Ann. Zool. Fennici 26:43–52. 1989

Simulated effects of the beaver on vegetation, invertebrates and ducks

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Nummi, P. 1989: Simulated effects of the beaver on vegetation, invertebrates and ducks. — Ann. Zool. Fennici 26:43–52.

The effect of beaver flood on the riparian vegetation, aquatic invertebrates and waterfowl broods of a creek was studied in southern Finland in a barren watershed area. The vegetation and invertebrate communities, as well as waterfowl brood use, in a section of a creek were monitored before artificial damming in 1984 and thereafter during the first three years of inundation (1985–1987). The flooding tolerance of floodplain trees differed markedly. As early as 1985, grey alders exhibited pronounced signs of stress, whereas willows were still in fairly good condition in 1987. Most of the macrophyte stands became considerably thinner during the three years of inundation, although the species composition was not radically altered. *Potentilla palustris* tolerated flooding very well. The benthic invertebrate communities of the littoral and river bed changed in slightly different directions during inundation. In the littoral, the most numerous forms were chironomids and *Asellus*. In the river bed *Pisidium* abounded, together with chironomids. The limnic forms of the littoral, particularly *Eurycercus*, were most abundant during the first year of flooding. The study suggests that the beaver can act as a keystone species by affecting the structure of riparian communities. The waterfowl can take advantage of these changes.

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1. Introduction

With their ability to build dams, the beavers *Castor fiber* L. and *C. canadensis* Kuhl can have a considerable effect on the riparian zone of creeks and ponds in particular. It is known that the flooding of watersides modifies their nutrient cycling, decomposition and vegetation dynamics, and allochtonous inputs, as well as the shape of the shore line (Kadlec 1962, Baxter 1977, Pederson & van der Valk 1984, Naiman et al. 1984). Beaver dams also increase the retention of sediment and organic matter, thereby influencing the character of the water and materials that are transported downstream (Naiman et al. 1986).

During one cycle of beaver impoundment, the riparian zone returns to an early stage of secondary succession twice: first, as the water rises on the shore, an aquatic ecosystem develops (Knudsen 1962, Danell & Sjöberg 1982). Second, the terrestrial succession begins on the exposed mud flat when the waters recede after abandonment by beavers (Neff 1957, Knudsen 1962).

In their study on the biogeochemical effects of beaver Naiman et al. (1986) concluded that the beaver acts as a keystone species in stream ecosystems. In this study I will examine the keystone effect of the beaver on animal and plant communities. This article concentrates on the first phases of succession in the flooded area. I will investigate the role of decomposing plant matter which forms the base of the food chain leading to waterfowl via invertebrates. In order to obtain a picture of the animal and plant life in the creek before the arrival of beaver a further study was made: a section of creek was monitored for one summer and then dammed.

2. Study area and methods

The fieldwork was performed in the barren watershed area of Evo (61°N, 25°E) in southern Finland. The water bodies of the area consist of small lakes and ponds, most of which are dystrophic or oligotrophic (Artimo 1960). The ponds are often surrounded by narrow peat bogs. The vegetation in the ponds and lakes is sparse but lush on the shores of creeks which run between lakes. The creek valleys are normally narrow but widen here and there to form a floodplain. Trees in the floodplains are mostly alders *Alnus incana* L. and *A. glutinosa* L., downy birch *Betula pubescens* Ehrh. and willows *Salix* sp. Scots pine *Pinus sylvestris* L. and Norwegian spruce *Picea abies* L. abound in the other parts of the area.

The work started in 1984 in two sections of Saukonoja creek. The lower section was flooded, while the upper was used as a control during the study. After damming in October 1984 the water rose about 50 cm and a flowage of 1 hectare was created. The inundated flood plain was normally under water during the high waters of spring, and during heavy rain parts of it may have been flooded also at other times. Saukonoja creek is a typical beaver habitat. Beavers dammed some sections of it in the 1960s, and, particularly in 1986 the beavers (introduced *C. canadensis*) foraged intensively in the man-made study pond.

2.1. Water analyses

The depth of the water was measured by the transects at intervals of 5 m. At the inflow and the outflow of the pond the water temperatures were measured and water samples collected in two glass bottles in July 1985-87. The samples were taken to the laboratory for pH and conductivity measurements. The water velocity was measured by floating a ball filled with water for 10 m; two trials were performed in July 1984 and 1985.

2.2. Vegetation analyses

Two line transects of 70 m and 55 m were laid across the flowage. Between 26 June and 10 August 1985–87, all the macrophytic species and shrubs under a height of 0.5 m which touched the line were noted at intervals of 0.5 m.

In 1984–87, the biomass of herbaceous vegetation in the floodplain was determined by harvesting the plants from 20 quadrats of 0.25 m^2 by the transect; the species present in these samples were recorded, too. The samples were dried for 1–2 days at 40°C before weighing. Also in 1984–87, leaf litter from trees in the flowage was collected in 12 buckets attached to floating plates; in 1984, the first collection was made from the ground in 0.25 m^2 quadrats (n = 12), which presumably bias the litter biomass values of 1984 to a slightly higher level in comparison with the later years. This is because some older leaves were also collected by this means. The collection period lasted about two months, from August to October. The buckets were emptied every second or third week. Litter samples were dried in the same way as the herbaceus vegetation.

Individual trees (n = 16 for each species, except for black alder n = 8) were marked in August 1985 and their condition monitored every year at the same time. The following classification was used: I = tree dead, without foliage; II = no more than 50% of the foliage left; III = some colour changes in the foliage, over 50% of the foliage left; IV = no apparent changes in the foliage. In 1984 the trees were studied by determining the coverage of the canopies.

2.3. Invertebrate sampling

During June, emerging insects in the flowage were collected in four floating hood traps (bottom area 0.5 m^2), which were emptied with a small vacuum cleaner. A hood trap was made of a ring shaped plastic tube over which a net (mesh size 0.5 mm) was stretched by the aid of a metal arch. In 1985–87, the traps were set for a total of 17 days (trapping periods lasted 5×3 and 2×1 day(s) every year); in 1984, the traps were set for only four periods of one day.

Freeswimming invertebrates and species living on the submerged vegetation were sampled in June in the littoral with a sweep net (aperture 177 cm^2, mesh size 0.5 mm). Four, eight and twelve samples were taken in 1985, 1986 and 1987, respectively. A water volume of about 33 litres was swept for each sample.

A tubular Hakala sampler (15.2 cm^2) was used in July for the collection of benthic invertebrates of the littoral at depths of 515 cm. The invertebrates of the creek bed were collected with an Ekman dredge (289 cm^2) at depths of 1.2–1.8 m. The animals were picked out by hand after sorting with an automatic sieve (smallest mesh size 0.5 mm).

2.4. Waterfowl observations

The data on use of the flooded area by the waterfowl broods was collected from a tower using observations of 15 and 60 minutes. These were performed almost daily at 0700–0900 hours or 1900–2100 hours from mid June to the beginning of August. During these periods waterfowl broods are usually feeding actively.

3. Results

3.1. Water

No differences were found in water pH, conductivity or temperature in the outflow of the pond as compared with the upper course. The pH of the water was 6.1–6.2 and the conductivity 4.4–4.5 mS/m(γ_{25}).

The mean depth of water in the flowage was 55 cm (range 15–78 cm; does not include the river bed). The water velocity in the creek section under study was about 0.4 m per second before the damming and about 0.03 m per second during the time of inundation. Water was not, then, stagnant, nor did it strongly erode the flooded area.

3.2. Vegetation

The flooding tolerance of trees

The only tree species growing in the flowage that showed pronounced signs of stress in the first year of

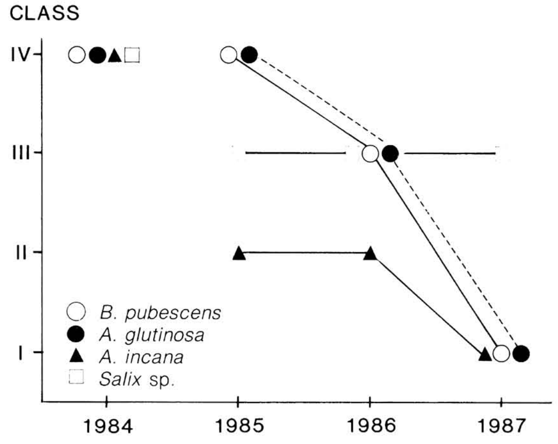

Fig. 1. Condition of different tree species in the flowage area during 1984–1987 (modes). *Betula pubenscens*, n = 16; *Alnus glutinosa*, n = 8; *A. incana*, n = 16; *Salix* sp., n = 16.

flooding was the grey alder *Alnus incana* L. (Fig 1, mode in class II). The colour of the foliage of willows *Salix* sp. had changed slightly but the quantity of leaves apparently had not diminished (class III). Very little signs of waterlogging were detected in downy birches *Betula pubescens* Ehrh. or black alder *Alnus glutinosa* L. (class IV). Before the inundation practically all the alders and birches were growing on dry ground (except during the spring run-off). In 1986 (2nd year) obviously more signs of stress were noted in birches and black alders ($P < 0.01$, Mann-Whitney U-test), and slightly more in grey alders (but no changes in the mode). During the third year of flooding willows were still in fairly good condition. The mode of all the other trees had dropped to class I, i.e. only a few trees had some foliage left.

Macrophytes

The species composition of macrophytes did not change very much during the three years of inundation (Tables 1–2), i.e. most of the species had at least some line contacts each year. However, most of the plant stands became considerably thinner. The most common species, which had already disappeared by the second year of flooding, was *Carex vesicaria* L. The number of line contacts of *Lysimachia vulgaris* L. also decreased considerably between the first and second year of flooding. The number of line contacts of initially common *Calamagrostis canescens*

Table 1. The number of contacts of macrophytic plant species (half meter by half meter) with two transects (70 m and 55 m) laid across the flowage. Species are shown in an arbitrary order of descending flooding tolerance.

	1985	1986	1987
Potentilla palustris	22	37	36
Lysimachia thyrsiflora	24	12	25
Nuphar lutea	–	6	7
Phalaris arundinacea	8	15	10
Utricularia vulgaris	4	15	5
Carex nigra	28	26	6
Lemna minor	–	6	1
Myriophyllum alterniflorum	–	2	2
Iris pseudacorus	2	4	1
Equisetum fluviatile	–	3	–
Phragmites australis	36	29	13
Calamagrostis canescens	43	33	10
C. purpurea	22	12	5
Scirpus sylvaticus	9	6	5
Lythrum salicaria	7	4	3
Calla palustris	9	9	2?
Sphagnum sp.	9	6	4
Lysimachia vulgaris	7	4	3
Carex globularis	5	–	–
C. vesicaria	16	–	1
Miscellaneous (9)	11	1	–
Salix sp.	34	29	47

Table 2. The frequencies of occurrence of herbaceous plants before and during the first year of flooding in 20 quadrats of 0.25 m^2.

	1984	1985
Potentilla palustris	0.2	0.3
Lysimachia thyrsiflora	0.1	0.15
Phalaris arundinacea	0.05	0.05
Utricularia vulgaris	–	0.05
Carex (nigra & vesic.)	0.4	0.3
Phragmites australis	0.2	0.2
Calamagrostis (can. & purp.)	0.6	0.3
Scirpus sylvaticum	0.2	0.05
Calla palustris	0.5	0.1
Lysimachia vulgaris	0.35	0.35
Equisetum sylvaticum	0.15	0.1
Filipendula ulmaris[1]	0.15	0.05
Deschampsia[1]	0.05	–
Caltha palustris	0.1	–
Viola palustris	0.2	–

[1] included in "Miscellaneous" in Table 1.

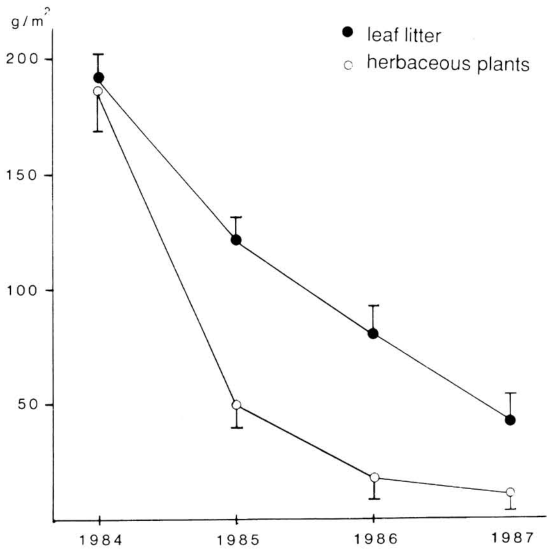

Fig. 2. Biomass (mean±*SE*) of autumnal leaf litter (n = 12) and herbaceous plants (n = 20) per square meter in flowage during 1984–1987.

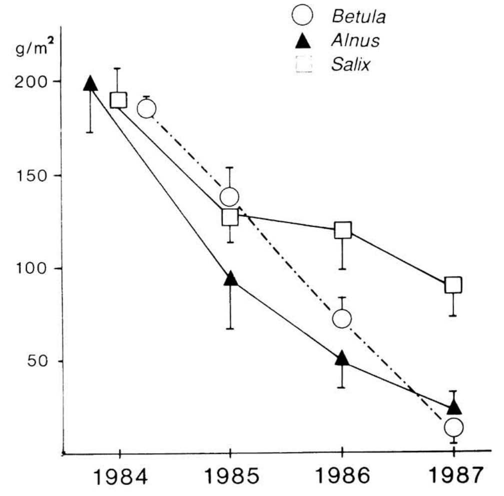

Fig. 3. Biomass (mean±*SE*) of autumnal leaf litter fall from different tree species in the flowage. (*Betula pubescens*, *Alnus glutinosa* and *A. incana*, *Salix* sp. n = 4.

(Weber) Roth and *Phragmites australis* (Cav.) Trin. did not decrease until 1987.

Two species that were spreading, at least according to the transects, were *Potentilla palustris* (L.) Scop. and *Nuphar lutea* (L.) Sibth. & Sm. The latter invaded from the deeper areas in the vicinity of the transect. The number of shoots of *Lysimachia thyrsiflora* L. decreased at first but then increased again. Quite the reverse was true for *Utricularia vulgaris* L.

The biomass of herbaceous vegetation and tree leaves

In 1984, the biomass of herbaceous plants per square metre and that of the dead leaves in the flood plain did not differ from each other (Fig. 2). But during inundation the production of herbaceous plants decreased at a faster rate, and in 1985–87 there was a marked difference ($P < 0.001$, Mann-Whitney) in the biomass of herbaceous plants and leaf litter.

The differences in biomass of leaf litter (Fig. 3) from stands of birches, alders (grey and black combined) and willows support the picture which emerged from the observations of the condition of the different trees (Fig. 1): the decrease in the biomass of leaves between 1984 and 1985, for example, was most pronounced in alders ($P < 0.05$), and the difference between the willows and the rest was greatest in 1987. The trend would be even more clear without the bias of two factors. Firstly, the buckets placed under, for example, birch stands often contained at least some leaves from other tree species growing nearby. Secondly, one alder bucket was placed under a black alder stand, and this particular bucket collected considerably more leaves than the rest during the last two years. Without the black alder, the average for alders in 1987 would fall below the biomass of birch leaves.

3.3. Invertebrates

Littoral

Littoral macro-benthos increased only in the second year of flooding (Fig. 4) whereas freeswimming invertebrates (Table 3) were most abundant in the first year ($P < 0.01$, Mann-Whitney). Thereafter the number of freeswimming invertebrates have decreased. The high number of invertebrates in the first year were due to the abundance of waterfleas of the large-sized genus *Eurycercus* (Table 3).

The significant increase ($P < 0.01$, Wilcoxon) in the number of benthic invertebrates in the second year of flooding was caused mainly by the increase of chironomid larvae and waterlice *Asellus aquaticus* L. (Fig. 4). Chironomids had already grown more nu-

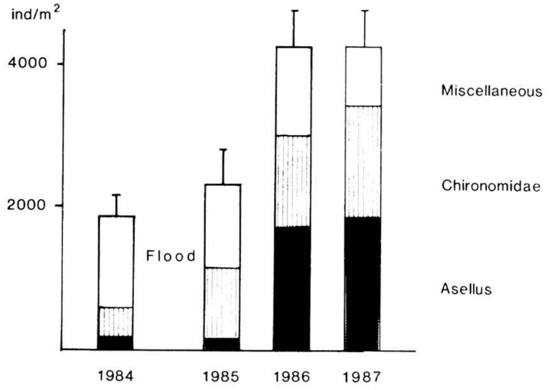

Fig. 4. Density (mean+*SE*) of benthic invertebrates of the littoral in flowage area in July during 1984–1987 (yearly sample size 30). The most important groups during inundation included in "Miscellaneous" are Oligochaeta and Cladocera.

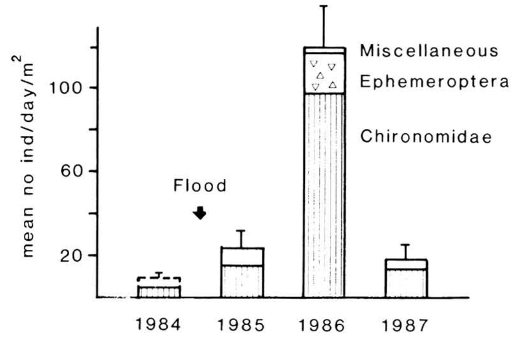

Fig. 5. Number of emerging insects (mean+*SE* for means of each collection) per day in June in the flowage. During 1985–1987 the trapping covered 17 days, in 1984 only 4. During 1985– 1987, *n* = 4; in 1984, *n* = 2. During 19841985 and 1987 Ephemeroptera are included in "Miscellaneous" as well.

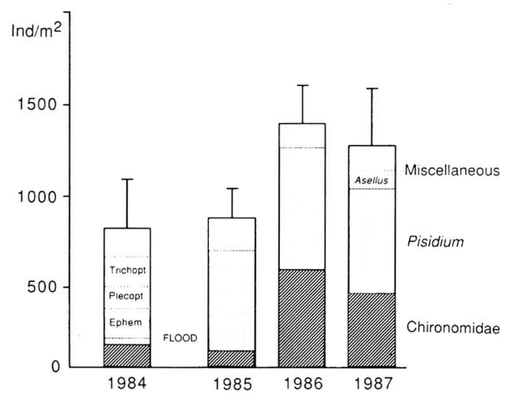

Fig. 6. Density (mean+*SE*) of benthic invertebrates of the creek bed in early August during 1984–1987. During 1984–1986, *n* = 6; in 1987, *n* = 5. Trichoptera and Plecoptera are included in "Miscellaneous" during 1985–1987, as are Ephemeroptera in 1987 and *Asellus* in 1984.

Table 3. Mean densities of freeswimming invertebrates (individuals/m³) in the flowage in 1985, 1986 and 1987.

	1985	1986	1987
Cladocera	3440	92	48
Chironomidae	480	128	8
Gerridae	–	256	8
Gastropoda	–	148	4
Ephemeroptera	–	8	40
Miscellaneous	120	228	112
Total (mean±*SE*)	4080±624	868±308	220±84
n	4	8	12

merous in 1985, but *Pisidium*-clams and the larvae of stoneflies (Plecoptera) and alderflies *Sialis*, all three of which were rather common prior to flooding, had disappeared at the same time. Emerging chironomids, especially large-sized *Chironomus* cf. *riihimaekiensis* Wülker, were also numerous in 1986 during a period of about three weeks in June (Fig. 5). Another group, mayflies (Ephemeroptera), had an equally high but clearly shorter emergence peak at the beginning of June (Nummi 1988).

In the community of benthic invertebrates of the littoral, the number of taxa was lowest (6) during the first year of inundation. Prior to flooding it was 14; in 1986 it was 11 and in 1987 it was 8. In limnic forms the number of taxa during flooding was also lowest (6) in 1985; in 1986 it was 10 and in 1987 it was 11.

River bed

In the river bed the number of invertebrates also increased significantly ($P < 0.05$, Mann-Whitney) only in 1986 (Fig. 6). *Pisidium* numbers grew higher in the first year of flooding but the larval densities of mayflies, caddis-flies (Trichoptera) and stoneflies decreased at the same time. The number of chironomids increased only in 1986. In 1987, there was a slight decrease in the invertebrate density in the river bed. However, there were substantially more waterlice in 1987 than in 1986.

The number of taxa varied less (10 in 1984–86, 11 in 1987) in the creek bed than in the newly flooded littoral. However, after flooding individuals of only two taxa *Pisidium* and Chironomidae together comprised 80–90% of the total.

3.4. Waterfowl

The use of the flooded section of the creek by the waterfowl broods was much higher during inundation than prior to it. During the first and second year of flooding slightly under two broods per hour were observed in the flowage and during the third about one; before the flooding only one brood was detected during the whole summer. In the first year apparently four different broods were using the flowage and in the second and third presumably six were seen. Teals *Anas crecca* L. were the most regular dwellers in the flowage, especially in 1985 (Nummi 1988). Other species present were the mallard *A. platyrhynchos* L. and the goldeneye *Bucephala clangula* L.

4. Discussion

4.1. Response of plants to flooding

Macrophytes

The plants growing in the flowage were species which would normally have to face periods of inundation, especially during the spring run-off, and the plant community did not change very rapidly. However, as the flooding continued, the numbers of most of the littoral macrophytes declined and some species disappeared altogether (Tables 1–2). Similar results have been obtained in earlier studies in North America (Harris & Marshall 1963, Millar 1973) and northern Europe (Sjöberg & Danell 1983).

Millar (1973) stated that macrophytes growing at greater than normal depths had to allocate extra energy to reach the surface; this will often weaken the plants and even cause some of the species to die off during continuous flooding. He also pointed out that growth of new shoots may be impeded by the increased water pressure. Additional effects of prolonged flooding are composed of changes in soil particle size, turbulence and light (Spence 1967) as well as the development of toxic conditions (Crawford 1969) caused by the lack of oxygen (Etherington 1983). Increase in water depth would, therefore, be the most important factor affecting the change of the flowage vegetation, as has also been suggested by others (Kadlec 1962, Harris & Marshall 1963, Munro 1967, Sjöberg & Danell 1983).

In this study, the effect of depth could perhaps best be seen in *Calamagrostis canescens*: in 1985, its stands grew at depths of 25–55cm but in 1987 there were shoots of this species only atdepths of 25–35 cm. The distribution of *Lysimachia thyrsiflora* in the flowage also changed interestingly in relation to depth. It was found initially in places where there was a water layer of 40–55 cm — from 1985 to 1986 its numbers decreased there. In 1987, *L. thyrsiflora* increased but now it was growing in places where the water depth did not exceed 40 cm. Sjöberg & Danell (1983) also found *L. thyrsiflora* to be susceptible to a prolonged rise in the water level.

The macrophytes differ substantially with respect to their flooding tolerance. While most of the plants in the flowage decreased, *Potentilla palustris* continued to flourish even at a depth of 70–80 cm and also increased there. Possibly the floating ability of the plant's rhizomes aided its survival.

Trees

Willows are known to have great flooding tolerance (Gill 1970) and in this study willows too were the only trees still in good condition in 1987 (Figs. 1, 3). Flooding in the dormant season has little or no effect on the trees (Hall & Smith 1955). However, survival through three growing seasons (480 days in total, Kalliola 1973) has not been reported very often, if one excludes trees growing in tropical swamp forests (Harms et al. 1980). One factor that apparently promoted good survival was that water in the flowage was not totally stagnant. In stagnant floods, the hypolimnion and submergent soil can be totally deficient in oxygen (Gill 1970).

Interestingly enough, the willows showed some signs of stress during the first year of inundation while birches and black alders did not (Fig. 1). The reason for this could be that willows were using resources to produce tussocks of adventitious roots which emerged close to the better oxygenated air/water interface. These "water roots" are common in many flood tolerant species (Gill 1970, Etherington 1983). It has been shown that the cutting of adventitious roots will eventually lead to cessation of shoot growth (Jackson 1955). In my study flowage *L. thyrsiflora* also had adventitious roots.

Further adaptations of willows to oxygen shortages include effective transportation of oxygen from shoot to roots (Huikari 1959). Water-tolerant trees are also suggested to control the toxicity of ethanol by diversication of the endproducts of glycolysis (Wilde et al. 1950, Crawford 1976).

4.2. The change in the invertebrate community

Disturbance is known to affect the structure of communities by reducing the number of species, and allowing populations of some of the survivors to reach very high levels (Patrick 1963). In this study the disturbance is caused mainly by the presence of large amounts of decaying organic matter. The effect of this organic loading could be seen in the littoral of the flowage during the first year of flooding: the number of species decreased but the numbers of one, the water flea *Eurycercus*, became very high (Table 3).

In other studies of flooded meadows, these water fleas have also been found to be extremely abundant (Brandl 1963, ref. Straskraba 1965). The food of *Eurycercus* is known to consist mainly of detritus (Smirnov 1962). As a filter feeder it apparently used the fine particulate organic matter (FPOM) which was released from the inundated litter (Nelson & Kadlec 1984). Because its ability to reproduce rapidly (Smirnov 1962) *Eurycercus* was the first macroinvertebrate species to reach high numbers in the flowage.

Another reason for the abundance of *Eurycercus* in 1985 was that fish apparently had not become very numerous by the first year of inundation. Fish are known to control populations of *Eurycercus*, as well as of other large-sized cladocerans (Straskraba 1965). In impoundments where fish have been present the abundance of *Eurycercus* has been of short duration (Runnström 1955).

During later years — 1986 and 1987 — the number of free-swimming invertebrates did not differ from that of a eutrophic pond situated nearby; they did differ from that of an oligotrophic lake, though (Nummi 1988).

Paterson & Fernando (1969) found chironomids to be rapid colonizers, as was also the case in this study (Figs. 4–5). In the streambed the lag in chironomid increase could be due to a slow rate of sedimentation (Fig. 6). A large number of chironomids are known to be associated with soft bottoms (Naiman et al. 1984) — they also feed on fine particulate organic matter (FPOM) (Anderson & Sedell 1979). *Pisidium* clams apparently benefited from the decrease in the water velocity more rapidly than chironomids. Drastic increases in the numbers of clams have also been reported in earlier studies of beaver ponds (Huey & Wolfrum 1956, Gard 1961). *Pisidium* filters fine grained detrital material (FPOM) by sucking in a current of watery sediment through its siphon (Moss 1980:123).

The number of *Asellus aquaticus* — a species which belongs to another functional group of detritivores — increased substantially only during the second year of flooding (Fig. 4). *Asellus* feeds on coarse particulate organic matter (CPOM) and is classified as a "shredder" (Williams 1962, Cummins 1974). Danell & Sjöberg (1982) also noted that *Asellus* grew numerous one year after it had appeared in their study flowage; *Asellus* colonized the more isolated water area of their study in the fourth year of flooding.

The reason for the benthic invertebrates failing to increase during the first year of flooding may be that they were influenced by the grazing of *Eurycercus*. Intensive grazing by large-sized *Daphnia* has been shown to effectively remove particles from the water column, and to reduce the rain of food for benthic animals (Korinek et al. 1987).

As we can see, the invertebrate fauna of the flowage was composed of two different elements: in the littoral chironomids were numerous in all three years and additional dominants were *Eurycercus* during the first, and *Asellus* during the second and third, year of flooding. In the streambed, however, there was a considerable increase of *Pisidium* in the first year of inundation which was followed by an increase of chironomids in the second. In addition, the streambed retained some forms, e. g. *Sialis*, which disappeared from the littoral.

According to Hynes (1963) a "pollution fauna" consists largely of oligochaetes (Tubificidae), *Asellus* and *Chironomus*; in addition, molluscs and *Sialis* can be numerous. In the context of this study "pollution" clearly means only the addition of organic matter. *Chironomus riihimaekiensis* has originally been described (Wülker 1973) from a forest pond but has later been found in running waste water of a certain grade (Hirvenoja, pers. comm.).

In this simulated beaver pond the autumnal leaf litter fall from trees presumably played an important role in the nutrition of invertebrates (Figs. 2–3). In addition, the input of organic material from the trees (mostly woody debris but also high-nutrient pollen) during other parts of the year can be considerable (Anderson & Sedell 1979).

4.3. Waterfowl

Ducks benefit from high invertebrate production of flooded areas (Whitman 1976, Danell & Sjöberg 1982, Nummi 1984). Both adults and young need the protein contained in invertebrates (Sugden 1973, Street 1978, Krapu 1979, Nummi 1985). Downy ducklings subsist mainly on insects caught on emergent vegetation and on invertebrates of the water surface. Thus, for them the structure of the vegetation is of importance. During the first years of flooding, the emergent shoots were distributed quite evenly in the pond. This meant that the ducklings were not obliged to concentrate their feeding efforts on the more dangerous shore line (Pehrsson 1979). In the open water, the trees were likely to conceal broods from raptors.

Adult ducks mainly search for invertebrates below the water surface (Swanson et al. 1979). In the study flowage, dabbling ducks — teals and mallards — fed exclusively in the flooded area, but the goldeneye adults apparently also obtained food from the streambed. The streambed becomes ice-free early. Hence, an increase in the invertebrates there could have been very beneficial to the goldeneyes, which were just starting to breed. Both chironomids and molluscs, which abounded in the streambed, are known to be important for goldeneyes (Bengtson 1971).

4.4. Beavers as keystone species

The keystone species often act by markedly changing the abundance of species in the communities (species assemblages) which they influence (Paine 1974, Järvinen et al. 1986). In this study it was found that in the early phase of simulated beaver flooding both the terrestrial (floodplain vegetation) and aquatic (stream invertebrates) communities are altered. As the beavers have a pronounced effect on small waters and watersides their widespread removal in Eurasia and North America in the 18th and 19th centuries has presumably influenced the abundance of many species. Naiman et al. (1986) underlined the fact that prior to this decline beaver occupancy was characteristic of many small streams of North America. It has been suggested, for example, that the recent increase of populations of wood ducks *Aix sponsa* L. and Canadian otter *Lutra canadensis* in parts of the United States is related to the recovery of beaver populations in these areas (Nevers 1968, Tumlison et al. 1982).

Acknowledgements. I am indebted to Kjell Danell, Olli Järvinen and Matti K. Pirhola for extensive help during this study. I also wish to thank Terhikki Alho for assisting with chemical analyses and Mauri Hirvenoja for chironomid identification. I am grateful to Heikki and Ritva Koivunen for the design and construction of the emergence traps. Kjell Danell, Mauri Hirvenoja, Olli Järvinen, Harto Lindén and Heikki Toivonen made valuable comments on the manuscript. The Finnish Cultural Foundation, the Finnish Game Foundation, the Hunters' Central Organization, and The Foundation for Research of Natural Resources in Finland provided financial assistance for this study.

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Received 15.VI.1988
Printed 23.VI.1989