BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

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JYVÄSKYLÄ 1994

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston vanhassa juhlasalissa (S212)
huhtikuun 29. päivänä 1994 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Natural Sciences of the University of Jyväskylä,
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UNIVERSITY OF JYVÄSKYLÄ

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URN:ISBN:978-951-39-8737-4
ISBN 978-951-39-8737-4 (PDF)
ISSN 0356-1062

ISBN 951-34-0239-8
ISSN 0356-1062

Jyväskylän yliopistopaino and
Sisäsuomi Oy, Jyväskylä 1994

ABSTRACT

Muotka, Timo
Patterns in northern stream guilds and communities
Jyväskylä: University of Jyväskylä, 1994, 24 p.
(Biological Research Reports from the University of Jyväskylä,
ISSN 0356-1062; 37)
ISBN 951-34-0239-8
Yhteenveto: Säännönmukaisuudet pohjoisten virtavesien ekologisten yhteisöjen ja kiltojen rakenteessa
Diss.

Patterns in northern stream communities are not yet well understood. Here, I document spatial patterns in predator-prey relationships and patterns in community structure of semi-sessile stream insects and stream bryophytes in northeastern Finland. Spatial distribution of predatory stoneflies was generally random, whereas caddisfly predators (*Rhyacophila* spp.) were aggregated to areas of highest density of larval black flies. After the emergence of black flies, the distribution of *R. obliterata* became random. The analysis of mapped point patterns proved more robust in detecting scales of predator-prey interaction than more conventional sampling techniques. Ontogenetic niche shifts in the microhabitat use by filter-feeding caddis larvae were detected in all five species studied. In particular, 5th instar larvae were clearly separated from the younger larval stages, irrespective of species. Ontogenetic niche shifts are probably nearly universal among benthic insects, and should be considered in any study of lotic insect community structure. It is further suggested that coexistence in the guild of filter-feeding caddis larvae is facilitated by independent aggregation of species to patchily distributed resources. Occurrence of stream bryophytes was strongly associated with the disturbance history (substratum movement, water level fluctuation) of a site. In the absence of disturbance, a few tall perennials (e.g. *Fontinalis* spp.), were able to monopolize space. Frequently disturbed habitats in large rivers were characterized by low-statured shuttle species, which either possess a high capacity for propagule dispersal or are able to withstand frequent scouring of substratum. In streams, small-scale disturbances leave patches open for colonization by facultatively aquatic species which tolerate both submersed and stranded conditions.

Keywords: Streams; predator-prey interaction; spatial patterns; filter-feeding caddisflies; bryophytes; disturbance; scale.

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List of original publications

This thesis is based on the following articles, which will be referred to by their Roman numerals:

I Muotka, T. 1993. Microhabitat use by predaceous stream insects in relation to seasonal changes in prey availability. - Ann. Zool. Fennici 30: 287-297.

II Muotka, T. & Penttinen, A. 1994. Detecting small-scale spatial patterns in lotic predator-prey relationships: statistical methods and a case study. - Can. J. Fish. Aquat. Sci. (accepted).

III Muotka, T. 1990. Coexistence in a guild of filter-feeding caddis larvae: do different instars act as different species? - Oecologia 85: 281-292.

IV Muotka, T. & Virtanen, R. 1994. Stream as a habitat templet for bryophytes: species distributions along gradients in disturbance and substratum heterogeneity. - Freshwat. Biol. (accepted).

CONTENTS

1 INTRODUCTION

Describing general patterns and finding mechanistic explanations for them are the twin goals of community ecology. It is a common practice to commence with studies aimed at "pattern detection" (see e.g. Wiens 1984, Tilman 1989). According to this "patterns first"-principle, one must first show that the community studied exhibits some discernible trends before any relevant questions about processes structuring the community can be posed. The more general a pattern is, the more interesting it becomes, because generality often implies a common underlying mechanism. This idea stems from the seminal work of MacArthur (1972): "To do science is to search for repeated patterns, not simply to accumulate facts". Especially in plant ecology the search for general patterns has been consistent during the last 15-20 years, and, occasional controversies notwithstanding, there seems to be a growing consensus that only a few environmental factors are influential in regulating the plant community structure (e.g. Grime 1979, Tilman 1982, Keddy 1989).

At the time ecology was taking its first steps toward theoretical maturation, stream ecologists were not represented in the frontline of the emerging science. Until early eighties, lotic ecology remained largely non-theoretical, descriptive enterprise, marginal to the rapidly progressing mainstream of ecology (see also Hildrew & Townsend 1987). Ever since that, lotic ecologists have had a distinct role in the application and testing of general ecological theories; books by Barnes & Minshall (1983) and Resh & Rosenberg (1984) stand out as cornerstones in the development of a more theoretically-oriented stream ecology. In recent years, stream ecologists have made increasingly important contributions to many central issues of ecology, e.g. predator-prey interactions and disturbance theory. However, stream ecology, as indeed most fields of ecology, has suffered from a serious geographical bias with a disproportionate amount of studies being conducted in the Temperate Zone. Studies of stream communities in northern areas, e.g. northern parts of

Scandinavia are largely lacking (but see Ulfstrand 1968, Kuusela 1979, Englund 1992). This thesis, which forms a part of an ongoing project on patterns and processes in northern stream communities, was started with the aim of filling this gap.

Disturbance is undoubtedly one of the leading themes in running water ecology (e.g. Resh et al. 1988, Lake 1990, Poff 1992). The patch dynamics models familiar from marine intertidal systems have been suggested to be applicable in stream communities also (Townsend 1989). However, these models are based on competitive hierarchies in communities of sessile organisms, where the resource competed for is space (Yodzis 1986). Stream macroinvertebrates, in contrast, are highly mobile organisms dependent upon a complex resource base. Competition for space among them, although demonstrably occurring in some cases (Hemphill & Cooper 1983, McAuliffe 1983, Hart 1985, Hemphill 1988), is generally regarded unlikely (Downes 1990). If patch dynamics models are to apply in any stream guilds, groups of sedentary organisms like filter-feeding caddis larvae (III) and stream bryophytes (IV) are probably the best candidates. Although the methods applied here can not demonstrate the existence of competitive hierarchies, the patterns observed in local guilds should be compatible with the model's expectations. To this end, evidence presented here should be considered as a necessary but not sufficient demonstration for the applicability of patch dynamic models in stream systems.

Another area of active research in lotic ecology has been the effects of predation on stream macroinvertebrate populations and communities. One explanation for the generally low impact of predators on prey communities has been that, because of a long shared history with fishes and other predators, lotic prey possess exceptionally well-developed antipredatory responses (Allan 1982). For example, behavioural observations of predator-prey interactions in laboratory conditions as well as field surveys have suggested that invertebrate predators, especially stoneflies, are not able to track the patchy distribution of their prey (Walde & Davies 1984, Peckarsky & Penton 1985, Peckarsky 1991a). In this thesis, I document the distribution patterns of lotic insect predators in relation to that of their most important prey at different times of the season (I and II). The objective was to see whether predators with different foraging strategies differ in their ability to aggregate to high-density prey patches, and whether prey with varied relative mobility are differentially susceptible to predator aggregation. Field sampling was performed by either classical quadrat sampling (I) or by a more sophisticated "plotless" sampling method (II). With this "full-pattern sampling" (cf. Hurlbert 1990) it was also possible to examine the scale-dependence of the predator-prey interactions.

2 STUDY AREA AND METHODS

The study area is located near the Arctic Circle in northeastern Finland. The study sites in papers I, II and III are in or near Oulanka National Park, whereas streams studied in paper IV are more widely distributed in the Koillismaa biological province. The area belongs to the northern boreal zone. The bedrock is characterized by frequent occurrences of calcareous rocks, which is reflected in exceptionally rich flora consisting of both northern and southern elements (Söyrinki & Saari 1980). Running waters of the area are mainly in close-to-pristine condition, River Kuusinkijoki (IV) being the only watercourse with some indication of slightly degraded water quality (Koutaniemi & Kuusela 1993). Because of the calcareous bedrock, small water bodies are often slightly alkaline with high conductivity and low colour of water (Myllymaa 1979). Discharge in rivers and streams of the area is characterized by a peak flow in early May soon after the snowmelt, with another, smaller peak in September-October (Koutaniemi 1979). More detailed descriptions of the study sites are given in respective papers.

2.1 Predator aggregation: quadrat sampling vs. point pattern analysis

Natural, cobble-sized stones were used as sampling units in study I, number of samples being 30-60. Samples were collected on 2-3 occasions from two streams. The dispersion patterns of predators (3 species) and their prey (4 prey groups) were analyzed with Lloyd's measure of "patchiness" (Lloyd 1967). Watanabe's (1988) modification of Lloyd's index for non-constant quadrat sizes was used.

The relative importance of biotic and abiotic variables on the microhabitat use by predators was investigated with Principal Component Analysis as described by Grossman & Freeman (1987).

Spatial patterns of natural populations are often too complicated to be detected by conventional sampling techniques. For example, a pattern may be clustered at one scale, yet regular at another. For these cases, second-order analyses of mapped point patterns are far more efficient than simple indices of dispersion. In study II, locations of all predators within a 1 m^2 "sampling window" were mapped. Spatial variation within the sampling window in the density of black fly larvae and pupae, the major prey available, and flow rate were quantified by intensive systematic sampling. Mapping was performed in an outlet of a small lake on two occasions, in mid-June (the time of the peak abundance of black flies) and in the beginning of July (after the emergence of black flies). The data were used (1) to estimate densities of the predators, (2) to analyse the spatial pattern of the predators (Ripley's L-function and the g-function approaches; Ripley 1981, Penttinen et al. 1992), and its relation to spatial variation in flow rate and prey density (an elementary GIS (Geographical Information Systems)-type of analysis; e.g. Johnson 1990), and (3) to assess the spatial interactions between the predatory species by means of a second-order analysis of bivariate point patterns (Lotwick & Silverman 1983).

2.2 Niche relationships and dominance patterns in lotic guilds and communities

The guild structure of semi-sessile, filter-feeding caddisfly larvae was studied in three lake-outlets (III). Samples (10 stones per site) were collected on five occasions in approximately 3-week intervals. Seven environmental variables were measured for each sample to quantify the microhabitats used by the larvae. The niche widths of and overlaps between species and species instars were examined by an application of the Principal Component Analysis as described by Rotenberry & Wiens (1980). Detrended Correspondence Analysis of the species/instars abundance data was also used to examine the species relationships in a multivariate niche space. Correlations between the derived axes and the original variables were used to find ecological interpretations for the DCA-axes.

Species distributions and dominance patterns in stream bryophyte communities along a disturbance gradient were examined in paper IV. First, a multivariate description of vegetation-environment relationships were constructed with the Canonical Correspondence Analysis. Material for this analysis was obtained from 11 river sites and 14 lake outlets and small streams. Eight to ten random sample plots (0.25 m^2) were collected from each site, resulting in 234 plots altogether. Nine environmental variables measured at the time of sampling or calculated from long-term records were used in the CCA. The existence of a disturbance gradient was verified by a quantitative analysis of disturbance regimes (in terms of substratum movement) based on long-term discharge records. These were available for only five sites, and more indirect measures of disturbance had to be used in other cases (the "instability index" of Cobb & Flannagan 1990). In addition, the elevational zonation patterns of bryophyte species in relation to water level fluctuation, another potential disturbance agent for stream bryophytes, was studied in 2 lake outlets and 2 small streams.

Standing crop of the bryophyte community was measured in 20 sites to test the 'hump-backed' model of species richness vs. standing crop relationship (Grime 1979) in stream bryophyte communities. Bryophyte stands were quantified in 10 0.1 m^2 quadrats per site. A finer-scale (within vegetation-type) analysis was conducted at two study sites, where 20 0.1 m^2 plots were collected, and species were separated and weighed individually for each quadrat. A bitonic relationship between species richness and biomass is predicted by theory, and to examine whether this expected pattern occurred among our data, second order polynomial regressions were fitted with species richness as the dependent variable.

3 RESULTS AND DISCUSSION

3.1 Aggregation of lotic invertebrate predators to their prey: considerations of scale

In the stream Putaanoja the distribution pattern of the stonefly predator *Diura nanseni* (Plecoptera) was random on all sampling occasions, and its microhabitat use was not affected by any of the prey variables. High moss cover and low flow rate were the physical habitat features most consistently associated with microhabitats used by *D. nanseni* (I). Predaceous stoneflies have often been observed to exhibit random distribution patterns in the field (Walde & Davies 1984, Peckarsky 1988, 1991a). Laboratory and field experiments by Peckarsky and her co-workers (Peckarsky & Penton 1985, Peckarsky 1991b) have shown that these tactile foragers are not able to aggregate to high-density prey patches because (1) there is mutual interference between the predators, and (2) prey patches are ephemeral, dispersing immediately once a predator enters a "patch". Lack of aggregation to less mobile prey (simuliid and chironomid larvae) could further result from avoidance of high velocity microhabitats by the predator or active defence by the prey (see Allan & Flecker 1988).

The caddis larva *Rhyacophila nubila* (Trichoptera) showed highest aggregation in October when chironomids and some case-bearing caddis larvae were contagiously distributed (I). Microhabitat use by this species was mainly affected by the availability of semi-sessile prey, which also formed the bulk of the diet of *R. nubila*. However, these prey mainly occurred within tufts of mosses, and the independent effects of biotic variables can not be separated without manipulative experiments.

At the lake outlet site (Rytipuro) black flies were by far the most abundant prey in mid-June. By the beginning of July, most black flies had already emerged, prey densities had declined abruptly, and the prey assemblage was dominated by more mobile prey types (e.g. *Baetis* mayflies). Black flies were highly aggregated on both sampling occasions, whereas the major predatory species, *Rhyacophila obliterata*, was aggregated only in mid-June. Microhabitat use by this species was mainly affected by the availability of black flies, and after the emergence of simuliids its distribution became random. None of the microhabitat variables had any observable effect on the microhabitat use by *R. obliterata* then. Black fly larvae are relatively sessile animals, which use their abdominal hooklets to attach to suitable filtering sites. They often form large aggregates in high velocity microhabitats to maximize the encounter rate with food (seston) particles (Chance & Craig 1986). Because of their life-style, black fly larvae are rather vulnerable, "cost-effective" prey for invertebrate predators (Feminella & Stewart 1986, Juntunen & Muotka, unpubl.). High flow rate may impair the foraging success of invertebrate predators (Hansen et al. 1991), and some predators have been observed to avoid high velocity microhabitats (Allan et al. 1987). Rhyacophilid larvae, in contrast, seem to possess the morphological apparatus (e.g. strong hind claws) for maneuvering even in the highest velocities. This sluggishly moving caddis larva is rather inefficient when foraging on mobile prey, and Otto (1993) observed a shift to 'sit-and-wait' strategy in *R. nubila* when only mobile prey were available. *R. obliterata* is apparently capable of aggregating to patches of larval black flies, and its gut contents indicated heavy feeding on black flies in mid-June. Strong selection for black flies was even more apparent in July, when simuliids, in spite of their much reduced availability in benthos, were still the dominant prey item for *R. obliterata* (I).

The analysis of the point patterns of two predatory species, *R. obliterata* and *Isoperla grammatica* (Plecoptera), showed distinct interspecific differences (II). The stonefly was randomly distributed throughout the scales studied, whereas the caddis larva exhibited a tendency towards clustering at two scales. Especially, aggregation was rather strong at the scale of 4-6 cm, which also was the scale of the most intense spatial association between the rhyacophilid and black fly larvae. Habitats of the predator and prey overlapped intensively in the velocity range of 40-60 cm/s, with no indication of avoidance of high velocity microhabitats by the predator. After the emergence of black flies, the point pattern of *R. obliterata* became random. Apparently, the outlet 'landscape' was much more more homogeneous in terms of prey patchiness once the simuliids had disappeared.

This study (II) stresses the importance of considering ecological patterns and processes at a wide range of spatial scales. The scale of aggregation of an insect predator would have gone undetected with the conventional sampling techniques commonly employed by benthic ecologists. The scale forced by traditional sampling devices may have little to do with the scale of biotic interactions or species-environment relationships. If this is so, the results are bound to be artifacts, and plotless sampling designs should be preferred whenever feasible.

3.2 Ontogenetic niche shifts and the guild structure of filter-feeding caddis larvae

Seven species of filtering caddis larvae occurred at the three study sites, three polycentropodids (Trichoptera: Polycentropodidae) and four hydropsychids (Trichoptera: Hydropsychidae) (III). *Hydropsyche saxonica* was the only species found in all three streams, but it was abundant in only one site, the outlet of the lake Rytilampi where it was the sole representative of the guild. *Polycentropus flavomaculatus* and *Hydropsyche pellucidula* were the core species of the guild at the other two lake outlets. Whenever a species was present in reasonably large numbers, instars 3, 4 and 5 co-occurred at any one site. Thus, it was expected that different instars of a species could function as "ecological species", and that the age-structure component of niche would make up a major proportion of the niche of the species in whole (see Polis 1984). This was shown to be so: in all four species used in the analysis, there were significant differences between instars in their microhabitat use. In DCA, the first axis mainly partitioned between instars, irrespective of species, so that the 3rd and 4th instars were widely separated from the 5th instars. Interspecific separation mostly took place along the second axis, where *H. pellucidula, P. flavomaculatus* and *Hydropsyche angustipennis* had non-overlapping distributions.

Differences between age-classes in resource use have traditionally been interpreted as a means of avoiding intraspecific competition. However, if based on field observations only, such a conclusion is problematic for at least two reasons. First, it implicitly assumes resource limitation, yet this is not usually documented (and, indeed, would be very difficult to document in the field). Another hidden assumption is that the divergence between age-classes has the same selective basis as the classical interspecific niche segregation. Besides being obviously untestable, this hypothesis is misleading, because ontogenetic niche shifts not only separate age-classes from each other, but also change the biotic as well as abiotic environment of a species during its larval development. Thus, because a species may belong to widely varying assemblages at different developmental stages, there may not have been opportunities for coevolutionary adjustments to a particular set of competitors (see also Maurer 1985). In species with size-structured populations species interactions should obviously be described as size-classes interacting with other size-classes of the same and of other species (Polis 1984). Because many benthic insects are characterized by long flight periods and asynchronous development, the kind of ontogenetic niche shifts described here are probably nearly universal and should always be taken into account when interspecific interactions among benthic insects are studied.

Petersen (1987) has suggested that the guild of filter-feeding caddis larvae is competitively structured with either *H. saxonica* or *H. pellucidula* as the keystone species. These two species would exclude other guild members from the best net-spinning sites, and coexistence would only be possible via temporal partitioning of the feeding sites. However, coexistence by life cycle differences is made improbable by the simultaneous occurrence of many instars. Furthermore, the "forbidden" combination of congeneric populations of *H. saxonica* and *H. pellucidula* (see Gatley 1988) was found in two of my study sites.

Townsend (1989) suggested that the classic patch dynamics models are applicable to the guilds of sessile filter-feeders in streams. It seems, however, that additional mechanisms must be provoked in order to understand the coexistence of up to 6-8 species which utilize the same resource base. Especially, the aggregation model of Atkinson & Shorrocks (1981) seems a promising alternative. Resources (i.e. suitable net-spinning sites) are certainly patchily distributed, and the species are probably independently aggregated over these resource patches. This leaves some patches free for colonization by inferior competitors ("probability refuges"; Shorrocks & Rosewell 1987). The aggregation model, possibly in concert with resource partitioning via differences in species phenologies, seems a likely mechanism promoting coexistence in the guild of filter-feeding caddis larvae. However, to corroborate this hypothesis, more information is needed about the population dynamics of the species involved, as are also experimental studies where the resource patchiness is manipulated.

3.3 Diversity and dominance patterns in stream bryophyte communities

The distribution patterns of bryophytes were studied in relation to disturbance regime and other habitat characteristics (IV). The first axis of the CCA of large rivers (11 sites) was mainly a current velocity-substratum roughness gradient, but no bryophyte species showed a strong response to it. The second axis was easier to interpret ecologically: it separated the most frequently disturbed sites in the River Oulankajoki from other, more stable habitats. In CCA, habitat stability was equated with a simple index, the "instability" index (Cobb & Flannagan 1990), which can only be used as a relative indicator of the substratum stability. A more thorough documentation of the disturbance regime was undertaken for a subset of the study sites where historical records of flow variation were available. This quantitative analysis was based on the examination of patch-scale disturbance, because, as emphasized by Poff (1992), flow variation as such may not be a meaningful way to describe disturbance as it is experienced by benthic organisms. Instead, one should use measures that are organism-related, yet independent of organism responses (Poff 1992; see also van der Steen & Scholten 1985). In this study, the flow needed to transport the median particle size of the stream bed was used as a measure of disturbance (see e.g. Rader & Ward 1989, Scarsbrook & Townsend 1993). The study sites in the three main channels (Rivers Oulankajoki, Kitkajoki and Kuusinkijoki) could be unambiguosly located on a disturbance gradient relative to each other. Rivers Kuusinkijoki and Kitkajoki, which are characterized by large, stable substrate particles and little variation in flow, showed much lower disturbance frequency and longer recurrence intervals between disturbance events than the frequently disturbed riffles in the River Oulankajoki. There were also drastic differences in the disturbance regime among riffles in the River Oulankajoki, this being mainly caused by differences in the stream gradient and the size of substratum particles. A parallel change was observed in the species composition of the bryophyte community, with low-statured, fast colonizers occurring at the disturbed, and large, perennial mosses at the stable end of the gradient.

In the ordination of small streams and lake outlets (14 sites) the first CCA-axis separated shallow streams with high substratum profile from the deeper, less rough-bedded streams. The former group was characterized by frequent occurrence of facultatively aquatic or semi-aquatic species (e.g. *Blindia acuta, Dichodontium pellucidum, Fissidens pusillus*), i.e. species tolerant of alternately submersed and emergent conditions (Vitt & Glime 1984). In contrast, the latter group of streams do not provide conditions for elevational segregation, and were thus dominated by obligatory aquatics. Species diversity in these streams was consistently lower.

Species zonation patterns along large boulders in two lake outlets and two headwater streams reflected the disturbance caused by water level fluctuations. Species richness was low in permanently submersed areas, which were exclusively dominated by obligatorily aquatic species, especially *Fontinalis antipyretica* and *Jungermannia exsertifolia*. In lake outlets, there was a sharp increase in species richness at or just above the water level where facultatively aquatic (e.g. *Palustriella commutata*) and semi-aquatic (e.g. *Schistidium rivulare*) species dominated the bryophyte community. In small headwater streams, the increase in species richness along elevational profiles was more gradual. Species living in the intermediate zone must either avoid flooding by completing their life cycle before the next flood, or else tolerate prolonged periods of submergence. Neither obligatorily aquatic nor semi-aquatic species are able to persist in these ever-changing conditions. In contrast, most facultative aquatics are gametophytically adapted to aquatic life, yet produce sporophytes mainly during the terrestrial phase (Vitt & Glime 1984). Thus, the availability of substratum particles that present an elevational gradient from continually submersed to truly terrestrial conditions effectively adds to the species richness of a local bryophyte community.

In the among-sites analysis, there was a significant positive regression between the standing crop and species richness of bryophyte communities in low standing crop habitats. At high standing crops, species richness decreased with biomass, but the relationship was not significant. The bitonic relationship predicted by theory (e.g. Grime 1979) was too weak to be detected by the polynomial regression. The standing crop - species richness relationship was more in concert with the predictions of the 'hump-backed' model when the analysis was conducted on a finer, i.e. within-habitat scale. The bitonic relationship was apparent and statistically significant at both sites where the data was collected. The maximum species density was achieved at around 30 g/m^2. Thereafter the relationship was negative, and the overall relationship was best described by regression equations including the second-order term.

The mechanisms causing the 'hump-backed' relationship between species richness and standing crop are presumed to be associated with gradients in habitat productivity and/or disturbance (e.g. Connell 1978, Grime 1979, Tilman 1982, Shipley et al. 1991). Only a few species are able to persist in continually disturbed habitats, and the biomass of the bryophyte community remains low. These species must either possess a capacity for efficient propagule dispersal (e.g. *B. acuta*) or be able to withstand frequent disturbances (e.g. *F. pusillus*). In the 'corridor' environments (Grime 1979), which sustain the highest diversity, disturbances (e.g. substratum movement, water level fluctuation) are usually fine-grained, leaving transient gaps among vegetation. High diversity is thus maintained by integration of patch-scale competition, disturbance and colonization, much like in the classic patch-dynamics models (see also Kimmerer & Allen 1982, Steinman & Boston 1993). Finally, stable, permanent habitats were dominated by tall, perennial mosses. These species are characterized by extensive clonal spread, and are clearly capable of monopolizing space.

The spatial extent of disturbance and the frequency of it seem to be the major forces determining the organization of stream bryophyte communities. The local disturbance regime acts as a filter, which eliminates traits and strategy types not able to persist in a given environment (see also Poff & Ward 1990, Keddy 1992). Highly permanent sites are occupied by obligatorily aquatic perennials (the '*Fontinalis*'-type), which rarely allocate recources to sexual reproduction. Facultative aquatics of the '*Leptodictyum-Bryum*'-type are characteristic representatives of frequently disturbed, species-rich habitats where the ability to fill gaps after small-scale disturbances is a particularly important trait. Reproduction is mainly asexual, but high investment to production of sporophytes may occur periodically, especially in stranded situations. In streams where disturbances recur frequently and affect rather large areas, only species possessing high colonization capacity and/or appropriate growth-form are able to persist. These short-lived '*Blindia*'-type species are low in stature, and produce spores frequently. Some highly flexible species (e.g. *F. antipyretica*) may occur at almost any point of the templet, but their growth-form varies according to the disturbance regime of a site. Finally, it must be stressed that the habitat templet scheme proposed here must be considered rather preliminary, and many more quantitative studies on stream bryophyte life histories are needed before any substantial progress in predicting lotic bryophyte community properties is possible.

4 CONCLUSIONS

Ecological theory has traditionally been grounded upon the precarious assumption of spatial homogeneity (McIntosh 1991). The growing demand for considering system heterogeneity and scale in ecological studies is a rather recent one, yet scale has in a short time become one of the keywords in ecological literature. Stream ecology is no less guilty of being 'mute to scale' (see Wiens 1989) than current ecology in general. For example, field experiments considering such an inherently spatial aspect of predator-prey interactions as the aggregative response of the predators to their prey have usually been conducted at only one scale. As already shown by Heads & Lawton (1983), it is nearly impossible to document even strong aggregative responses, if the scale of the study is inappropriate. Accordingly, it is highly hazardous to interpret the results of these single-scale experiments in a more general context; patterns observed at one scale may not prevail when the scale is changed (see e.g. Rose & Leggett 1990). Stream ecologists are highly tradition-bound, with a tendency to use quadrats or experimental cages of a certain size. Unfortunately, traditional sampling techniques often scale the environment in a profoundly different way than the study organisms do; in other words, the scale of our measurements and that of the organisms' responses do not fall within the same domain (Wiens 1989). For example, while there were some hints of aggregation by *R. obliterata* to its simuliid prey when quadrat sampling was employed (I), the real scale and intensity of this particular predator-prey interaction could be revealed only by a multiscale, plotless sampling design (II). Clearly, to avoid untenable generalizations, spatial aspects of predator-prey interactions must be studied across several different scales (see also Hurlbert 1990).

Another central issue in stream ecology which would benefit from the multiscale perspective is the study of disturbance. Patch-scale studies where individual stones or small areas of the stream bed are experimentally disturbed can be neatly replicated, and are relevant for studies considering the patch dynamics nature of lotic communities. However, natural disturbances that affect can be neatly replicated, and are relevant for studies considering the patch dynamics nature of lotic communities. However, natural disturbances that affect the structure of benthic communities likely operate on a much larger scale. At these scales, controlled experiments are often logistically unfeasible, and one must content with monitoring of the benthic recovery rates after an exceptional disturbance event. At a still larger scale, only comparisons between rivers with different disturbance histories are possible ('natural experiments' sensu Diamond 1983). Thus, disturbance in lotic environments would probably be better understood by adopting a pluralistic approach (e.g. Haila 1988), pluralism in this context meaning a parallel change in the methods employed with changes in the scale of the study.

Acknowledgements

This work was initiated at the Department of Zoology, University of Oulu and completed at the Department of Biology, University of Jyväskylä. The field work was carried out at Oulanka Biological Station, University of Oulu.

First, I express my gratitude to the members of our stream ecology group, some of them in Oulu, some in Jyväskylä. Their efforts in collecting and processing hundreds of samples (and never letting me forget who did the tedious part of the job) is hereby acknowledged. Special thanks go to my closest co-worker Pertti Tikkanen who has contributed to most of the ideas presented in this book. He never hesitated to show me how wrong I was and how I could improve my study designs. Kalevi Kuusela originally introduced me to the fascinating world of aquatic insects. Jaakko Lumme taught me that ecology is much more than a mere collection of facts, and that no branch of biology can be meaningful unless firmly based on evolution. My intellectual background stems from the Club of Mutual Praise whose members Jouni Aspi, Heikki Haavi, Kari Koivula, Kyösti Lempa, Mikko Mönkkönen, Seppo Rytkönen, Pertti Tikkanen and Risto Virtanen all deserve to be mentioned here. During endless hours of discussions they have given me all sorts of critiques, using all available tools to make me think of alternative hypothesis. Thanks guys, you're really good. I also thank my coauthors Antti Penttinen and Risto Virtanen, without whose expertise two of the papers included in this thesis could not have been completed. Finally, I thank Katri Kärkkäinen for always being there when I needed her most.

This study was supported by Emil Aaltonen Foundation, Heikki and Hilma Honkanen Foundation, Alfred Kordelin Foundation, Finnish Cultural Foundation and the Academy of Finland.

I dedicate this thesis to the late Professor Olli Järvinen whose support at the early stages of my scientific endeavour was more important than he probably ever came to realize.

Yhteenveto

Säännönmukaisuudet pohjoisten virtavesien ekologisten yhteisöjen ja kiltojen rakenteessa

Säännönmukaisesti toistuvien rakenteiden kuvaaminen ja niihin johtavien mekanismien löytäminen ovat yhteisöekologian kaksi rinnakkaista päämäärää. Mitä yleisemmästä säännönmukaisuudesta on kyse, sitä mielenkiintoisempi se on, koska yleisyys usein ilmentää yhteistä selitysmekanismia. Virtavesiekologiassa yleisten rakenteiden löytämistä on kuitenkin hidastanut ekologista tutkimusta yleisemminkin vaivaava maantieteellinen vinouma. Ylivoimaisesti suurin osa tutkimuksesta on tehty lauhkealla vyöhykkeellä, ja esimerkiksi Fennoskandian pohjoisosien virtavesiyhteisöjä on tutkittu niukalti. Tämän tutkimuksen tavoitteena on ollut selvittää säännönmukaisesti toistuvia rakenteita eräissä pohjoisten virtavesien ekologisissa yhteisöissä ja killoissa, erityisesti suhteessa ympäristöhäiriöteorioihin ja peto-saalisteoriaan.

Selkärangattomien petojen ja niiden tärkeimpien saaliskohteiden välistä vuorovaikutusta tarkasteltiin useilla eri mittakaavoilla ja useina ajankohtina. Eräissä aiemmissa tutkimuksissa on havaittu, että petohyönteisten esiintyminen keskittyy mikrohabitaatteihin, joissa saalistiheydet ovat suurimmat. Laboratorio- ja kenttäkokeissa on toisaalta osoitettu, että petojen keskinäinen häirintä ja saalislaikkujen lyhytaikaisuus voivat estää aggregatiivisen vasteen muodostumisen. Tutkimukseni osoittivat, että petojen esiintyminen on laikuttaista, ja laikut ovat keskittyneet suurimpiin saalistihentymiin silloin, kun saaliskohde on suhteellisen liikkumaton. Siten laikuttaisuutta esiintyy suhteessa mäkärätoukkiin, mutta ei sen sijaan esimerkiksi tehokkaasti liikkuvien päivänkorentotoukkien suhteen. Numeerisen vasteen havaitseminen oli riippuvainen tutkimuksen mittakaavasta. *Rhyacophila obliterata*-vesiperhosen esiintyminen oli laikuttaista mittakaavalla, joka vastaa mäkärätoukkien muodostamien toukkatihentymien kokoa, mutta sitä pienemmällä tai suuremmalla mittakaavalla laikuttaisuutta ei havaittu. Tämä korostaa oikean mittakaavan merkitystä peto-saalissuhteen tarkastelussa.

Suodattajavesiperhosten kiltarakennetta selvitettiin erilaisten monimuuttuja-analyysien avulla. Kaikkiaan näytteistä tavattiin seitsemän suodattajavesiperhoslajia, joista useimmilla esiintyi rinnakkain vähintään kolme eri toukkavaihetta. Tämän perusteella oli ennakoitavissa, että toukkavaiheet toimisivat "ekologisina lajeina", ja ikärakennekomponentti muodostaisi huomattavan osan kunkin lajin ekolokerosta. Jokaisella neljällä analyysiin mukaan otetulla lajilla toukkavaiheiden väliset erot elinympäristön valinnassa olivat todellakin huomattavat. Tällaisten kasvun myötä tapahtuvien ekolokeron muutosten vuoksi vuorovaikutuksia kokorakentuneiden populaatioiden muodostamissa yhteisöissä tulisikin tarkastella eri kokovaiheiden, ei niinkään eri lajien välillä.

Virtavesisammalten esiintymistä ja runsaussuhteita tarkasteltiin ns. häiriöteorioiden valossa. Häiriön frekvenssin ja voimakkuuden mittana käytettiin alustan liikkumistodennäköisyyttä. Tällainen lähestymistapa edellyttää verrattain pitkiä virtaamamittaussarjoja, joita oli saatavilla vain tutkimusalueen kolmesta pääuomasta (Oulankajoki, Kitkajoki ja Kuusinkijoki). Analyysin mukaan koskipaikan häiriöalttiuteen vaikuttavat ennen muuta joen gradientti ja alustan partikkelikoko. Sammalyhteisöissä paikan häiriöalttius näkyi siten, että herkästi häiriintyvillä paikoilla menestyivät ainoastaan matalakasvuiset kolonisoijalajit, kun taas pitkäikäiset, laajoja kasvustoja muodostavat lajit dominoivat vakaampia ympäristöjä. Vesisammalyhteisöissä suurin lajistollinen monimuotoisuus näyttää kehittyvän ympäristöissä, joissa häiriöt ovat verraten tavallisia, mutta pienen mittakaavan tapahtumia. Vegetatiivisen kasvun kautta tapahtuvaan lyhyen etäisyyden kolonisaation kykenevät lajit ('*Leptodictyum-Bryum*' tyyppi) säilyttävät asemansa näissä yhteisöissä, mutta tulevat syrjäytetyiksi hyvin vakaista ympäristöistä, joita dominoivat pitkäikäiset, puhtaasti akvaattiset lajit ('*Fontinalis*'-tyyppi). Puroissa, joissa häiriöt ovat laaja-alaisia ja usein toistuvia tapahtumia, vain lyhytikäiset, itiöittensä avulla vapaita alueita tehokkaasti kolonisoivat, matalakasvuiset lajit ('*Blindia*'-tyyppi) kykenevät tulemaan toimeen, mutta nekään eivät muodosta kovin laajoja kasvustoja. Vesisammalten ryhmittely elinstrategioiden mukaan tarjoaa potentiaalisesti tehokkaan menetelmän paikallisten yhteisöjen lajikoostumuksen ja dominanssisuhteiden ennustamiseen. Mallin testaamiseksi ja edelleenkehittämiseksi tarvitaan kuitenkin lisävalaistusta monista erityisesti vesisammalten lisääntymisbiologiaan liittyvistä seikoista, ja siksi esitettyä mallia onkin toistaiseksi pidettävä alustavana.

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https://doi.org/10.1111/j.1365-2427.1995.tb01156.x