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Investigation on competitors and predators of herbivorous aquatic Lepidoptera (*Acentria ephemerella*) on submersed macrophytes in a large prealpine lake

E. M. Gross and R. Kornijów

Introduction

Submersed macrophytes offer a large colonization area for many macroinvertebrates. Numerous studies investigated the interaction between plant species, growth and leaf form and the abundance and species composition of invertebrates (e.g. SOSZKA 1975, KORNIJÓW & KAIRESALO 1992). Grazers and detrivores assist the plants by removing epiphyton and allowing more light to reach the photosynthetic tissue. Only recently has the paradigm that aquatic angiosperms are not subjected to a high degree of herbivory been challenged (LODGE 1991, NEWMAN 1991, KORNIJÓW 1996, LODGE et al. 1998). A detailed study of the literature reveals that aquatic insects were frequently observed feeding on submersed macrophytes. For example, *Acentria ephemerella*, a true shredder–herbivore, was found associated with pondweeds and other macrophytes in several studies (BERG 1942, MÜLLER-LIEBENAU 1956, SOSZKA 1975). *Acentria* seems to prefer large lakes to small ponds as habitat (JOHNSON et al. 1998). Data on its abundance in different lakes range from a few dozen to many hundred species per square meter (SOSZKA 1975, HEDAL & SCHMIDT 1992, BÄNZIGER 2000, JOHNSON et al. 2001, GROSS et al. in prep.).

In Lake Constance, *Acentria* is the major invertebrate herbivore and regularly develops exponentially increasing densities during the vegetation period (GROSS et al. in prep.). However, information is still lacking on the relationship between the abundance of this herbivore and the resulting damage to different macrophyte species (JOHNSON et al. 2001, GROSS et al. 2001). Very little is also known on the interactions with other invertebrates, especially competitors and predators. Therefore, the aim of this study was to learn the guild structure of the epiphytic macroinvertebrate communities inhabiting various elodeids in Lake Constance with analyses of potential competitors and predators of *Acentria*.

Methods

Lake Constance is the second largest (571 km^2) prealpine lake in Europe. The lake has three major basins, the Überlinger See, the Upper Lake and the Lower Lake. The Lower Lake (71 km^2) is shallow (max. depth 46 m, 28% littoral area defined as area above 10 m water depth). This part supports luxurious submersed macrophyte growth.

In order to determine the seasonal and spatial dynamics of *Acentria ephemerella*, macrophyte stands at different sites in the Überlinger See and Lower Lake Constance were sampled regularly during the vegetation period from 1998 to 2000 (GROSS et al. in prep.). The samples for analyses of the animal guild structure were collected during August–September 2000 from *Potamogeton perfoliatus*, *P. pectinatus* and *Myriophyllum spicatum* at the western tip of the island, from two different locations. They were situated about 300 m from each other, at a depth of between 2 and 2.5 m, depending on the water gauge level of the lake.

In addition to the 0.1-m^2 samples taken for the evaluation of *Acentria* abundance, one or two shoots of each macrophyte were carefully selected at the sediment interface and pushed gently in an upward moving sweep net (mesh width 240 µm) to avoid loss of highly mobile macroinvertebrates. Three replicate samples from each macrophyte were collected at each sampling location .

All samples were taken snorkelling. Samples were concentrated in mesh beakers and transferred with water into 1-L sealable (Ziploc ™) bags. After sorting, the macroinvertebrates were preserved in 70% ethanol. The absolute number of *Dreissena polymorpha* is probably underestimated because not all specimens were preserved. The dry weight of the macrophyte shoots was determined after drying at 100 °C for 48 h. The density of macroinvertebrates was calculated per 100 g of plant dry weight.

Results

Density of Acentria

In 1998, *Acentria* developed densities, in dense stands of both *Potamogeton perfoliatus* and *Myriophyllum spicatum,* of 10–8000 ind./m^2 lake area. That year exhibited extremely low summer water levels allowing lush macrophyte growth. In late spring and early summer of 1999, Lake Constance exhibited a very high water level (2 m higher than normal for this time of the year) due to massive precipitation in the northern catchment area. This severely interfered with normal submersed macrophyte growth, which usually starts in May. Consequently, maximum densities of *Acentria* found in 1999 reached only about 100 ind./m^2 from August until the end of October. During 2000, water levels were close to the long-term annual mean, and pondweeds developed normally. Only *M. spicatum* failed to build up the dense stands observed in the previous years and reached only 150–175 g DW per m^2 in September 2000 compared with ca. 350 g DW per m^2 in 1998. *Acentria* density dropped from 2420 ind./100 g DW at the end of September 1998 to 243 ind./100 g DW at the same time in 2000. The mean summer percentage of *Acentria* in the total density of epiphytic fauna on *Potamogeton perfoliatus*, *P. pectinatus* and *Myriophyllum spicatum* in 2000 differed considerably and amounted to 11%, 31% and 1.3%, respectively.

Guild structure of the animal epiphytic communities

The analysis of the plant-associated macrofauna occurring on the vegetation during late summer 2000 exhibited a diverse community, composed of 27 taxa, of which 25 were found on *Potamogeton perfoliatus*, 6 on *P. pectinatus* and 12 on *Myriophyllum spicatum.* The total mean faunal densities amounted to 2819, 397 and 2137 ind./100 g DW, respectively.

The communities can be pooled into three groups: vascular plant feeders (two species), omnivores (18 taxa) and predators (seven taxa). The most abundant were omnivores (Table 1) with predominating chironomid larvae *Endochironomus albipennis* (81%, 24% and 71% by numbers, respectively). The second most numerous group was the herbivores, represented by only two species, among which *Acentria ephemerella* predominated (98%, 100% and 87%) over *Macroplea appendiculata* (Chrysomelidae). Predators occurred in relatively low numbers and only on *P. perfoliatus* and *M. spicatum.*

Discussion

Acentria ephemerella is an important invertebrate herbivore in Lower Lake Constance, causing extensive damage to aquatic vegetation. Since its abundance increases almost exponentially during the vegetation period, other members of the macroinvertebrate community are potential competitors or predators of this species. In previous studies, the only predators found associated with *Acentria* were planaria (*Dugesia* sp.) and dytiscid larvae (Buckingham & Ross 1981). In studies of lakes in the US, *Acentria* was frequently associated with the herbivorous cucurlionid *Euhrychiopsis lecontei* (26 out of 34 lakes shared both herbivores (Johnson et al. 1998).

Many species classified in this study as omnivores consume plant tissue, also, although in small quantities. They can interact with *Acentria* in various ways. For example, the predominating photophilous larvae *Endochironomus albipennis* occur mainly in the upper stem sections of submersed macrophytes (Zhgarieva 1982), the same habitat used by *Acentria* (Gross et al. 2001). They overwinter in the bottom sediments but live on various macrophytes during the vegetation period, with maximum abundance during midsummer (Kornijów 1992). The larvae may benefit from herbivory by *Acentria* due to damage of the leaves causing leaching of cell sap and the production of faecal pellets still rich in nutrients, which can lead to the subsequent higher production of bacterial and algal epiphytes. On the other hand, *Acentria* benefits from epiphyte grazers since they remove dense layers of algae, especially filamentous species, which can severely interfere with the feeding on macrophyte tissue.

Table 1. List of invertebrates (per 100 g DW) associated with the herbivorous *Acentria ephemerella* (Lepidoptera: Pyralidae) on *Potamogeton perfoliatus*, *P. pectinatus* and *Myriophyllum spicatum* in late summer in Lower Lake Constance. *Indicates potential predators.

Taxa	*P. perfoliatus*	*P. pectinatus*	*M. spicatum*
Hirudinea			
Erpobdella sp.*	17		
*Glossiphonia heteroclita**	1		
*Helobdella stagnalis**	17		
Oligochaeta			
Stylaria lacustris	9		21
Naididae n. det	84	71	
Gastropoda			
Bithynia tentaculata	106		
Gyraulus albus	3		
Planorbis planorbis			
Bivalvia			
Dreissena polymorpha	140	95	306
Sphaeridae	2		
Crustacea			
Gammarus sp.*	10		
Hydracarina*			63
Ephemeroptera			
Caenis sp.	7		
Zygoptera			
Trichoptera			
Athripsodes atterimus l.	53	44	37
Athripsodes atterimus p.	57	9	332
Trichoptera non. det.	6		
Lepidoptera			
Acentria ephemerella l.	283	123	12
Acentria ephemerella p.	34		16
Chrysomelidae			
Macroplea appendiculata	5		11
Chironomidae			
Ablabesmyia sp.*			7
Corynoneura lobata	5		
Cricotopus sp. (gr. *silvestris*)	25		7
Endochironomus albipennis	1801	43	1163
Limnochironomus sp.	39	11	14
Orthocladiinae non. det.	5		
Paratanytarsus sp. (gr. *lauterborni*)	6		71
Parachironomus varus	10		42
Psectrocladius gr. *sordidellus*	4		
Chironomidae pupa	185		35
Fauna total per 100 g DW	2819	397	2137

Colonization of macrophytes by *Dreissena* should not interfere with the active feeding of *Acentria*. However, dense *Dreissena* coverage at lower stem sections could interfere with stem boring of *Acentria* for winter diapause. The same *Dreissena* cover may prevent predation by invertebrate omnivores or predators on stems containing *Acentria*. Anyhow, predatory macroinvertebrates present in association with *Acentria* larvae, due to their low size and densities, seem unlikely to threaten larger instar larvae. Only egg clutches and young instar larvae might be susceptible to predation, e.g. by leeches and predatory chironomid larvae of the midge larvae. *Acentria* larvae are very cryptic: first and second instars mine in leaves. Older instars build retreats with leaf material, either by cutting a disk of leaf material and attaching it 'sandwich-like' to their back or by connecting leaflets of milfoil in a tube-like manner. Mortality of *Acentria* was assumed to be low during the active feeding period (May to early September), which was reflected in the almost exponential increase of density. Mortality was obviously high during the winter months when larvae stayed in remnants of lower shoot sections.

The only other true macrophyte herbivore, *Macroplea appendiculata*, usually occurs in much lower densities than *Acentria* on *P. perfoliatus* (5 *Macroplea* compared to 283 *Acentria* larvae and 34 pupae per 100 g DW). Approximately the same density of both species was observed on *M. spicatum* (11 *Macroplea* versus 16 *Acentria* larvae and 12 pupae per 100 g DW). Larvae of *Macroplea* usually feed on midstem sections or move to the root area in the late fall. Not much is known about the life history and feeding preferences of this species (GRILLAS 1988) It has only be found on *P. perfoliatus* (this study), *P. pectinatus* and *M. spicatum* (GRILLAS (1988) and this study).

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Authors' addresses:

E. M. GROSS, Limnological Institute, University of Konstanz, 78457 Konstanz, Germany.
E-mail: Elisabeth.Gross@uni-konstanz.de

R. KORNIJÓW, Department of Hydrobiology and Ichthyobiology, University of Agriculture, Akademicka 13, 20–950 Lublin, Poland.
E-mail: rkorn@ursus.ar.lublin.pl