Limnologica 45 (2014) 24–32

Contents lists available at ScienceDirect

Limnologica

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

Flexibility in feeding periodicity of a grazing mayfly in response to different concentrations of benthivorous fish

Jana Schneider[a,*], Susanne Worischka[a], Claudia Hellmann[b], Jürgen Benndorf[a], Carola Winkelmann[b]

[a] *Institute of Hydrobiology, Dresden University of Technology, Helmholtzstrasse 10, 01069 Dresden, Germany*
[b] *Department of Biology, University of Koblenz-Landau, Universitätsstrasse 1, 56070 Koblenz, Germany*

ARTICLE INFO

Article history:
Received 11 April 2013
Received in revised form 9 October 2013
Accepted 9 October 2013
Available online 19 October 2013

Keywords:
Behavioural response
Avoidance behaviour
Predator–prey interactions
Chemical cues
Consumption
Baetis rhodani

ABSTRACT

Flexibility is an important adaptive attribute of the feeding periodicity of grazing mayfly larvae because most natural environments offer a wide variation in local predation risk in terms of space, time or predator species. In this study any changes of diel feeding periodicity and consumption rates of *Baetis rhodani* (Ephemeroptera) were analysed in response to different densities of benthivorous fish (*Barbatula barbatula*, *Gobio gobio*) by quantifying gut fullness using the fluorescence of algal pigments. Laboratory experiments with the grazer species *B. rhodani* were conducted by using different concentrations of chemical fish cues. In order to assess the transferability of the results to a larger scale, the experimental results were compared with field observations in two second order streams using different densities of freely foraging benthivorous fish. During the presence of chemical fish cues in the laboratory experiments the feeding periodicity of the *B. rhodani* larvae were mostly diurnal while in the absence of fish chemicals nocturnal feeding was observed. The same patterns could be detected in the field during the experiments with the different fish densities. These findings indicate that the larvae were able to assess variations in the predation risk and to alter their feeding habits by making flexible behavioural adjustments. The results from the laboratory experiments further suggested that the behavioural response is controlled by fish density. Behavioural changes were observed for medium and high concentrations of the fish cues but not for a very low concentration. In the field however, the mere presence of fish seemed to be sufficient to induce the observed behavioural shifts. Although the presence of benthivorous fish seemed to cause a lower consumption rate of the *B. rhodani* larvae in the field, such a reduction could not be found in the laboratory experiments. A conclusion from this study is that the identification of behavioural modifications is an essential component needed for a better understanding of complex trophic interactions in benthic communities. Accurate evaluation and detailed observation of direct and indirect effects cannot be made without the consideration of such behavioural mechanisms.

Introduction

Predation in stream ecosystems can have far-reaching effects on prey populations, either directly via predator-induced mortality and indirectly via sublethal effects such as behavioural adaptations (Peckarsky and McIntosh 1998; Allan and Castillo 2007) or alterations of prey life-styles (Sih 1987). The risk of mortality during the feeding process is an important influence on prey which causes them to alter their behaviour in order to reduce their vulnerability to predators (Sih 1980; Holomuzki et al. 2010). One of the avoidance responses towards predators is to change activity times (e.g. Gentry 1974; Nelson and Vance 1979; Bertness et al. 1981). The benefit of this strategy clearly lies in the reduction of direct predation risk due to a decrease of time exposed to the predator. However, predator avoidance involves some costs, such as a reduction in the time spent foraging, which makes it necessary to balance the potentially conflicting demands of maximising feeding rates and minimising predation risk (Sih 1987). Therefore, many prey species in streams facing benthivorous fish show trade-offs between foraging efficiency (energy intake) and predation risk (mortality) (e.g. Sih 1980; Lima 1985; Lima et al. 1985; Abrahams and Dill 1989). Dahl and Greenberg (1996) and Dahl (1998b) additionally suggested that benthic-feeding predators might be more efficient at finding and capturing benthic prey than drift-feeding predators. It was suggested that they might have a more intense impact on benthic prey. However, experiments which have used exclusively benthivorous fish to determine the behavioural effects of mayflies are rare. Kohler and McPeek (1989)

* Corresponding author. Tel.: +49 351 463 32329; fax: +49 351 463 37108.
E-mail address: Jana.Schneider2@mailbox.tu-dresden.de (J. Schneider).

0075-9511/$ – see front matter © 2013 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.limno.2013.10.002

conducted a predation experiment with visually feeding benthic fish and observed strong behavioural effects of *Baetis* sp. during the day, when fish fed most actively. In a study with nocturnal benthic fish Culp et al. (1991) found two anti-predator responses of nocturnally active mayfly (*Paraleptophlebia heteronea*): movement into the drift and retreat into interstitial crevices.

The majority of predation experiments were, however, conducted with *Baetis* sp. larvae with visually hunting and drift-feeding fish predators (mostly brown or brook trout, less frequently European minnow). They were focused mainly on the drift and exposure times of the larvae (e.g. Cowan and Peckarsky 1994; Douglas et al. 1994). The higher predation risk caused by visually hunting fish during the day leads *Baetis* sp. larvae to retain their nocturnal periodicity (Peckarsky and McIntosh 1998). In trout streams more larvae of *Baetis* sp. were found feeding on stone tops during the night than during the day (Cowan and Peckarsky 1994). Several other studies have described an increased propensity for nocturnal drift of *Baetis* sp. larvae (e.g. Douglas et al. 1994; Tikkanen et al. 1994; Huhta et al. 1999; Miyasaka and Nakano 2001; McIntosh et al. 2002), and a reduced exposure and drift activity during the daytime in the presence of visually feeding predators (e.g. McIntosh and Peckarsky 1996, 1999, 2004; McIntosh et al. 1999). All the above mentioned predation experiments applied various approaches using either freely foraging fish or fish chemicals. However, a combined approach with different concentrations and densities of freely foraging benthivorous fish which integrates small and large spatial scales has still not been undertaken.

Flexible avoidance behaviour, linked to a specific predation threat, is an essential trait for most prey organisms. Moreover, it is a common and widespread solution (Lima and Dill 1990). Its importance in benthic stream communities has been supported by many recent studies, which have shown flexible antipredator responses of stream insects to fish (e.g. Kohler and McPeek 1989; Douglas et al. 1994; McIntosh and Townsend 1994; Tikkanen et al. 1994, 1996; McIntosh et al. 1999). Individual prey often show a pronounced flexibility with regard to their antipredator response, also known as short-term response, to predators (Sih 1987), e.g. highlighted by the alterations to their activity schedules. Consequently, prey is able to adjust its behaviour to short-term changes in predator density perceived by predator cues (Douglas et al. 1994). For *Baetis* sp. chemical signals seem to be the most effective cue for predator detection (McIntosh and Peckarsky 1999; McIntosh et al. 1999). Previous experiments have shown that *Baetis* sp. larvae are able to detect different concentrations of brook trout cues in stream water (McIntosh et al. 1999, 2002) and that chemical cues alone can cause an avoidance response (McIntosh and Peckarsky 1999, 2004; Peckarsky et al. 2002). However, contradictory findings suggest that changes in the drift rates of *Baetis* sp. were strongest during the direct presence of fish and that responses to live predators differed from the responses to predator cues only (Tikkanen et al. 1994, 1996).

Most experiments on the predator avoidance behaviour of benthic invertebrates in streams are conducted for small temporal and spatial scales, probably because of practical reasons. Therefore, such experiments cannot fully capture the consequences of predator avoidance behaviour on the ecosystem functions, due to experimentally necessary reductions in time, space and complexity (Carpenter et al. 1995; Petersen and Hastings 2001). Thus, in such cases it is difficult to transfer obtained results to processes on the ecosystem scale (Carpenter et al. 1995; Schindler 1998; Petersen and Hastings 2001). In this work laboratory experiments were used to record the behavioural responses of mayflies to nocturnal feeding fish on the small scale and field observations were used to assess the possible effects of behavioural changes on a larger scale. The objective of this study was the identification of behavioural predator responses with regard to the feeding periodicity of *Baetis rhodani* (Pictet) under the influence of different concentrations of fish cues (*Barbatula barbatula*, (L.), *Gobio gobio*, L.) which was analysed in laboratory feeding experiments. The study also included an evaluation of the consequences of predator avoidance behaviour on the general grazing intensity (consumption rate) and an assessment of the transferability of predator effects on natural stream ecosystems. In order to achieve this goal an analysis was made of the grazing activity and the consumption rate of *B. rhodani* in the field in two small mountain streams containing different densities of benthivorous fish over a three-year period. It was hypothesised that larvae of *B. rhodani* would change their feeding periodicity pattern in order to avoid nocturnal feeding fish predators. It was assumed that this predator avoidance behaviour would result in reduced grazing rates in natural stream ecosystems.

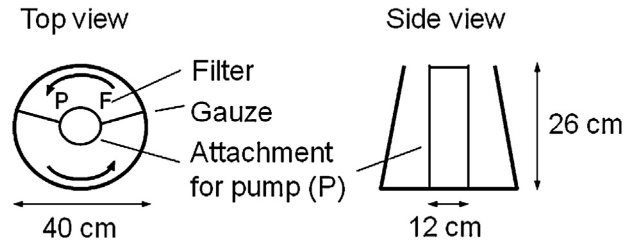

Fig. 1. Design of the circular stream tanks used in the laboratory experiments (not to scale, P: Pump, F: Filter). Arrows in the top view indicate the flow direction.

Materials and methods

Laboratory experiment setup

In the laboratory experiments the influence of chemical fish cues on the feeding periodicity of *B. rhodani* larvae was investigated in April 2011. The experimental setup involved four treatments each with a different concentration of fish chemicals, which were replicated three times each: control (no fish cues), low, medium and high concentration. The trials were conducted in black circular stream tanks (Fig. 1). In each experimental tank at least 40 larvae of *B. rhodani* were introduced, after a measurement of their body length to the nearest 0.1 mm (TSO-VID-MESS-HY, Leica WILD M3C, Pulsnitz, Germany). The larvae had a mean body length 9.5 ± 1.0 mm ($\pm$SD, $n = 240$). The larvae (nymphs with black wing pads were excluded) were collected in the morning between 09:00 and 11:00 a.m. from the upstream fishless site of the Gauernitzbach (see *study site*) and kept for 24 h in a glass tank with algae-covered rocks from the same site. These provided a food supply. Subsequently, the experiment was run for 48 h using a light regime of 12/12 h (light/dark) which was similar to the natural conditions at the time of the year.

Water containing chemical fish cues was taken from a 150 L aquarium including three fishes (this corresponded to a fish density of 200 Ind m^{-2}): one gudgeon (110 mm long) and two stone loaches (95 mm and 100 mm long), which were fed daily with frozen chironomids. On the basis of the average fish density of 0.6 ± 0.1 Ind m^{-2} (mean from 2007 to 2010 $\pm$ SD, $n = 8$) in the Tännichtgrundbach (see *study site*) with a mean of depth 0.1 m, a low (mean value divided by 10), a medium (corresponded to the mean value), and a high (mean value multiplied by 10) fish density was assigned. In order to reach a final water volume of 12 L in each experimental tank and to have the required fish density treatment, a calculated amount of fish-conditioned water from the aquarium was added to the fish-free water from the upper fishless site of the Gauernitzbach. The experimental tanks were filled shortly before the experiment was started. The water temperature of 10.0 ± 0.1 °C (mean $\pm$ SD, $n = 12$) was similar to the natural stream