Limnologica 62 (2017) 132–139

Contents lists available at ScienceDirect

Limnologica

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

Vertical migration of *Daphnia galeata* – Evidence for the use of an alternative resource from a lethal environment

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ARTICLE INFO

Article history:
Received 27 April 2016
Received in revised form
18 November 2016
Accepted 21 November 2016
Available online 15 December 2016

Keywords:
Diel vertical migration
Daphnia galeata
Hydrogen sulfide
Gravel pit lake
Anaerobic environment
Field experiments
Mortality

ABSTRACT

Metazoans normally avoid anaerobic environments, at least when they are combined with toxic stress due to hydrogen sulfide. In Lake Speldrop, a small but deep gravel pit lake at the Lower Rhine, *Daphnia galeata* was found not only to dominate the zooplankton community, but was also regularly found in anoxic and even sulfidic layers during summer. We conducted field experiments with a newly developed "Zooplankton *In-situ* Incubator", simulating vertical migrations of *D. galeata*. When daphnids were exposed to sulfidic conditions, mortality increased with exposure time, revealing LT_{50}-values between 129 and 42 min in relation to increasing concentrations of sulfide. Additionally, those experimental individuals originating from 12.5 m depth showed significantly higher mortality rates than those from 7.5 m depth. Further migration experiments showed that an interruption period of sulfidic exposition in less stressful environments reduced mortality rates significantly. Daphnids found in the hypolimnion belonged partly to moribund parts of the population; however, the majority of daphnids showed regular mowing activity and was able to withstand sulfidic conditions in the hypolimnion for a limited time. It is so far unclear what maybe the major ultimate factor for this type of short term migratory behavior, to seek for shelter or to use high amounts of sulfur bacteria as an alternative food resource.

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1. Introduction

Anaerobic environments are normally avoided by metazoans. However, there are some exceptions. For example, the central mud minnow (*Umbra limi*) was found to dive regularly into the anoxic bottom waters of lakes to forage on phantom midge larvae of the genus *Chaoborus* (Rahel and Nutzman, 1994), a genus that make use of this anaerobic environment in order to avoid fish predation (*e.g.*, Voss and Mumm, 1999). This example illustrates the two major reasons for organisms to make use of a harsh environment, which are food resources and predator avoidance. This represents a typical and important tradeoff situation in the behavior of organisms (*e.g.*, Magnhagen and Borcherding, 2008). During the last two decades it has become evident that some invertebrates and ectothermic vertebrates successfully cope with a fluctuating supply of ambient oxygen (for review see Gorr et al., 2010).

In freshwater lakes, many zooplankton species stay in deeper zones during the day and migrate to surface areas during the night for feeding on algae that accumulated nutrients and grow during day (Stich and Lampert, 1981; Ringelberg, 1999). Several models on this diel vertical migration (DVM) have been hypothesized that take into account all aspects of ecology like temperature dependence of physiological rates of the algae and the zooplankton, feeding rates and the energy balance including the cost of migration, or aspects of competition and predator avoidance (Lampert et al., 1988; Lampert, 1989; Loose and Dawidowicz, 1994). Among these aspects, avoidance of predation seems to be the major ultimate factor for DVM (induced by kairomones, Loose et al., 1993; von Elert and Loose, 1996), especially in daphnid species. Changes in light intensity have been shown to trigger the behavior (van Gool and Ringelberg, 1998; Ringelberg, 1999; Effertz and von Elert, 2014).

Apart from kairomones and light intensity, the concentration of oxygen is also thought to play an important role for the vertical distribution of daphnids, as areas of low oxygen may serve as a refuge against fish predation (Kobayashi and Gonoi, 1985 Wright and Shapiro, 1990). The occurrence of daphnids in anaerobic layers is generally restricted to short periods as filtering and respiration rates decrease below a threshold concentration of about 3.5 mg O_2 l^{-1} (*e.g.*, *Daphnia pulex*, Weider and Lampert, 1985). The production of hemoglobin in some daphnid species was shown to allow the extension of such periods under unfavorable conditions (Paul et al., 1998; Sell, 1998; Pirow et al., 2001; Schwerin et al., 2010).

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http://dx.doi.org/10.1016/j.limno.2016.11.010
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Anoxic conditions during summer are common in the hypolimnion of eutrophic lakes (Vanderploeg et al., 2009). Extended anaerobic conditions, may lead to increased levels of sulfidic conditions (Volpers and Neumann, 2005) through the production of sulfide through dissimilatory sulfate reduction. Due to the high affinity of the sulfide ion to the cytochrome-c-oxidase it is a strong inhibitor of the respiratory chain and, thus highly toxic to many organisms (Reiffenstein et al., 1992; Bagarinao, 1992). Daphnids have been described to sometimes occur in these sulfidic layers (Mazumder and Dickman, 1989), however, these individuals were assumed to be the moribund part of the population. Other reports found daphnids to be voracious predators on the microbial community in the sulfidic zone, though of negligible importance in the anaerobic layers (Massana et al., 1994).

Anoxic and sulfidic conditions are typical for some gravel pit lakes at the Lower Rhine (Volpers, 1995). One of these lakes with a typically anaerobic hypolimnion is Lake Speldrop, where mining stopped about 50 years ago (Beeck et al., 2002). Summer stratification forms an anoxic hypolimnion up to about 5 m depth which is usually fully established by the beginning of July (*e.g.*, Beeck et al., 2002). First surveys on the zooplankton of Lake Speldrop in 1997 revealed that a certain amount of daphnids were always present in the deep anaerobic layers in which sulfidic conditions were expected. These observations raise the questions (1) whether the occurrence of daphnid species in the anaerobic and potentially sulfidic depth during summer may be a common phenomenon in a hypertrophic lake such as Lake Speldrop, (2) whether these individuals are not only the moribund part of the population, but healthy and active individuals, and (3) how long daphnids are able to survive such toxic conditions. The results were hoped to provide cues as to whether an active migration of daphnids into sulfidic layers can be assumed and what the ultimate reasons for such behavior may be. Consequently, the vertical distribution of the zooplankton in Lake Speldrop was studied for two successive years from April until October. In addition, a newly developed method was utilized to allow the experimental simulation of vertical migration for zooplankton in the lake. Using this method, field experiments were performed to analyze the relationship between sulfide concentrations and mortality of *Daphnia galeata*, the dominant daphnid species in Lake Speldrop.

2. Material and methods

2.1. Study site

Lake Speldrop in the Lower Rhine area is a gravel pit lake between Emmerich and Rees (Germany), with an area of 7 ha and a maximum depth of 16 m, depending on the water level of the River Rhine which affects the water level of Lake Speldrop *via* groundwater. There is no surface inflow. With the exception of one small bay, the bank has a steep slope of >60°. The substratum of the bank is dominated by sand and gravel and submersed vegetation is virtually absent (*cf.* Beeck et al., 2002; Borcherding et al., 2007).

2.2. Abiotic factors and chlorophyll

Between April and October 1999 and 2000, weekly measurements were taken at a fixed buoy at the deepest point of Lake Speldrop. In 1999, vertical profiles were recorded using a submersible 12 V pump that pumped the water into a small measuring container where it flowed around three probes to measure temperature and conductivity (WTW LF91, Germany), oxygen (WTW Oxi 320, Germany) and pH (WTW pH 320, Germany). In 2000, the vertical profiles were recorded with a multi-parameter probe (Yellow Spring Instrument Incorporated, USA). The transparency was measured at least once a week with a white standard secchi disk. Water samples from 1, 5, 9 and 13 m depth were taken fortnightly with the above mentioned submersible pump. Samples were stored cool and dark in plastic bottles and subsequently analyzed for orthophosphate (MERCK, Spectroquant 14848) and nitrate (MERCK, Spectroquant 14773). In 1999, the same water was used to determine the chlorophyll *a* concentration according to the method described by Nusch (1984). In 2000, chlorophyll *a* was measured with the multi-parameter probe. Starting seasonal sampling in May 1999 or in July 2000 respectively, water samples were taken from the bottom of the lake up to the end of the anoxic layer at 1 m intervals. These samples were stored cool and dark in tightly closed glass bottles which were completely filled with no air remaining (bottles closed with ground-in glass stoppers). The samples were analyzed photometrically for their sulfide concentration (MERCK, Spectroquant 14779). When comparing these sulfide concentrations to other studies on the toxicity of hydrogen sulfide, one has to consider that, depending on the pH, three sulfide species can be found: H_2S, HS^- and S^{2-}. At a pH of around 7.3, as it was found in the hypolimnion of Lake Speldrop, the dominant toxicant H_2S is assumed to make up roughly 60% (Vismann, 1996), however, this percentage was not quantified in our study. Therefore, we have to assume that the daphnids in Lake Speldrop were probably affected by somewhat lower toxic concentrations of H_2S than those derived from the analysis of total sulfide.

2.3. Zooplankton

From April until October, samples of the zooplankton were collected fortnightly with a 20 l Schindler-Patalas trap. Triplicate replicate samples were taken around midday and 1.5 h after sunset at the buoy over the deepest point of the lake from depths of 1, 5, 9 and 13 m. The samples were concentrated with a 200 μm-net and preserved with sucrose-formalin according to Haney and Hall (1973). Samples were diluted in 250 ml water and subsamples of 5 ml were counted under an inverted microscope for determining abundances. Before subsampling, larger organisms (*Chaoborus* and *Leptodora*) were counted for each sample. Each species of zooplankton was grouped into size classes for estimating the dry weight according to Bottrell et al. (1976).

2.4. Incubation and migration experiments

To carry out *in-situ* experiments with daphnids in the hypolimnion of Lake Speldrop, a new method was developed that uses the Zooplankton *In-situ* Incubator (ZII, Fig. S1, Suppl. material). The ZII is a rectangular box, the bottom of which consists of two flaps. Each flap has five round holes in which standard sample chambers (200 ml) can be fitted. The sample chambers were prepared by cutting two holes (2 × 3 cm) into opposite sides of each container which were sealed with a 250 μm mesh. Equipped with ten sample chambers, the ZII can be lowered into the water. The flaps then lift upwards and water flows through the chambers. When the incubation depth is reached, the flaps return to their initial position. To terminate an experiment, the ZII is pulled out the water. The flaps remain in position keeping the water of the experimental depth in the sample chambers. Preliminary tests with blue ink were carried out revealing the total replacement of colored water after lowering the ZII for one meter, proving the steady water exchange in the chambers when lowering the ZII.

Starting in mid-September, daphnids for the experiments were caught with a Schindler-Patalas trap (20 l volume, 500 μm mesh size) in depths of 7.5 and 12.5 m (Table 1). During the experimental periods in September and October in 1999 as well as in 2000, only *D. galeata* was found in Lake Speldrop, thus, all experiments were obviously conducted with this species in both years. They were

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