Limnologica

Extended larval development compensates for sublethal effects of fish predation in a mayfly population (*Rhithrogena semicolorata*, Ephemeroptera)

Claudia Hellmann*, Carola Winkelmann, Susanne Worischka, Jürgen Benndorf

Technische Universität Dresden, Institut für Hydrobiologie, 01062 Dresden, Germany

ARTICLE INFO

ABSTRACT

Many predation experiments in streams are carried out in enclosures. Hence, the relevance of their results to predict population dynamics is often unclear due to the relatively small spatial and temporal scale of the experiments. To enhance the transferability of experimental results on the ecosystem scale the impact of fish predators on a prey population was observed in a reach scale approach over 2 years in a natural stream. A 400-m reach inhabited by the small benthivorous fishes gudgeon (*Gobio gobio*) and stone loach (*Barbatula barbatula*) was compared with a fishless reference reach.

It was shown that fish predation may affect the population of the grazing mayfly *Rhithrogena semicolorata* on the ecosystem scale. Although the larvae grew slower in the fish reach than in the fishless reach, the adults reached the same size and fecundity because they emerged 2–3 weeks later. By this compensation, the prey species avoided a reduction of their individual fecundity. On the other hand, the extended exposure to the fish predators resulted in an enhanced mortality and a reduced density of adult mayflies. Thus, there was obviously a trade-off between maximising fecundity and minimising mortality from fish predation.

The observed differences were almost certainly caused be fish predation and not by natural differences of the reaches. This was concluded from results gained after eliminating all benthivorous fish from the former fish reach.

With the help of scenario analyses based on our empirical data and simple model assumptions we could demonstrate that compensating the potential loss in fecundity by extending development time led to higher average fitness of the prey population than emerging at an earlier fixed time to avoid additional predation losses. Therefore, we concluded that this strategy was adaptive in the presence of benthivorous fish.

© 2010 Elsevier GmbH. All rights reserved.

Introduction

The predation risk of a prey organism depends on a variety of environmental factors such as substrate and habitat complexity (Dahl and Greenberg, 1996, 1997; Nyström and Pérez, 1998; Rosenfeld, 2000a; Turnbull and Barmuta, 2002), temperature (Kishi et al., 2005), spatial scale (Englund and Cooper, 2003; Bergström and Englund, 2004) and biotic factors such as interactions between multiple predators (Griffen and Williamson, 2008) or between the predator and its prey (Vance-Chalcraft and Soluk, 2005). It has been shown in enclosure experiments that fish densities and fish species determined the strength of the lethal impact on the invertebrate community (Dahl, 1998a,b; Rosenfeld, 2000b; Ruetz et al., 2004).

Reviewing the literature describing predation experiments with benthic invertebrate prey suggests that strong predation effects are likely at low habitat complexity or area size and optimal temperature for the predators (Power, 1992; Bechara et al., 1993; Englund and Cooper, 2003; Kishi et al., 2005). The effects in enclosures may be exaggerated due to simplified habitats, and predator effects at the ecosystem scale in the absence of artefacts may be quite different. Parallel, former large-scale field studies have recorded weak or no lethal fish effects on the invertebrate community (Thorp and Bergey, 1981; Allan, 1982; Flecker, 1984) most likely because of high habitat heterogeneity or a community well adapted to fish. Therefore, our first goal was to assess whether fish predation has an impact on a potential invertebrate prey in the heterogeneous environment of natural streams with natural densities of benthivorous fish.

The second goal of this study was to determine the magnitude of sublethal and lethal effects of fish predation on a prey population and how these two types of effects might interact. Lethal impact of predation has been reported to be a major factor

* Corresponding author. Present address: Helmholtz Centre of Environmental Research GmbH - UFZ, Department River Ecology, Brueckstraße 3a, 39114 Magdeburg, Germany. Tel.: +49 391 810 9221; fax: +49 391 810 9150.
E-mail address: claudia.hellmann@ufz.de (C. Hellmann).

structuring benthic communities in both mesocosm experiments (Flecker, 1984; McIntosh and Townsend, 1996; Dahl, 1998a,b; Rosenfeld, 2000b) and field studies (Allan, 1982; Nyström et al., 2003) and generally mean an increased mortality by consumption. However, some field and laboratory studies suggested that sublethal predation effects can have even a stronger impact on the dynamics of prey populations than lethal effects (Werner and Peacor, 2006) especially if the size of adults is correlated to their fecundity (McPeek and Peckarsky, 1998). Sublethal effects mean consequences of predation for behaviour, growth and fitness of the prey organisms and have been reported also from both mesocosm experiments (*Baetis* spp.: Peckarsky et al., 1993, 2001; Scrimgeour and Culp, 1994; Peckarsky and McIntosh, 1998) and large-scale investigations (*Baetis bicaudatus*: Peckarsky et al., 2002; *Drunella coloradensis*: Dahl and Peckarsky, 2002). A variety of sublethal predation effects potentially resulting in a fecundity loss of the prey have been described. Fish can alter prey behaviour by inducing escape and higher drift activity (Forrester, 1994; Tikkanen et al., 1994; Peckarsky, 1996; Huhta et al., 2000) or by decreasing mobility and encounter to predators (Power, 1992; Muotka et al., 1999; McIntosh and Peckarsky, 1999, 2004; Vance-Chalcraft et al., 2004). Increased drift as well as reduced activity has been observed (Malmqvist, 1992; Peckarsky et al., 1993; Scrimgeour and Culp, 1994; McIntosh and Townsend, 1994; Peckarsky, 1996; Koperski, 1997; Winkelmann et al., 2008). Especially, due to the effort spent for escaping and hiding behaviours energy reserves for growth and reproduction may be reduced (Briegel, 1990; Peckarsky et al., 1993; Cavaletto et al., 2003). Besides behavioural responses, life history patterns of prey might change for instance by delaying emergence because of slow larval growth and development (Scrimgeour and Culp, 1994; Peckarsky and McIntosh, 1998; Tseng, 2003). This delay might enable the individuals to reach the same size and fecundity like individuals from fishless experimental units (Tseng, 2003) while in other cases prey organisms emerged smaller and with lower fecundity (Scrimgeour and Culp, 1994; Peckarsky and McIntosh, 1998). That means, due to predator avoidance of prey in risky habitats, like the reduction of foraging activity, growth and potentially also fecundity will be reduced (costs due to increasing sublethal effects) but at the same time low vulnerability to predation and high survival probability will be achieved (benefit due to decreasing lethal effects). There are, however, also experiments showing a shorter development time indicating acceleration of larval maturation (Peckarsky et al., 2001). In this case, the resource intake and therefore growth and fecundity will increase by reduced avoidance effort (benefit due to decreasing sublethal effects). However, that results in a high predation risk (costs due to increasing lethal effects). These different findings are assumed to be different realisations of the trade-off between maximising the reproduction effort (being as large as possible at emergence) and minimising the mortality due to predatory consumption (shortening the larval period). The synthesis of both effect types, lethal and sublethal, reflects the outcome of the mayfly population called average fitness of a population. Similarly to our study, Greig and McIntosh (2008) have also measured the lethal and sublethal effects by trout on a caddisfly population and estimated the net effect by calculating a total egg number potentially produced. This can be understood as the result of the fish effects on both the adult density and the individual fecundity, and represents the theoretically possible offspring of one generation.

To assess the importance of lethal and sublethal predation effects of benthivorous fish on a mayfly population and the possible interaction between the two effects, we observed the density and life history of the mayfly *Rhithrogena semicolorata* Curtis (Ephemeroptera, Heptageniidae) in its natural habitat. We expected that the combined survey of sublethal and lethal effects could show the benefit and costs of predator avoidance behaviour

and life history changes and thus the fitness consequences for the development of a prey population. Therefore, we observed a population of *R. semicolorata* on a reach-scale study over a two-year period. A 400-m-long stream reach stocked with the small benthivorous fishes, gudgeon (*Gobio gobio*) and stone loach (*Barbatula barbatula*), was compared with a fishless reference reach. In a second phase about two years after the initial study period we identified the natural differences in the mayfly population dynamics between these two reaches when all fish were absent.

Methods

Study design

To assess the effect of benthivorous fish on a prey population we compared a fish reach with the fishless reference reach. The field study was conducted in a second-order stream over two years (November 2004 to October 2006). The investigated part of the stream was divided into three sections separated by grids of high-grade steel (5 mm mesh size). The lower, 400 m long, section (fish reach) was stocked with the benthivorous fishes, gudgeon (*G. gobio* L., Cyprinidae) and stone loach (*B. barbatula* (L.), Cobitidae). The mean fish density over the two-year period (fish density: 0.47 ± 0.07 fish m^{-2}; fish biomass: 3.52 ± 0.59 g m^{-2}; mean $\pm$ SE, weighted by time) was similar to natural densities of small benthivorous fish species reported from Europe and North America (Santoul et al., 2005: up to 0.76 stone loach m^{-2}; Fairchild and Holomuzki, 2005: 0.3–1 sculpin m^{-2}; Erös et al., 2003: 0.21–0.95 stone loach m^{-2}, 0.0–0.14 gudgeon m^{-2}; Huhta et al., 2000: 0.5–0.8 bullhead m^{-2}). Upstream of the fish reach a 400 m long reference reach was installed and kept almost completely fishless by electrofishing (fish density: 0.007 ± 0.0003 fish m^{-2}; fish biomass: 0.14 ± 0.003 g m^{-2}; mean $\pm$ SE). The reach upstream of the reference reach that was suitable for fish (500–700 m) was also fished to ensure that the reference reach did not receive fish kairomones. Between the two reaches a 200 m long buffer reach was inserted to avoid edge effects. The buffer reach was stocked with a similar biomass of the same fish species as the fish reach. To assess the effect of benthivorous fish on a prey population we compared the fish reach with the fishless reference. To minimise confounding effects of the electrofishing procedure on invertebrate abundances all reaches were fished four times a year. Stunned fish were removed from the reference reach but not from the fish reach. The fish and buffer reach were restocked in spring and autumn every year to compensate for fish losses due to the sampling for gut content analyses, winter mortality, migration and bird predation.

After October 2006 we manipulated the fish, buffer and fishless reach similarly by eliminating all benthivorous fish. We controlled the fishless conditions regularly to exclude potentially migrating fish. To check the natural differences in larval growth and emergence of *R. semicolorata* we compared both, the former fish reach and fishless reach, again in spring 2009 after eliminating benthivorous fish for two years.

Study site

The field study was conducted in a small second order stream (Gauernitzbach) draining into the river Elbe about 15 km downstream of Dresden (Saxony, Germany, 51°06′N, 13°32′E, altitude of source 225 m). The land use in the 400 ha catchment area is predominantly agriculture. The stream has a length of 4.6 km and runs through a woodland valley (mainly alder, maple, beech, ash, and oak trees). The geological bedrock was formed by syenite and granite whereas the upper layer is dominated by loess and loam with a high proportion of calcium carbonate (Schmidt et al., 2008). At the

manipulated reaches, the stream has a mean width of 1.2 m and an average discharge of 27 ± 37 L s^{-1} (mean $\pm$ SD, November 2004 to October 2006, $n = 40$). The water temperature ranged between 0 and 16 °C with the maximum occurring in August (mean $\pm$ SD: 8.7 ± 4.8 °C, November 2004 to October 2006, $n = 41$). Other environmental factors did not show strong seasonal changes during the study period (means $\pm$ SD, November 2004 to October 2006: pH 8.4 ± 0.3, $n = 35$; electrical conductivity 872 ± 42 μS cm^{-1}, $n = 35$; oxygen saturation $95 \pm 16\%$, $n = 28$).

Studied organisms

The predators feeding on the *R. semicolorata* population were mainly the two stocked fish species stone loach and gudgeon. While gudgeon is mostly dwelling in pool sections (Erös et al., 2003; Winkelmann et al., 2007), stone loach prefers riffle sections (Mastrorillo et al., 1996; Watkins et al., 1997; Erös et al., 2003). Gut analyses showed that both species were benthivorous and used among others *R. semicolorata* as food (Winkelmann et al., 2007, unpublished data: S. Worischka, Institute of Hydrobiology of TU Dresden).

The univoltine stream-dwelling mayfly *R. semicolorata* exhibited a highly synchronised life cycle in the studied stream. The larvae grew rather slowly after hatching (autumn, winter) and accelerated their growth during a short time span in spring until adults emerge in May (Winkelmann and Koop, 2007). During spring, *R. semicolorata* was the most abundant grazer and mayfly species in the study stream followed by *Baetis* spp. (Winkelmann et al., 2007).

Field sampling and laboratory analyses

The fish and the reference reach each contained three randomly distributed floating emergence traps (type "week", 0.16 m^2, LeSage and Harrison, 1979). Animals were fixed in the trap chamber with a mixture of 2/3 ethanol (80%) and 1/3 ethylene glycol. All traps were sampled weekly from March to September. Insects caught in the emergence traps must not necessarily have developed at the sampling point but in the stream section upstream from each trap (30–50 m; Illies, 1983). Therefore we did not assume a habitat specific sampling (pools or riffles). The habitats used for positioning the traps seemed to be less important for the emergence composition but we ensured a sufficient distance between the traps to avoid a high dependence between the samples.

In the laboratory all adults of *R. semicolorata* (mostly subimagoes) were counted. In addition to body length and sex determination, the eggs were counted in all females. The eggs were removed from the abdomen, filled in 1 mL water and separated from each other by short ultrasonic pulses (UW 70, Badelin Electronic, Berlin). The water with the detached eggs was filtered (cellulose acetate, 0.45 μm) and the eggs were made more visible by staining the filter with a drop of ink. All eggs of at least three out of eight parts of the filter were counted under a dissecting microscope.

Six benthic samples were taken in each study reach with a Surber sampler (0.12 m^2, 500 μm mesh size) every four weeks throughout the study period. Three samples were taken in randomly chosen riffles and three in randomly chosen pools because the distribution of riffle and pool areas in the studied stream was very similar. Larval body length, density, and biomass of *R. semicolorata* larvae were determined in each sample.

Data analyses

The adult density was calculated by averaging the three emergence samples on every date. For analyses of the individual adult size and fecundity on the other hand, all measured individuals were treated as replicates. The average fitness of the population was esti-

mated as the number of eggs produced annually by one mayfly generation. This was calculated as the sum of all eggs of female individuals emerged from an area of 1 m^2 for each study reach in one year (egg production m^{-2} a^{-1}). This value served as a total estimate of the average population fitness because lethal fish effects on the adult density as well as sublethal fish effects on the adult fecundity were included. Thus, the average population fitness was no true mean but the total amount of eggs theoretically produced during one emergence period.

To describe differences in larval size and growth between the reaches all measured individuals were treated as replicates. The individual growth rate g (d^{-1}) was estimated from the linear slope of larval size (*BL* in mm) in the spring (t in days after beginning of the year) according to the equation $BL = g \cdot t + a$. This was done exclusively from end of March until May when the larval growth was highest probably due to increased temperatures and food supply. From this linear relationship we calculated a theoretical larval size at the actual beginning of emergence period in each stream reach. To define the initial population density of mayfly larvae for the adult emergence in both reaches we compared the mean larval density (from 6 samples each) in March before starting the rapid growth in springtime.

To estimate the consumptive mortality of *R. semicolorata* larvae, we compared the fish consumption with the biomass production of prey (for details see Winkelmann et al., 2007). This was exemplarily analysed for spring 2005 (April to June) shortly before and during the emergence period because food analyses for the fish were available for this period. Secondary production of *R. semicolorata* (mg dry mass m^{-2} month^{-1}) was estimated using a model approach, which calculates the individual growth rate as a function of mean temperature and larval body size (Morin and Dumont, 1994). The consumption of benthivorous fish in spring 2005 on *R. semicolorata* (mg dry weight m^{-2} per 3 month) was estimated from the proportion of mayfly larvae in the fish guts analysed in April (gudgeon: $n = 10$; stone loach: $n = 9$), the daily food ration of fish (mg dry weight g wet weight^{-1} d^{-1}), and the mean fish biomass in spring (mean from April until June 2005: 1.27 g wet weight m^{-2}). The daily food ration was estimated in spring following the method of Elliott and Persson (1978) using one 24 h-field-sampling of each fish species with 4 h-time segments (gudgeon: 25.05.2004, $n = 63$; stone loach: 08.06.2005, $n = 30$) and gut evacuation experiments (see details in Winkelmann et al., 2007). All fish for food analyses were caught by electrofishing in the fish reach of the study stream.

Model approach

The consequences of sublethal and lethal fish effects on the egg production of the mayfly population (average population fitness) were simulated using two scenarios. Regarding the interaction of the two effect types, two basic realisations are theoretically conceivable: (1) unchanged emergence time with the result of reduced individual fecundity of the adults but no additional mortality, and (2) delayed emergence time with the result of compensated (unchanged) individual fecundity of the adults but enhanced mortality due to prolonged exposure to predation risk. Thus, both scenario 1 (Sc 1) and scenario 2 (Sc 2) simulate lethal and sublethal effects though in Sc 2 the consequences of sublethal effects on individual fecundity are compensated (Table 1). Even though the two compared scenarios are hypothetical, they contain assumptions and estimations derived from our observations during this study in 2005. The lethal effect of benthivorous fish on the prey abundance (m) is part of both scenarios and estimated by the difference between the mean female abundances at emergence of the two reaches (m_t: 6.2 females m^{-2}). This value is assumed to represent the mortality due to fish consumption during the larval growth. It includes an additional larval mortality (m_a) in the

Table 1
Parameter values for the estimation of "population fitness" consequences of lethal and sublethal predation effects used in the scenario analysis.

m	Consumptive mortality	Females m^2	5	Sc 1, Sc 2
m_a	Additional consumptive mortality due to emergence delay	Females m^2	1.2	Sc 2
F	Fecundity loss (lethal effects)	Eggs m^2	7675	Sc 1, Sc 2
F_s	Fecundity loss (sublethal effects)	Eggs m^2	12 995	Sc 1
F_a	Additional fecundity loss (lethal effects) due to emergence delay	Eggs m^2	1842	Sc 2

Table 2
Growth rates g (d^{-1}) of *R. semicolorata* derived from linear relationships between larval size and time (number of days from end of March to May in 2005 and 2006, respectively). Using these parameters theoretical larval sizes at the actual beginning of the emergence (as number of day after the beginning of the year) were estimated.

Stream reach (year)	g (d^{-1})	a	r^2	P-value (n)	Emergence (d)	Larval size (mm)
Fish (2005)	0.048	1.248	0.21	<0.001 (200)	144	8.2
Reference (2005)	0.082	−1.733	0.45	<0.001 (240)	124	8.4
Fish (2006)	0.092	−3.477	0.54	<0.001 (81)	144	9.8
Reference (2006)	0.122	−5.888	0.69	<0.001 (52)	130	9.8

fish reach due to the delayed emergence, which therefore must be subtracted ($m = m_t - m_a$). This additional mortality is calculated using Eq. (1) including the consumption rate of the fish predators (c: 0.36 mg dry weight d^{-1}), an average delay of emergence (t) of 20 days exemplarily following the measured data for the study year 2005, and the mean individual dry weight of larvae in May (bm: 2.9 mg). The sex ratio of adults and larvae is assumed to be nearly 1:1 ($m_a/2$):

$$m_a = \frac{c \cdot t}{bm} \qquad (1)$$

The annual fecundity loss due to lethal effects (F, in eggs m^{-2}) is calculated as: $F = m \cdot \bar{E}$ using the assumed mortality (m) and the mean individual egg number ($\bar{E} = 1535$ eggs per female) derived from direct measurements in 2005. The additional fecundity loss (F_a) in scenario 2 is calculated similarly by using m_a instead of m. The sublethal predation effect is estimated to be a size reduction of 1.0 mm (BL_R) at emergence. This value was derived from the lower larval growth observed in the fish reach which resulted in a difference in larval body length of 1.0 mm at the actual (measured) and the theoretical (20 days earlier) beginning of emergence in 2005 (Table 2). It is assumed that this larval size difference would have translated in a similar adult size difference if the emergence time had not differed between the stretches. The loss of fecundity due to size reduction (F_s) is calculated according to Eq. (2):

$$F_s = BL_R \cdot b \cdot (A + m_a) \qquad (2)$$

where b is obtained from the correlation $E = b \cdot BL - a$ of female body length (BL in mm) and individual egg number (E) observed in our study ($b = 822.5$, $a = 5160$; $n = 31$; $r^2 = 0.79$; 2005 and 2006); and A is the mean adult female abundance measured in the fish stretch 2005 ($A = 14.6$ females m^{-2}) which must be corrected by the additional mortality (m_a) to exclude the effects of the delayed emergence.

Statistical analysis

All statistics were calculated using R computer software (Version 2.4.1, R Development Core Team, 2006). To test the effects of the factors 'fish presence' (f_1) and 'study year' (f_2) on the body length of larvae and adults, time of emergence and the egg number, a maximum likelihood model selection method was applied (Johnson and Omland, 2004; Hobbs and Hilborn, 2006). Starting with the full linear model containing all factors and possible interactions we derived simplified models omitting one of the two factors or the interaction between them. The alternative models were compared using F-tests according to the ANOVA which were performed between consecutive models, testing if the more complicated of the two models was significantly better compared to the simpler one. With this model selection technique we were able to

identify the most adequate linear model from the candidate model set, which explained the data reasonably well. This method was used when the number of samples was not equal between the factors and a two-way ANOVA was not feasible. The differences in larval density in March between the stream reaches (factor 'fish presence') were tested with a two-way ANOVA also considering the factor 'study year'. The variable 'emergence time' was reciprocally transformed and the larval density was transformed by $\log(y + 0.0001)$ to achieve the best approximation to normal distribution and homogeneity of variances.

Results

Potential environmental differences between the two study reaches

Although differences in the abiotic and biotic environmental conditions between both reaches cannot be completely excluded they seemed unlikely. The physical and chemical measures did not show differences between both experimental reaches (Table 3). Substrate, habitat distribution, riparian vegetation and consequently the light supply were very similar in the two reaches of the experimental stream. The biomass of periphyton measured as ash free dry mass (AFDM), the main food resource of the grazing mayfly larvae, was similar between the study reaches in spring (March to June) in the two study years (mean $\pm SE$, $n = 7$; 2005: fish 0.92 $\pm$ 0.35 mg AFDM cm^{-2}, reference 0.62 $\pm$ 0.23 mg AFDM cm^{-2}; 2006: fish 0.57 $\pm$ 0.21 mg AFDM cm^{-2}, reference 0.52 $\pm$ 0.20 mg AFDM cm^{-2}). Due to the short distance between the fish and the reference reach (buffer reach 200 m) and some measurements we assumed a similar temperature regime in both reaches. Therefore, the conditions for growth and development of the benthic grazing insects seemed to be very similar between the reaches.

Sublethal effects of benthivorous fish

The presence of fish resulted in a slower growth and a longer larval development time of *R. semicolorata*. The factor 'fish pres-

Table 3
Physical and chemical characteristics (means $\pm$ SD) of the fish and the fishless stream reach measured in spring 1999 and 2010 (n = number of measures).

Characteristics	Fish reach	Reference reach	n
Temperature (°C)	14.5 $\pm$ 2.1	14.2 $\pm$ 2.1	15
Oxygen (mg L^{-1})	9.4 $\pm$ 1.0	9.6 $\pm$ 2.0	9
Electrical conductivity (μS cm^{-1})	729 $\pm$ 63	726 $\pm$ 65	15
pH	8.3 $\pm$ 0.006	8.3 $\pm$ 0.09	14

Table 4
Results of the model selection using F-tests. The dependent variable (y = larval or adult body length, time of emergence or number of eggs) was modelled as a function of two factors (f_1 = fish: presence or absence; f_2 = study year: 2005 or 2006). The unconstrained model ($y \sim f_1 \cdot f_2$) was simplified by stepwise eliminating the factors f_1, f_2 or the interaction and pairwise comparing the more complex model with the simpler one. Significant differences due to the elimination of the respective factor indicate that this factor is necessary to explain the variation in the dependent variable.

Dependent y	Eliminated factor	F	P-value
Larval body length	Fish	13.41	<0.001
	Study year	0.38	0.541
	Interaction	0.40	0.529
Emergence time	Fish	10.22	0.002
	Study year	0.71	0.403
	Interaction	0.23	0.637
Adult body length	Fish	1.85	0.179
	Study year	109.24	<0.001
	Interaction	6.66	0.013
Individual number of eggs	Fish	0.16	0.696
	Study year	58.02	<0.001
	Interaction	2.15	0.154

Table 5
Differences between the fish and the reference reach regarding the larval and adult size, individual egg number, adult densities and annual egg production of *Rhithrogena semicolorata* in 2005 and 2006 (mean $\pm$ *SE*, n = number of replicates). Larval size was measured at the end of April, shortly before the start of the emergence. All other factors were measured over the whole emergence period.

Measurement	Year	Fish	n	Reference	n
Larval size (mm)	2005	6.9 ± 0.3	55	8.1 ± 0.2	85
	2006	7.1 ± 0.3	36	8.5 ± 0.4	22
Adult size (mm)	2005	8.5 ± 0.2	15	8.0 ± 0.1	18
	2006	9.9 ± 0.3	7	10.2 ± 0.2	13
Egg number (per individual)	2005	1663.3 ± 343.3	7	1444.6 ± 115.3	10
	2006	3068.4 ± 276.1	6	3538.7 ± 221.0	8
Adult density, both sexes (individuals $m^{-2} a^{-1}$)	2005	22.9 ± 19.9	3	39.6 ± 19.9	3
	2006	14.6 ± 11.6	3	27.1 ± 7.5	3
Adult density, females only ($m^{-2} a^{-1}$)	2005	14.6 ± 11.6	3	20.8 ± 12.7	3
	2006	12.5 ± 9.5	3	16.6 ± 5.5	3
Annual egg production (eggs $m^{-2} a^{-1}$)	2005	24 257	–	30 096	–
	2006	38 356	–	58 978	–

ence' caused a significantly better fit of the model to our data of larval body length and time of emergence than the simpler model neglecting this factor (Table 4). At the last sampling date before the beginning of emergence in the fishless reach, *R. semicolorata* larvae were significantly smaller in the presence of fish than in the reference reach in both study years (Table 5). These size differences seemed to be caused by the lower growth rates in the fish reach during the last weeks before the beginning of emergence (Fig. 1 and Table 2). In general, the larvae in both stretches

showed the highest growth in this spring period (March to May). The beginning of the emergence period was delayed by two to three weeks in the fish reach compared to the reference reach (Fig. 2 and Table 4; 2005: fish 24.05.2005, reference 04.05.2005; 2006: fish 24.05.2006, reference 10.05.2006). Therefore the larvae in the fish reach had a longer growth period that enabled them to achieve a similar body length at the actual beginning of the emergence as the larvae in the reference reach (Table 2). In the model selection procedure the factor 'fish presence' was not necessary to explain the
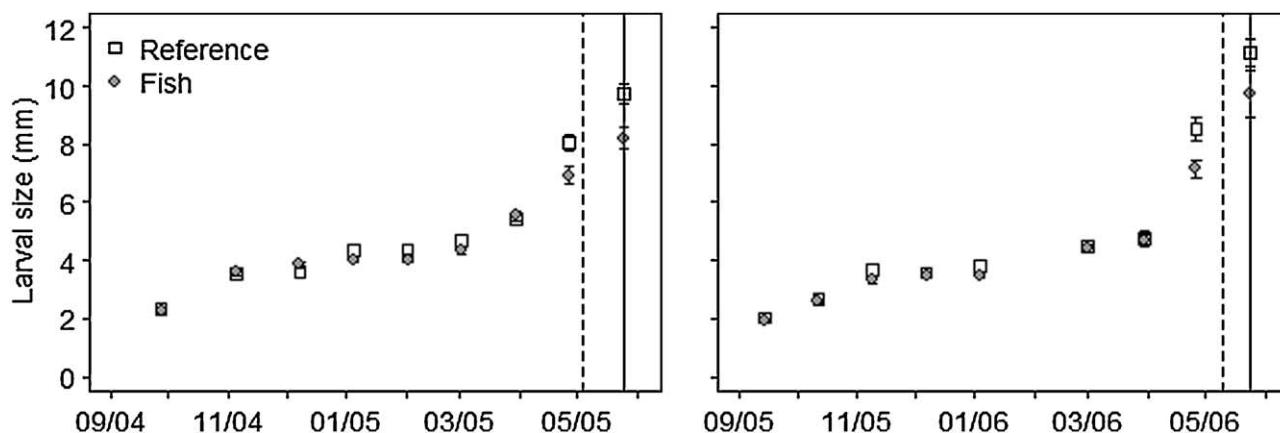

Fig. 1. Mean larval size (mm) $\pm$ *SE* of the mayfly *R. semicolorata* after hatching in autumn until spring in the following year in 2004/05 (left) and 2005/06 (right) in the fish and reference reach. The highest growth was observed in the last weeks (last three points) before the beginning of emergence (fish reach: solid lines, reference reach: dashed lines) from March to May.
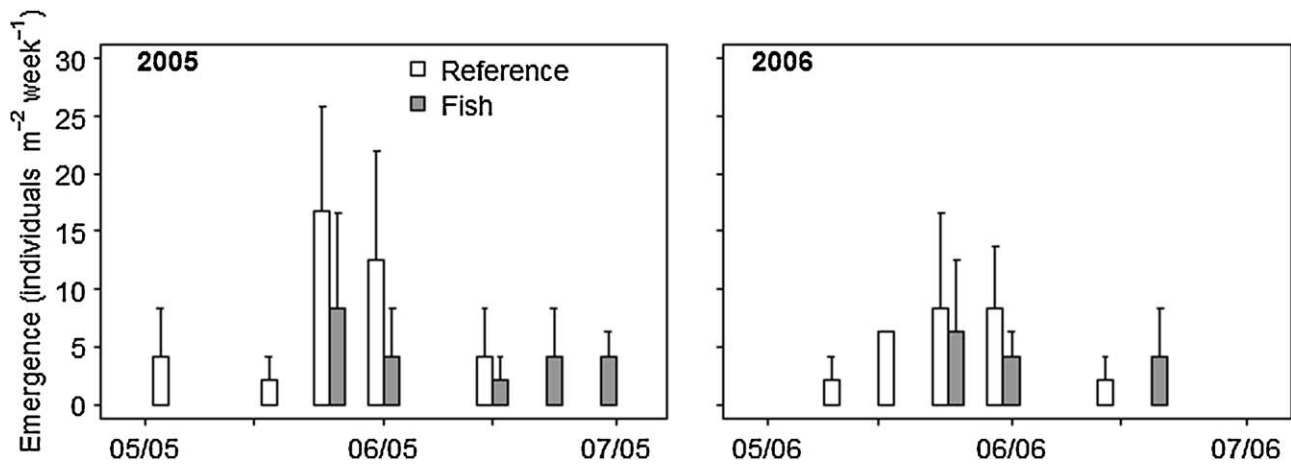
Fig. 2. Mean emergence (individuals m^{-2} week^{-1}) of *R. semicolorata* (+*SE*, *n* = 3) in the reference and the fish reach in 2005 and 2006.

data (Tables 4 and 5). Consequently, the adult body length and the fecundity measured as egg number per female were not affected by fish predation. In contrast, the factor 'study year' was important for the model fit indicating strong interannual variation of adult body length and individual egg number. Additionally, a significant interaction between 'study year' and 'fish presence' reflected opposed differences in the adult length between the reaches in both years.

Lethal effects of benthivorous fish

Predation by benthivorous fish was an important cause of mortality at least for mature stages of *R. semicolorata* larvae. This was indicated by the relatively high consumption of mayfly larvae by their fish predators. From April to June 2005 17.5% of the biomass production of *R. semicolorata* was consumed by fish predators (fish consumption: 34.8 mg dry mass m^{-2} per 3 months; mayfly production: 198 mg dry mass m^{-2} per 3 months), wherein stone loach consumed much more than gudgeon (stone loach: 16.1%, gudgeon 1.4%). For benthivorous fish, *R. semicolorata* was an important food source in spring (April 2005: 22.3% of the gut content, stone loach alone: 18.9%). This parallels with the observation that the density of emerged adults was reduced in the fish reach by about 40% compared to the reference reach in both study years (Fig. 3a and Table 5). The assumption that the predation mainly affected the mature larvae was supported by the comparison of the initial larval densities in March (2005: fish 274 ± 115 ind m^{-2}, reference 336 ± 156 ind m^{-2}; 2006: fish 63 ± 18 ind m^{-2}, reference 37 ± 10 ind m^{-2}; mean ± *SE*, *n* = 6). Then all larvae still had no black

wing pads and the same size in both reaches. At this time no significant differences in the densities were found between the reaches (ANOVA; *F* = 0.99, *P* = 0.33) or the years (ANOVA; *F* = 0.02, *P* = 0.88), and no interaction between the factors was recorded (ANOVA; *F* = 0.31, *P* = 0.58).

The reduced adult density resulted in a lower average fitness of *R. semicolorata* at the population level in the presence of benthivorous fish. This was indicated by a lower annual egg production per m^2 in the fish stretch compared to the reference stretch (Table 5 and Fig. 3b). The reduced annual egg production was a consequence of both the individual egg numbers (sublethal) and the number of all emerged females per area and year (lethal). Because only the emergence abundance and not the individual egg number per female were reduced in the presence of benthivorous fish, the reduced average population fitness is interpreted as a lethal predation effect.

Consequences of lethal and sublethal predation effects on average population fitness

The fish-induced sublethal fitness losses were predicted to be 43% of the average population fitness using our simple model (scenario 1 in Table 6). In the model the reduced body length of the adults that would have occurred without the delay in the emergence caused this loss in egg production. The total loss of the average population fitness in scenario 1 including sublethal and lethal predation effects was calculated to be about 68%. The compensation of the sublethal fitness consequence on the other hand, was predicted to reduce the average population fitness much less (6%, scenario 2 in Table 6). This loss was caused in our model by
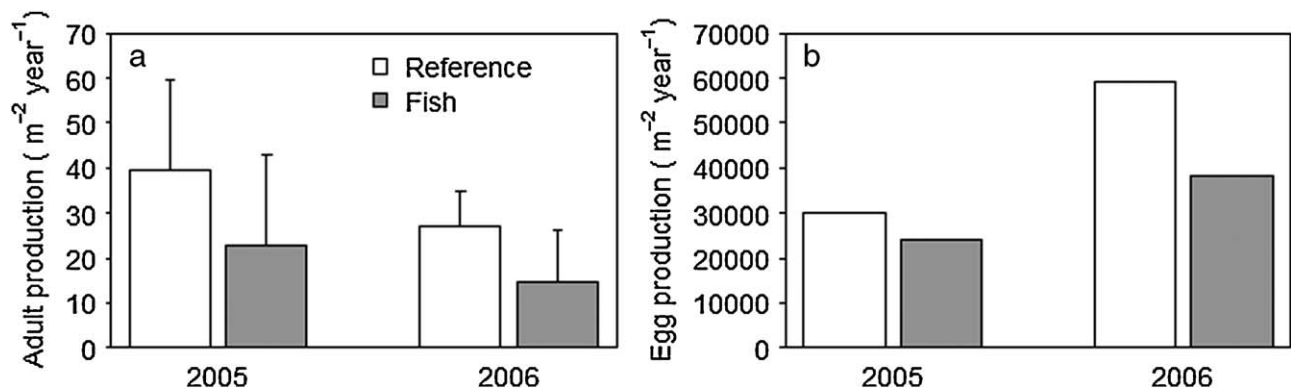

Fig. 3. (a) Annual production of adults of *R. semicolorata* (adults produced m^{-2} year^{-1}) (+*SE*, *n* = 3) emerging from the fishless reference and the fish reach. (b) Estimation of the average fitness of the *R. semicolorata* population measured as the total egg production m^{-2} year^{-1} in the fishless reference (open columns) and the fish reach (grey columns) in 2005 and 2006.

Table 6

Extrapolations of collected data to estimate the importance of lethal effects, sublethal effects and the interaction between the two effect types. Scenario 1 contains the observed lethal and assumed sublethal effect. Scenario 2 contains the lethal effect (as in scenario 1), the sublethal effect of delayed larval development (compensation), including the additional mortality caused by this extended larval development according to our field data.

Reduction of	Scenario 1			Scenario 2		
	Lethal	Sublethal	Total	Lethal	Compensation	Total
Annual egg production (eggs m^{-2} a^{-1})	7675	12 995	20 670	7675	1842	9517
Average population fitness (%)	25.5	43.2	68.7	25.5	6.1	31.6

mortality of larvae consumed by fish during the time period of delayed emergence. The combined losses of average population fitness due to the lethal predation and the compensation of sublethal fish effects were predicted to be 32%. This predicted value approximated the loss of 19–35% of average population fitness observed in this study (Fig. 3b).

Natural differences in the mayfly population between the study reaches

About two years after eliminating benthivorous fish from the fish reach the mean production of adults of *R. semicolorata* was clearly higher in the former fish reach compared to the reference reach (fish 389.6 ± 154.4 individuals m^{-2} a^{-1}, reference 10.4 ± 7.5 individuals m^{-2} a^{-1}, mean ± *SE*, *n* = 3). In addition, larvae were significantly bigger in the former fish reach than in the reference reach in April 2009 shortly before the beginning of emergence (fish 8.0 ± 0.2 mm, *n* = 88, reference 7.3 ± 0.2 mm, *n* = 107; mean ± *SE*; Student's *t*-test, *t* = −2.56, *P* = 0.01) because their growth rate in the last weeks was slightly higher (fish: *g* = 0.061 d^{-1}; reference: *g* = 0.05 d^{-1}; Fig. 4a). The emergence period started two weeks earlier in the fish reach compared to the reference (fish 29.04.2009, reference 13.05 2009; Wilcoxon test, *P* = 0.01; Fig. 4b). Due to the later emergence in the reference reach the mayfly larvae could theoretically achieve a mean body length of 7.9 mm in the reference reach at the actual beginning of emergence, and therefore the same body length like larvae in the former fish reach. However, a significantly higher mean adult size of *R. semicolorata* was measured in the former fish reach than in the reference reach (fish 8.9 ± 0.08, *n* = 139, reference 7.7 ± 0.28, *n* = 5; mean ± *SE*; Student's *t*-test, *t* = −2.8, *P* = 0.005).

Discussion

In this study two main goals were pursued. Firstly, we asked whether benthivorous fish had any impact on an invertebrate prey

population in the heterogeneous environment of a natural stream. Secondly, the relative importance of sublethal and lethal effects of fish predation on the prey population was assessed. The first question could be answered clearly positive. Under natural conditions the results showed dramatic consequences of fish predation on survival and reproduction of a mayfly prey population. It is important to emphasise that this result was found under natural conditions because high habitat complexity as well as temporal and spatial variation of environmental factors are assumed to blur prey responses (Power, 1992; Bechara et al., 1993; Englund and Cooper, 2003; Kishi et al., 2005). Nevertheless, *R. semicolorata* emerged later and in lower densities in the fish reach. We assume this phenomenon to be caused by the fish predator. Comparing the two studied reaches without fish (after the experiment) revealed naturally higher abundances and earlier emergence in the former fish reach. Therefore, the lower performance of the prey population in the fish reach during the experiment seems not to be caused by some unfavourable environmental factors but by the presence of benthivorous fish instead. Lethal and sublethal effects of fish predators on stream mayflies have been reported from laboratory and mesocosm experiments (e.g. Power, 1990; McIntosh and Townsend, 1996; Dahl, 1998a,b; Peckarsky and McIntosh, 1998). There are, however, only few field studies analysing both types of predation effects in natural streams (but see: Peckarsky et al., 2001, 2002; Dahl and Peckarsky, 2002; Winkelmann et al., 2007; Greig and McIntosh, 2008) and in most of them drift feeding fish species were used. Thus, the clear negative net effect of predation on the abundance and on the reproduction of the grazing mayfly *R. semicolorata* in this study underlines the importance of benthivorous fish as predators in streams. Further on, the presence of the observed fish effects in this field study was a categorical prerequisite for our second objective regarding the relative importance of sublethal and lethal effects.

It has been argued that sublethal effects would result in fitness consequences if the female fecundity depends on the size at emergence and that they might be even more important for the sur-
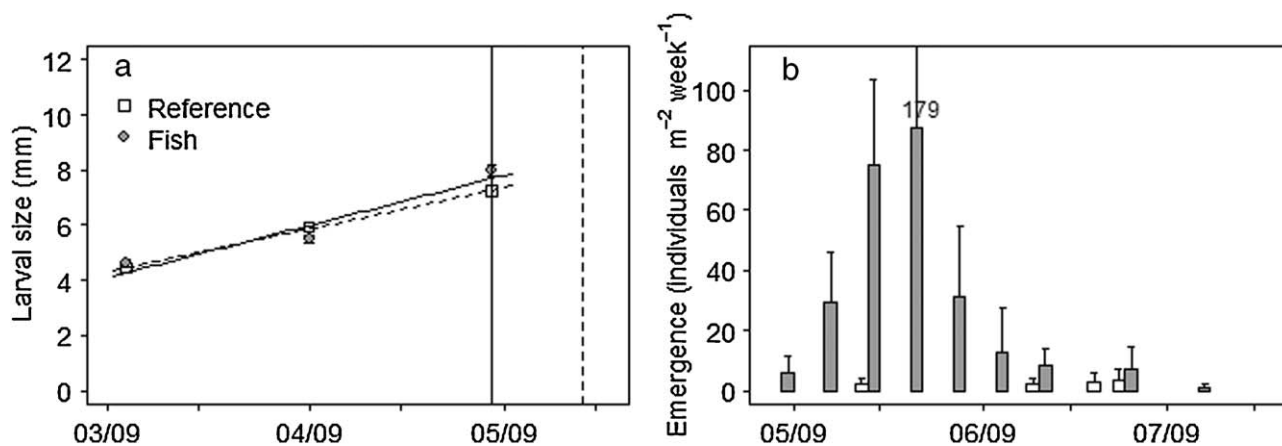

Fig. 4. (a) Mean larval size (mm) ± *SE* of the mayfly *R. semicolorata* in the former reference and fish reach after elimination of benthivorous fish for two years. Data from March to May 2009. Growth rates were calculated in the last weeks before the beginning of emergence (fish reach: solid line, reference reach: dashed line) from the linear relation between the larval size and the number of days during growth (fish: *r²* = 0.41, *P* < 0.001, *n* = 269; reference: *r²* = 0.32, *P* < 0.001, *n* = 339). (b) Mean emergence (individuals m^{-2} week^{-1}) of *R. semicolorata* (+*SE*, *n* = 3) in the former reference and fish reach in 2009 (highest value showed as number).

vival of a prey population than mortality (McPeek and Peckarsky, 1998). However, no reduction of female fecundity due to fish predation was observed in our study. Even though this result seems to contradict McPeek and Peckarsky's statement, in fact it underlines the importance of sublethal fitness consequences. As our scenario analysis revealed, the compensation of sublethal predation effects regarding the individual fitness by a prolonged larval development was highly adaptive (6% reduction of the average population fitness vs. 43% reduction without prolongation). Thus, sublethal effects were largely compensated on the population level because they otherwise would have had an enormous negative effect on the average fitness of the population. It seems that other forms of compensation are also possible. Greig and McIntosh (2008) observed a partial compensation of strong lethal effects due to trout predation by enhanced individual fecundity of a caddisfly. Although lethal effects cannot be neglected in our case (25% loss of the average population fitness) the sublethal effects seem to pose the greater risk for the population. Therefore, the compensation of sublethal effects regarding the individual fitness was more important to reduce the potential loss of egg production of the whole population than the larval mortality due to predation during the prolonged larval development.

In general, aquatic insects with a flexible life history seem to follow two different strategies of predator avoidance to optimise their reproduction and chance of survival. The first strategy is to accelerate larval development to escape the predation risk by earlier emergence (Peckarsky and McIntosh, 1998; Peckarsky et al., 2001, 2002). This strategy may cause smaller size at metamorphosis (Peckarsky and McIntosh, 1998; Peckarsky et al., 2001, 2002) which consequently leads to lower female fecundity (Wickman and Karlsson, 1989; Honèk, 1993; Bonduriansky and Brooks, 1999), shorter adult life span (Taylor et al., 1998; Sokolovska et al., 2000) or a lower mating success of males (Flecker et al., 1988; Sokolovska et al., 2000). The benefit of this strategy seems to be a reduced time spent in the risky habitat and therefore less mortality by the faster larval development (Peckarsky et al., 2002). If the mortality by predation is very high it seems to be best to emerge sooner even if the adults are undersize with low fecundity (first strategy). In most studies this strategy was shown using drift-feeding fish (e.g. trout) and the drifting mayfly *Baetis* spp. as main prey in these (enclosure) experiments. This combination might have resulted in a high predation pressure. Our scenario analysis demonstrated that the first strategy does not seem to be adaptive for the prey under the given predation regime, because it would more than halve the average fitness of the population. The second strategy is to delay metamorphosis to reach optimal size in spite of slower larval growth (Scrimgeour and Culp, 1994; Tseng, 2003). Similarly to the first strategy, if larval mortality by fish predation is relatively low, sustaining the mortality risk to achieve a larger size and higher fecundity (second strategy) might be a strategy that pays off. In our study, *R. semicolorata* larvae followed the second strategy, as they needed a longer time for larval development in the presence of fish. This almost certainly enabled them to achieve the optimal adult size and fecundity, similarly to Tseng's speculation (Tseng, 2003). Thus, a loss of individual fecundity, which would have caused a reduction of the average population fitness by nearly 43%, was avoided. The enhanced mortality due to the longer development time under fish predation pressure reduced the annual egg production to a much smaller extent (6%). As the comparison of the two scenarios demonstrates, only the second behaviour (compensation of sublethal effects on the individual fitness) was adaptive for the prey population. Individuals following the second strategy will be able to contribute much more offspring (exactly 11 153 eggs per m^2 and year in 2005) to the next generation. The difference of this field study compared to most mesocosm studies was the high supply of alternative prey for the benthivorous fish

out of a diverse benthic community in a natural environment (see Appendix A), which might reduce the mortality risk for one prey species. This finally resulted in the observed response in the life history of the prey population to the presence of benthivorous fish. Therefore, the predation rate, specific for each predator-prey pair, relative to the potential sublethal predation consequences in a specific set of environmental factors might account for the differences between the results of the various studies.

In ecosystem research, we have to consider that environmental conditions form a complex network that determines ecological processes (Petersen and Englund, 2005). Hence, working under artificial conditions in microcosms or laboratory experiments reduces the transferability of the results to natural ecosystems (Carpenter, 1996; Schindler, 1998; Petersen and Hastings, 2001; Petersen and Englund, 2005). Undoubtedly, small-scale experiments are an important tool to test hypotheses or gain special ecological insights. Their main advantage is the possibility of replication of the experimental units and therefore statistical analysis of the results. Nevertheless, spatial scale and duration of ecological processes might often be too large to investigate them adequately in mesocosm experiments (Carpenter, 1996; Benndorf et al., 2002). Especially when effects on the population level are to be observed, a large-scale field experiment seems to be the preferred solution. The best way to do this would be a spatially and temporally replicated experiment by investigating a sufficient number of manipulated ecosystems at the same time over a longer time period. This, however, requires a huge sampling and analytical effort. To analyse predation effects on population level with a maintainable effort, we decided to use two reaches of the same stream. This design benefited from the natural environmental conditions and a complex food web. However, due to the lack of real sample replicates statistical analysis was complicated. Nevertheless, we used three emergence traps within each reach to estimate spatial variation. The high substrate heterogeneity led to large differences between the traps. This variability was reflected in the mean emergence abundances and in the outcome of the population (net production). We chose to compare two reaches of one stream rather than two streams (one with fish, one without fish) because we assumed a higher similarity between the reaches within one stream. Because there is no general agreement which environmental factors trigger emergence (e.g. temperature: Langford, 1975; Watanabe et al., 1999) we thought it was best to use reaches with environmental factors as similar as possible. Therefore the two reaches of only one stream allowed us to compare the development of the studied mayfly under very similar environmental preconditions.

However, the study was not replicated and therefore it cannot be excluded that other environmental factors (e.g. temperature, food, competition) might have affected the differences in the mayfly population dynamics between the study reaches. Nevertheless, we assume that the observed pattern was mainly caused by the different fish regimes. By comparing both reaches about two years after the elimination of the benthivorous fish we observed that the differences concerning the mayfly populations developed in an opposite direction than during the experimental study period. While *R. semicolorata* in the fish reach grew more slowly and produced less adults and potential offspring than in the fishless reach in 2005 and 2006, it showed a slightly faster larval growth, an earlier emergence and a higher net production (number of adults per unit time) without fish predation in 2009 in the former fish reach. The mayfly population in the reach, which was fishless from 2005 through 2009 (the former fishless reference reach) developed in 2009 similar to 2005 and 2006. Therefore, we assume that the environmental conditions controlling the larval development besides predation were initially better in the former fish section. In the presence of fish this advantage for the mayfly population was not only compensated but also inverted.

We conclude that predation of benthivorous fish (stone loach and gudgeon) can affect the survival of their prey *R. semicolorata* in natural streams in spite of high spatial heterogeneity and temporal variation of environmental factors. Even though the observed reduction of the average population fitness was caused by prey mortality alone, sublethal predation effects, such as a slower larval growth rate, were important for the survival of the population as shown by the scenario analysis. The observed compensation of potential fecundity loss by a delay of emergence was highly adaptive. We argue that compensation of fecundity loss is evolutionary meaningful when mortality risk is not too high. That might be the reason why consequences of predation regarding the average fitness of a prey population are not that apparent in natural systems where mortality risk of a single prey species is somewhat reduced by the presence of numerous other prey organisms.

Acknowledgments

Appendix A. The composition of the benthic community and the invertebrate biomass (mg dry mass m^{-2}) found in the fish and the fishless reach during the study period from November 2004 to October 2006 (means ± *SE*, *n* = 25 samplings)

Taxon	Fish reach	Reference reach
Ancylus fluviatilis	7.2 ± 1.9	4.9 ± 1.1
Baetis muticus	20.8 ± 3.8	32.1 ± 6.5
Baetis rhodani	18.6 ± 3.9	14.5 ± 2.3
Capnia bifrons	30.0 ± 10.3	27.0 ± 9.7
Ceratopogonidae	9.3 ± 1.6	9.7 ± 1.4
Chironomidae	66.9 ± 25.1	54.2 ± 17.8
Dugesia gonocephala	17.3 ± 3.9	39.2 ± 7.8
Ecdyonurus subalpinus	3.1 ± 1.0	3.9 ± 1.0
Electrogena ujhelyii	12.4 ± 2.2	22.8 ± 3.9
Elmis spp.	1.6 ± 0.5	2.2 ± 0.4
Ephemera danica	85.3 ± 20.7	45.7 ± 11.4
Gammarus pulex	259.6 ± 38.5	400.7 ± 70.7
Hydraena spp.	30.4 ± 4.2	31.3 ± 4.4
Hydropsyche spp.	38.4 ± 7.4	29.3 ± 4.7
Isoperla grammatica	4.3 ± 0.9	2.6 ± 0.8
Leuctra spp.	9.7 ± 1.8	6.9 ± 1.6
Limnephilidae	87.2 ± 26.7	64.7 ± 15.6
Limoniidae	13.5 ± 6.0	32.4 ± 9.7
Nemoura cambrica	12.7 ± 3.8	14.9 ± 6.4
Odontocerum albicorne	16.2 ± 4.8	0.02 ± 0.02
Oligochaeta	0.9 ± 0.2	0.5 ± 0.1
Ostracoda	0.9 ± 0.5	7.4 ± 4.6
Pisidium spp.	0.6 ± 0.2	2.8 ± 0.5
Plectrocnemia conspersa	4.6 ± 2.6	5.7 ± 1.6
Psychodidae	10.4 ± 9.5	2.7 ± 1.4
Ptychopteridae	5.8 ± 2.4	44.5 ± 17.4
Rhithrogena semicolorata	65.7 ± 13.7	78.8 ± 20.0
Rhyacophila fasciata	23.2 ± 3.9	30.9 ± 11.0
Rhyacophila tristis	0.9 ± 0.4	0.5 ± 0.2
Scirtidae	1.4 ± 0.5	1.6 ± 0.4
Sericostoma spp.	71.1 ± 17.7	49.5 ± 10.2
Silo pallipes	8.1 ± 3.6	2.8 ± 4.2
Simuliidae	6.6 ± 2.6	21.8 ± 16.1
Tinodes rostoki	5.5 ± 2.1	1.4 ± 0.5
Tipulidae	38.5 ± 23.1	57.7 ± 24.9

References

Allan, J.D., 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. Ecology 63 (5), 1444–1455.

Bechara, J.A., Moreau, G., Hare, L., 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refuge. J. Anim. Ecol. 62, 451–464.

Benndorf, J., Boing, W., Koop, J.H.E., Neubauer, I., 2002. Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. Freshw. Biol. 47, 2277–2281.

Bergström, U., Englund, G., 2004. Spatial scale, heterogeneity and functional responses. J. Anim. Ecol. 73, 487–493.

Bondurianski, R., Brooks, R.J., 1999. Reproductive allocation and reproductive ecology of seven species of Diptera. Ecol. Entomol. 24, 389–395.

Briegel, H., 1990. Metabolic relationship between female body size, reserves, and fecundity of *Aedes aegypti*. J. Insect Physiol. 36 (3), 165–172.

Carpenter, S.R., 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77 (3), 677–680.

Cavaletto, J.F., Nalepa, T.F., Fanslow, D.L., Schloesser, D.W., 2003. Temporal variation of energy reserves in mayfly nymphs (*Hexagenia* spp.) from Lake St. Clair and western Lake Erie. Freshw. Biol. 48, 1726–1738.

Dahl, J., 1998a. Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. Oecologia 116, 426–432.

Dahl, J., 1998b. The impact of vertebrate and invertebrate predators on a stream benthic community. Oecologia 117, 217–226.

Dahl, J., Greenberg, L.A., 1996. Effects of habitat structure on habitat use by *Gammarus pulex* in artificial streams. Freshw. Biol. 36 (3), 487–495.

Dahl, J., Greenberg, L.A., 1997. Foraging strategies of a vertebrate and an invertebrate predator in stream enclosures. Oikos 78, 459–466.

Dahl, J., Peckarsky, B.L., 2002. Induced morphological defenses in the wild: predator effects on a mayfly, *Drunella coloradensis*. Ecology 83 (6), 1620–1634.

Elliott, J.M., Persson, L., 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47, 977–991.

Englund, G., Cooper, S.D., 2003. Scale effects and extrapolation in ecological experiments. Adv. Ecol. Res. 33, 161–213.

Erös, T., Botta-Dukát, Z., Grossmann, G.D., 2003. Assemblage structure and habitat use of fishes in a Central European submontane stream: a patch-based approach. Ecol. Freshw. Fish 12, 141–150.

Fairchild, M.P., Holomuzki, J.P., 2005. Multiple predator effects on microdistributions, survival, and drift of stream hydropsychid caddisflies. J. N. Am. Benthol. Soc. 24 (1), 101–112.

Flecker, A.S., 1984. The effects of predation and detritus on the structure of a stream insect community: a field test. Oecologia 64, 300–305.

Flecker, A.S., Allan, J.D., McClintock, N.L., 1988. Male body size and mating success in swarms of the mayfly *Epeorus longimanus*. Holarctic Ecol. 11 (4), 280–285.

Forrester, G.E., 1994. Diel patterns of drift by five species of mayfly at different levels of fish predation. Can. J. Fish. Aquat. Sci. 51, 2549–2557.

Greig, H.S., McIntosh, A.R., 2008. Density reductions by predatory trout increase adult size and fecundity of surviving caddisfly larvae in a detritus-based stream food web. Freshw. Biol. 53, 1579–1591.

Griffen, B.D., Williamson, T., 2008. Influence of predator density on nonindependent effects of multiple predator species. Oecologia 155, 151–159.

Hobbs, N.T., Hilborn, R., 2006. Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. Ecol. Appl. 16 (1), 5–19.

Honèk, A., 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66, 483–492.

Huhta, A., Muotka, T., Tikkanen, P., 2000. Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. Freshw. Biol. 45, 33–42.

Illies, J., 1983. Ökosystemforschung an einem Mittelgebirgsbach (Emergenzanalyse). Verhandlungen der Gesellschaft für Ökologie (Mainz 1981) 10, 247–253.

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends Ecol. Evol. 19 (2), 101–108.

Kishi, D., Murakami, M., Nakano, S., Maekawa, K., 2005. Water temperature determines strength of top-down control in a stream food web. Freshw. Biol. 50, 1315–1322.

Koperski, P., 1997. Changes in feeding behaviour of the larvae of the damselfly *Enallagma cyathigerum* in response to stimuli from predators. Ecol. Entomol. 22, 167–175.

Langford, T.E., 1975. The emergence of insects from a British river, warmed by power station cooling-water. Hydrobiologia 47 (1), 91–133.

LeSage, L., Harrison, A.D., 1979. Improved traps and techniques for the study of emerging aquatic insects. Entomol. News 90 (2), 65–78.

Malmqvist, B., 1992. Stream grazer responses to predator odour – an experimental study. Nordic J. Freshw. Res. 67, 27–34.

Mastrorillo, S., Dauba, F., Belaud, A., 1996. Utilisations des microhabitats par le vairon, le goujon et la loche franche dans trois rivières du sud-ouest de la France. Ann. Limnol. 32 (3), 185–195.

McIntosh, A.R., Townsend, C.R., 1994. Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. Ecology 75 (7), 2078–2090.

McIntosh, A.R., Townsend, C.R., 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour. Oecologia 108, 174–181.

McIntosh, A.R., Peckarsky, B.L., 1999. Criteria determining behavioural responses to multiple predators by a stream mayfly. Oikos 85, 554–564.

McIntosh, A.R., Peckarsky, B.L., 2004. Are mayfly anti-predator to fish odour proprtional to risk? Arch. Hydrobiol. 160 (2), 145–151.

McPeek, M.A., Peckarsky, B.L., 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. Ecology 79 (3), 867–879.

Morin, A., Dumont, P.J., 1994. A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. J. N. Am. Benthol. Soc. 13 (3), 357–367.

Muotka, T.G., Huhta, A., Tikkanen, P., 1999. Diel vertical movements by lotic mayfly nymphs under variable predation risk. Ecol. Entomol. 24, 443–449.

Nyström, P., Pérez, J.R., 1998. Crayfish predation on the common pond snail (*Lymnaea stagnalis*): the effect of habitat complexity and snail size on foraging efficiency. Hydrobiologia 368 (1–3), 201–208.

Nyström, P., McIntosh, A.R., Winterbourn, M.J., 2003. Top-down and bottom-up processes in grassland and forested streams. Oecologia 136, 596–608.

Peckarsky, B.L., 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. Ecology 77 (6), 1888–1905.

Peckarsky, B.L., Cowan, C.A., Penton, M.A., Anderson, C., 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74 (6), 1836–1842.

Peckarsky, B.L., McIntosh, A.R., 1998. Fitness and community consequences of avoiding multiple predators. Oecologia 113, 565–576.

Peckarsky, B.L., Taylor, B.W., McIntosh, A.R., 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology 82 (3), 740–757.

Peckarsky, B.L., McIntosh, A.R., Taylor, B.W., Dahl, J., 2002. Predator chemicals induce changes in mayfly life history traits: a whole-stream manipulation. Ecology 83 (3), 612–618.

Petersen, J.E., Englund, G., 2005. Dimensional approaches to designing better experimental ecosystems: a practitioners guide with examples. Oecologia 145, 216–224.

Petersen, J.E., Hastings, A., 2001. Dimensional approaches to scaling experimental ecosystems: designing mousetraps to catch elephants. Am. Nat. 157, 324–333.

Power, M.E., 1990. Effects of fish in river food webs. Science 250, 811–814.

Power, M.E., 1992. Habitat heterogeneity and the functional significance of fish in river food webs. Ecology 73 (5), 1675–1688.

R Development Core Team, 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rosenfeld, J.S., 2000a. Effects of fish predation in erosional and depositional habitats in a temperate stream. Can. J. Fish. Aquat. Sci. 57, 1369–1379.

Rosenfeld, J.S., 2000b. Contrasting effects of fish predation in a fishless and fish-bearing stream. Arch. Hydrobiol. 147, 129–142.

Ruetz III, C.R., Vondracek, B., Newman, R.M., 2004. Weak top-down control of grazers and periphyton by slimy sculpins in a coldwater stream. J. N. Am. Benthol. Soc. 23 (2), 271–286.

Santoul, F., Mengin, N., Céréghino, R., Figuerola, J., Mastrorillo, S., 2005. Environmental factors influencing the regional distribution and local density of a small benthic fish: the stone loach (*Barbatula barbatula*). Hydrobiologia 544, 347–355.

Schindler, D.W., 1998. Replication versus realism: the need for ecosystem-scale experiments. Ecosystems 1, 323–334.

Schmidt, S.I., König-Rinke, M., Kornek, K., Winkelmann, C., Wetzel, M.A., Koop, J.H.E., Benndorf, J., 2008. Finding appropriate reference sites in large-scale aquatic field experiments. Aquat. Ecol. 43, 169–179.

Scrimgeour, G.J., Culp, J.M., 1994. Feeding while evading predators by a lotic mayfly: linking short-term foraging behaviours to long-term fitness consequences. Oecologia 100, 128–134.

Sokolovska, N., Rowe, L., Johansson, F., 2000. Fitness and body size in mature odonates. Ecol. Entomol. 25, 239–246.

Taylor, B.W., Anderson, C.R., Peckarsky, B.L., 1998. Effects of size at metamorphosis on stonefly fecundity, longevity, and reproductive success. Oecologia 114, 494–502.

Thorp, J.H., Bergey, E.A., 1981. Field experiments on responses of a freshwater benthic macroinvertebrate community to vertebrate predators. Ecology 62 (2), 365–375.

Tikkanen, P., Muotka, T., Huhta, A., 1994. Predator detection and avoidance by lotic mayfly nymphs of different size. Oecologia 99, 252–259.

Tseng, M., 2003. Life-history responses of a mayfly to seasonal constraints and predation risk. Ecol. Entomol. 28, 119–123.

Turnbull, K.R., Barmuta, L.A., 2002. Substrate complexity influences the preference of a predatory stonefly, *Eusthenia costalis* Banks (Plecoptera: Eustheniidae), for its prey. Arch. Hydrobiol. 155 (3), 481–492.

Vance-Chalcraft, H.D., Soluk, D.A., Ozburn, N., 2004. Is prey predation risk influenced more by increasing predator density or predator species richness in stream enclosures? Oecologia 139, 117–122.

Vance-Chalcraft, H.D., Soluk, D.A., 2005. Multiple predator effects result in risk reduction for prey across multiple prey densities. Oecologia 144, 472–480.

Watanabe, N.C., Mori, I., Yoshitaka, I., 1999. Effect of water temperature on the mass emergence of the mayfly *Ephoron shigae*, in a Japanese river (Ephemeroptera: Polymitarcyidae). Freshw. Biol. 41, 537–541.

Watkins, M.S., Doherty, S., Copp, G.H., 1997. Microhabitat use by 0+ and older fishes in a small English chalk stream. J. Fish Biol. 50 (5), 1010–1024.

Werner, E.E., Peacor, S.D., 2006. Lethal and nonlethal predator effects on an herbivore guild mediated by system productivity. Ecology 87, 347–361.

Wickman, P.-O., Karlsson, B., 1989. Abdomen size, body size and the reproductive effort of insects. Oikos 56, 209–214.

Winkelmann, C., Koop, J.H.E., 2007. The management of metabolic energy storage during the life cycle of mayflies: a comparative field investigation of the collector-gatherer *Ephemera danica* and the scraper *Rhithrogena semicolorata*. J. Comp. Physiol. B 177, 119–128.

Winkelmann, C., Worischka, S., Koop, J.H.E., Benndorf, J., 2007. Predation effects of benthivorous fish on grazing and shredding macroinvertebrates in a detritus-based stream food web. Limnologica 37, 121–128.

Winkelmann, C., Petzoldt, T., Koop, J.H.E., Matthaei, C.D., Benndorf, J., 2008. Benthivorous fish reduce stream invertebrate drift in a large-scale field experiment. Aquat. Ecol. 42, 483–493.