Limnologica 44 (2014) 49–57

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

The effect of trophic state and depth on periphytic nematode communities in lakes

Ardeshir Kazemi-Dinan[a], Fabian Schroeder[a], Lars Peters[a], Nabil Majdi[b,c], Walter Traunspurger[a,*]

[a] University Bielefeld, Animal Ecology, Morgenbreede 45, 33615 Bielefeld, Germany
[b] Université de Toulouse, INP, UPS, EcoLab, 118 route de Narbonne, 31062 Toulouse, France
[c] CNRS, EcoLab, 31062 Toulouse, France

ARTICLE INFO

Article history:
Received 19 March 2013
Accepted 27 May 2013
Available online 10 September 2013

Keywords:
Biofilm
Community ecology
Trophic structure
Meiofauna
Algae
Grazing

ABSTRACT

The aim of this study was to investigate whether nematode community patterns are shaped by nutrient and light availability. Accordingly, nematode communities inhabiting periphyton were investigated at gradual water depths (50, 150 and 250 cm) in three Swedish lakes showing graded trophic states. It was hypothesized that: (1) nematode density correlates positively with increasing nutrient availability and negatively with increasing depth; (2) increasing nutrient availability favors species and feeding type richness; (3) increasing depth favors deposit-feeders; and (4) differences in the algal composition of the periphyton affect the diet of algal-feeders. Our results showed that the biomass of periphytic algae increased with nutrient availability and decreased with increasing depth. Nematode density also increased with increasing trophic state. Species richness decreased with increasing depth in the investigated oligotrophic lake, while the opposite pattern was determined in the other two lakes. Lake trophic state significantly affected the trophic structure of the nematode community, with more algal-feeders occurring in the eutrophic lake whereas chewers were found only in the meso- and eutrophic lakes. Water depth was also shown to influence nematode feeding type structure, as in all lakes the abundance of deposit-feeders was greater at increasing depth. While diatoms dominated the periphytic algal community at all lakes and depths, analyses of the gut pigment content of nematodes showed that their diet shifted toward green algae in the oligotrophic lake and in shallow zones of the mesotrophic lake.

Hard substrates in the euphotic littoral zones of lakes are often coated by periphyton, which consists of autotrophic and heterotrophic organisms embedded in a slimy organic matrix. The conventional view of energy transfers in lakes is based mostly on pelagic food web functioning (e.g., Hairston 1993; Mittelbach et al. 1995; Brett and Goldman 1997; Vander Zanden and Vadeboncoeur 2002). However, it has long been acknowledged that benthic communities are also involved in the total production of lakes (e.g., Lindeman 1942; Bergtold and Traunspurger 2005a). In recent years, periphytic communities have drawn particular attention, as several studies have demonstrated the pivotal contribution of benthic algae to lake total primary production, food webs, and nutrient cycling (e.g., Strayer and Likens 1986; Wetzel 1996; Vadeboncoeur et al. 2001, 2002; Hillebrand et al. 2002; Ask et al. 2009). Periphyton productivity, however, remains constrained by light and nutrient availability (Hillebrand and Kahlert 2001; Rodusky et al. 2001) and its transfer through food webs involves species assemblages that are more complex than those inhabiting the water column (Warren 1989; Havens et al. 1996).

Minute metazoan meiofauna densely colonize lake periphyton (Peters and Traunspurger 2005; Schroeder et al. 2012a). In stream periphyton, meiofauna specifically prey on microalgae (Borchardt and Bott 1995; Majdi et al. 2012b), thereby constituting relevant trophic intermediaries between micro- and macro-organisms (Schmid-Araya et al. 2002). Nematodes usually dominate meiobenthic communities in freshwater (Traunspurger 1996a,b; Bergtold and Traunspurger 2004; Michiels and Traunspurger 2004; Traunspurger et al. 2012) and, given their diverse feeding types, are able to exploit multiple food resources, including periphytic microorganisms such as bacteria, protozoans, and micro-algae (Montagna 1995). Yet, the combined ecological consequences of nutrient and light availability on periphytic nematodes have thus far been overlooked.

The decrease in light availability with increasing water depth causes a switch in periphyton composition, from photoautotrophic (e.g., diatoms) to heterotrophic (e.g., bacteria) micro-organisms (Vadeboncoeur et al. 2008). Light penetration depends on the trophic state of the lake, with increasing nutrient concentrations

* Corresponding author. Tel.: +49 5211062702.
E-mail address: traunspurger@uni-bielefeld.de (W. Traunspurger).

0075-9511/$ – see front matter © 2013 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.limno.2013.05.011

Table 1
Morphometric and physico-chemical characteristics of the study lakes. TN: total nitrogen, TP: total phosphorus, O_2: dissolved oxygen, *T*: temperature.

Lake and location	State	Area (km^2)	Mean depth (m)	Max. depth (m)	TN (μg/l)	TP (μg/l)	O_2 (mg/l)	*T* (°C)
Largen (59°59′ N, 18°52′ E)	Oligotrophic	1.5	8.3	21.0	500	8	8.6	5.8
Erken (59°51′ N, 18°36′ E)	Mesotrophic	24.0	9.0	21.0	670	28	11.8	5.6
Limmaren (59°72′ N, 18°73′ E)	Eutrophic	5.4	4.6	7.8	1100	44	11.2	6.5

reducing water transparency (Mazumder and Havens 1998). However, the potential negative effects on periphytic algae of a reduction in light are overcome by high nutrient availability. Thus, the periphyton in eutrophic lakes sustains a higher productivity than in less nutrient-enriched lakes (Vadeboncoeur et al. 2008). Furthermore, the periphytic algal community is also affected by lake trophic state: Liboriussen and Jeppesen (2005) reported a shift under an increasing nutrient availability gradient, from a predominance of diatoms and cyanobacteria toward one of green algae. Periphytic algal composition also changes with depth in response to differences in light availability (Jonsson 1987).

These variations in the periphytic community structure may affect the diet of invertebrate consumers. Hence, the autotrophic vs. heterotrophic content of the periphyton has the ability to drive the distribution of algal- vs. bacterial-feeders. In addition, the diet of algal-feeders might correspond to the availability of the different algal groups within the periphyton. This latter possibility can be verified by using high-performance liquid chromatography (HPLC) to quantify algal biomarker pigments contained in the guts of grazers. Indeed, this technique yields *in situ* information on the diet of grazers and was previously applied to unravel the algal diet of small invertebrates such as planktonic and benthic copepods, chironomids (Buffan-Dubau et al. 1996; Irigoien et al. 2000; Goldfinch and Carman 2000) and, more recently, nematodes (Majdi et al. 2012c). In their study of the Garonne River (SW France), the latter authors showed that the algal diet of periphytic nematodes is restricted to diatoms, which also dominate the periphytic algal assemblage.

Against this background, our study investigated the vertical changes occurring in the meiobenthic community structure of the periphyton sampled in three Swedish lakes with graded differences in their trophic states. The nematode community in particular was detailed (species composition and feeding types), and nematode gut pigment contents were compared to the algal biomarker pigment composition of the periphyton. We specifically hypothesized that: (1) meiofauna (and nematode) density increases with increasing lake trophic state and decreases with increasing depth; (2) nematode species and feeding type richness should increase with increasing lake trophic state; (3) a switch from a dominance of algal- toward bacterial-feeders should be detected with increasing depth; and (4) the diet of periphytic nematodes should match the availability of the algal groups present in the periphyton.

Materials and methods

Study site and sampling

In April 2010, three Swedish lakes differing in their trophic state, size, and mean depth were sampled (Table 1). The periphytic meiobenthos in these lakes is dense and diverse (Peters and Traunspurger 2005). In each lake, a site was sampled at three depths (50, 150, and 250 cm) along a depth transect from the littoral zone. All samples below 50 cm were taken by a scuba-diver. However, in the eutrophic lake, high water turbidity prevented sampling at 250 cm. At each depth, five replicate periphyton samples were retrieved from hard substrates (stones) using a brush-sampler (Peters et al. 2005); these samples were used to measure periphytic dry mass (DM) and ash-free dry mass (AFDM), chlorophyll *a* (Chl *a*), and algal pigments content, as well as meiofaunal density and nematode density, diversity, and feeding types. In addition, at each depth two or three stones were carefully slid, underwater, into 20-μm sieve bags, packed in buckets containing lake water, and then transported to the laboratory. During sampling, the light quantity (μmol/s/m^2) was measured underwater at different depths (50, 100, 200, and 300 cm) using a LI-250A photometer (LI-COR, Lincoln, NE, USA). Light measurements were carried out at about 1 p.m. during slightly overcast but sunny weather. Water temperature and dissolved oxygen were measured at 15 cm depth using a Hanna HI 9828 probe (Hanna Inc., RI, USA). Total phosphorus and nitrogen concentrations were measured following the Swedish Standard Institute guidelines at the Erken Laboratory (Uppsala Universitet, Sweden).

Periphyton biomass and algal composition

Periphyton samples retrieved with the brush-sampler were adjusted to a defined volume (100 ml). For each sample, one aliquot (5–10 ml) was filtered onto a pre-combusted (550 °C, 7 h) glass-fiber filter (Whatman GF/C, ∅ 25 mm, Whatman, Maidstone, UK) and then dried (105 °C, 24 h) and weighed to calculate dry mass (DM). To measure the AFDM content of the periphyton the sample was combusted by 550 °C for 7 h.

Another aliquot (5–10 ml) was centrifuged (3000 × *g*, 5 min), and Chl *a* was extracted from the pellet with 90% EtOH during 24 h at 4 °C in the dark following the method of Nusch (1980). The Chl *a* concentration was measured spectrophotometrically at 644 nm and 750 nm and determined on the basis of the uncorrected pheophytin values (Stich and Brinker 2005).

Another aliquot (5–10 ml) was centrifuged (3000 × *g*, 5 min) and the pellet was freeze-dried and thoroughly homogenized. A 250-mg subsample was retrieved from the pellet and algal pigments were extracted from each subsample three times (−20 °C, 15 min) with a total of 25 ml (10, 10, and 5 ml) of 98% cold-buffered methanol (with 2% 1 M ammonium acetate) by sonication, after Buffan-Dubau and Carman (2000). One ml of the pigment solution was then filtered through a 0.2-μm PTFE syringe filter and the filtrate was analyzed using HPLC (LC1200 series, Agilent Technologies, Santa Clara, CA, USA). The mobile phase was prepared and programmed following Barlow et al. (1997). Algal pigments were identified by comparing their retention time and absorption spectra with those of pure standards (DHI LAB products, Hørsholm, Denmark; see Majdi et al. 2011 for further details). The HPLC-analysis of algal biomarker pigments was coupled with a chemotaxonomic analysis using CHEMTAX software (version 1.95; Mackey et al. 1996) to estimate the biomass of algal groups in the periphyton in terms of their contribution to total Chl *a* biomass. The biomarker pigment ratios of periphytic microalgal groups reported in Majdi et al. (2011) were used to supply the initial matrix needed to run the chemotaxonomic analysis.

Meiofauna and nematode communities

The remaining periphyton suspension was poured through a 20-μm sieve. The organisms retained on the sieve were preserved with 4% formaldehyde and stained with Rose Bengal. Invertebrates were counted und classified into major taxonomic groups (Nematoda, Rotifera, Crustacea, Tardigrada, Hydrachnidia, and Oligochaeta)