

CONSEQUENCES OF PREDATOR-PREY INTERACTIONS IN BOREAL STREAMS

Scaling up from processes to large-scale patterns

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Abstract

In this thesis I studied lotic trout predation and its ecological effects, and investigated invertebrate predator-prey interactions under natural and anthropogenically modified flow conditions. Given the growing concern about the reliability of extrapolations from small-scale studies to larger spatio-temporal scales, results of mechanistic small-scale experiments were scaled up by linking them to large-scale field surveys.

An intensive survey assessed changes in diel feeding periodicity, prey selection and daily ration of juvenile brown trout (*Salmo trutta* L.) over the course of the open water period. This survey provides the first field estimates of juvenile brown trout daily rations and indicates crepuscular feeding peaks. Trout selectively preyed on medium- to large-sized prey, shifting towards epibenthic feeding with increasing availability of suitable prey. In a small-scale field experiment, trout displayed clear size-related predation concentrating on invertebrate predators and cased caddisflies, a pattern that scaled up successfully in large-scale surveys. Further, predation effects on large-sized prey were also repeated in a meta-analysis on lotic salmonid predation.

While dense blackfly populations in lake-outlet streams are common, mass outbreaks of blackflies in short-term regulated rivers are poorly studied. In our studies the principal invertebrate predator of vernal benthic communities, the caseless caddisfly *Rhyacophila*, displayed significant preference for blackflies and was almost unable to capture any other prey, thus resulting in passive selection for larval blackflies.

Rhyacophila larvae displayed highest capture success in intermediate current velocities, whereas further increases in current velocities decreased capture success. Short-term regulation releases increased both predator and prey drift but, unlike for *Rhyacophila*, magnitude of drift was unrelated to substrate for blackflies. Indeed, field observations indicated that blackflies rarely face detrimental effects of short-term regulation due to their fast growing rates and early emergence. Moss was the most preferred habitat of *Rhyacophila* and provided the best buffer against sudden increases in current velocities. These results suggest that several factors maintain spring-time outbreaks of blackfly populations in short-term regulated rivers: exaptation of the dominant blackfly species to prevailing conditions, degradation of the key habitat of the predator, and recurring annual drift losses and diminished capture success of *Rhyacophila* during short-term regulation releases.

Keywords: blackfly larvae, brown trout, macroinvertebrates, predation, prey selection, *Rhyacophila*, spatial scale, streams

To my family

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List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Kreivi P, Muotka T, Huusko A, Mäki-Petäys A, Huhta A & Meissner K (1999) Diel feeding periodicity, daily ration and prey selectivity in juvenile brown trout in a subarctic river. *J Fish Biol* 55: 553-571.
- II Meissner K & Muotka T (2005) The role of trout in stream food webs: integrating evidence from field surveys and experiments. *Journal of Animal Ecology* (accepted).
- III Muotka T, Juntunen A & Meissner K (2005) Differential vulnerability determines prey preference by a predatory caddis larva, *Rhyacophila obliterata* McL. Manuscript, submitted.
- IV Meissner K, Muotka T & Kananen I (2002) Drift responses of larval blackflies and their predators to short-term flow regulation. *Arch Hydrobiol* 154: 529-542.
- V Meissner K, Juntunen A, Malmqvist B & Muotka T (2005) Predator-prey interactions in a variable flow environment: responses of a predatory caddis larva and its black fly prey to variations in flow. Manuscript, submitted.

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1 Introduction

Predation has been shown to be a major regulatory force in some lotic communities (Power 1990, 1992, Bechara *et al.* 1992) but its general importance remains controversial (Cooper *et al.* 1990, Wooster 1994 and Dahl & Greenberg 1996). In their review, Cooper and coauthors (1990) showed a strong relation between the mesh size of experimental units and the observed predator impact. While this result implied that most of the observed predation effects were artifacts of the experimental design, later meta-analysis on lotic predation were unable to reproduce this relationship (Wooster 1994, Dahl & Greenberg 1996). In his meta-analysis, Wooster (1994) recorded much stronger predation effects for invertebrate than vertebrate predators, thus stressing the importance of ecological factors over physical design features. Similarly, in a meta-analysis on fish predation, Dahl & Greenberg (1996) found that the feeding mode of fish significantly influenced the observed predation effect. However, in yet the most detailed meta-analyses on stream predation, Englund and coauthors (1999) attributed differences between their and earlier reviews to problems related to meta-analytic methodology, namely data inclusion criteria and metric choice. Thus, while past reviews have put forward several explanatory factors about lotic predation impacts, their conclusions are neither general nor consistent, stressing the continuous need for more detailed research on the mechanisms underlying the observed patterns.

Research on predation effects in lotic systems has relied heavily on the use of well-replicated, small-scale experiments because the relevant spatial and temporal scale(s) of experiments is seldom known a priori. While convenient, the use of small-scale experiments to interpret large-scale effects has come under growing criticism because such experiments may be forced to scales inappropriate for the study of system-wide effects (e.g., Englund & Olsson 1996). Behavioural responses of prey can influence predator impacts (Sih & Wooster 1994) and Englund (1997) noted that at small scales, predator-induced prey dispersal may obscure the detection of true (i.e., consumptive) predator impacts. Therefore “scaling-up”, i.e., extrapolating from small-scale effects to larger scales (i.e., stream scale) may be impossible. The problems associated with scaling-up from small-scale studies to more relevant spatial and temporal scales are not exclusive to lotic systems (Thrush *et al.* 1997, Raffaelli & Møller 2000). While large-scale, preferably whole-system, manipulations solve dispersal-related problems, such

studies are plagued by ethical, financial and logistical problems. Increasing the extent of a study increases variation (Wiens 1989) and the interpretation of large-scale studies is often complicated by the vast number of interaction pathways typical of complex systems (Sarnelle 1997). To directly assess whether small-scale effects can be scaled up, studies should ideally conduct the same manipulation concurrently on multiple spatial and/or temporal extents. As both whole-system and multi-scale studies are still exceptional in aquatic systems (but see Thrush *et al.* 1997), other solutions to scaling issues have been suggested (e.g., Polis *et al.* 1998, Power *et al.* 1998, Werner 1998). These approaches explicitly link process-related small-scale experiments to large-scale surveys of community structure, an approach that was adopted in this thesis to examine the effects of trout and invertebrate predation in boreal lotic systems.

In the Fennoscandian shield, brown trout (*Salmo trutta* L.) is the principal salmonid predator in most pristine stream systems. As trout predation may have profound ecosystem level effects, it is surprising that only few studies have investigated the community-level effects of trout predation in this area. In particular, little is known about the ecological consequences of ontogenetic and temporal changes in trout foraging behaviour and the consistency of observed patterns over a range of scales. In a large-scale survey we investigated seasonal changes in diel feeding periodicity, daily ration and prey selectivity of brown trout (I). In addition, a small-scale experimental study examined the potential community-wide effects of size selective trout predation (II). To scale up from small-scale patterns, experimental results were directly compared to large-scale surveys at different spatial scales and they were then set into a global context using meta-analysis (II).

Studies of invertebrate predation in lotic systems often focus on predatory stoneflies (e.g., Huhta *et al.* 1999 and references therein) whereas comparatively little is known about impacts of predatory caddisflies on their prey's densities and habitat choice. In natural streams in the Fennoscandian shield, caseless caddisfly larvae of the genus *Rhyacophila* feed selectively on, and aggregate with, larval blackflies in spring and early summer. As *Rhyacophila* larvae represent the main top-level predators in many of these streams they can potentially exert strong regulatory effects on their blackfly prey. While blackflies occur naturally in dense populations in stream outlets, human regulation of flow and channel modification have caused mass outbreaks of blackfly larvae in many streams worldwide (e.g., Nyman 1995, de Moor 1997, Zhang *et al.* 1998). In a series of studies, we studied the mechanisms of *Rhyacophila* prey selection, hunting behaviour and dietary composition (III). These results were applied in studies where we examined the causes of blackfly mass-outbreaks in a regulated river. In particular, these studies focused on the interference of short-term regulation with predator-prey interactions by assessing macroinvertebrate drift responses to anthropogenic modification of stream flow (IV) and habitat choice and current preferences (V) of the rhyacophilid predator and its prey.

Overall, this thesis focuses on two major issues in stream ecology: (i) the impact of a visually hunting fish predator on invertebrate prey communities, attempting to relate community-wide predation effects to fish diet preferences; (ii) behavioural aspects of the predator-prey interaction between larval blackflies and their major invertebrate predators, *Rhyacophila* caddis larvae. The second theme does not directly test for the impact of the invertebrate predator on its prey communities, but using a combination of behavioural laboratory experiments and direct field observations of interacting animals, it provides

the basis for understanding the relative importance of this type of predator to the regulation of prey communities in boreal streams and rivers.

2 Methods

2.1 Study area

The studies of this thesis were conducted at several locations in northeastern (I, II, III, V), central (II) and western (IV, V) Finland. Due to the large geographical extent, there are distinct differences in physical and chemical characters between the sampling sites. Streams in the Kuusamo area (NE Finland) are oligotrophic, oligohumic, near-pristine or modestly-impacted (I, II, III, V) and they drain mainly forested watersheds. Discharge varies from 0.1 to 65 m³ and streams are ice-covered for 5-6 months each year. The unique calcareous geology of the drainage areas in the Kuusamo region makes these second and third order streams slightly alkaline. Streams in central and western Finland drain bogs, forested or cultivated areas and are either slightly, moderately (II) or severely (IV, V) impacted by land use practices. Stream discharge varies from 0.1 to 165 m³, water is humic and oligo-to-mesotrophic. In the second-to-third order streams, pH is circumneutral (II), whereas pH in the fourth order river in studies IV and V is slightly acidic. Ice covers streams (II, IV, V) for 3-5 months each year. More detailed site descriptions of the field sites are provided in the respective papers.

Laboratory experiments were conducted at two locations: (i) Oulanka Research Station, Kuusamo (III) and (ii) the West-Finland Environment Centre Laboratory in Kokkola (IV, V). Experiments were conducted in unheated warehouses and stream water used in the experiments was changed daily. Thus, diel water temperature variations in aquaria paralleled those of local streams. Experiments at Oulanka Research Station were conducted in recirculating stream tanks (40 x 20 x 19 cm) modified from Soluk & Collins (1988). Current velocity in the experimental arena ranged from 5 to 45 cm/s. To provide a foothold for the animals, we fastened a mesh cloth to the experimental arena and added eight small, flat stones (ca. 5 x 5 x 1 cm) to each stream tank.

In experiments conducted in Kokkola we used four replicate flumes (240 x 14 cm). Water to the flumes was recirculated using two pumps with a total capacity of 46 m³/h. Discharge to the individual flumes was adjusted through ball valves. Substrate patches, either stone or moss, covering 29 % of the total experimental arena were attached at regularly spaced intervals to alternating sides of the flume bottom using non-toxic silicon.

Three types of substrates were used in the experiments: (i) bare concrete, (ii) natural stones, and (iii) strips of plastic doormat (Finnturf®), hereafter referred to as “moss”.

2.2 Trout predation: scaling up from small-scale patterns

Patterns of prey selection and predatory impact by trout were directly assessed by stomach content analysis (I, II) and a controlled field experiment (II), respectively. Patterns of prey selection, daily ration and diel feeding periodicity of juvenile trout (0+ and 1+) were investigated during eight sampling occasions in the summer and autumn of two consecutive years (I). Sampling was conducted by electrofishing at three hour intervals for 24 hours (I). Stomach contents were immediately preserved, wet-weighed, and later sorted, keyed and dry weighed (I, II). To assess trout prey selection, prey availability from both benthos and drift was studied. Densities of benthic macroinvertebrates were estimated from five replicate Surber samples taken on each sampling date (I) and drift was sampled at three hour intervals concurrent with electrofishing (I).

In the fall of 1997, a field experiment was conducted to evaluate trout predation effects on prey density and prey size using a replicated enclosure-exclosure design with open-to-trout controls (II). In combination with the experiment, a dietary survey of trout was made to evaluate local prey selection. Prey availability was assessed by both drift and benthic samples taken from open-to-trout controls. Drift samples were taken to quantify emigration and immigration into experimental units (II). Direct effects of trout predation were assessed from benthic samples (five stones per experimental unit). Periphyton chlorophyll-a content of tiles introduced to each experimental unit prior to the experiment was sampled to reveal possible indirect effects of trout predation on benthic algae. Macroinvertebrate samples were keyed to the lowest feasible taxonomic level, typically genus or species. Head widths of macroinvertebrates were measured to assess size-related impacts of trout predation.

Trout feeding rhythmicity (I) was analyzed by analysis of covariance (ANCOVA). ANCOVA of diel differences in food consumption was performed on log-transformed mean weights and prey numbers, using fish length as the covariate. Diel variation in trout diet was estimated through Chesson's (1983) index of selection, calculated for individual fish and tested against deviation from randomness using sequentially corrected, paired t-tests (Tikkanen *et al.* 1997). To assess diel variations in prey selectivity we correlated day- and night-time preference for each sampling date (Spearman rank) and tested for overall trends across dates using Fisher's combined probability tests (I).

Daily ration estimates were calculated using Elliott & Persson's (1978) equation. The proportional error estimate of Post (1990) was subsequently used to obtain 95 % confidence intervals for the daily ration estimates. Relationships between drift density and (i) the mean relative dry weight of stomach contents and (ii) the number of prey consumed were assessed using Spearman rank correlations.

Overlap in taxonomic composition between drift and trout diet was calculated for every three-hour sampling interval using Schoener's (1970) index, for randomly paired stomach and drift samples, without replacement (Linton *et al.* 1989). Average overlap

values were subsequently tested for diel differences using one-way analysis of variance (ANOVA) followed by Tukey's tests.

In the field experiment (II) differences in macroinvertebrate densities and algal biomass between treatments were tested using a randomized block design ANOVA. The six most abundant prey groups representative of the size spectrum of macroinvertebrates were chosen for analysis (II). Per capita drift rates of each prey group were related to predator impact to assess whether prey mobility influenced predation impact (see Englund 1997). Trout prey selection was calculated using Chesson's (1983) index and deviation from random selection was tested using sequentially α -level adjusted t-tests (Tikkanen et al 1997). To evaluate the across-scale generality of the experimental findings we examined benthic densities of three prey groups differing in size, mobility and trophic status (i.e., invertebrate predators, grazing mayflies and Chironomidae) in 18 trout streams and six fishless streams in Central Finland. Finally, in an attempt to evaluate the findings of this study in a global context, a meta-analysis on salmonid predation experiments was conducted using the same three focal groups.

2.3 Invertebrate predation: assessing key factors influencing predator-prey interactions

A series of laboratory experiments and field surveys was conducted to assess the prey selection and habitat choice of a key invertebrate predator and its main prey under varying flow regimes. The diet of fifth instar rhyacophilid caddis larvae was examined at three stream sites in NE-Finland (III). Prey items ingested by *Rhyacophila* larvae were identified from sclerotized fragments. Availability of prey was estimated by concurrent Surber samples and selection was calculated using Chesson's (1983) index. Deviations from random selection were tested with sequentially adjusted t-tests (Tikkanen *et al.* 1997). In the laboratory experiments *Rhyacophila* larvae were confronted with four principle prey types that differ in their inherent mobility and are abundantly available in the stream benthos. In a series of single species feeding trials fifth instar *Rhyacophila* larvae were offered *Helodon ferrugineus* Wahlberg, *Cnephia pallipes* (Fries) (Diptera: Simuliidae), *Amphinemura borealis* (Morton) (Plecoptera: Nemouridae), and small and large *Baetis rhodani* Pictet (Ephemeroptera: Baetidae), at densities equivalent to those in natural streams. During these trials, we recorded the number of attacks, capture success and handling times by *Rhyacophila* and antipredatory responses by the prey. In mixed-species trials, *Rhyacophila* larvae were offered a mixture of *Cnephia pallipes*, *Amphinemura borealis* and large *Baetis rhodani*, and only prey consumption was recorded. Data from the feeding trials were analyzed with one-way ANOVA followed by post-hoc Tukey's tests, using prey species as the treatment factor (III).

Flow during short-term regulation releases in River Perhonjoki is roughly fivefold compared to low-flow conditions. Effects of flow variation on drift, benthic densities and habitat choice of *Rhyacophila* and blackfly larvae were investigated in a series of laboratory experiments and a field survey (IV, V). In the field survey, effects of the commencement of short-term regulation on the four main groups of the spring-time benthic community (i.e., *Rhyacophila nubila* Zetterstedt, blackflies, Chironomidae and

Hydropsychoidea) were evaluated on replicate drift- and benthic samples. Drift was sampled immediately prior and during six consecutive short-term regulation intervals (IV). Differences in drift densities between flow levels and sampling occasions were analyzed using repeated measure ANOVA. When sphericity was not met, Greenhouse-Geisser corrected degrees of freedom were used (Huynh & Feldt 1976, Rogan *et al.* 1979). Changes in benthic densities were assessed by Surber samples taken on three dates before, during and after short-term regulation and one-way ANOVA was used to assess differences between these periods (IV). To examine mechanisms underlying the observed patterns, the effects of substrate and simulated peaking flows were studied for larval blackflies and 5th instar *Rhyacophila* larvae in four experimental flumes (IV). Flumes in the blackfly trials had either concrete or concrete and moss as substrate, whereas in trials with *Rhyacophila* the substrate factor had two additional levels (i.e., concrete and stone or concrete, moss and stone). We simulated short-term regulation releases by adjusting the discharge to individual flumes through valves. The flow factor had two levels: (i) high and (ii) low flow. The effects of flow and habitat on the proportion of emigrating larvae were analyzed using a randomized block ANOVA followed by Tukey's test (IV).

We examined the influence of current velocity on the feeding behaviour of fifth instar *Rhyacophila* larvae in direct field observations (V). Individual larvae were randomly chosen and observed for 20 minutes. During the observations we recorded activity (i.e., time spent moving), distance moved, number of attacks and number of captures by *Rhyacophila*. Current velocities along five equidistant spots on the trail chosen by individual *Rhyacophila* were measured and averaged. Observations were grouped into four categories according to current velocity regimes. Velocity categories were (i) slow (<45 cm/s), (ii) medium (45-69 cm/s), (iii) high (70-100 cm/s) or (iv) very high (>1 m/s). Differences in behavioural parameters between velocity categories were analyzed using one-way ANOVA followed by Tukey's tests. In addition, laboratory experiments were used to estimate whether overlap of current and habitat preferences of *Rhyacophila* and their blackfly prey change with flow, habitat structure or simultaneous presence of the other species (V). The four flumes were divided into a grid of 6 times 55 cells. Each flume contained a mixture of different substrate types (concrete, stone and moss). Current velocities were measured in each cell during both peak- and low-flow treatments. *Rhyacophila* and blackfly larvae were introduced to the flumes and subjected to flow releases simulating those experienced during short-term regulation. Larval positions in the grid were mapped after one hour. Both single species as well as mixed *Rhyacophila* and blackfly trials were conducted. Current preferences of the two species in each flow treatment were calculated using Chesson's index for evenly spaced (i.e., 25 cm/s) increments. The deviation of each increment's preference value from random expectation was tested using paired t-tests with sequentially adjusted α -levels (Tikkanen *et al.* 1997). To analyze habitat selection, animal presence and the substrate class of cells were crosstabulated. Standardized residuals were used to evaluate whether the choice of animals for a particular substrate type deviated significantly from randomness. Differences between substrate type preferences were tested separately, both blackflies and larvae using a-priori contrasts for log- linear models on data combined across the flow treatments. Contrasts compared: (i) concrete substrate to the combination of moss and stone, (ii) stone to moss, (iii) stone to concrete, and (iv) moss to concrete. In addition, exploratory hierarchical log-linear models with backward selection were conducted to

assess the most parsimonious model describing the patterns of animal distribution in response to habitat and flow fluctuations. The fit of individual models was evaluated using likelihood-ratio tests.

3 Results and Discussion

3.1 Trout predation: ecological consequences of feeding behaviour and prey preference

No diel variation in juvenile brown trout prey selection was observed in an extensive field survey, but significant differences between age classes and sampling dates were evident (I). Young-of-the-year trout (0+) preferred *Ephemerella* mayfly larvae in early summer and semi-sessile case-bearing caddisfly *Micrasema* in autumn, while 1+ trout preferred caddisfly larvae on all sample dates. In early summer, 1+ trout preyed selectively on larger prey (i.e., *Rhyacophila* and Hydropsychoidea caddis larvae) until the more preferred intermediately-sized *Micrasema* larvae became abundant. Although *Baetis* mayfly and blackfly larvae made up 25 to 50 % of trout diet, these prey items were mostly avoided when compared to their availability.

The extensive dietary survey is to our knowledge the first one to document estimates of daily rations for juvenile brown trout (I) in the field. Similar to other salmonid species (Allan 1981, Walsh *et al.* 1988) the average estimates of daily rations per fish dry body weight of juvenile brown trout declined from summer towards late fall. However, our estimates of juvenile trout daily rations are higher than those of other lotic salmonids (Sagar & Glova 1988, Forrester 1994). During the diel cycle, trout showed a significant periodicity in food intake with the highest intake usually coinciding with periods of twilight (i.e., at dusk or dawn). This result was expected since trout have been described as crepuscular fish that display distinct activity peaks around dusk and dawn (Eriksson 1978). Even though peak drift densities in our survey coincided with the periods of heightened trout activity, correlation between trout feeding and drift rates was low. A possible explanation for this result is that trout switch to a predominantly epibenthic feeding mode when epibenthic prey are abundant. Thus, the increase in drift at twilight may not be needed to acquire sufficient food. Rather, heightened activity under low-light conditions that still permit the use of visual cues for foraging may, in itself, suffice to ensure adequate capture success from both epibenthos and drift (Fraser & Metcalfe 1997).

Trout rely mainly on visual cues to catch prey (McIntosh & Townsend 1995, Fraser & Metcalfe 1997), therefore large-sized or otherwise conspicuous prey should be disproportionately selected for. Indeed, predation effects in the enclosure-exclosure experiment were positively related to prey size (II). Densities of large invertebrate predators (mainly *Rhyacophila* larvae) and medium-sized *Micrasema* caddis larvae were lower in trout enclosure than exclosure treatments, whereas densities of small-sized *Baetis* and Chironomidae larvae were unaffected by trout presence. Trout predation can trigger trophic cascades (Power 1990, Bechara *et al.* 1992), but we observed no changes in periphyton chlorophyll-a levels in response to trout presence, suggesting a lack of cascading effects by brown trout in our study system.

Recent criticism suggests that at small experimental scales, observed effects of predation may arise mainly as a function of prey movement rather than direct predator consumption. As a result, findings of small-scale studies may be artifacts of the scale of observation and extrapolation to larger scales can be misleading (see review by Englund & Cooper 2003). We observed no differences in either emigration or immigration rates for any prey type in response to experimental treatments, thus precluding predation effects due to different emigration rates (Englund & Olsson 1996). To further examine patterns of prey selection, trout diet was divided into major prey groups representing different increments of the prey size spectrum. As in the field experiment, results of the dietary survey showed that larger prey were significantly selected for (aerial insects, predatory invertebrates), whilst prey types at the lower end of the size spectrum were avoided (small *Baetis* sp., Chironomidae). Thus, size-related predatory impacts of our small-scale experiment scaled up to the stream-wide scale (II) and mirror patterns of juvenile trout prey selection on a regional scale (I). Experimental results were also compared to those in an across-system survey. In this survey macroinvertebrates were sampled in streams containing vs. lacking trout. Trout streams supported significantly lower densities of large invertebrate predators and five times lower densities of *Baetis*. However, the difference of *Baetis* densities between trout streams and fishless streams only bordered significance due to very high variability in the data and low power of the test. Finally, on a global scale, meta-analysis of published data revealed reduced densities of large invertebrate predators and intermediately-sized mobile grazers (mostly epibenthic mayflies) in the presence of trout. While not significant the small Chironomidae midges displayed increased densities in the presence of trout. Different metrics and data selection criteria had no influence on the pattern of reduced invertebrate predator densities in the presence of trout, whereas meta-analytic results for *Baetis* were not always significant.

An important implication of the extensive trout dietary survey is that the feeding mode of juvenile trout may be more flexible than earlier studies have indicated, resulting in the inclusion of predominantly epibenthic prey whenever these are abundant. Furthermore, feeding of juvenile trout seemed partly unrelated to availability since abundant prey items (e.g., *Baetis* and aerial prey) were often significantly avoided. Significant impacts on large prey by lotic salmonids have been reported in many instances and were also observed in our studies (I, II). The reduction of epibenthic grazers in the presence of lotic salmonids was an obvious, yet variable pattern in our across-stream survey. However our small- and intermediate scale within stream survey studies gave no indication of such an effect. Our study thus demonstrates the need for a multi-scaled approach in the study of

fish predation. Future studies should concentrate on ecological consequences of predation using not only single predator manipulations but including the range of fish predators typically encountered in streams. Such studies are rare (but see Dahl 1998) but can provide valuable insights into prey responses under conflicting risks of predation.

3.2 Invertebrate predator-prey interactions: prey selection, habitat choice, and influences of flow

Rhyacophila larvae displayed a pronounced preference for blackflies in all three streams studied (III). This result parallels the findings of Muotka (1993) who noted *Rhyacophila* to aggregate with and selectively feed on blackfly prey in the early summer. Other abundant prey types (i.e., Chironomidae, *Baetis* and *Amphinemura*) in the streams were either avoided or used in proportion to their availability in the benthos (III). In single- and mixed- species feeding trials, *Rhyacophila* larvae always showed significantly higher capture success for blackfly larvae than any other taxa, despite higher attack rates on mobile prey. Capture success of *Rhyacophila* for *Helodon ferrugineus* was significantly lower than for *Cnephia pallipes*. This is probably due to active defence (i.e., biting the predator) used by *Helodon* which accounted for 25 % of its successful escapes. *Baetis* and *Amphinemura* larvae escaped attacks by crawling away or drifting. Compared to *Helodon*, *Baetis* and *Amphinemura* larvae avoided encounters more often before the predator came within striking distance (III).

Commencement of short-term flow regulation in River Perhonjoki has caused massive outbreaks of larval blackflies and the disappearance of some sensitive taxa (Nyman 1995). In a series of studies we investigated whether environmental stress explained the observed patterns. Blackflies exhibit high resistance to flow changes (Hart *et al.* 1996), relative to their invertebrate predators and competitors. Flow resistance could therefore be a key mechanism causing outbreaks of blackflies in River Perhonjoki. The field survey indicated that the main two blackfly species found in River Perhonjoki are *Simulium noelleri* and *Cnephia pallipes* (IV). Both species exhibit rapid larval growth (Malmqvist 1994) and often emerge prior to the onset of short-term regulation in River Perhonjoki (IV). These blackfly species are therefore “exapted” (sensu Gould & Vrba 1982) to exploit the prevailing environmental conditions in short-term regulated rivers. When faced with effects of short-term regulation in the field, however, blackfly larvae displayed the highest drift densities during the peak flows in the beginning of the short-term regulation. Similarly, *Rhyacophila* always displayed higher drift densities during peak flows, but due to low statistical power this result only bordered significance. Benthic densities of blackflies did not vary for the duration of the regulation period. However, benthic densities were significantly higher before, rather than after the short-term regulation period. To assess the effect of drifting on the reduction of benthic densities we estimated drift loss based on Pearson & Franklin’s (1968) assumptions regarding the short-term regulation related drift behaviour of blackflies. Estimates of blackfly drift loss tracked the observed daily reduction in benthic blackfly densities. In the laboratory, simulations of flow releases resulted in significantly higher drift densities for both blackflies and *Rhyacophila* when compared to low flow conditions. While blackflies drift

densities were unaffected by substrate treatments, drift of *Rhyacophila* was significantly higher in the structurally simple concrete treatment, than in structurally more complex treatments (IV).

Field observations of *Rhyacophila* predation on blackflies demonstrated a clear inverse relationship between attack rates and current speed (V). Capture success in the field was highest at intermediate velocities (50 cm/s), a finding well in line with that by Malmqvist & Sackmann (1996). Similarly, in our laboratory flumes *Rhyacophila* preferred currents <50 cm/s while higher currents were avoided under both low-flow and high-flow conditions. This suggests that *Rhyacophila* only enter habitats with higher than optimal velocities for short feeding bouts, thus maximizing their capture success, while at even higher velocities capture success significantly decreases. The use of more sheltered habitats by *Rhyacophila nubila* when not feeding has been demonstrated before (Malmqvist 1993) and there is strong evidence for diel periodicity in hunting behaviour of congeners (Elliott 2005). Elliott (2005) found diel periodicity to be less pronounced for smaller *Rhyacophila dorsalis* (Curtis) instars, pointing to ontogenetic shifts in this either fixed or chemically induced behaviour. As *Rhyacophila* in streams of the Fennoscandian shield attain last instars close to the summer solstice, diel periodicity is unlikely to affect our experiments. More generally, periodicity and use of sheltered habitats in *Rhyacophila* may be the consequences of active fish predator avoidance by last instar *Rhyacophila* larvae. Unfortunately we still lack the data to test either hypothesis.

Under low-flow conditions blackflies always avoided the lowest current regime and displayed preference for velocities of 25-100 cm/s, thus partly overlapping with the velocity preference of their predators. Increasing experimental flow decreased blackfly preference for currents lower than 75 cm/s and reduced overlap with the current preferences of *Rhyacophila*. The shift in current preferences of blackflies rendered more than half of the population virtually inaccessible to their predators. This contrasts with results for *Plectrocnemia* caddisfly (Lancaster 1996) and *Cosmioperla* stonefly predators (Thompson *et al.* 2002), which display increased predatory effects in response to flow increases. While spate-induced aggregation of predator and prey into flow refugia can increase encounter rates and consumption (Lancaster *et al.* 1990, Lancaster 1996), increased encounter rates can also lead to higher post-encounter prey emigration, thus resulting in apparently higher predator impact (Englund & Olsson 1996, Thomson *et al.* 2002). We noted neither aggregation into low flow zones in response to flow releases, nor a difference in prey emigration between treatments with vs. without predators.

Irrespective of flow treatment, distributions of blackflies and *Rhyacophila* larvae in different substrates always differed from those expected by chance. Concrete was always avoided whereas moss was always selected for by both species. A-priori contrasts showed no differences between stone and moss patches for blackflies. *Rhyacophila* larvae significantly preferred moss over stone. In mixed predator-prey trials, the presence of *Rhyacophila* larvae caused a shift in blackflies from stone habitats towards moss. This apparent distributional shift of prey towards the preferred habitat of their predators was related to the grain (sensu Wiens 1989) of the study. At the scale of a single cell, *Rhyacophila* and blackflies shared the same habitat but a reduction in grain size revealed that predator and prey occupied different microhabitats within the same cell. Larval blackflies were mainly found on tops of the bristles whereas *Rhyacophila* occurred in the sheltered microhabitats within the moss tufts. Blackflies on top of bristles faced

considerably higher currents than *Rhyacophila* larvae at the base of the tufts. Similar to our results, Fuller & DeStaffan (1988) noted blackflies to shift distributions away from exposed surfaces towards safer habitats which still permitted adequate feeding in the presence of an invertebrate predator. While a trade-off may be involved with the observed habitat shifts of blackflies in the presence of *Rhyacophila*, its duration and relative importance to populations in the field remain unknown.

4 Conclusions and challenges for future research

Aquatic studies examining the role of predation have mainly focused on the identification of mechanisms influencing the outcome of predator-prey interactions, often with the tacit intention of developing predictive rules. Such studies, however, have almost solely relied on small-scale designs under the implicit assumption that results can be generalized to larger scales. Nevertheless, since aquatic communities are highly variable any observations on ecological patterns and processes are ultimately scale-dependent.

As different sets of factors operate at different ranges of scale, recent attention has been attributed to identifying scale ranges in which processes remain constant (spatial domains, *sensu* Wiens 1989). Theoretically, individual domains are likely to be separated by sharp transitions due to the shift in predominant factors influencing the patterns (Wiens 1989). In an attempt to identify and evaluate the relative importance of factors influencing scale domains for lotic predation, Englund (1997) constructed a model based on published stream predation experiments. The model identified three scale domains of lotic predation (small, intermediate and large) and predicted that only at large scales will consumptive effects of predation control prey densities. At small scales prey densities are controlled by prey movements and, more specifically, prey emigration at these scales is likely to cause artefactual predatory impacts (Englund 1997). Relying on the model predictions Englund & Cooper (2003) concluded that results of small-scale predation designs cannot accurately predict responses at the ecosystem scale. Contrary to Englund's (1997) assumptions, we found no evidence of pronounced emigration from predator treatments in our experiment (II). In addition, our studies (I, II) suggest that at least the effect of salmonids on invertebrate predators is caused by the same factors (i.e., preference for large prey) in all domains identified by Englund's (1997) model. We cannot be sure, however, whether predatory effects of salmonids are consumptive in other published studies on salmonid predation. Certainly, if results of individual studies contributing to the meta-analysis were in many cases influenced by behavioural rather than consumptional effects, we would likely make "the right decision for the wrong reasons" when concluding that size-selective predation by salmonids is a universal factor influencing benthic communities at all spatial scales.

A closer re-examination of the studies in our meta-analysis (II) tested whether small scale studies, indeed, cause stronger predation effects; this would likely manifest in a

negative correlation of predation effect with experimental unit size. However, we observed no correlation between predation effect (PI) and experimental unit length for any of the target groups included in the meta-analysis (II). A rerun of meta-analysis on two new data pools that encompassed either studies belonging to the small spatial domain or large spatial domain as identified by Englund's (1997) model equally provided no evidence for larger predation effects in shorter experimental units as opposed to long ones.

Only a replicated multi-scale experiment would be able to directly test Englund's (1997) hypothesis. However, our findings for the invertebrate predators suggest that Englund's (1997) model predictions may apply only to certain groups and for certain domains of scale. If, indeed, domains of scale for predation effects are not equal for different groups of the benthic community, the search for the "right" experimental scale of predation studies examining community level responses is an insurmountable task. Thrush and coauthors (1997) reached a similar conclusion regarding the spatial scale of marine experiments and called for a shift of focus from the search of the single right scale of experiments towards the scalability of results. While the effects of trout predation on the invertebrate predators appear to scale up over at least the three spatial scales identified by Englund's (1997) model, further studies are needed to assess the spatial domains over which predation acts for other groups of lotic macroinvertebrates. Multi-scale studies in particular should prove useful in this regard, allowing tests for the predominance of antipredator behaviour over consumptive effects of predation on many spatial scales simultaneously.

While multi- or large-scale experiments would undoubtedly solve many of the problems related to the spatial dimension of field experiments, the equally important influence of the temporal extent is still largely neglected. Current knowledge on lotic predation is based largely on single snapshots of limited temporal extent. Our findings indicate, however that the timing of a study may affect the results observed (I, II, IV). The short growth season and drastic seasonality of the boreal region renders most aquatic insect taxa univoltine. This forces size selective predators, such as trout, to be flexible in the inclusion of prey into their diet over the annual cycle (I). An illustration of the significance of timing on observations of prey size and predation experiments is given by the discrepancy of the results between our experiment and the across-stream survey for mayflies (II). The dietary survey of juvenile brown trout (I) indicated that baetid mayflies were often avoided but can be temporarily a preferred prey item. This finding was paralleled by lower mayfly densities in trout streams in both the across-scale survey and the meta-analysis (II). In sharp contrast, as a consequence of small individual prey size, our field experiment suggested that trout had no effect on baetid mayflies (II). This example clearly indicates the caveats in generalizing predation impacts beyond the temporal extent of a study.

Because of its effect on prey size, the timing of studies not only influences prey preference by different predators but also the prey's behaviour in boreal systems. While small-sized baetid mayflies in late summer are unresponsive to fish presence (Meissner, pers. obs.), antipredator responses commonly change with increasing body size (Culp & Scrimgeour 1993, Tikkanen *et al.* 1994, Huhta *et al.* 1995). Avoidance of encounters with visually hunting fish often leads to diel avoidance of risky feeding patches (e.g., Muotka *et al.* 1999) which is not necessarily reflected as numerical responses in small-scale

experiments. Invertebrate predators may also induce similar habitat shifts in prey. Examples of such shifts include mayflies in the presence of predatory stoneflies (e.g., Soluk & Collins 1988) and simuliids in the presence of rhyacophilid predators (V). Such antipredator behaviours can result in lowered fitness and life-time reproductive success on a stream-wide scale (Peckarsky *et al.* 1993, Dahl & Peckarsky 2002). In a comparative study of mayflies in fishless vs. trout-containing streams, Peckarsky *et al.* (1993) noted that female egg- weight and thus lifetime reproductive success was lower in fish streams compared to fishless streams. Therefore, future large-scale studies of lotic predation should incorporate experimental assessment of macroinvertebrate fitness.

Different feeding modes of fish predators may pose conflicting demands for macroinvertebrate prey. Recent studies have suggested that combinations of multiple predators can cause “emergent effects”, i.e., effects that are not obvious when studying single predators alone (Sih *et al.* 1998). Most fish predation experiments have examined the effects of a single fish predator and used only presence/absence designs. Certainly such simple designs can be valid (e.g., II) and allow to test the specific hypotheses of the effects of predator presence on prey densities. However, it is likely that many fish predation experiments have overlooked the complexity and intensity of the fish predation regimes that prey face in most natural systems. To date, only few experimental studies have manipulated the range of fish species encountered in the target system (e.g., McIntosh & Townsend 1995, Dahl & Greenberg 1996). Without knowledge about the spatiotemporal prevalence of fish predation from quantitative field data (e.g., II) the results of single fish predator experiments may state little about the actual consequences, strength, magnitude and relevance of emergent, direct or indirect predator effects in a multi-predator system and thus may be of mere academic value (see Bernardo 1998).

Foodweb theory and numerous lentic predation studies have suggested that strong predation on one trophic level may cause indirect regulatory effects on lower trophic levels, amounting to trophic cascades (e.g., Carpenter *et al.* 1985). Stream predation studies have mainly reported predation effects on the adjacent trophic levels. In some streams, however, strong direct effects of trout predation (e.g., Power 1990, Bechara *et al.* 1992) and the presence of non-native trout (McIntosh & Townsend 1996) are known to cause trophic cascades. In a series of predation experiments in Californian intermittent streams, Power (1990, 1995) noted annually recurring physical factors to be the prerequisite for the manifestation of trophic cascades. Fish predation following scouring floods led to a trophic cascade (Power 1990) while the absence of floods during a prolonged period of drought dramatically changed the outcome of similar experiments (Power 1995). More generally, trophic cascades appear to be special cases of predation in systems with low overall diversity and relatively direct food-chains (Petchey *et al.* 2004). A number of factors are likely to prevent the formation of trophic cascades in boreal forest streams. First, in comparison to systems where cascades are observed, the benthic community of boreal forest streams is generally quite diverse (Meissner, pers. obs.). High species diversity increases the probability of substitutability and compensation among species (Strong 1992), and as theoretical models show, may obscure direct effects of higher trophic levels (Borrvall *et al.* 2000, Montoya *et al.* 2003). A recent meta-analysis on the top-down effects of grazers in freshwater ecosystems has similarly shown that grazer effects on periphytic biomass decrease with increases in algal diversity (Hillebrand & Cardinale 2004). A meta-analysis examining effects of diversity in lotic

macroinvertebrate communities is still lacking, but could provide interesting insights on the possible role of biodiversity as a mediating factor of predation effects.

Second, lotic systems expressing trophic cascading are not only often low in biodiversity but also rely heavily on autochthonous energy. In deciduous forest streams a large degree of the energy budget is made up of allochthonous terrestrial inputs of leaf litter (e.g., Wallace *et al.* 1999) and invertebrates (Nakano *et al.* 1999). Allochthonous inputs in boreal forest streams result in donor-control, which is prevalent from autumnal leaf fall until icebreak when the role of autotrophic production may temporarily increase. It is likely that this shift in the relative importance of energy sources on an annual cycle further contributes to biodiversity, omnivory, and consequently to buffering of trophic cascades. Indeed, Hall and coauthors (2000) noted higher per-biomass consumption coefficients in streams experimentally deprived of allochthonous inputs, suggesting stronger interactions among taxa than in the reference streams. Similarly, in stream sections where terrestrial arthropod inputs had been excluded Nakano and coauthors (1999) noted a shift in fish impacts towards lowered herbivorous biomass and concurrent increases in periphyton. To test whether the reliance on autochthonous inputs and concurrent low biodiversity facilitate strong effects or even trophic cascades one should conduct fish predation experiments similar to study II in small streams north of the tree-line. In these low-diversity lotic systems the influence of autotrophic production should be pronounced given the minute influence of the riparian zone on energy budgets.

In larger rivers, terrestrial inputs from leaf fall decline in relative importance. In these rivers vernal blackfly populations condition huge amounts of otherwise unavailable, minutely sized material to be used by other members of the community (Malmqvist *et al.* 2001), making blackflies an integral part of the food web (ecosystem engineers). The extensive input of organic carbon through blackfly faecal pellets dramatically affects downstream communities (Wotton *et al.* 1998), and dense blackfly populations can also be of crucial importance to non-aquatic life (Yoerg 1994, Rodway 1998). More generally, allochthonous inputs of adult aquatic insects to terrestrial systems are known to shift the avian predator pressure in riparian forests (Murakami & Nakano 2002) and provide seasonally important prey for terrestrial arachnid predators (Kato *et al.* 2003, Sanzone *et al.* 2003).

Early observations note that harnessing of boreal rivers for hydroelectric purposes usually reduces blackfly populations (Müller 1968). The reverse, however, has been observed in reaches downstream of the man-made impoundments in River Perhonjoki (Nyman 1995). The dramatic increases in blackfly densities increase the retentive potential in River Perhonjoki which not only affects lotic ecosystem dynamics but also can cause profound effects on the adjacent terrestrial systems. Long-term radioactive tracer studies assessing energy fluxes to terrestrial invertebrates and birds in both natural and disturbed parts of River Perhonjoki could provide important information on the spatial extent of the consequences of blackfly outbreaks. In addition, the importance of blackfly-conditioned organic material for the macroinvertebrate community should be assessed in detailed instream studies. Information on the role of these fluxes could help predict short- and long-term consequences of planned hydroelectric power plants and guide restoration measures in similarly affected waterways.

To minimize the introduction of confounding factors, studies of predation effects on ecosystem structure are mostly conducted in pristine environments. Anthropogenic

interferences with predation and ecosystem function, however, pose an equally challenging field of research. Given the often limited understanding of ecological consequences of anthropological disturbance and scarce funding, the study of human interventions in lotic ecosystems has often been restricted to the post-impact monitoring of species densities, indices of biodiversity or surrogates of such. Nonetheless, it is equally important to gain information on the processes behind the observed patterns of anthropogenic disturbances. Providing answers on ecosystem function, or changes therein, requires a good basic knowledge of the study system, often specialized approaches and an integrative use of differently scaled studies (Werner 1998). As indirect effects make it difficult to pinpoint causal pathways, experimental ecology is, and will be, vital to the advance of general and applied aquatic ecology.

Realistic assessments of predation effects in the boreal region will have to include the temporal dimension due to its potentially profound influence on results. Clearly, manipulative multi-scale studies using the range of predators typically encountered in lotic systems will be the basis of future knowledge on the ecological consequences of predation in streams. More generally, future experimental studies of lotic processes should use seasonally and annually repeated designs, imply realistic treatments levels and be strictly linked to surveys at larger temporal and spatial scales. This approach will shift focus from merely demonstrating links, towards assessing and predicting the relevance and influence of ecological processes for the formation of patterns in streams.

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