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Studies of aquatic insects in the Atna River 1987–2002

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Abstract

River Atna is situated in south-eastern Norway and stretches from approx. 1400 m a.s.l. in the Rondane Mountains, through Lake Atnsjøen, at 701 m a.s.l.; to the confluence with River Glomma at 338 m a.s.l. The catchment area is 1323 km^2, oligotrophic and very susceptible to acid precipitation. The river water is very poor in nutrients and ions, and pH varies from 5.0 to 7.2. Samples were taken each year from 1987 to 2002 at three to five localities from 1280 to 380 m a.s.l. Insect larvae were collected by Surber sampling and by kick sampling. Malaise traps were used to collect adults of Plecoptera, Trichoptera, Chironomidae and Limoniidae. A total of 16 taxa of Ephemeroptera, 24 taxa of Plecoptera, 39 taxa of Trichoptera, 125 taxa of Chironomidae and 52 taxa of Limoniidae, were identified. Our results from Atna provide some support for a zonation of the river based on zoobenthos. The occurrence and abundance of functional groups among the Plecoptera, Trichoptera, and Chironomidae are discussed in relation to the River Continuum Concept (RCC). Our conclusion is that grazers dominate in the zoobenthos in streams in the treeless alpine region in Norway. Natural lakes, which occur in most watercourses in Norway, appear to cause a disturbance in relation to the original RCC concept, as the zoobenthos community in and below the lake outlet is dominated by collectors (filter feeders). The pattern found in the Atna watercourse is probably a general pattern for a northern watercourse in the Holarctic, where the glacial periods created lakes in most watercourses. The results of the long term sampling in Atna are discussed in relation to the practicalities and the cost-benefit of zoobenthos in efficient bio-monitoring in rivers.

Introduction

Longitudinal distribution and community structure of invertebrates in rivers have been discussed in several papers over the last 40 to 50 years. The earliest papers were descriptive and focused mainly on the distribution of benthic communities (Müller, 1953; Illies, 1956, 1961; Illies & Botosaneanu, 1963). However, Webster (1975) pointed out that nutrients in a stream do not cycle in place, but are transported downstream as they complete a cycle; this coupling of transport and energy cycling was described as a 'spiralling' effect. This idea was further developed by Vannote et al. (1980) who introduced the River Continuum Concept (RCC). RCC takes into consideration not only the species composition, but also the production, respiration and feeding habits of the species, providing a more holistic and dynamic view of the running water ecosystem. The RCC classifies the zoobenthos in functional groups based on their feeding habits, i.e. grazers, shredders, collectors (filter feeders), and predators. Vannote et al. (1980) postulated a gradual change in community structure from the source of the river to its end in the ocean. In their study, the river source was in forest, i.e. heavily shaded, and they demonstrated a gradual change in the production/respiration ratio along the river. At the source, respiration was larger than production. Some distance downstream, production increased to become larger than respiration, while even further downstream respiration again became larger than production. Other authors, e.g., Statzner & Higler (1986) and Statzner (1987) focused on the stream hydraulics as an important factor governing the distribution of species. Townsend (1989) introduced the patch dynamics concept of stream community organization, stressing the importance of competition, succession, predation, grazing and disturbance.

Norway (and Scandinavia) has been classified into several biotic zones based on terrestrial vegetation (Moen, 1999). Subsequently, the vertical zonation of Plecoptera and Trichoptera in rivers in relation to the zonation in adjacent terrestrial ecosystems was discussed by Lillehammer (1974) and Solem (1985). In this study we have collected zoobenthos from the river Atna, which runs through several vegetation zones (Table 1), in order to analyse the spatial and temporal changes in the community structure of Ephemeroptera, Plecoptera and Trichoptera. We have also included data on the species composition of Diptera families Chironomidae and Limoniidae.

The objectives of the study were:

(1) to document the species inhabiting the river;
(2) to describe the longitudinal zonation in the aquatic insect communities and relate the aquatic fauna to the terrestrial biotic zonation;
(3) to discuss the occurrence and dominance of functional groups in the different biotic zones in relation to the RCC concept; and
(4) to evaluate the monitoring value of a low effort long term study.

Methods

Insect larvae were collected by Surber sampling and by kick sampling. The net meshes in the 0.1 m^2Surber sampler and kick sampling net were 0.5 mm. Caddis larvae (Trichoptera) were also handpicked, mostly in the upper parts of the river system. Mayflies (Ephemeroptera) are best caught with the kick sample method (Engblom, 1996). The use of the Surber sampler is probably one of the reasons for a relatively low specimen number in the samples. A careful use of the Surber method has nevertheless been shown to increase the number of rare taxa collected on heterogeneous substrates, while the number of specimens is lower in Surber samples compared to kick samples (Storey et al., 1991).

Malaise traps were used to collect adults of stoneflies (Plecoptera), caddis flies, limonids and chironomids. This adds information on species occurrence to facilitate community analyses and to reveal distribution patterns. One argument against sampling with Malaise traps for community analyses, is that species may fly in from other habitats than the one targeted by the sampling. However, Solem (1985) tested the validity of the Trichoptera collections in Malaise traps against emergence traps in the stream Raubekken, Dovrefjell, and concluded that Malaise trap collections are adequate for community analyses. Although the Malaise trap will always capture a few specimens of species that do not belong to the nearby community, these specimens are so few that they will not seriously disturb the general community analyses. An obvious advantage of Malaise traps is that they may sample continuously during the whole flying season, from late June, through July, August and September. During our sampling programme, the traps were emptied every week and the animals were conserved in ethanol.

Study area and sampling sites

River Atna is situated in southeastern Norway and originates in the Rondane Mountains well above the tree line, which is at 1100 m a.s.l. The river is 97 km long, and Lake Atnsjøen, at 701 m a.s.l., is situated in the middle of the water course. Atna joins River Glomma at 338 m a.s.l. Our sampling sites are situated between approximately 62° N, 9° 45′ E and 61° 45′ N, 10° 45′ E (Fig. 1). Surber samples were taken each year from 1987 to 2002 at three localities; Dørålseter, Vollen, and Solbakken, and covered a nearly 80 km stretch of the river. Surber samples have also been taken in some of the later years at Skranglehaugan (Table 1). The material of benthic insect larvae from these samples has been identified mostly to the species or genera level for the groups Plecoptera, Ephemeroptera and Trichoptera.

Material of adult insects was collected with Malaise traps at Vidjedalsbekken Skranglehaugan, Dørålseter, Vollen, the outlet of Lake Atnsjøen and Solbakken (Table 1). Imagines of Trichoptera and Plecoptera were identified from all these localities, while imagines of Ephemeroptera and males of Chironomidae and Limoniidae were identified from Vidjedalsbekken, Skranglehaugan, Dørålseter, Vollen and Solbakken.

The water in the river is very poor in nutrients and ions, and pH varies from 5.0 to 7.2 (cf. Lindstrøm et al., 2004). The catchment area is 1323 km^2, oli-

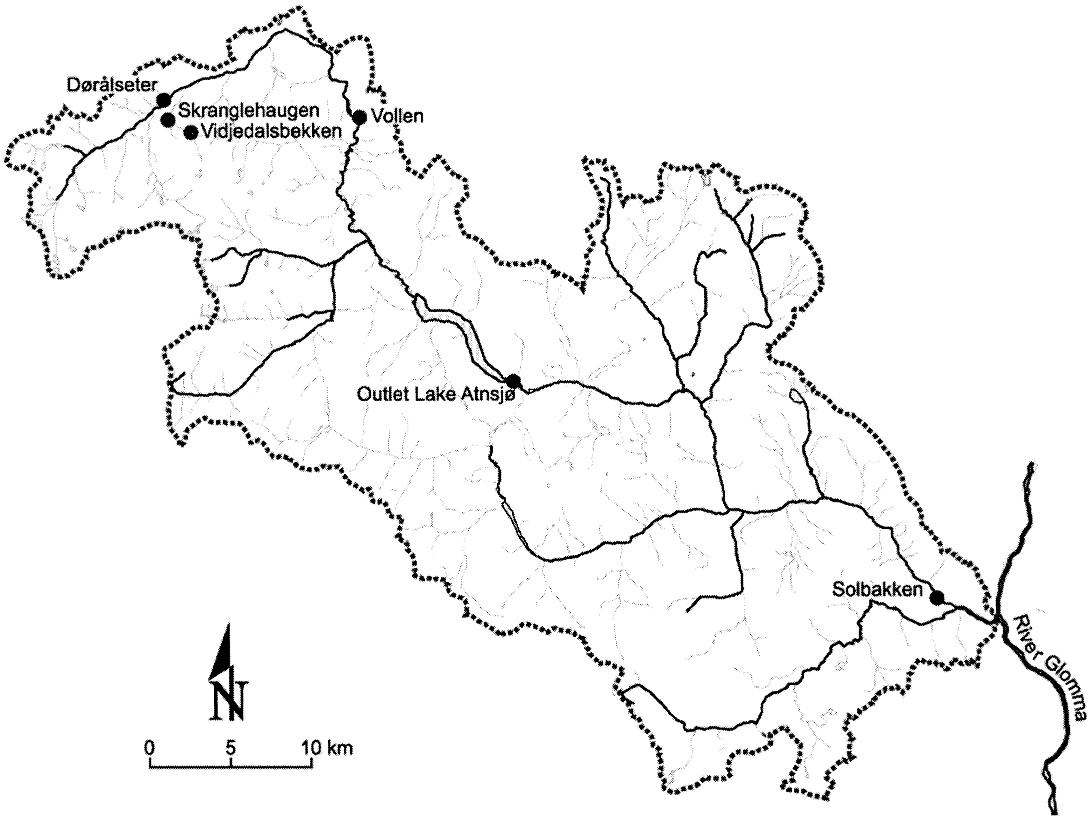

Figure 1. Map of the Atna watershed with sampling localities (cf. Table 1).

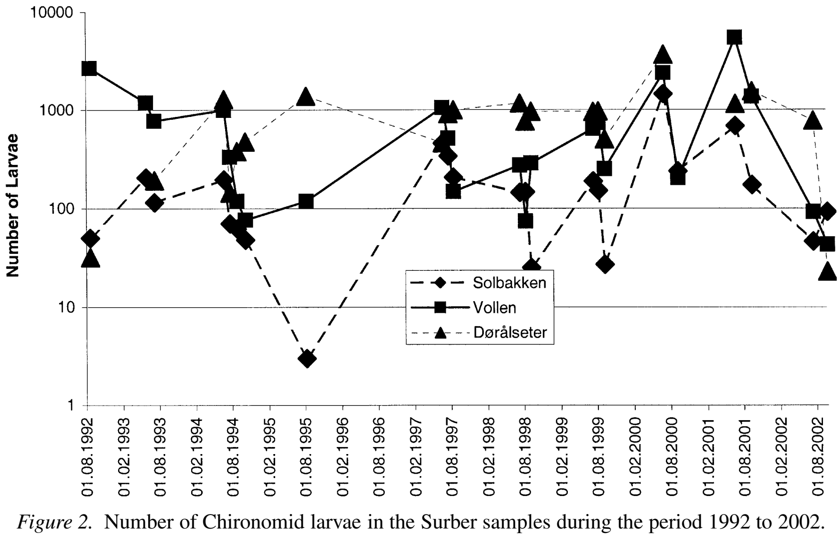

Figure 2. Number of Chironomid larvae in the Surber samples during the period 1992 to 2002.

Table 1. Sampling sites with altitude, vegetation type, vegetation zone and -section according to Moen (1999), and zoobenthos sampling program.

Station	Altitude (m a.s.l)	Vegetation type	Vegetation zones	Vegetation sections	Surber samples	Malaise traps
Vidjedals-bekken	1280	Treeless area	Alpine	Continental to oceanic	–	1986 and 1987
Skrangle-haugan	1120	Birch woodland belt	Northern boreal	Continental to oceanic	1997–2002	1986 and 1987
Dørålseter	1060	Birch woodland belt	Northern boreal	Continental to oceanic	1987–2002*	1986 and 1987
Vollen	710	Coniferous area	Northern boreal	Slightly continental	1987–2002*	1986
Atnsjøen	700	Coniferous area	Northern boreal	Slightly continental	–	1986
Solbakken	380	Coniferous area	Middle boreal	Slightly continental	1987–2002*	1986

*The material from 1996 was lost in an accident.

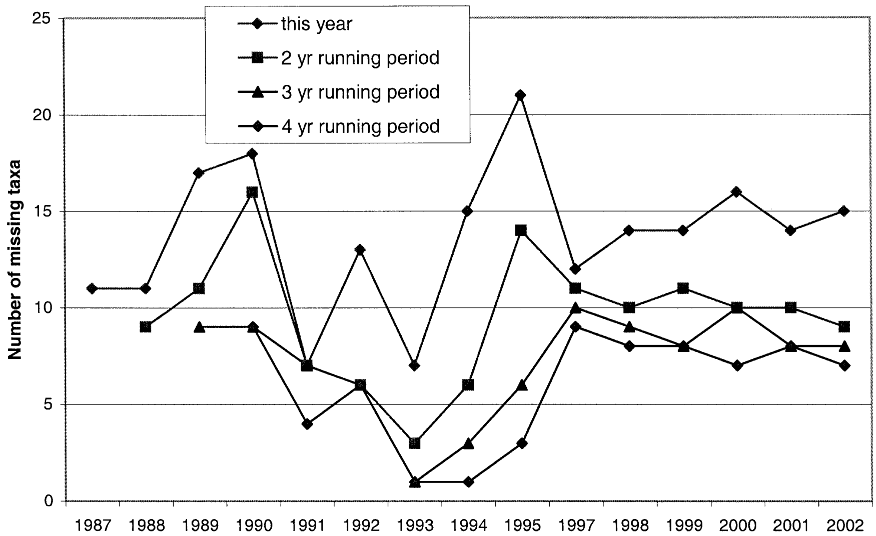

Figure 3. Number of missing taxa in the Surber samples at Solbakken for each year and running periods for the last 2, 3 and 4 years.

gotrophic and very susceptible to acid precipitation (Blakar et al., 1997). The water temperature in the lower part of the river, below the lake, may reach 20 °C during summer, with mean temperatures in June to August at 10–12 °C. Upstream of Lake Atnsjøen, the water temperature may reach 10 °C only for short periods during summer. At Vidjedalsbekken, in the subalpine birch woodland belt, maximum water temperature may reach 7–8 °C during summer, with mean temperatures during July and August of 4–6 °C. At Dørålseter a little further downstream, maximum summer temperatures may reach 10–11 °C. The increase in water temperatures during spring occurs nearly two months later at Vidjedalsbekken than at Solbakken, and there is a corresponding difference in summer temperature of 6 °C (Tvede, 2004). River Atna and its tributaries, including Vidjedalsbekken, is unregulated, and only to a very limited extent influenced by human activities. No part of the tributary or river is significantly shaded by terrestrial vegetation. Consequently, the light conditions are very good for periphyton growth on the substratum.

Results

Distribution and abundance of Ephemeroptera

A total of 16 taxa of mayflies were identified in the material collected during the years 1986–2002 (Table 2). This includes an unidentified Leptophlebidae collected at Solbakken. *Baetis rhodani* is by far the most common species in the river. In fact 30 000 individuals out of a total of 36 000 collected mayfly nymphs belonged to this species, which is by far Norway's most common running water mayfly species. *B. rhodani*

Table 2. Distribution of Ephemeroptera species in the river Atna. Species records at each of the localties quantified as very abundant or abundant (xxxx or xxx), less abundant (xx) or rare (x). An *i* indicates that the species are identified from imago.

Locality	Skranglehaugan	Dørålseter	Vollen	Solbakken
Baetis lapponicus	x	x		x
Baetis rhodani	xx	xxxx	xxxx	xxxx
Ephemerella aurivillii		x	xxx	xxxx
Heptagenia joernensis		x	xx	xxx
Baetis muticus		x	x	xxx
Baetis fuscatus/scambus		x	x	xxxx
Ameletus inopinatus		x	xx	xx
Siphlonurus lacustris		*i*	*i*	*i*
Baetis subalpinus			xx	xxx
Heptagenia dalecarlica			x	xxx
Siphlonurus aestivalis			x	
Baetis scambus				xx
Ephemerella mucronata				xx
Heptagenia sulphurea				x
Leptophlebiidae				x
Parameletus chelifer *				
Number of species	2	8	10	14

*Imago found in a Malaise trap at the outlet of Lake Atnasjøen.

is a collector-gatherer and grazer (scraper) (Bækken, 1981; Elliott et al., 1988).

At the site Skranglehaugan, 1120 m a.s.l., only nymphs of *B. rhodani* and *B. lapponicus* were recorded in the Surber and kick samples. At this elevation mayflies are at their extreme altitudinal limit in Norway. The third species of this genus known from high altitudes, *B. subalpinus*, was not found at the two high altitude sites (Vidjedalsbekken, Skranglehaugan) in Atna. This is somewhat surprising, since this species is characterised as a northern, high altitude species in Norway (Nøst et al., 1986).

Eight species of Ephemeroptera were found at Dørålseter, which is situated in the birch woodland belt (1060 m a.s.l.) (Table 2). The site with most mayfly species was Solbakken in the middle boreal zone, where 14 species were recorded. At this site, *Baetis fuscatus/scambus* were caught in considerable numbers. Nymphs of the two species may not be easily separated (Elliott et al., 1988). However, as no *B. fuscatus* imagines has yet been recorded in Atna, it appears reasonable that the nymphs collected mainly were *B. scambus* The two species *Heptagenia dalecarlica* and *H. joernensis* were present in large numbers at Solbakken, while only one specimen of *H. sulphurea* was caught during all the sampling years. All mayfly species recorded in Atna during our sampling period (1986–2002) are common in Norway, except the species *Parameletus chelifer* that was found in a Malaise trap at the outlet of Atnsjøen. This species is missing in large parts of western and northern Norway, although it is not formally listed as rare or uncommon. *Ameletus inopinatus* has not previously been recorded from the area (Brittain et al., 1996).

Distribution and abundance of Plecoptera

The stonefly fauna must be considered well documented through this investigation. In our material we identified 24 of the 28 species previously recorded in the region (Table 3; Aagaard et al., 2002). Stoneflies generally prefer cold, clean, running waters, and a few species occur at all altitudes in all parts of Norway. The four species not recorded in this study is either a lake dweller (*Diura bicaudata*), or they are species with a distribution mainly restricted to lowland areas. (*Dinocras cephalotes* occurs in brooks and large rivers, *Isoperla difformis* has a wide, but sparse distribution, and *Isogenus nubecula* has a southern and eastern distribution in Scandinavia and is therefore rare in Norway).

A total of 7048 stonefly nymphs were recorded in the Surber samples. *Capnia atra* was the most abundant species with a maximum at Dørålseter, while

Table 3. Distribution of Plecoptera species in the river Atna. Species records at each of the localties quantified as very abundant or abundant (xxxx or xxx), less abundant (xx) or rare (x). An *i* indicates that the species are identified from imago.

Locality	Skranglehaugan	Dørålseter	Vollen	Solbakken
Capnia bifrons	*i*			
Arcynopteryx compacta	xx	xx		
Brachyptera risi	x	xxx	xx	
Nemoura cinerea	x	xx	*i*	*i*
Capnia atra	xx	xxxx	xxx	x
Protonemura meyeri	xx	xxx	xx	x
Nemurella pictetii	xx	xx	x	x
Amphinemura borealis	x	x	xx	xxx
Diura nanseni	x	x	xxx	xxx
Isoperla obscura	x	x	xxx	x
Isoperla grammatica	x	*i*	xxx	x
Leuctra fusca	*i*	x	x	xx
Capnia pygmaea	*i*	*i*	*i*	*i*
Amphinemura standfussi		*i*	*i*	
Leuctra digitata		xx	x	xx
Leuctra nigra		x	xx	x
Leuctra hippopus		x	xx	x
Taeniopteryx nebulosa		x	xxx	xx
Nemoura avicularis			x	*i*
Capnopsis schilleri			x	
Siphonoperla burmeisteri			x	xx
Amphinemura sulcicollis			xx	x
Nemoura flexuosa				*i*
Xanthoperla apicalis				*i*
Number of species	13	17	20	19

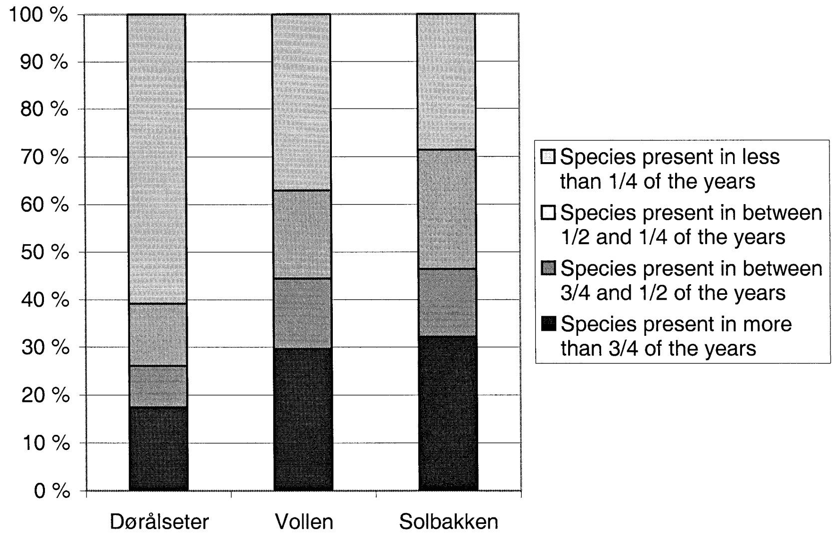

Figure 4. Number of species with different frequency of occurrence in the annual Surber samples at the three localities Dørålseter, Vollen and Solbakken in Atna, 1986–1998.

Diura nanseni dominated the samples from Vollen and Solbakken. No species were recorded in Malaise traps at Vidjedalsbekken, 1290 m a.s.l. in the midalpine zone. In the birch woodland belt (Skranglehaugan and Døràlseter) 17 species were found, and the fauna was dominated by *Capnia atra*, *Brachyptera risi* and *Protonemura meyeri*. *B. risi* is a grazer (scraper) on periphyton in streams. *P. meyeri* is a grazer and shredder. All the 24 species, except *Arcynopteryx compacta*, were collected in the boreal zone. *A. compacta* is an alpine species, and was only found at the two uppermost sites, Døràlseter and Skranglehaugan.

Capnia species dominated at high altitudes. This genus includes three species in Atna, *C. atra*, *C. bifrons* and *C. pygmaea*. *C. atra* is the dominating species, according to our Malaise trap catches along the river. Other species caught in large numbers are *Amphinemura borealis*, *Leuctra fusca*, *Isoperla obscura* and *Taeniopteryx nebulosa*, all common species in Norway.

Distribution and abundance of Trichoptera

A total of 39 species of caddis flies were identified in our material from Vidjedalsbekken and the river Atna. One species was collected in the alpine zone, 14 species in the birch woodland belt, and 38 species in the boreal zone (Table 4). At the high altitude site Vidjedalsbekken, 1280 m a.s.l., the parthenogenetic *Apatania zonella* was the only caddis fly caught in the Malaise traps. At Skranglehaugan, the collecting site in the upper part of the birch woodland belt, the Scandinavian endemic, *Apatania hispida*, was the dominant species with more than 90% of the total number of individuals. In the lower part of the birch woodland belt at Døràlseter, 14 species were collected, with three species fairly equally represented. *A. hispida*, *Potamophylax cingulatus* and *Ecclisopteryx dalecarlica* each made up between 20 and 31% of the catches.

There are no conspicuous changes in the caddis fauna at the collecting sites from Døràlseter, at 1060 m a.s.l., and downstream to Vollen, at 710 m (Table 4). However, an obvious change in the caddis fly community was found at the outlet of Lake Atnsjøen, where the collector or filter feeder (i.e. netspinning caddis) *Polycentropus flavomaculatus* constituted more than 70% of the total number of individuals. The highest number of caddis fly species, 34, was recorded at the site Solbakken in the mid-boreal zone, at 380 m elevation.

Distribution and abundance of Limoniidae

We captured 52 taxa of Limoniidae during this study (Table 5). This family includes both aquatic and terrestrial species. Six species were recorded in the alpine zone, 21 in the birch woodland belt, and 41 species in the boreal zone (Solem & Mendel, 1989). At Vidjedalsbekken, in the birch woodland belt, the dominant species in the Malaise traps, *Phyllolabis macrura*, is a terrestrial species, but the *Orimarga* and *Ormosia* species are aquatic. They are probably shredders and collectors/gatherers, respectively. *Dicranota guerini* is a predator, and dominates (about 64%) the Limoniidae fauna in the birch woodland belt. *Ormosia fascipennis, Rhaphidolabis exclusa* and *Molophilus flavus* are subdominant here.

Distribution and abundance of Chironomidae

A total of 125 species of Chironomidae were found in the Malaise trap samples from the five localities. Twentyeight species were recorded at Vidjedalsbekken, 54 at Skranglehaugan, 62 at Døràlseter, 54 at Vollen, and 52 species at Solbakken. Due to the traps' positions at the different sampling sites, the samples are more representative for the stream fauna at the alpine sites than at Vollen and Solbakken. At the boreal sites, a larger number of the species caught are most probably 'tourists' from other habitats. However, the impression of a clear zonation of the species composition is not seriously effected by this problem.

The chironomids are always an important component of the fauna in alpine streams. Although Vidjedalsbekken is not glacier feed, it shares many similarities with such brooks, which is reflected in the chironomid fauna. A chironomid community of ten *Diamesa* species and several species of *Pseudodiamesa*, *Tokunagaia*, *Tvetenia*, *Eukiefferiella* and *Chaetocladius* characterizes the three uppermost alpine localities. A total of 33 species were only captured in this region (Table 6). While only five species were found at both Vidjedalsbekken and Solbakken, 39 other species occurred both in the alpine and boreal part of the river (Table 7). A surprisingly high number of species, 48 in all, where captured only in the lower part of the river at Vollen or Solbakken (Table 8). The common occurrence of 'tourist species' originating from other habitats is most probably the main reason for this. The material of Chironomidae larvae taken in the Surber samples was not identified below the family level in this study. The number of individuals in five Surber samples was mostly found to be between 100 and

Table 4. Distribution of Trichoptera species in the river Atna. Species records at each of the localties quantified as very abundant or abundant (xxxx or xxx), less abundant (xx) or rare (x). An *i* indicates that the species are identified from imago.

Locality	Skranglehaugan	Dørålseter	Vollen	Solbakken
Potamophylax cingulatus	x	xx	x	
Chaetopteryx villosa	x	x	x	
Halesus digitatus		x	x	
Apatania hispida	xx	xx		
Apatania zonella	xx	xxx	xx	xx
Apatania muliebris	xx	xx	xx	xx
Limnephilus coenosus	x	x	x	x
Oxyethira flavicornis		x		x
Ecclisopteryx dalecarlica	x	xx	xxx	x
Potamophylax latipennis	xx	x	x	x
Lepidostoma hirtum	xx	xx		xxx
Apatania stigmatella	xx	xx	xx	xx
Glossosoma spp.(intermedia)	x		xx	xx
Rhyacophila nubila	x	xx	xxx	xxx
Arctopsyche ladogensis		x		xxx
Philopotamus montanus	x			x
Polycentropus flavomaculatus			x	xxx
Micropterna sequax			x	x
Annitella obscurata			xx	x
Halesus radiatus			x	
Ceratopsyche nevae				xx
Micrasema nigrum				*i*
Micrasema gelidum				*i*
Hydroptila simulans				*i*
Hydroptila forciptata				*i*
Sericostoma personatum				xx
Hydropsyche pellucidula				x
Hydroptila tineoides				x
Ceraclea spp.				x
Psychomyia pusilla				x
Athripsodes commutatus				x
Hydropsyche siltalai				x
Hydropsyche silfvenii				x
Apatania wallengreni				x
Phacopteryx brevipennis				x
Ithythricia lamellaris				x
Glossosoma conformis				x
Agapetus ochripes				x
Silo pallipes				x
Number of species	13	14	15	34

Table 5. Distribution of Limonidae species found only at the localities in the river Atna. Species recorded at each of the localities quantified as very abundant (xxxx or xxx), less abundant (xx) or rare (x).

Locality	Vidjedalsbekken	Skranglehaugan	Dørålseter	Vollen	Solbakken
Phyllolabis macroura	xxx	x	x		
Ormosia fascipennis	xx	xx	x	x	x
Limonia macrostigma	x	x	xx	xxx	x
Dicranota guerini	x	xxx	xxx	x	
Orimarga attenuata	x				
Melanolimonia caledonica	x				
Rhaphidolabris exclusa		xx	xx	x	x
Trichyphona immaculata		x	x		
Dicranota bimaculata		x	x	x	
Rhiphidia duplicata		x	x	x	xx
Brachylimnophila nemoralis		x	x		xx
Rhabdomastrix parva		x	x		
Symplecta hybrida		x	x	x	x
Gonomyia sp.		x			x
Paradicranota subtilis		x			
Paradicranota gracilipes		x			
Molophilus flavus			xx		
Euphylidorea phaeostigma			x	x	
Dicranomyia incisurata			x		
Dicranomyia distendens			x	x	
Erinocopa trivialis			x		
Ormosia ruficauda			x		
Idioptera macropteryx			x	x	
Molophilus propinquus					xx
Parilisia vicina				xxx	x
Neolimnophila (placida?)				x	x
Dicranomyia halterata				x	
Limonia sylvicola				x	x
Metalimnobia zetterstedti				x	x
Dicranomyia terranovae				x	x
Paradicranota robusta				x	
Erioptera lutea				x	
Phylidorea squalens				x	
Erioconopa diaturna				x	
Dicranomyia modesta					xx
Metalimnobia 4-notata					xx
Dicranomyia frontalis					xx
Metalimnobia bifasciata					x
Limonia flavipes					x
Ula sylvatica					x
Limonia tripunctata					x
Empeda cinerascens					x
Euphylidorea fulvonervosa					x
Archilimnophila unica					x
Melanolimonia morio					x
Ula mollisima					x
Ormosia staegeriana					x
Melanolimonia rufiventris					x
Dicranomyia zernyi					x
Dicranomyia sp.					x
Number of species	6	14	18	20	29

Table 6. Distribution of Chironomidae species found only at the upper tree localities in the river Atna.Species recorded at each of the localties quantified as very abundant (xxxx or xxx), less abundant (xx) or rare (x).

	Vidjedalsbekken	Skranglehaugan	Dørålseter
Bryophaenocladius inconstans (Brundin, 1947)	x		
Tokunagaia rectangularis (Goetghebuer, 1940)	x		
Pseudodiamesa nivosa (Goetghebuer, 1928)	xx	xx	
Chaetocladius laminatus Brundin, 1947	x	xx	xx
Diamesa incallida (Walker, 1856)	x	xx	x
Diamesa gregsoni Edwards, 1933	xx	x	x
Eukiefferiella spp.	x		x
Chaetocladius dissipatus (Edwards, 1929)	xx		xx
Limnophyes brachytomus (Kieffer, 1922)	x	xx	x
Parametriocnemus sp.		x	
Tokunagaia scutellata (Brundin, 1956)		x	
Eukiefferiella dittmari Lehmann, 1972		x	
Tvetenia bavarica (Goetghebuer, 1934)		xx	
Thienemanniella indet.		xxx	xxxx
Chaetocladius piger (Goetghebuer, 1913)		xx	xxxx
Rheocricotopus effusus (Walker, 1856)		xx	xx
Krenosmittia camptophleps (Edwards, 1929)		xx	xx
Tokunagaia parexcellens Tuiskunen, 1986		xxx	xx
Parochlus kiefferi (Garrett, 1925)		xx	xx
Pseudodiamesa branickii (Nowicki, 1873)		xx	x
Corynoneura lobata Edwards, 1924		x	x
Smittia edwardsi Goetghebuer, 1932		x	x
Rheocricotopus chapmani (Edwards, 1935)		x	x
Limnophyes aagaardi Sæther, 1990			x
Natarsia punctata (Meigen, 1804)			x
Prodiamesa olivacea (Meigen, 1818)			x
Chaetocladius grandilobus Brundin, 1956			x
Corynoneura indet.			x
Micropsectra boralis (Kieffer, 1922)			x
Protanypus caudatus Edwards, 1924			x
Chaetocladius gracilis Brundin, 1956			x
Chaetocladius acuminatus Brundin, 1956			xx
Tvetenia calvescens (Edwards, 1929)			xx
Number of taxa	9	19	26

1000 at all three localities, and the annual variation is synchronic with a maximum abundance in spring. In 1995, the extreme flood in spring (Tvede, 2004) clearly influenced the samples taken in August at the lower sampling sites (Fig. 2). At this date, the abundance at Dørålseter was normal, while the results from Solbakken showed the lowest number of chironomid larvae recorded during the ten year period. The effect of the flood was also seen in the low number of other insect groups this year.

Discussion

Zonation of the benthic communities

Because most Norwegian rivers run through a considerable altitudinal gradient over a relatively short distance, the question of biological zonation have been extensively discussed for several groups of organisms. Lillehammer's (1974) studies of Plecoptera included a variety of localities with different environmental conditions and species composition. He did not, however, find it feasible to establish a Plecoptera-based classi-

Table 7. Distribution of Chironomidae species found at five or four localities in the river Atna. Species recorded at each of the localities quantified as very abundant (xxxx or xxx), less abundant (xx) or rare (x).

Locality	Vidjedalsbekken	Skranglehaugan	Dørålseter	Vollen	Solbakken
Eukiefferiella claripennis (Lundbeck, 1898)	x	xxx	xxxx	xx	
Diamesa bertrami Edwards, 1935	xx	xxx	xxxx	xx	
Orthocladius (Euorthocladius) saxosus (Tokunaga, 1939)	x	xxx	x	xx	
Eukiefferiella brevicalcar (Kieffer, 1911)	x	x	x	x	
Diamesa hyperborea Holmgren, 1869	xx	xxx	xx	x	
Eukiefferiella devonica (Edwards, 1929)	x	xx	x	x	
Chaetocladius suecicus (Kieffer, 1916)	x	xx	xxxx	x	
Diamesa lindrothi Goetghebuer, 1931	xxx	xxx	xx	x	
Diamesa latitarsis (Goetghebuer, 1921)	xx	xxx	xxxx	x	
Eukiefferiella minor (Edwards, 1929)	xx	x	xxx	x	
Orthocladius (Eudactylocladius) mixtus (Holmgren, 1869)	xx	xx	x	x	
Diamesa bohemani Goetghebuer, 1932	xx	xx	xx	x	
Limnophyes bidumus Sæther, 1990	x	x	x	x	
Limnophyes minimus (Meigen, 1818)	x		x	x	
Pseudosmittia recta (Edwards, 1929)		x		x	
Chironomus (Chironomus) longistylus Goetghebuer, 1921		x		xx	
Limnophyes natalensis (Kieffer, 1914)		x		x	
Limnophyes pumilio (Holmgren, 1869)		x		xx	
Paratrichocladius skirwithensis (Edwards, 1929)		x	xx	x	
Trichotanypus posticalis (Lundbeck, 1898)		x	x	x	
Diamesa serratosioi Willassen, 1985	x	xxxx	xxxx	xxx	x
Diamesa tonsa (Walker, 1856)	x	xxx	xx	xx	x
Bryophaenocladius nitidicollis (Goetghebuer, 1913)	x				x
Diamesa aberrata Lundbeck, 1889	xx	xxx	xx		x
Gymnometriocnemus volitans (Goetghebuer, 1940)	xx	xx	x		x
Orthocladius (Euorthocladius) thienemanni Kieffer, 1906		xxx	x	x	x
Micropsectra groenlandica Andersen, 1937		xxx	xx	x	x
Micropsectra lacustris Säwedal, 1975		xx		x	x
Metriocnemus indet.		xx	x		x
Orthocladius (Orthocladius) frigidus (Zetterstedt, 1838)		xx	x	x	x
Limnophyes asquamatus Andersen, 1935		xx		x	x
Bryophaenocladius indet.		x			x
Parametriocnemus stylatus (Kieffer, 1924)		x	xx		x
Limnophyes edwardsi Sæther, 1990		x	x	x	x
Psectrocladius (Psectrocladius) indet.		x	x	x	x
Cricotopus (Isocladius) indet.		x	x		xx
Parapsectra nana (Meigen, 1818)		x	x		x
Heterotrissocladius marcidus (Walker, 1856)			x	x	
Micropsectra radialis Goetghebuer, 1939			x	xx	
Diplocladius cultriger Kieffer, 1908			x	x	x
Heterotanytarsus apicalis (Kieffer, 1921)			xx		x
Rheocricotopus fuscipes (Kieffer, 1909)			xx		x
Micropsectra atrofasciata (Kieffer, 1911)			x		x
Smittia sp.			x		x
Number of taxa	19	35	36	32	22

Table 8. Distribution of Chironomidae species found only at the lower two localities in the river Atna.Species recorded at each of the localities quantified as very abundant (xxxx or xxx), less abundant (xx) or rare (x).

Locality	Vollen	Solbakken
Thienemannimyia fusciceps (Edwards, 1929)	x	
Eukiefferiella ilkleyensis (Edwards, 1929)	x	
Tokunagaia excellens (Brundin, 1956)	x	
Parametriocnemus boreoalpinus Gouin, 1942	x	
Micropsectra notescens (Walker, 1856)	x	
Tanytarsus gregarius Kieffer, 1909	x	
Tanytarsus lestagei Goetghebuer, 1922	x	
Ablabesmyia monilis (Linnaeus, 1758)	x	
Orthocladius (Orthocladius) indet.	x	
Corynoneura edwardsi Brundin, 1949	x	
Saetheria reissi Jackson, 1977	x	
Ablabesmyia phatta (Egger, 1863)	x	
Odontomesa fulva (Kieffer, 1919)	x	
Endochironomus indet.	x	
Stictochironomus maculipennis (Meigen, 1818)	x	
Einfeldia longipes (Stæger, 1839)	x	
Thienemanniella majuscula (Edwards, 1924)	x	
Limnophyes schnelli Sæther, 1990	x	
Chironomus riparius Meigen, 1804	xx	x
Paraphaenocladius impensus impensus (Walker, 1856)	x	x
Procladius (Holotanypus) indet.	x	x
Smittia aterrima (Meigen, 1818)	x	x
Krenopelopia binotata (Wiedemann, 1817)		x
Macropelopia nebulosa (Meigen, 1804)		x
Nilotanypus dubius (Meigen, 1804)		x
Orthocladius decoratus (Holmgren, 1869)		x
Heleniella ornaticollis (Edwards, 1929)		x
Dicrotendipes tritomus (Kieffer, 1916)		x
Paracladopelma laminata (Kieffer, 1921)		x
Constempellina brevicosta (Edwards, 1937)		x
Micropsectra lindebergi Säwedal, 1976		x
Micropsectra recurvata Goetghebuer, 1928		x
Paratanytarsus penicillatus (Goetghebuer, 1928)		x
Rheotanytarsus muscicola Thienemann, 1929		x
Tanytarsus fimbriatus Reiss & Fittkau, 1971		x
Potthastia longimana (Kieffer, 1922)		x
Pseudosmittia indet.		x
Demicryptochironomus vulneratus (Zetterstedt, 1838)		x
Rheotanytarsus ringei Lehmann, 1970		x
Chaetocladius perennis (Meigen, 1830)		x
Polypedilum albicorne (Meigen, 1838)		x
Metriocnemus hygropetricus (Kieffer, 1912)		x
Virgatanytarsus arduennensis (Goetghebuer, 1922)		x
Cardiocladius capucinus (Zetterstedt, 1850)		x
Rheopelopia maculipennis (Zetterstedt, 1838)		xx
Polypedilum convictum (Walker, 1856)		xx
Stempellinella brevis (Edwards, 1929)		xx
Limnophyes pentaplastus (Kieffer, 1921)		x
Number of taxa	22	30

fication or zonation for Norwegian rivers similar to that developed by Illies & Botosaneanu (1963) for Central Europe.

Our results from Atna provide some support for a zonation based on zoobenthos. Both the Trichoptera genus *Apatania,* and several species of the chironomid genera *Diamesa*, *Pseudodiamesa*, *Tokunagaia*, *Tvetenia*, *Eukiefferiella* and *Chaetocladius*, are restricted to localities in or above the birch woodland belt. However, there were no typical alpine species of Ephemeroptera, and only one high mountain species of Plecoptera; *Arcynopteryx compacta*. In total, there is a zonation shift in benthic communities from the alpine and birch woodland belt area to the lower boreal zone, coinciding with the vegetation regions. The shift from the north boreal zone at Vollen to the middle boreal zone at Solbakken is more obscure. This may partly be due to the difference in dominating mesohabitats between these two localities. However, both localities belong to the boreal zone, and it should perhaps be expected that the finer classification based on terrestrial vegetation is not well reflected in the aquatic fauna. The aquatic environment is, after all, more continuous in temperature and nutrient level.

Trophic relationships and the RCC concept

The trophic relationship among the zoobenthos can be discussed based on taxa shifts of Plecoptera, Trichoptera, and Chironomidae along the watercourse. The Ephemeroptera do not provide useful data in this context because *Baetis rhodani* was the dominant species at all sampling localities. In Atna, the grazers (the stoneflies *Brachyptera risi*, *Protonemura meyeri*, and the caddis flies *Apatania hispida* and *A. zonella*) dominated in the birch woodland belt. The reason is most probably the unshaded river channel together with low water temperature. *Protonemura meyeri* may also partly be a shredder, feeding on detritus. The Chironomidae species that inhabit the alpine zone and the birch woodland belt are either grazers or collectors. A similar pattern in the alpine zone and the birch woodland belt was found for Trichoptera also at Dovrefjell, further west in the Norwegian mountains (Table 9). In the boreal zone, shredders, represented by the stoneflies *Amphinemura sulcicollis* and *Ecclisopteryx dalecarlica* and the caddis fly *Annitella obscurata*, was the dominant functional group. In this zone, however, Lake Atnsjøen has a great influence on the occurrence of the various functional groups. At the outlet of the lake, the trichopteran collector or filter feeder, *Polycentropus flavomaculatus*, dominates the community.

The River Continuum Concept (RCC) (Vannote et al., 1980) states that the shredders should dominate among the functional feeding groups when the source of the river is within a shaded area, e.g. in a forest. The RCC was further developed by Minshall et al. (1985), who included a treeless area (desert) at the source of the river. In this case, the different functional feeding groups (grazers, shredders, collectors, predators) constituted approximately one fourth of the community each. Our results from Atna, as well as the results reported from Dovrefjell (Solem 1985) (cfr. Table 9) differ from the pattern described both by Vannote et al. (1980) and Minshall et al. (1985). Our conclusion is that grazers dominate in the zoobenthos in streams in the treeless alpine region in Norway. The reason is most probably that the supply of dead organic material (detritus) from the heather-like riparian vegetation is restricted, while the light conditions provide a good environment for periphyton production (cf. Lindstrøm et al., 2004).

Natural lakes, which are found in most water courses in Norway, may be considered a disturbance in relation to the original RCC concept. The lake causes a shift in the stream ecosystem structure and function. The export of particulate organic matter (phyto- and zooplankton) from the lake (Sandlund 1982) changes the relationships between the functional feeding groups, as the filter feeders (i.e. the caddis fly *Polycentropus flavomaculatus*) come to dominate the aquatic insect community.

The RCC concept was intended as an universal model, but local topography must be taken into consideration when applying the concept. Lakes obviously constitute important elements in this. In Atna, there is a gradual change in the caddis fly community structure from the alpine to the boreal zone, but at the lake outlet there is a sudden and pronounced change in community dominance (Table 9). Therefore there is no obvious connection between the functional groups in the zoobenthos and the zonation in terrestrial vegetation given by Moen (1999). Still, the trophic relationships in the caddis fly communities are different in the alpine and boreal zones.

The pattern found in the Atna water course is probably a general pattern for a northern water course in the Holarctic, where the glacial periods created lakes in most water courses.

Table 9. Proportion of functional groups (in per cent) of Trichoptera in vegetation zones along Atna River and rivers in the Dovre mountains (from Solem 1999).

Functional group	Grazers	Shredders	Predators	Collectors
Atna				
Alpine zone	95	5	+	0
Birch woodland belt	70	24	5	1
Lower boreal zone	25	38	21	15
Outlet of Lake Atnsjøen	7	8	10	74
Dovre				
Alpine zone	90	10	0	0
Birch belt	10	40	40	10

The monitoring value of a low effort long term study

The aim of an efficient bio-monitoring is to detect possible impacts of human activities on a natural system with the lowest possible level of effort. However, as ecological systems are heterogeneous and variable at all spatial and temporal scales (Brown, 2003), the problem of all monitoring inventories is to distinguish between natural and human induced variation. In addition, nearly all sampling procedures introduce additional methodological uncertainties.

The composition of the zoobenthos in a stream varies in time on a seasonal as well as on an annual scale, and in space from the scale of bioregions to that of mesohabitats (Beisel et al., 1998). This long time study of benthic animals covers bioregional differences from the alpine to the boreal region. Mesohabitat variation was not considered a recordable parameter when the studies started in 1986, and such information is consequently not available. The intention was to cover seasonal variation through a sampling program of two or three sampling periods during the ice-free season. However, in some years the budget allowed only one sampling period. The quality of this long-term study is therefore strongly influenced by the project economy. The information gained on the number of species recorded in a single year (Appendices A, B, C) is of limited value. However, if the material is seen as information data covering longer time periods, a fundamental question of a biodiversity monitoring survey might be answered: Did species disappear or did the dominant species composition change during the monitoring period?

The Plecoptera and Ephemeroptera of this region are well known and it is therefore feasible to use these two groups in a methodological analysis. Few or no additional species are expected to be found in this watercourse in the future, unless there is a considerable change in the environmental factors. The sampling program during 15 years in the lower and middle parts of the river, at Solbakken and Vollen, and 13 years in the upper part at Dørålseter, gave a total of 28, 27 and 23 known taxa, respectively, as most of the nymphs were identified to species. The uncertainty of the species identity of some small nymphs leaves us with some uncertainty considering the exact number of species recorded in each sample or year. The following considerations are therefore based on the number of *missing taxa*, i.e., species that have been recorded in the total material, but which in a particular year were not identified among larvae or present as a possible member of an unidentified larva group (Appendices A, B, C).

Several questions of relevance for monitoring programme designs could now be answered:

- What is the mean number of missing taxa for each year?
- If two, three or four years are seen together, what is then the mean number of missing taxa?
- How does the number of sampling periods in each year affect the number of missing taxa?

Number of missing taxa

The mean numbers of taxa not included in the samples for any one year were 13.7 at Solbakken, 13.9 at Vollen and 14.3 at Dørålseter. This is nearly 50% of the total recorded number of species at Vollen and Solbakken, and 62% at Dørålseter.

Combining samples from two, three, and four years, results in a substantial decrease in the number of

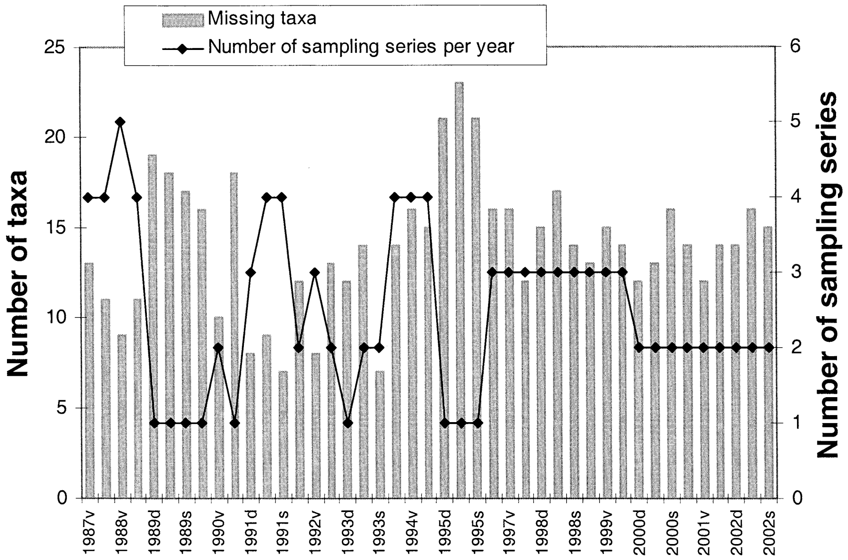

Figure 5. Number of sampling series and missing taxa at Døràlseter (d), Vollen (v) and Solbakken (s) for each year and locality.

missing taxa. At Solbakken, two, three and four years running intervals result in mean numbers of 9.5, 7.3, and 5.9 missing taxa respectively (cf. Fig. 3).

The actual results from each period show that four-year periods unveiled most of the taxa in the years before 1995. For the last 6 years, i.e. the period after 1995, the four-year running interval resulted in the relatively stable number of 7 to 9 missing taxa for each sampling period. The most dominant or abundant species where found nearly every year while more than 60% of the species at Dørålseter and about 30% of the species at Vollen and Solbakken were present in only 25% of the years (Fig. 4).

Rare species constitute a general problem in monitoring programmes. Species which occur only in a few samples are often supposed to be 'tourists' in the sense that they do not have a complete life cycle at the locality. Species with a low abundance that do not occur every year in the samples due to sampling error and/or annual variation of the population, are 'real' rare species. These species are often of great interest from a biodiversity conservation aspect. Beisel et al. (1998) found that more than 46% of the species at a given locality had both low abundance and were present in only one or a few mesohabitats on the river bed. They recommended that the sampling program was designed to include a sufficient number of mesohabitats. However, as this study indicates, species with low abundance may even then not be detected unless the sampling effort is increased beyond all practical means.

When the results are evaluated in this way, there is no evidence for a shift in dominance or a real disappearance or extinction of any species in Atna. The most extreme results are from the year 1995 when the low number of individuals collected also resulted a high number of missing taxa at all localities. The low number of individuals was most likely a result of the extreme spring flood in this year.

Seasonal sampling and number of missing taxa

Sampling was done one to five times per year. One sampling series per year always results in a high number of missing taxa. While two sampling series per year results in a lower number of missing taxa, there is no clear difference between two and tree series per year. Four or five sampling series most often results in a low number of missing taxa, but not in all years (Fig. 5).

Monitoring of human-induced disturbance

In addition to a species by species analysis of changes in the Plecoptera and Ephemeroptera communities, there are several other methods available for describing or testing changes in community structure. Diserud & Aagaard (2002) found that the results were affected by the way the community structure was measured and that the conclusion depended heavily on the estimate of the environmental variation. Even with a moderate expectation of environmental variation, the results could vary a great deal and still be within the limits of the expected range.

In general, monitoring a large number of rare species will always be an expensive and difficult task. Monitoring environmental changes or pollution effects, on the other hand, could be done with much lower effort through methods based on models of community structure or diversity indices. Most methods for monitoring freshwater insects are best suited for detection of pollution impacts on community structure or species composition. So far, no index of rare species, or predictive models for the occurrence of rare species, have been suggested. The methods for rare species monitoring are all based on observation of the actual species in samples, which renders these methods expensive and cumbersome.

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Annex A. Plecoptera and Ephemeroptera larvae in Surber samples from Dørålseter. Species not identified but possibly present as a component of an unidentified taxon are marked by □. Species not present in the samples are indicated as missing taxa (m.t.).

Year	1989	1990	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	Total	%
# sampling series per year	1	1	3	2	1	4	1	3	3	3	2	2	2	28	
Baetis rhodani	1	19	24	22	3	14	m.t.	m.t.	m.t.	30	10	4	1319	1446	36,88
Capnia atra	□	15	151	8	77	□	□	□	□	507	226	110	31	1125	28,69
Protonemura meyeri	m.t.	1	19	2	9	6	14	15	4	24	24	21	34	173	4,41
Brachyptera risi	12	m.t.	17	m.t.	6	7	m.t.	5	m.t.	m.t.	38	14	2	101	2,58
Arcynopteryx compacta	m.t.	6	16	4	m.t.	5	m.t.	2	3	9	3	m.t.	6	54	1,38
Nemoura cinerea	□	2	8	m.t.	□	m.t.	m.t.	□	□	□	3	6	20	39	0,99
Nemurella pictetii	m.t.	m.t.	4	m.t.	4	3	m.t.	m.t.	2	10	3	3	m.t.	29	0,74
Leuctra digitata	m.t.	m.t.	m.t.	m.t.	m.t.	2	m.t.	1	3	8	□	m.t.	6	20	0,51
Diura nanseni	m.t.	m.t.	1	m.t.	3	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	3	m.t.	7	0,18
Leuctra nigra	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	3	1	5	0,13
Heptagenia joernensis	m.t.	m.t.	2	2	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	4	0,10
Ephemerella aurivillii	m.t.	2	m.t.	1	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	4	0,10
Baetis muticus	m.t.	m.t.	1	2	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	3	0,08
Amphinemura borealis	m.t.	m.t.	1	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	3	0,08
Leuctra fusca	m.t.	m.t.	m.t.	m.t.	m.t.	□	m.t.	m.t.	□	1	1	m.t.	m.t.	2	0,05
Ameletus inopinatus	m.t.	1	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	0,05
Baetis lapponicus	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	m.t.	m.t.	m.t.	2	0,05
Leuctra hippopus	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	2	0,05
Isoperla obscura	m.t.	m.t.	m.t.	□	□	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	1	0,03
Taeniopteryx nebulosa	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	1	0,03
Baetis fuscatus	m.t.	m.t.	□	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	0	0,00
Baetis scambus	m.t.	m.t.	□	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	0	0,00
Siphlonurus aestivalis	m.t.	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	0	0,00
Identified individuals	13	46	245	43	103	38	14	23	12	591	310	165	1420	3023	77,10
Siphlonurus sp	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0,03
Perlidae	1	0	0	0	1	0	0	0	3	0	0	0	0	5	0,13
Isoperla sp.	0	0	0	6	5	0	0	0	0	0	0	0	0	11	0,28
Nemoura sp	1	0	0	0	6	0	0	5	6	8	16	1	0	43	1,10
Capnias sp	2	63	69	21	0	127	18	300	223	0	0	9	0	832	21,22
Leuctra sp.	0	0	0	0	0	1	0	0	2	0	3	0	0	6	0,15
Total number of individuals	17	109	315	70	115	166	32	328	246	599	329	175	1420	3921	100,00
Number of missing taxa	19	16	8	12	12	14	21	16	15	13	12	14	14	14,3	

Annex B. Plecoptera and Ephemeroptera larvae in Surber samples from Vollen. Species not identified but possibly present as a component of an unidentified taxon are marked by □. Species is not present in the samples are indicated as missing taxa (m.t.).

Year	1987	1988	1989	1990	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	Total	%
# sampling series per year	4	5	1	2	4	3	2	4	1	3	3	3	2	2	2	41	2,73
Baetis rhodani	1255	637	98	474	4415	1556	2586	728	18	1390	1249	2411	1726	1814	1699	22056	88,43
Diura nanseni	59	14	3	25	32	31	11	36	6	19	128	83	47	22	27	543	2,18
Capnia atra	1	□	□	4	51	24	2	□	m.t.	□	□	115	16	46	□	259	1,04
Isoperla obscura	m.t.	□	m.t.	□	1	2	45	10	□	16	5	□	14	48	68	209	0,84
Ephemerella aurivillii	42	6	1	2	20	43	6	5	m.t.	2	m.t.	1	1	4	15	148	0,59
Taeniopteryx nebulosa	28	6	m.t.	25	11	18	m.t.	7	m.t.	2	1	1	10	1	17	127	0,51
Isoperla grammatica	m.t.	□	m.t.	□	27	2	2	□	□	□	□	7	72	3	m.t.	113	0,45
Protonemura meyeri	1	1	m.t.	2	25	14	10	2	m.t.	m.t.	1	2	5	m.t.	2	65	0,26
Amphinemura borealis	□	□	m.t.	6	18	26	2	1	m.t.	1	1	m.t.	2	1	4	62	0,25
Ameletus inopinatus	3	1	m.t.	m.t.	26	13	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	2	m.t.	46	0,18
Brachyptera risi	m.t.	m.t.	1	1	14	2	10	m.t.	m.t.	2	m.t.	5	1	4	2	42	0,17
Baetis subalpinus	2	m.t.	m.t.	m.t.	27	2	m.t.	m.t.	m.t.	1	m.t.	5	m.t.	m.t.	m.t.	37	0,15
Leuctra nigra	3	8	m.t.	m.t.	m.t.	m.t.	16	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	27	0,11
Amphinemura sulcicollis	□	□	m.t.	1	8	1	6	m.t.	m.t.	1	m.t.	1	m.t.	3	m.t.	21	0,08
Leuctra hippopus	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	18	18	0,07
Heptagenia joernensis	m.t.	m.t.	m.t.	m.t.	1	10	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	12	0,05
Leuctra fusca	1	□	□	□	1	1	m.t.	m.t.	m.t.	m.t.	m.t.	5	1	m.t.	m.t.	9	0,04
Capnopsis schilleri	m.t.	m.t.	m.t.	1	m.t.	7	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	8	0,03
Heptagenia dalecarlica	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	7	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	8	0,03
Leuctra digitata	1	□	□	2	□	□	m.t.	m.t.	m.t.	m.t.	□	m.t.	□	1	2	6	0,02
Siphonoperla burmeisteri	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	3	m.t.	m.t.	m.t.	m.t.	4	0,02
Baetis muticus	m.t.	m.t.	m.t.	m.t.	m.t.	4	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	4	0,02
Nemurella pictetii	m.t.	1	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	0,01
Siphlonurus aestivalis	□	□	□	□	m.t.	m.t.	2	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	0,01
Nemoura avicularis	m.t.	□	1	1	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	□	m.t.	2	0,01
Baetis fuscatus/scambus	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	0,00
Nemoura cinerea	m.t.	□	m.t.	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	□	m.t.	0	0,00
Identified individuals	1396	674	104	545	4677	1757	2699	797	24	1434	1388	2636	1897	1949	1854	23831	95,54
Diura sp.	17	2	0	0	0	0	0	0	0	0	2	0	44	0	0	65	0,26
Amphinemura sp.	3	6	0	0	2	0	0	0	0	0	0	0	0	1	0	12	0,05
Isoperla sp.	0	5	0	25	134	137	41	9	4	14	24	172	0	13	0	578	2,32
Nemoura sp.	0	2	0	0	91	0	0	0	0	0	0	0	0	3	0	96	0,38
Capnia sp.	15	13	4	37	53	0	0	5	0	24	8	0	0	0	110	269	1,08
Leuctra digitat/fusca	2	5	1	13	26	9	0	0	0	0	1	0	2	0	0	59	0,24
Siphlonurus sp.	9	22	1	1	0	0	0	0	0	0	0	0	0	0	0	33	0,13
Baetis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,00
Total number of individuals	1442	729	110	621	4983	1903	2740	811	28	1472	1423	2808	1943	1966	1964	24943	100,00
Number of missing taxa	13	9	18	10	9	8	14	16	23	16	17	15	13	12	16	13,9	0,06

Annex C. Plecoptera and Ephemeroptera larvae in Surber samples from Solbakken. Species not identified but possibly present as a component of an unidentified taxon are marked by □. Species not present in the samples are indicated as missing taxa (m.t.).

Year	1987	1988	1989	1990	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	Total	%
Sampling series pro year	4	4	1	1	4	2	2	4	1	3	3	3	2	2	2	38	
Baetis rhodani	138	118	16	109	788	121	91	480	4	166	203	1120	757	830	123	5064	45,04
Ephemerella aurivillii	128	38	24	14	25	1	47	26	3	11	71	31	732	52	116	1319	11,73
Baetis fuscatus/scambus	50	393	47	m.t.	70	m.t.	89	95	4	182	124	83	m.t.	m.t.	61	1198	10,66
Heptagenia dalecarlica	46	15	2	2	17	9	6	63	m.t.	47	122	110	86	33	66	624	5,55
Diura nanseni	111	22	26	13	58	1	16	68	7	57	65	72	27	19	15	577	5,13
Heptagenia joernensis	68	19	32	□	44	1	31	39	14	72	16	22	m.t.	1	m.t.	359	3,19
Baetis subalpinus	2	8	26	m.t.	11	m.t.	3	63	1	53	65	16	11	5	52	316	2,81
Baetis muticus	19	15	2	4	13	8	5	83	m.t.	22	50	6	21	11	m.t.	259	2,30
Amphinemura borealis	□	4	1	16	74	14	1	4	m.t.	12	m.t.	m.t.	17	25	m.t.	168	1,49
Ameletus inopinatus	m.t.	m.t.	m.t.	m.t.	28	11	30	9	m.t.	9	1	m.t.	m.t.	3	m.t.	91	0,81
Ephemerella mucronata	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	□	m.t.	m.t.	1	16	18	1	m.t.	m.t.	36	0,32
Leuctra fusca	2	5	□	3	□	2	□	□	m.t.	4	7	9	□	m.t.	2	34	0,30
Taeniopteryx nebulosa	1	1	m.t.	m.t.	8	1	m.t.	m.t.	m.t.	m.t.	2	6	2	2	2	25	0,22
Leuctra digitata	□	□	□	□	1	□	3	□	m.t.	□	1	m.t.	□	m.t.	5	10	0,09
Siphonoperla burmeisteri	1	2	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	1	m.t.	m.t.	m.t.	4	1	10	0,09
Amphinemura sulcicollis	m.t.	m.t.	m.t.	m.t.	7	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	m.t.	9	0,08
Capnia atra	□	□	m.t.	m.t.	2	1	m.t.	□	m.t.	m.t.	m.t.	2	m.t.	4	□	9	0,08
Leuctra nigra	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	7	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	7	0,06
Protonemura meyeri	m.t.	m.t.	m.t.	m.t.	5	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	6	0,05
Leuctra hippopus	4	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	5	0,04
Nemoura sp.	m.t.	m.t.	m.t.	m.t.	4	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	5	0,04
Isoperla grammatica	m.t.	□	m.t.	m.t.	1	1	2	m.t.	m.t.	m.t.	□	m.t.	□	m.t.	□	4	0,04
Isoperla obscura	m.t.	m.t.	m.t.	m.t.	1	m.t.	1	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	1	4	0,04
Heptagenia sulphurea	□	m.t.	m.t.	□	□	□	m.t.	m.t.	m.t.	□	m.t.	3	m.t.	m.t.	m.t.	3	0,03
Baetis lapponicus	□	1	m.t.	m.t.	m.t.	m.t.	□	m.t.	□	m.t.	m.t.	1	m.t.	1	m.t.	3	0,03
Siphlonurus sp.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	0,01
Nemurella pictetii	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	0,01
Leptophlebiidae	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	0,01
Identified individuals	570	642	176	161	1158	172	336	930	33	638	743	1499	1654	992	444	10148	90,26
Isoperla sp.	0	1	0	0	122	11	0	0	0	0	2	0	5	0	3	144	1,28
Perlodidae(=nanseni?)	0	9	0	0	0	0	2	0	0	25	0	0	84	0	0	120	1,07
Amphinemura sp	4	12	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0,14
Baetis sp.	2	0	0	0	0	0	1	0	2	0	0	0	0	0	0	5	0,04
Heptagenia sp.	13	0	0	3	8	2	0	0	0	15	0	0	0	0	0	41	0,36
Ephemerella sp.	0	0	0	0	0	0	2	0	0	0	0	0	525	0	0	527	4,69
Leuctra fusca/digiata	17	3	6	74	78	2	2	10	0	24	12	0	14	0	0	242	2,15
Total number of individuals	606	667	182	238	1366	187	343	940	35	702	757	1499	2282	992	447	11243	100
Number of missing taxa	11	11	17	18	7	13	7	15	21	12	14	14	16	14	15	13,7	