J. Limnol., 2012; 71(1): 216-227
DOI: 10.4081/jlimnol.2012.e23

Temporal changes in periphytic meiofauna in lakes of different trophic states

Fabian SCHROEDER,* Walter TRAUNSPURGER, Kurt PETTERSSON,[1] and Lars PETERS

Animal Ecology, Bielefeld University, Morgenbreede 45, 33615 Bielefeld, Germany; [1]Department of Ecology and Genetics, Erken Laboratory, Uppsala University, Norr Malma 4200, 76173 Norrtälje, Sweden
*Corresponding author: fabian.schroeder@uni-bielefeld.de

ABSTRACT

Meiofaunal organisms in the periphyton of stony hard-substrates (epilithon) were studied in three Swedish lakes with different trophic states (oligo-, meso- and eutrophic) with respect to seasonal successions in abundance, biomass, and production. Over a period of 2 years, the meiofaunal population of all three lakes fluctuated greatly, with densities varying up to nine-fold within a season. In the oligotrophic lake, a significant decrease in meiofauna in winter was striking, whereas in the other two lakes, richer in nutrients, there was a pronounced peak in early summer. Although the lakes, on average, did not differ in epilithic organic and inorganic material, the differences in meiofaunal abundance, biomass, and production were significant. Correlation analysis revealed that altogether the meiofaunal biomass was positively related to the lakes' trophic state (total phosphorus), while the meiofaunal abundance and production along the trophic spectrum displayed a humped-shape distribution, with maximum values measured in the mesotrophic Lake Erken (1324 ind cm^{-2} and 2249 μg DW cm^{-2} y^{-1}). Nematodes were the dominant meiofaunal group in the epilithon of all three lakes, accounting for up to 58% in abundance, 33% in biomass and 55% in production of the whole meiofaunal community. However, their relative importance tended to decrease with increasing trophic state. Beside nematodes, rotifers, oligochaetes, copepods and tardigrades were also found in large numbers in the epilithon. Overall, the results demonstrated that, due to their high abundance, biomass, and production, meiofaunal organisms play an important role in epilithic communities.

Key words: nematodes, meiofaunal production, epilithon, seasonal succession, Lake Erken.

Received: November 2011. Accepted: January 2012.

INTRODUCTION

In freshwater ecosystems nearly every surface is covered by periphyton, which consists mainly of algae but also of heterotrophic components including bacteria, fungi, protozoans, and small metazoans, as well as dead organic material (Wetzel 2001). In recent decades, it has become increasingly apparent that periphyton is of great importance for lake ecosystems. Especially in shallow lakes, periphyton can account for a large proportion of whole-lake primary production, by the fixation of carbon and essential nutrients such as nitrogen and phosphorus (Vadeboncoeur, and Steinman 2002), in addition to providing a habitat and major food source for many macrozoobenthic organisms and fish (Hecky, and Hesslein 1995; Hillebrand 2009). The temporal development of periphytic communities with regard to autotrophic and heterotrophic microorganisms has been well studied (Cattaneo 1987; Harrison, and Hildrew 2001; Kahlert et al. 2002). However, one important group of organisms has been largely neglected, namely, the meiofauna.

In lentic habitats, meiofaunal organisms (benthic invertebrates between 50 and 1000 μm), mainly nematodes, rotifers, and microcrustaceans, are known to account for approximately 25% of the total biomass of all benthic organisms (Hakenkamp et al. 2002), and due to their high turnover rates and short generation times, they can be responsible for up to 50% of the total benthic secondary production (Strayer, and Likens 1986). As primary consumers, meiofauna influence lake ecosystem processes by reducing microfauna (Perlmutter, and Meyer 1991; Borchardt, and Bott 1995) and by stimulating microbial activity through moderate grazing, bioturbation, and excretion (Traunspurger et al. 1997; Hakenkamp et al. 2002; Mathieu et al. 2007). Meiofaunal organisms are not only closely linked to the lowermost trophic level, but also constitute an important food source for larger vertebrates and invertebrates (Schmid, and Schmid-Araya 2002; Dineen, and Robertson 2010; Spieth et al. 2011). However, nearly all studies of freshwater meiofauna published so far have dealt with sediment-associated meiofauna whereas general information on meiofauna in the periphyton of lakes is scarce, with only a few studies reported to date (*e.g.*, Meschkat 1934). Peters and Traunspurger (2005) documented that meiofaunal organisms are a numerically abundant component of lake periphyton. They are able to quickly colonize new, growing periphyton habitats (Peters et al. 2007) and to increase in abundance with increasing periphytic biomass (Hillebrand et al. 2002; Peters, and Traunspurger 2005). A detailed description of the seasonal variations in population density and community composition, however, is still lacking despite the fact that precisely such investigations are needed to improve our understanding of freshwater periphytic communities.

Also, in soft sediments, little is known about the seasonal succession of meiofauna (Bergtold, and Traunspurger 2004; Michiels, and Traunspurger 2004; Witthöft-Mühlmann et al. 2005). In contrast to the benthos, the seasonal succession of zooplankton in the pelagic zone has been extensively described in the literature (Wetzel 2001; Scheffer 2004). Those studies have shown that, beside the lake's morphometry and fish stock, the trophic state is an important factor influencing seasonal patterns of zooplankton populations (Sommer et al. 1986). Overall, empirical models predict that with increasing trophic state primary production and hence also the abundance and biomass of zooplankton will increase (Hanson, and Peters 1984; Rasmussen, and Kalff 1987). The rare data on littoral meiofaunal communities so far did not confirm this result gained for zooplankton (Ristau, and Traunspurger 2011). In profundal sediments, the trophic state actually negatively affected meiofaunal densities through the related changes in oxygen concentration (Prejs 1977). How the trophic state, one of the most important factors influencing lentic communities, shapes the periphytic meiofauna is still unknown.

As even the most basic knowledge about the meiofauna in periphytic biofilms is lacking, we carried out a 2-year (2008-2010) pilot study of the periphyton of stony hard-substrates (epilithon) in three dimictic lakes with different trophic state, focusing particularly on meiofaunal abundance, biomass, and secondary production. Specifically, the following questions were addressed: 1) What are the patterns in seasonally changing meiofauna communities? 2) How does the trophic state of a lake shape the meiofaunal community and its seasonal succession?

MATERIALS AND METHODS

Study sites

Epilithic communities in the littoral zone of three differently productive lakes were analyzed over a 2-year period. The lakes are located close to each other, approximately 70 km northeast of Stockholm, Sweden (Fig. 1). The sampled lakes differ in trophic state and in morphometric parameters (see Peters, and Traunspurger 2005). The oligotrophic Lake Largen is the smallest of the three lakes (location: N59°35.631' E18°32.158', surface area: 1.5 km^2, mean depth: 8.3 m, max. depth: 21 m) followed by the eutrophic Lake Limmaren (location: N59°42.843' E18° 42.960', surface area: 5.4 km^2, mean depth: 4.6 m, max. depth: 7.8 m); the largest lake is the mesotrophic Lake Erken (location: N59°51.584' E18°38.194', surface area: 24 km^2, mean depth: 9 m, max. depth: 21 m).

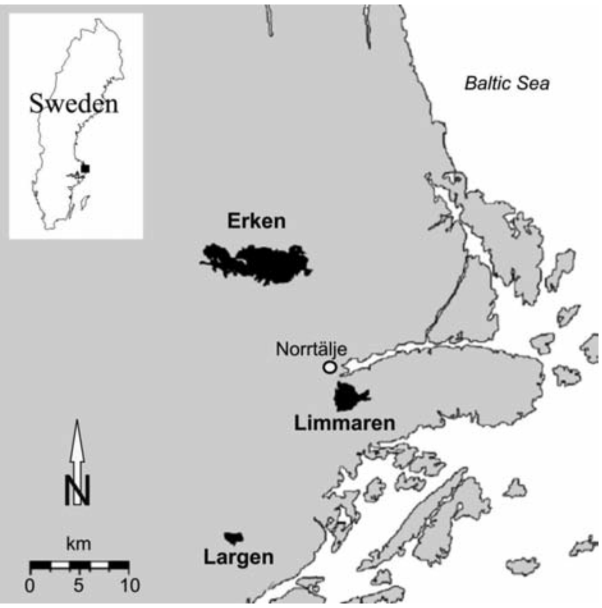

Fig. 1. Location of the three analyzed lakes in Sweden. Map modified from Peters, and Traunspurger (2005).

Sampling procedure and analyses

From April 2008 to April 2010, samples were collected bimonthly, except between August 2009 and February 2010, during which the epilithon was sampled every third month. In each lake and at each sampling date, four epilithon samples were obtained at a water depth of 50 cm by using a brush sampler, as described in Peters et al. (2005). This syringe-like sampler scrapes off a defined area (3.14 cm^2) on hard-substrates and collects all sampled epilithic material, including biofilm-dwelling meiofauna, without loss and without contamination by zooplankton. Each epilithon sample was transferred into a 100 mL polyethylene bottle and stored in the dark at 4°C until all processing was completed, within 12 h. To analyze total phosphorus (TP) and nitrogen (TN) of the water column water samples from each sampling location were taken by using a 10 mL syringe close to the hard-substrates. TP and TN of the taken water samples were analyzed following the Swedish Standard guidelines (Swedish Standards Institution 1995). In the lab, the epilithic material of each brush sample was transferred into beakers, which were then filled with tap water to a defined volume (100-150 mL). To ensure a homogeneous distribution of the material for further analyses, algal conglomerates were carefully separated with scissors and forceps (Peters et al. 2005).

For the determination of algal biomass, organic and inorganic material (OM, IOM), measured as chlorophyll-*a* (Chl-*a*), ash-free dry mass (AFDM) and ash, two aliquots (5-10 mL) from each sample were filtered onto glass-fiber filters (Schleicher, and Schuell GF6, ø 25 mm). Using the method of Marker et al. (1980), Chl-*a* was extracted with 90% ethanol and Chl-*a* concentrations were measured spectrophotometrically without correcting for phaeophytin (Stich, and Brinker 2005). For OM analyses, pre-combusted (5 h at 550°C) glass-fiber filters were used and the filtered material was dried at 105°C for 24 h, followed by combustion at 550°C for 5 h. Meiofauna OM was removed from the epilithic OM by subtracting the specific meiofaunal dry weight (see below). Epilithic meiofauna were identified by sieving the remainder of each sample through a 10 μm mesh and then fixing the content of the mesh with formaldehyde (4% final concentration) followed by staining with rose Bengal.

Meiofaunal organisms were counted and classified into taxonomic groups based on stereomicroscopic (40× magnification) observations. To calculate the biomass of the meiofaunal groups, excluding nematodes, the organisms were grouped into taxon-specific size classes and the body volume of 20 randomly chosen individuals of each taxon and size class was measured. Body volumes of oligochaetes, mites, tardigrades, ostracods and copepods were calculated by using the formula of Feller, and Warwick (1988). For rotifers, the formula of ellipsoid/oval individuals from Herzig (1984) was applied. Body volume was converted to dry weight using the specific gravity (1.13 g cm^{-3}) and a dry/wet weight ratio of 0.25 (Feller, and Warwick 1988). The body lengths of benthic cladocerans and nauplii were converted directly to dry weight using published regression equations from Dumont et al. (1975) and Stead et al. (2003). For nematode biomass calculation, 50 individual nematodes per replicated sample were identified to species level (data not presented here), and the species-specific bio-mass was calculated using length and width specifications from the literature (Andrássy 1984; Bongers 1987), the formula of Andrássy (1956), and a dry/wet weight ratio of 0.25 (Feller, and Warwick 1988). Males, females, and juveniles were treated separately. If length and width data for nematode juveniles were not specified in the literature, biomass was assumed to be a quarter of the adult biomass (Ristau, and Traunspurger 2011).

Estimates of the secondary production of each meiofaunal group were based on the allometric relationships between annual production and body mass (P/B), using equation 3 of Banse and Mosher (1980). Hence, for each meiofaunal taxon the maximum body mass was used, converting dry biomass from kJ to kcal according to Cummins, and Wuycheck (1971). Multiplying P/B by the mean biomass yields the secondary production value. As suggested by Banse and Mosher (1980), the product was divided by four since meiofaunal organisms tend to have a lower P/B than predicted by equation 3.

Statistical analyses

To test for differences among sampling dates, a repeated measurement analysis of variance (rmANOVA) was applied to epilithic biomass parameters (Chl-*a*, OM) and to meiofaunal abundance, biomass, and production. First, the data were log-transformed (x + 1) and then tested for normality. Repeated measurement analysis was followed by pairwise post-hoc comparisons using Tukey's honestly significant difference (HSD) test. Spearman's rank correlation test was used to determine whether epilithic biomass (algal biomass and OM) correlated with seasonal fluctuations in the nutrient content (TP, TN) and temperature of the water column. Furthermore it was tested whether the seasonal variations in meiofaunal abundance were linked to the amount of algal biomass, OM and IOM in the epilithon (Spearman's rank correlation test).

To test for overall differences between the lakes, the data were analyzed by a univariate test of significance (one-way-ANOVA) followed by post-hoc comparisons (Tukey's HSD test). The assumption of homogeneous variance was confirmed with Bartlett's test. If variances were not equal, the Kruskal-Wallis ANOVA and the Mann-Whitney U-test were used. Spearman's rank correlation test was used to find out if the amount of epilithic algal biomass, OM and IOM as well as meiofaunal abundance, biomass and production, and the relative abundance of each meiofaunal group correlated with lake trophy (TP concentrations). All tests were performed using the STATISTICA software package (version 9.1, StatSoft Inc., Tulsa, OK, USA).

RESULTS

Seasonal fluctuations

Between April 2008 and April 2010, both algal biomass and OM showed significant temporal variations in the epilithon of all analyzed lakes (rmANOVA, Tab. 1). Whereas only slight seasonal changes in algal biomass were detected in the oligotrophic lake with the lowest values recorded in the winter, larger fluctuations were recorded in the meso- and eutrophic lakes, where the lowest values were measured in the summer (Fig. 2). Particularly noticeable was the significant decline of algal biomass in mesotrophic Lake Erken in August 2009 in contrast to the two large peaks in June and November (Tukey's HSD, $p<0.001$). In all three lakes, OM fluctuations in the epilithon were of the same order of magnitude, with maximum values in oligotrophic Lake Largen in autumn, in mesotrophic Lake Erken in summer, and in eutrophic Lake Limmaren during or directly after the ice-cover period in winter or spring. Spearman rank correlations revealed that in the oligotrophic lake the increases in epilithic algal biomass and OM were positively related to temperature

Tab. 1. Annual means (±SD) of different water parameters (temperature, total-P, total-N) of epilithic biomass (algal biomass, organic material, inorganic material) and of meiofaunal abundance, biomass, and production in the three study lakes, together with the minimum and maximum ranges of the means measured at each sampling date. rmANOVA was applied to test for significant differences between sampling dates. n.s.=not significant, *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$.

	Mean±SD	Min	Max	rmANOVA			
				df	MS	F	*p*
Oligotrophic							
Water parameters							
Temperature (°C)	9.5±7.0	0.5	21.5				
Total-P (μg L^{-1})	8.9±5.1	5	24				
Total-N (μg L^{-1})	497±94	370	760				
Epilithic biomass							
Algal biomass (μg cm^{-2})	41.0±20.3	18.7	67.9	11	0.1	2.4	*
Organic material (mg cm^{-2})	9.8±6.4	2.9	19.7	11	0.2	7.9	***
Inorganic material (mg cm^{-2})	32.5±31.5	4.5	175.8	11	0.2	3.9	**
Meiofauna values							
Abundance (ind cm^{-2})	254±179	41	476	11	0.5	10.8	***
Biomass (μg DW cm^{-2})	31±22	5	96	11	0.4	7.6	***
Production (μg DW cm^{-2} y^{-1})	500±335	125	1016	11	0.4	7.7	***
Mesotrophic							
Water parameters							
Temperature (°C)	9.0±6.7	0.5	20.4				
Total-P (μg L^{-1})	33.1±10.8	16	50				
Total-N (μg L^{-1})	787±117	590	991				
Epilithic biomass							
Algal biomass (μg cm^{-2})	100.7±59.0	21	277	11	0.3	10.2	***
Organic material (mg cm^{-2})	12.1±7.4	2.8	41.7	11	0.1	3.1	**
Inorganic material (mg cm^{-2})	21.5±18.0	0.6	110.8	11	0.2	2.9	**
Meiofauna values							
Abundance (ind cm^{-2})	448±381	231	1324	11	0.1	4.1	***
Biomass (μg DW cm^{-2})	102±61	31	364	11	0.1	4.3	***
Production (μg DW cm^{-2} y^{-1})	1092±646	621	2249	11	0.1	5.3	***
Eutrophic							
Water parameters							
Temperature (°C)	9.2±6.8	0.5	19.5				
Total-P (μg L^{-1})	66.3±25.7	33	120				
Total-N (μg L^{-1})	1255±187	960	1600				
Epilithic biomass							
Algal biomass (μg cm^{-2})	95.2±52.3	28.8	261.1	11	0.2	6.7	***
Organic material (mg cm^{-2})	10.9±5.5	5.5	31.5	11	0.1	3.8	**
Inorganic material (mg cm^{-2})	23.3±13.6	5.7	58.0	11	0.1	2.0	n.s.
Meiofauna values							
Abundance (ind cm^{-2})	336±257	84	717	11	0.5	4.8	***
Biomass (μg DW cm^{-2})	98±77	15	262	11	0.4	3.5	**
Production (μg DW cm^{-2} y^{-1})	875±661	237	2092	11	0.4	7.8	***

($R=0.6$, $p<0.05$; $R=0.67$, $p<0.05$ respectively), while the algal biomass in the mesotrophic lake correlated positively with fluctuations in the TP content of the water column ($R=0.65$, $p<0.05$). In contrast, in the eutrophic lake epilithic biomass did not correlate with any of the environmental parameters, *i.e.*, temperature and nutrient content (TP, TN).

The abundance of the whole meiofaunal community in the epilithon also exhibited strong seasonal variations (rmANOVA, Tab. 1). In all three lakes, meiofaunal abundance increased in spring or early summer (Fig. 3), with maximum densities of 476 ind cm^{-2} (Lake Largen, June 2008), 1324 ind cm^{-2} (Lake Erken, June 2009), and 717 ind cm^{-2} (Lake Limmaren, June 2008). In oligotrophic Lake Largen, meiofaunal abundance remained more or less constant during summer and autumn until the start of the ice cover, after which, in winter, the density declined to a very low level.

The seasonal patterns of the meso- and eutrophic lakes included a pronounced peak in meiofaunal abundance in spring or summer but, in contrast to the oligotrophic lake, there was no significant decrease in winter. The seasonal variations in meiofaunal abundance were positively re-

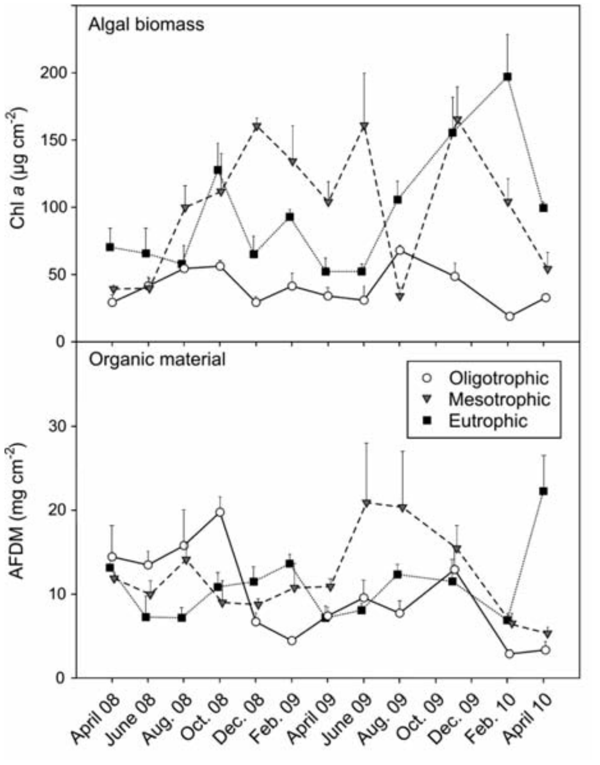

Fig. 2. Seasonal fluctuations in algal biomass (Chl-*a*) and organic matter (AFDM) in epilithic biofilms of an oligotro-phic, a mesotrophic, and a eutrophic lake over a period of 2 years (2008–2010). Mean±SE.

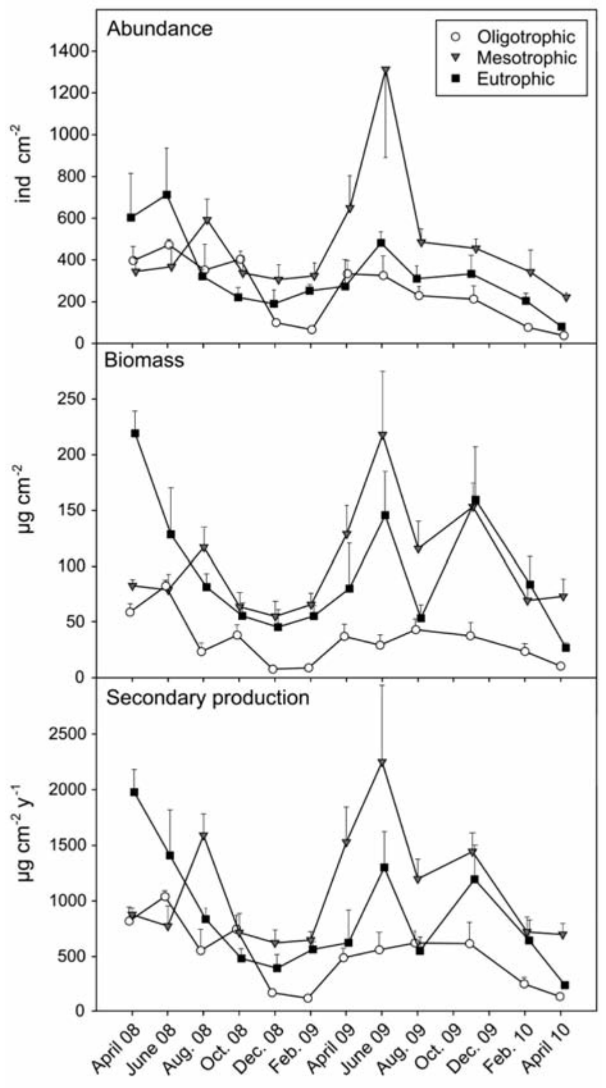

Fig. 3. Seasonal fluctuations in abundance (ind cm^{-2}) biomass (µg cm-2) and secondary production (µg cm^{-2} y^{-1}) of epilithic meiofauna in an oligotrophic, a mesotrophic, and a eutrophic lake over a period of 2 years (2008-2010). Mean±SE.

lated to the amount of epilithic OM and IOM in the oligotrophic (OM: R=0.87, p<0.001; IOM: R=0.80, p<0.01) and mesotrophic lakes (OM: R=0.82, p<0.01; IOM: R=0.63, p<0.05), but not in the eutrophic lake (OM: R=0.15, p=0.63; IOM: R=0.06, p=0.85). No correlations, however, were found between meiofaunal abundance and algal biomass.

Nearly all meiofaunal groups followed the above-described seasonal fluctuations, forming one general peak in summer (Fig. 4, Tab. 2). Only the tardigrades of the eutrophic lake were more frequent in the winter than in the summer months. In addition, in the first year the tardigrade population peaked twice within a season. In the mesotrophic lake, copepods, also peaked twice within a year, with a maximum in summer and a smaller increase in autumn.

Nematodes were by far the most abundant meiofaunal group in the epilithon, ranging from 47% of the meiofaunal abundance in eutrophic Lake Limmaren to 58% in oligotrophic Lake Largen, and were therefore mainly responsible for the temporal variations of the meiofaunal community (Tab. 2). For example, in mesotrophic Lake Erken the remarkable maximum abundance of 1324 meiofaunal individuals per cm² in June 2009 can be primarily attributed to the rapid increase in nematode abundance (1014 ind cm^{-2}; Fig. 4). Second to the nematodes were rotifers, accounting on average for 26% of the total meiofaunal community of the epilithon. In addition to these two most abundant groups, abundances over 10% were determined only for copepods and tardigrades in Lake Limmaren.

As with abundance, seasonal fluctuations were observed for the biomass and production of meiofaunal organisms (rmANOVA, Tab. 1), reaching maximum values of 96 µg DW cm^{-2} and 1016 µg DW cm^{-2} y^{-1} in the oligotrophic lake, 364 µg DW cm^{-2} and 2249 µg DW cm^{-2} y^{-1} in the mesotrophic lake, and 262 µg DW cm^{-2} and 2092 µg DW cm^{-2} y^{-1} in the eutrophic lake. However, in the latter two lakes, both biomass and production peaked twice, in

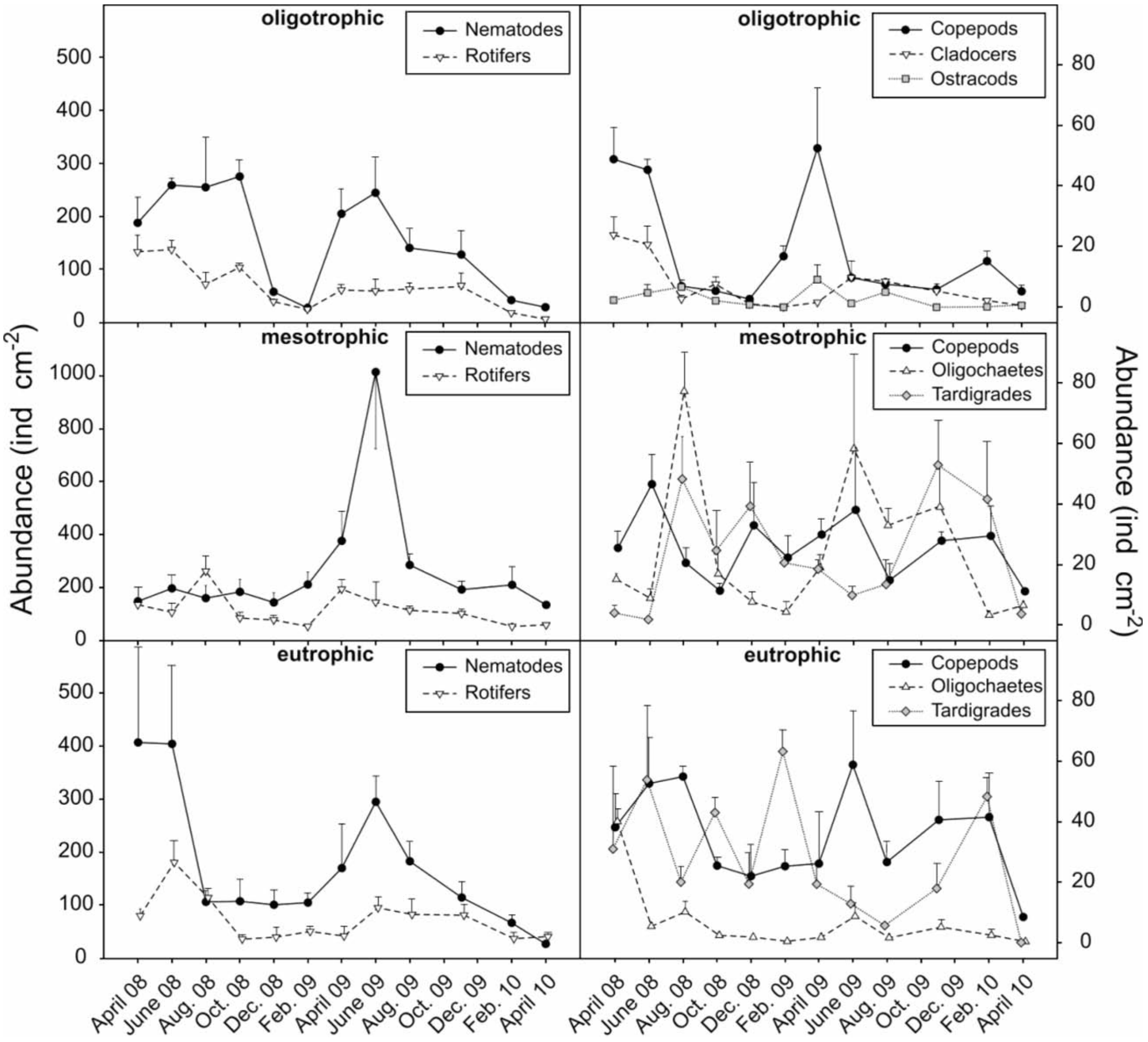

Fig. 4. Seasonal fluctuations in abundance (ind cm^{-2}) of the five most frequent meiofaunal groups in the epilithon of an oligotrophic, a mesotrophic, and a eutrophic lake over a period of 2 years (2008-2010). Note the different dominance structures within the meiofauna in the lakes and of the differently scaled axes. Mean±SE.

the summer and autumn of 2009 (Fig. 3), but without significant differences between the months (Tukey's HSD). With respect to abundance, the relative proportion of biomass decreased for meiofaunal groups with a low body weight (nematodes, rotifers and tardigrades) but increased for groups with a higher body weight (copepods, oligochaetes, ostracods and mites; Tab. 3). Despite their low individual body weight, nematodes still accounted for 22-33% of total meiofaunal biomass and therefore, together with copepods and oligochaetes, remained the most important group. Also, in terms of meiofaunal production, a large proportion was contributed by nematodes. This was especially the case in oligotrophic Lake Largen, where nematodes accounted for more than half of the total meiofaunal production (55%), while in Lake Limmaren and Lake Erken rotifers were approximately as productive as nematodes (Tab. 3).

Comparisons between lakes

The differences in nutrient supply among the lakes mirrored the significant differences in epilithic algal biomass (one-way ANOVA: $F_{2,141}$=35.1, p<0.001), with values significantly higher in the mesotrophic and eutrophic lakes (Tukey's HSD both: p<0.001) than in the oligotrophic lake. Spearman's rank correlation among all lakes revealed that the higher the TP content, the higher the algal biomass in the epilithon (R=0.62, p<0.001). In contrast, the lakes did not differ in the amount of epilithic IOM and OM, and no correlations with nutrient content (TP) were observed.

Tab. 2. Mean (±SD) abundance (ind cm^{-2}) of each meiofauna taxon and its relative proportion (%) in the epilithon of an oligotrophic, mesot-rophic and eutrophic lake. To test for time effects, the rmANOVA was applied. n.s.=not significant, *=p<0.05, **=p <0.01, ***=p<0.001.

Meiofauna	Abundance		rmANOVA			
	(ind cm^{-2})	(%)	df	MS	*F*	*p*
Oligotrophic						
Nematodes	154±121	58±14	11	0.6	8.7	***
Rotifers	65±50	26±10	11	0.6	11.4	***
Copepods	19±22	9±8	11	0.6	11.7	***
Tardigrades	2±3	1±1	analysis not possible			
Oligochaetes	3±4	1±1	analysis not possible			
Cladocerans	7±9	2±2	11	0.7	10.2	***
Ostracods	3±4	1±2	analysis not possible			
Mites	2±3	1±1	11	0.2	2.3	*
Mesotrophic						
Nematodes	271±292	52±15	11	0.2	4.2	***
Rotifers	115±84	26±11	11	0.2	4.3	***
Copepods	26±19	6±4	11	0.1	1.6	n.s.
Tardigrades	23±25	5±5	11	0.9	4.6	***
Oligochaetes	24±30	5±4	11	1.5	9.6	***
Cladocerans	11±4	2±3	11	0.7	7.7	***
Ostracods	5±4	1±1	11	0.2	1.8	n.s.
Mites	12±9	3±2	11	0.3	2.4	*
Eutrophic						
Nematodes	174±181	47±16	11	0.2	5.5	***
Rotifers	73±55	23±12	11	0.3	3.2	**
Copepods	35±25	11±6	11	0.2	2.2	*
Tardigrades	28±29	10±10	10	0.4	3.4	**
Oligochaetes	7±11	2±3	11	0.8	5.9	***
Cladocerans	8±28	2±7	analysis not possible			
Ostracods	5±5	2±2	11	0.2	2.3	*
Mites	6±4	2±3	11	0.1	2.0	n.s.

A comparison of meiofaunal abundance (a), biomass (b), and production (pd) among the lakes also showed significant overall differences between the lakes (Kruskal-Wallis, a: χ^2=12.2, p<0.01; b: χ^2=38, p<0.001; pd: χ^2=20.2, p<0.001). Meiofaunal abundance and production were significantly higher in the mesotrophic lake than in the oligo- and eutrophic lakes (Tab. 4). In the absence of a linear correlation between abundance or production and lake trophic state (TP) (a: *R*=0.09, p=0.58; pd: *R*=0.28, p=0.1), distribution was rather unimodal. Copepods and tardigrades, however, diverged from this unimodal distribution since their abundance (copepods: *R*=0.45, p<0.01; tardigrades: *R*=0.69, p<0.001) and production (copepods: *R*=0.53, p<0.001; tardigrades: *R*=0.73, p<0.001) correlated positively with lake trophy. In contrast to abundance and production, a significant positive relationship between meiofaunal biomass and lake trophy was determined (*R*=0.56, p<0.001), as meiofaunal biomass was significantly higher in the meso- and eutrophic lakes compared to the oligotrophic lake (Tab. 4).

The individual body weights of meiofaunal organisms also varied between lakes (Kruskal-Wallis: χ^2=24.5, p<0.001). Organisms in the eutrophic lake were significantly heavier than those in the less productive lakes (Tab. 4). However, a significant positive relation-ship with lake trophy could not be demonstrated (*R*=0.19, p=0.28). The individual body weights of nematodes and oligochaetes diverged from this overall pattern because they correlated significantly with lake trophy (nematodes: *R*=0.50, p<0.01; oligochaetes: *R*=0.55, p<0.001).

The structures of the meiofaunal communities in the three lakes can be compared by using the relative abundances of the meiofaunal organisms. Except for rotifers, whose percentage of the whole meiofaunal community was the same in all three lakes, meiofaunal groups were differently distributed within the lakes. For example, the proportion of nematodes and cladocerans decreased tendentially (*R*=0.32, p=0.06) and significantly (*R*=0.46, p<0.01) with increasing lake trophy, respectively, whereas the proportion of tardigrades (*R*=0.68, p<0.001) and mites (*R*=0.49, p<0.01) increased. The percentage of oligochaetes was highest in the mesotrophic lake.

DISCUSSION

Seasonal fluctuations

Ours is the first comparative study addressing the seasonal succession of meiofaunal organisms in the periphyton of stony hard-substrates in three lakes differing in trophic state.

Over a 2-year period, the epilithic meiofauna of all three lakes were characterized by strong fluctuations, with densities varying up to nine-fold within a season. Meiofaunal abundance in oligotrophic Lake Largen was constant from spring to autumn, but exhibited a pronounced minimum in winter. For the two nutrient-richer lakes, a large peak in meiofaunal abundance in early summer was characteristic and, in contrast to the oligotrophic lake, meiofaunal populations did not decrease significantly in winter. This is consistent with the findings of Sommer et al. (1986), who reported that the seasonal succession of zooplankton in the pelagic zone differs in lakes of different trophic state. For example in oligotrophic lakes, zooplankton populations were shown to fluctuate more slowly than in eutrophic lakes (Sommer et al. 1986). Furthermore, in oligotrophic lakes they typically peak only once a year, whereas in eutrophic lakes two maxima are often observed, namely, a large one in spring and a smaller one in autumn (Sommer et al. 1986). In our study, the most common seasonal pattern in the epilithon seemed to be a single maximum but the temporal variations in meiofaunal biomass and production in the meso- and eutrophic lakes in the second year (2009) revealed that populations can also peak twice yearly.

In the oligotrophic and mesotrophic lakes, but not in

Tab. 3. Mean (±SD) individual body weight (μg) of each meiofauna taxon together with the total and relative biomass (μg DW cm^{-2}) and secondary production (μg DW cm^{-2} y^{-1}) in the epilithon of three lakes of different trophic states (oligotrophic, mesotrophic, and eutrophic).

Meiofauna	Indiv. body weight (μg)	Biomass (μg cm^{-2})	Biomass (%)	Production (μg cm^{-2} y^{-1})	Production (%)
Oligotrophic					
Nematodes	0.08±0.04	10±7	33±15	271±189	55±14
Rotifers	0.05±0.01	3±2	12±7	98±75	20±10
Copepods	0.63±0.45	9±9	31±21	46±55	11±9
Tardigrades	0.04±0.02	< 1	< 1	2±4	< 1
Oligochaetes	0.75±0.67	2±5	5±9	25±50	3±5
Cladocerans	0.41±0.55	3±4	7±9	30±48	5±6
Ostracods	1.31±2.31	3±5	7±9	15±28	3±5
Mites	0.88±0.79	2±2	6±6	13±18	3±4
Total	0.15±0.09	31±22		500±335	
Mesotrophic					
Nematodes	0.09±0.03	23±24	22±13	273±222	24±19
Rotifers	0.09±0.02	10±7	10±6	286±105	27±10
Copepods	0.77±0.57	18±14	18±11	76±64	8±9
Tardigrades	0.06±0.01	1±2	2±2	28±48	3±2
Oligochaetes	1.11±0.84	23±24	20±16	224±347	18±18
Cladocerans	0.36±0.36	5±8	4±7	49±38	4±6
Ostracods	3.28±0.43	14±19	11±12	80±66	7±6
Mites	0.84±1.41	9±11	10±13	75±34	8±4
Total	0.23±0.09	102±61		1092±646	
Eutrophic					
Nematodes	0.14±0.08	20±17	24±12	200±193	24±11
Rotifers	0.08±0.03	5±3	7±6	145±105	20±12
Copepods	0.86±0.59	29±31	28±12	118±106	14±7
Tardigrades	0.11±0.09	3±3	4±4	54±54	8±8
Oligochaetes	2.30±1.38	20±37	12±18	203±369	14±20
Cladocerans	0.42±0.39	3±12	2±6	36±129	3±7
Ostracods	2.09±1.67	10±14	11±12	58±78	8±9
Mites	1.13±0.66	7±7	10±8	61±57	9±8
Total	0.31±0.20	98±78		875±661	

Tab. 4. Statistical differences between lakes in abundance, biomass, and production of the meiofaunal community (Mann-Whitney U-test). *=p<0.05, **=p<0.01, ***=p<0.001.

	Abundance	Biomass	Indiv. body weight	Production
Oligotrophic - Mesotrophic	***	***	***	***
Oligotrophic - Eutrophic	0.122	***	***	**
Mesotrophic - Eutrophic	**	0.16	*	*

the eutrophic lake, meiofaunal abundance was closely linked to fluctuations in the IOM and OM of the epilithon. With the amount of IOM and OM serving as an estimate of habitat size and food availability, the positive correlation with meiofaunal abundance in the oligotrophic and mesotrophic lakes might be indicative of the bottom-up regulation of the meiofaunal community. In contrast, this cannot be claimed for the eutrophic lake, as there was no correlation between meiofaunal abundance and epilithic IOM and OM. In this case, a greater role for predation in regulating meiofaunal communities might be expected. As reported by Magnusson, and Williams (2009) and Peters, and Traunspurger (2011), predatory insect larvae as well as grazing macroinvertebrates can negatively affect meiofaunal communities. Whereas several authors established a positive relationship between the meiofaunal abundance and algal biomass of the epilithon (Hillebrand et al. 2002; Peters, and Traunspurger 2005), this was not confirmed in the present study. This might have been because changes in the biomass of highly edible algae were masked by concurrent changes in biomass of larger non-edible algae. Therefore the resolution of chlorophyll a measurements was too low to establish a link between meiofauna and their autotrophic food resource, because meiofaunal organisms are highly specialized with respect to their food resources. Nematodes, for example, can pierce filamentous algae or fungi, ingest small diatoms, or feed on everything that passes through their buccal cavity (Traunspurger 2002). Gaudes et al. (2006) and Majidi et al. (2011) found a positive correlation between the most common periphytic nematode species and the availability of diatoms and cyanobacteria. Bacteria are another important food resource for meiofaunal organisms (Schmid, and Schmid-Araya 2002), and thus the increase in bacterial production, as observed in the epilithon of Lake Erken by Haglund, and Hillebrand (2005) during summer, might also have been responsible for the observed changes in meiofaunal densities.

Altogether, meiofaunal densities were on average considerably higher in the epilithon compared to those measured in soft sediments (Bergtold, and Traunspurger 2004; Michiels, and Traunspurger 2004; Witthöft-Mühlmann et al. 2005). Moreover, average densities exceeded the values reported in the epilithon study of Peters, and Traunspurger (2005), who analyzed 17 lakes, including the same lakes studied here, but only in autumn. This highlights the necessity to include temporal variations when describing meiofaunal communities. Especially remarkable was that as many as 1324 meiofaunal individuals, as found in the epilithon of mesotrophic Lake Erken in June 2009, can coexist in an area of only one square centimeter. Those high abundances show that the epilithon is clearly an important habitat for meiofaunal organisms, providing them with shelter and an ample food supply.

Consistent with the findings reported for almost every freshwater habitat, including the epilithon (Traunspurger 2002; Peters, and Traunspurger 2005), nematodes were the most abundant meiofaunal group in the present study. Some of the most common periphytic nematode species in the epilithon are perfectly adapted to this habitat as they are attached to the substrate by a sticky structure and are therefore independent of the surrounding hydrodynamics (Meschkat 1934; Majdi et al. 2011). Mathieu et al. (2007) documented that only 50 nematodes per cm^2 are sufficient to have a positive effect on the oxygen turnover of diatom biofilms. Since in our study the number of meiofaunal organisms was higher than 50 individuals per cm^2 at every time point in all three lakes, it is likely that meiofauna play an important role in these environments by enhancing matrix permeability and recycling of essential nutrients. Nevertheless, at densities of 1324 ind cm^{-2}, such as those recorded in our study, meiofauna could negatively alter epilithic biofilms through its grazing pressure. Evidence for such an effect comes from mesotrophic Lake Erken, where algal biomass rapidly decreased following the large meiofaunal peak in June 2009. Likewise, Borchardt, and Bott (1995) showed that, especially during periods of high densities, periphytic meiofauna is able to remove a significant amount of microfaunal biomass.

Although meiofaunal biomass accounted for only 1 2% of the total OM in the epilithon, the high secondary production values measured for the lakes indicate the importance of meiofauna in the energy-flow within the epilithon and probably also at the level of the whole lake. In contrast to numerous macrozoobenthic studies (reviewed in Benke, and Huryn 2010), there have been very few estimates of meiofaunal production rates. The present study determined average production values of 5 g DW m 2 y^{-1}, 10.9 g DW m 2 y^{-1}, and 8.8 g DW m 2 y^{-1} in the epilithon of the sampled lakes. These values are in the same range as those reported for sediment-dwelling meiofauna in lakes (Strayer, and Likens 1986; Bergtold, and Traunspurger 2005) and even higher than those obtained in lotic studies (Stead et al. 2005; Reiss, and Schmid-Araya 2010; Tod, and Schmid-Araya 2009). Further evidence for the importance of meiofaunal organisms in freshwater ecosystems comes from the studies of Bergtold, and Traunspurger (2005) and Strayer, and Likens (1986), in which sediment-dwelling meiofauna were shown to account for up to 50% of the total benthic secondary production. However, the proportion of meiofauna and macrofauna on the whole benthic secondary production in the epilithon of lakes remains to be determined in further investigations.

Comparisons between lakes

Lake-specific differences in the average amount of algal biomass but not in the average amount of OM provide evidence of differences in the composition of the epilithic biomass. While the amount of algal biomass and thus its relative proportion of the total epilithic organic material increased with increasing trophic state, the proportion of other organic components like epilithon-associated bacteria decreased. These results are in good agreement with observations from the pelagic zone, where phytoplankton biomass and production are much greater relative to heterotrophic bacteria in nutrient-richer mesotrophic and eutrophic lakes than they are in oligotrophic lakes (Biddanda et al. 2001). Also, the relative importance of benthic algae in periphytic communities of running waters was found to increase with increasing phosphorus concentrations (Hill et al. 2011).

While among the lakes the same average amount of OM and IOM and hence the same habitat size was determined for the epilithon, the abundance, biomass, and production of the associated meiofauna were highly different. With increasing trophic state meiofaunal abundance and production showed a unimodally shaped curve, since the average values were highest in the mesotrophic lake. Whereas several studies of macroinvertebrates and zooplankton reported that these populations were positively related to lake trophy (McCauley, and Kalff 1981; Hanson, and Peters 1984; Rasmussen, and Kalff 1987), this cannot be claimed for sediment-dwelling meiofauna based on the rare data describing these organisms (Särkkä 1996; Ristau, and Traunspurger 2011). Especially in the profundal zone, the trophic state can even negatively affect meiofaunal densities due to the lower oxygen concentrations (Prejs 1977). In a microcosm study of Ristau et al. (submitted), meiofaunal abundance also had a humped-shaped distribution along a nutrient enrichment gradient, with a peak at a TP concentration of 30 μg L^{-1}. On average, almost the same TP concentration (33.1 μg L^{-1}) was measured in the present study in Lake Erken, in which the highest meiofaunal abundance was determined. Ristau et al. (submitted) suggested a coupling between the nutrientrelated pattern of meiofaunal abundance and the characteristic development of primary producers, which in their study showed an obvious shift along the nutrient enrichment gradient, from low densities of edible diatoms and unicellular green-algae to large standing stocks of inedible forms. In the periphyton, the proportion of taxa comprising larger-sized algae also increases with increasing nutrient concentrations (Cattaneo 1987; De Nicola et al. 2006); similarly, it might well be the case that primary producers differing in composition alter meiofaunal abundance in the epilithon of the present study. Unlike the nutrient-related pattern of meiofaunal abundance and production, the relationship between meiofaunal biomass and trophic state was linear. The difference can be explained by the fact that the higher abundance in mesotrophic Lake Erken was compensated by a higher individual body weight of organisms in eutrophic Lake Limmaren.

The differences in the individual body weight, *i.e.*, a meiofaunal individual in the oligotrophic lake weighed, on average, half as much as one in the eutrophic lake, probably mirrors the different compositions of the meiofaunal groups among the three lakes. While in oligotrophic Lake Largen the relative proportion of nematodes was higher than in Lake Erken or Lake Limmaren, the proportion of heavier meiofaunal groups, such as oligochaetes, ostracods, and mites, was lower. A higher percentage of nematodes at nutrient-poor than at nutrient-rich locations was also observed by Traunspurger (2002) and Wu et al. (2004). Due to their small body size nematodes may be better adapted than larger meiofaunal species to environments in which nutrients are scarce, as smaller species require less food to attain positive growth rates. Conversely, under eutrophic conditions larger species dominate and are able to outcompete smaller ones (Romanovsky, and Feniova 1985). However, this explanation is not applicable to epilithic rotifers and tardigrades. Indeed, for rotifers the same relative abundance among lakes was determined while for tardigrades the trend was reversed. Even within some meiofaunal groups the individual body weight differed between lakes. For example for nematodes and oligochaetes the individual body weight increased with increasing trophic state, indicating that the species community composition of these groups changed with changing trophic state.

The observed differences in meiofaunal abundance, biomass, production, and community composition lends support for the trophic state as an important factor in shaping epilithic communities. But it should be noted that beside the different lake trophy, also other factors might be just as responsible for differences in meiofaunal values. For example the different size of the analyzed lakes might affect wind and wave exposure, and therefore also the meiofauna abundance and community composition.

CONCLUSIONS

The present study showed that meiofaunal populations vary greatly between seasons as well as between lakes of different trophic states. Not only the remarkable abundances but also the high production rates underline the importance of small meiofaunal organisms in the littoral food web. This long-term study provides a solid basis for further investigations of epilithic meiofaunal communities and their function in ecosystem processes.

ACKNOWLEDGMENTS

We thank Dominik Kathöfer, Michael Faupel, and Stefanie Horsthemke for their help during field sampling and Stefanie Gehner for nematode preparation. We are grateful to all members of the Norrmalma Field Station for their friendly support during our time at Lake Erken. We thank also two anonymous referees for helpful comments. Financial support from the German Research Foundation (DFG - PE 1522/2-1) is gratefully acknowledged.

REFERENCES

Andrássy I. 1984. Klasse Nematoda (Ordnungen Monhyste-rida, Desmoscolecida, Araeolaimida, Rhabditida). Gustav Fischer Verlag. Stuttgart.

Andrássy I. 1956. Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoda). Acta Zool. Hung. 2: 1-15.

Banse K, and Mosher S. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50: 355-379.

Benke AC, and Huryn AD. 2010. Benthic invertebrate production - fascilitating answers to ecological riddles in freshwater ecosystems. J. N. Am. Benthol. Soc. 29: 264-285.

Bergtold M, and Traunspurger W. 2005. Benthic production by micro-, meio-, and macrobenthos in the profundal zone of an oligotrophic lake. J. N. Am. Benthol. Soc. 24: 321-329.

Bergtold M, and Traunspurger W. 2004. The benthic community in the profundal of Lake Brunnsee: seasonal and spatial patterns. Arch. Hydrobiol. 160: 527-554.

Biddanda B, Ogdahl M, and Cotner J. 2001. Dominance of bacterial metabolism in oligotrophic relative to eutrophic waters. Limnol. Oceanogr. 46: 730-739.

Bongers T. 1987. De Nematoden van Nederland. Stichting Uitgeverij Koninklijke Nederlandse Natuuhistorische Vereniging. Utrecht.

Borchardt MA, and Bott TL. 1995. Meiofaunal grazing of bacteria and algae in Piedmont stream. J. N. Am. Benthol. Soc. 14: 278-298.

Cattaneo A. 1987. Periphyton in lakes of different trophy. Can. J. Fish. Aquat. Sci. 44: 296-303.

Cummins KW, and Wuychuck JC. 1971. Caloric equivalents for investigations in ecological energetics. Int. Ver. theor. angew. Limnol., Mitt. 18: 1-158.

DeNicola DM, de Eyto E, Wemaere A, and Irvine K. 2006. Periphyton response to nutrient addition in 3 lakes of different benthic productivity. J. N. Am. Benthol. Soc. 25: 616-631.

Dineen G, and Robertson AL. 2010. Subtle top-down control of a freshwater meiofaunal assemblage by juvenile fish. Freshwater Biol. 55: 1818-1830.

Dumont HJ, Van de Velde I, and Dumont S. 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from plankton, periphyton and benthos of continental waters. Oecologia 19: 75-97.

Feller,RJ, and Warwick RM. 1988. Energetics. In: Higgins, R.P., and H. Thiel (Ed.), Introduction to study of meiofauna. Smithsonian Institution Press, Washington D.C.: 739-759.

Gaudes A, Sabater S, Vilalta E, and Munoz I. 2006. The nematode community in cyanobacterial biofilms in the river Llobregat, Spain. Nematology 8: 909-919.

Haglund A, and Hillebrand H. 2005. The effect of grazing and nutrient supply on periphyton associated bacteria. FEMS Microbiol. Ecol. 52: 31-41.

Hakenkamp CC, Morin A, and Strayer DL. 2002. The functional importance of freshwater meiofauna. In: Rundle, S.D., A.L. Robertson, and J.M. Schmid-Araya (Eds), Fresh-water meiofauna: Biology and Ecology. Backhuys Publishers, Leiden: 321-335.

Hanson JM, and Peters RH. 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. Can. J. Fish. Aquat. Sci. 41: 439-445.

Harrison SSC, and Hildrew AG. 2001. Epilithic communities and habitat heterogeneity in a lake littoral. J. Anim. Ecol. 70: 692-707.

Hecky RE, and Hesslein RH. 1995. Contributions of Benthic Algae to Lake Food Webs as Revealed by Stable Isotope Analysis. J. N. Am. Benthol. Soc. 14: 631-653.

Herzig A. 1984. Fundamental requirements for zooplankton production studies. Limnologisches Institut Österreichische Akademie der Wissenschaften: 83 pp.

Hill WR, Roberts BJ, Francoeur SN, and Fanta SE. 2011. Resource synergy in stream periphyton communities. J. Ecol. 99: 454-463.

Hillebrand H. 2009. Meta-analysis of grazer control of periphyton biomass across aquatic ecosystems. J. Phycol. 45: 798-806.

Hillebrand H, Kahlert M, Haglund A, Berniger UG, Nagel S, and Wickham S. 2002. Control of microbenthic communities by grazing and nutrient supply. Ecology 83: 2205-2219.

Hynes HBN, and Coleman MJ. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13: 569-573.

Kahlert M, Hasselrot AT, Hillebrand H, and Pettersson K. 2002. Spatial and temporal variation in the biomass and nutrient status of epilithic algae in Lake Erken, Sweden. Freshwater Biol. 47: 1191-1215.

Magnusson KA, and Williams DD. 2009. Top-down control by insect predators in an intermittent pond - a field experiment. Ann. Limnol. -Int. J. Lim. 45: 131-143.

Majdi N, Traunspurger W, Boyer S, Mialet B, Tackx M, Fernandez R, Gehner S, Ten-Hag L, and Buffan-Dubau E. 2011. Response of biofilm-dwelling nematodes to habitat changes in the Garonne River, France: influence of hydrodynamics and microalgal availability. Hydrobiologia 673: 229-244.

Marker A, Nusch E, Rai H, and Riemann B. 1980. The measurement of photosynthetic pigments in freshwater and standardization of methods: conclusions and recommendations. Arch. Hydrobiol.–Beih. Ergebn. Limnol. 14: 91-106.

Mathieu M, Leflaive J, Ten-Hage L, de Wit R, and Buffan-Durban E. 2007. Free-living nematodes affect oxygen turnover of artifical diatom biofilms. Aquat. Microb. Ecol. 49: 281-291.

McCauley E, and Kalff J. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes Can. J. Fish. Aquat. Sci. 38, 458-463.

Meschkat A. 1934. Der Bewuchs in den Röhrichten des Plattensees. Arch. Hydrobiol. 27: 436-513.

Michiels IC, and Traunspurger W. 2004. A three year study of seasonal dynamics of a zoobenthos community in a eutrophic lake. Nematology 6: 655-669.

Perlmutter DG, and Meyer JL. 1991. The impact of a stream-dwelling harpacticoid copepod upon detritally-associated bacteria. Ecology 72: 2170-2180.

Peters L, Scheifhacken N, Kahlert M, and Rothhaupt KO. 2005. An efficient *in situ* method for sampling periphyton in lakes and streams. Arch. Hydrobiol. 163: 133-141.

Peters L, and Traunspurger W. 2011. Temporal patterns in macrograzer effects on epilithic algae and meiofauna: a comparative approach to test for single species and whole grazer community effects. Aquatic Sciences, DOI 10.1007/s00027-011-0214-7.

Peters L, and Traunspurger W. 2005. Species distribution of free-living nematodes and other meiofauna in littoral periphyton communities of lakes. Nematology 7: 267-280.

Peters L, Wetzel MA, Traunspurger W, and Rothhaupt KO. 2007. Epilithic communities in a lake littoral zone: the role of water-column transport and habitat development for dispersal and colonization of meiofauna. J. N. Am. Benthol. Soc. 26: 232-243.

Prejs K. 1977. The littoral and profundal benthic nematodes of lakes with different trophy. Ekol. Pol. 25: 21-30.

Rasmussen JB, and Kalff J. 1987. Empirical models for zoobenthic biomass in lakes. Can. J. Fish. Aquat. Sci. 44: 990-1001.

Reiss J, and Schmid-Araya JM. 2010. Life history allometries and production of small fauna. Ecology 91: 497-507.

Ristau K, and Traunspurger W. 2011. Relation between nematode communities and trophic state in southern swedish lakes. Hydrobiologia 663: 121-133.

Romanovsky JE, and Feniova IY. 1985. Competition among Cladocera: effect of different levels of food supply. Oikos 44: 243-252.

Särkkä J. 1996. Meiofauna of the profundal zone of the northern part of Lake Ladoga as an indicator of pollution. Hydrobiologia 322: 29-38.

Scheffer M. 2004. Ecology of shallow lakes. Kluwer Academic Publishers, Dordrecht.

Schmid PE, and Schmid-Araya JM. 2002. Trophic relationships in temporary and permanent freshwater meiofauna. In: Rundle SD, Robertson AL, and Schmid-Araya JM (Eds), Freshwater meiofauna: Biology and Ecology. Backhuys Publishers, Leiden: 295-319.

Sommer U, Gliwicz ZM, Lampert W, and Duncan A. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106: 433-471.

Spieth HR, Möller T, Ptatscheck C, Kazemi-Dinan A, and Traunspurger W. 2011. Meiobenthos provides a food resource for young cyprinids. J. Fish Biol. 78: 138-149.

Stead TK, Schmid-Araya JM, and Hildrew AG. 2005. Secondary production of a stream metazoan community: does the meiofauna make a difference. Limnol. Oceanogr. 50: 398-403.

Stead TK, Schmid-Araya JM, and Hildrew AG. 2003. All creatures great and small: patterns in the stream benthos across a wide range of metazoan body size. Freshwater Biol. 48: 532-547.

Stich HB, and Brinker A. 2005. Less is better: Uncorrected *versus* pheopigmentcorrected photometric chlorophyll-a estimation. Arch. Hydrobiol. 162: 111-120.

Strayer D, and Likens GE. 1986. An energy budget for the zoobenthos of Mirror Lake, New Hampshire. Ecology 67: 303-313.

Swedish Standards Institution. 1995. Swedish Standard. Water Quality. Swedish Standard Institution, Stockholm.

Tod SP, and Schmid-Araya JM. 2009. Meiofauna *versus* macrofauna: secondary production of invertebrates in a lowland chalk stream. Limnol. Oceanogr. 54: 450-456.

Traunspurger W. 2002. Nematoda. In: Rundle SD, Robertson AL, andSchmid-Araya JM (Eds), Freshwater meiofauna: Biology and Ecology. Backuys Publishers, Leiden: 63-104.

Traunspurger W, Bergtold M, and Goedkoop W. 1997. The effects of nematodes on bacterial activity and abundance in a freshwater sediment. Oecologia 112: 118-122.

Vadeboncoeur Y, and Steinman AD. 2002. Periphyton function in lake ecosystems. The Scientific World JOURNAL, 2: 1449-1468.

Wetzel RG. 2001. Limnology. Academic Press, San Diego.

Witthöft-Mühlmann A, Traunspurger W, and Rothhaupt KO. 2005. Influence of river discharge and wind field on the freshwater meiofauna of a dynamic river mouth area. Arch. Hydrobiol. 163: 307-327.

Wu J, Cuizhang F, Liang Y, and Chen J. 2004. Distribution of the meiofaunal community in a eutrophic shallow lake of China. Arch. Hydrobiol. 159: 555-575.