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Long-term changes in the littoral benthos of a Norwegian subalpine lake in relation to the introduction of the European minnow (*Phoxinus phoxinus*)

Frode Næstad[1*] & John E. Brittain[2, 3]

[1]Department of Forestry and Wildlife Management, Hedmark University College, 2480 Koppang, Norway

[2]Natural History Museum, University of Oslo, PO Box 1172 Blindern, NO-0318 Oslo, Norway.

[3]Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Ås, Norway.

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*Corresponding author, e-mail: frode.nastad@hihm.no

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Abstract

The littoral benthos of the subalpine lake, Øvre Heimdalsvatn, has been documented in a series of investigations carried out in 1972, 1976, 1985 and 2000. During this 28 year period there have been major changes in the lake's fish population following the introduction of European minnow into the lake where brown trout was formerly the sole species.

In 1972 Ephemeroptera, Trichoptera, Plecoptera and *Gammarus lacustris* dominated the macrobenthos, constituting 85% of faunal numbers, while Chironomidae and Oligochaeta made up only c. 6%. However, by 1976 chironomids and oligochaetes had increased in relative abundance, while *G. lacustris* declined. This trend towards a dominance of chironomids and oligochaetes was confirmed in 1985 and 2000, although absolute numbers of Ephemeroptera, Plecoptera and Trichoptera increased in 2000 relative to 1972 values.

Gammarus lacustris had a two-year life cycle in Øvre Heimdalsvatn. In 1972 there were significantly more females than males, but by 1976 and through to 2000 there were greater numbers of males. Despite this reduction in females, numbers of juveniles increased, although mortality, probably due to increased predation from minnows, was higher than previously.

There have been major changes in the benthos of Øvre Heimdalsvatn over the 28 years from 1972 to 2000. These changes have occurred at the same time as the European minnow has been introduced to the lake and increased substantially in numbers. The effect of the introduction of minnows on the benthic macroinvertebrates of the lake littoral was clearly seen in the major reduction in the population of *G. lacustris* and the increased proportions of smaller forms, especially chironomids and oligochaetes in relation to Ephemeroptera and Trichoptera.

Introduction

The stony littoral zone of arctic and alpine lakes has been little studied despite its importance in lake production processes. The utilisation of allochthonous inputs in the littoral zone by aquatic invertebrates is often crucial to the energy budget of such lakes (Stockner & Hynes, 1976; Larsson et al.1978; France, 1995). The retention and processing of particulate organic matter is considered to be higher than in running waters (Johnson et al. 2004).

The littoral benthos may show considerable spatial and temporal variability in a structurally complex environment and this presents sampling problems (Reid et al., 1995; Tolonen et al. 2001; Johnson & Goedkoop, 2002; Johnson et al., 2004; Klemetsen & Elliott, submitted). The amount of detrital biomass is important for most macroinvertebrate taxa and its distribution is a major determinant of macroinvertebrate distribution and abundance (Brittain & Lillehammer, 1978; Weatherhead & James, 2001).

Recently, there has been increasing focus on arctic and alpine freshwaters, many of which are susceptible to anthropogenic impacts, both local and global (Brittain & Milner, 2001; Füreder et al., 2006; Maiolini et al., 2006). The introduction of alien fish species is one of such impacts. In New Zealand predation by large trout has probably eliminated small-bodied galaxids, and affected the distributions of crayfish and other large invertebrates from many streams (McIntosh, 2000; Townsend, 2003). Fish are frequently introduced into high elevation, headwater localities and this enables them to spread downstream to threaten native fish and invertebrate populations far removed from the site of introduction (Hesthagen et al., 1992; Adams *et al.,* 2001). However, the relationship between zoobenthic biomass and fish abundance is not always clear (Ramcharan et al., 1995).

Norwegian mountain lakes usually contain few fish species, and brown trout, *Salmo trutta* (L.), is often the sole species. However, during the last 40 years, the distribution of the European minnow, *Phoxinus phoxinus* (L.), has expanded in Norway, and its expansion has been particularly apparent in mountain areas (Borgstrøm 1973; Hesthagen & Sandlund 1997; Saltveit & Brabrand 1991; Museth et al., 2002), and it is in such ecosystems that the spread of the European minnow seems to have had the greatest ecological consequences (Saltveit & Brabrand, 1991). Because minnows often form large populations in these lakes and are restricted to littoral habitats where they often forms shoals, it has been concluded that they consume more littoral benthos than the original fish species (Hesthagen et al., 1992; Saltveit & Brabrand, 1991; Borgstrøm et al., 1985).

The aim of this paper is to document possible long-term changes in macroinvertebrate fauna of a subalpine lake during the period 1972-2000, during which there were major changes in the lake's fish population. It was hypothesised that the introduction and spread of the European minnow would change the composition and structure of the littoral macroinvertebrate benthos.

Lake description, methods and sampling sites

Øvre Heimdalsvatn is situated 1090 m a.s.l. in central southern Norway at the upper limit of the subalpine birch forest. The lake has a surface area of 0.775 km^2, a mean depth of 4.7 m and a maximum depth of 13 m. Øvre Heimdalsvatn is ice covered for 8 months of the year and is characterized by low autochthonous production and major allochthonous inputs. Three distinct depth zones are distinguishable in Øvre Heimdalsvatn (Brettum 1972; Brittain & Lillehammer 1978; Vik 1978). The uppermost littoral, termed the exposed zone because it is affected by wave and ice erosion has a substrate varying from boulders to sand, although stones are predominant. The lower limit of this zone varies in depth from 0.75m in the sheltered bays, to 4.5m in more exposed areas, but the major part is situated at depths less than 2 m. Below this zone is the macrophyte zone, extending up to the shoreline in the most sheltered bays where *Carex rostrata* occurs. This macrophyte zone is dominated by *Isöetes lacustris* that extends down to 5-5.5m around the whole lake, but in the western part *Scorpidium scorpoides* dominates. Below the macrophyte zone soft sediments dominate, although there are areas of stony and rocky substrates.

The benthos of Øvre Heimdalsvatn has been sampled several times since the initial survey in 1972, when 20 stations around the lake were sampled monthly during the ice free period (Fig. 1, Brittain & Lillehammer 1978). A single station (st. 15) was subsequently re-sampled in 1976, seven stations in 1985 (stns 2, 5, 11, 13, 14, 17 & 20), one station (st. 14) in 1986 and five stations in 2000 (stns 2, 11, 13, 14 & 17). An overview of sampling dates is given in Table 1. In the present analysis of long-term changes in the benthic fauna, only data from the same five littoral stations sampled in 2000 are included in addition to a single station in 1976. A more comprehensive treatment of the 1972 survey was given in Aagaard (1978), Aarefjord et al. (1978), Brittain (1978a, b, c, d), Brittain & Lillehammer (1978) and Lillehammer (1978a, b).

Because of the variety of substrates, several different methods depending on the aim and nature of the study have been used to sample the benthos in Øvre Heimdalsvatn (Aarefjord et al.1978, Brittain & Lillehammer 1978). In the present long-term analysis data from kick samples (Brittain 1978c; Frost et al. 1971) are compared. These samples were taken per unit time using nets with a mesh size of 450µm and at depths between 0 and 1 m.

Specimens of *G. lacustris* collected in 1972 were only sexed and measured from stations 14 and 15, while all specimens collected in subsequent years were sexed and measured. The generations of *G. lacustris* are designated after the number of summers, e.g. newborn are 0^+, last years generation 1^+ and the reproducing generation 2^+.

Despite intensive brown trout population studies since 1957, minnows were not observed until1969. The population increased rapidly, and in 1973 small shoals could be seen in some sheltered bays around the lake. The population continued to occupy new areas, but in 1979 minnows were still restricted to a few sheltered bays (Lien 1981). However, by 1985 minnows were found all around the whole lake (Bruun 1988), indicating that the population had continued to expand.

Results

In 1972, Ephemeroptera, Trichoptera, Plecoptera and *G. lacustris* were the dominant macroinvertebrate taxa in the shallow littoral of Øvre Heimdalsvatn (Fig. 2). Ephemeroptera constituted 31 % of faunal numbers, followed by *G. lacustris* with 29 %, Trichoptera 18 % and Plecoptera 7 %. Chironomidae and Oligochaeta numbers constituted only 6 and 0.3 %, respectively.

In 1976 the benthic fauna at st. 15 was dominated by Ephemeroptera and Chironomidae. Ephemeroptera were recorded in high densities in June and the beginning of July, while Chironomidae dominated in early July. Oligochaeta had increased in relative abundance and in numbers compared to 1972, while *G. lacustris* had declined in both relative abundance and numbers (Figs 2, 3).

In 1985 there was a marked change in the composition of the fauna, compared to 1972 (Fig 2). Chironomidae and Oligochaeta were the dominating taxa, and constituted 63 and 20 %, respectively. This was due to a significant increase in densities of these taxa (Table 2). Ephemeroptera, Trichoptera and Plecoptera had decreased in relative numbers (%), although there was a significant increase of Plecoptera numbers. Ephemeroptera and Trichoptera also showed a non-significant increase in densities at four out of five stations (Table 2).

Gammarus lacustris continued to decrease both in relative and absolute numbers (Figs 2, 3), although the decrease was not significant since the frequency at one station had increased (Table 2).

In 2000 the faunal composition was similar to 1985. The fauna was dominated by Chironomidae and Oligochaeta (66 % and 11 %, respectively) (Fig. 2). The numbers of

Ephemeroptera, Plecoptera, Trichoptera, Chironomidae and Oligochaeta had increased significantly compared with numbers from 1972 (Fig. 2, Table 2). *Gammarus lacustris* had decreased in relative terms and there was also a significant decrease in numbers (Table2). Compared to 1985, Oligochaeta showed a rather large and significant decrease in relative and absolute numbers (Figs 2, 3; Table 2). Chironomidae had increased relative to the other taxa, but showed a small decrease in absolute numbers (Figs 2, 3).

Gammarus lacustris had a small but non-significant increase in total numbers compared to 1985 (Fig. 4), due to an increase of juveniles of the year (0^+). Ephemeroptera and Trichoptera showed an increase both in absolute and relative numbers compared to 1985 (Figs 2, 3), although the increase was only significant for Ephemeroptera (Wilcoxon signed rank test, P=0.043)(Table 2). Plecoptera showed a non-significant decrease (Table 2), although there were exceptionally high numbers of Plecoptera at a single station in 2000. This manifested itself in the percentage distribution and the absolute numbers in that year (Figs 2, 3), but not in the overall statistics (Table 2).

In Øvre Heimdalsvatn, the *G. lacustris* population had a two year life cycle spanning three summers. Station 14 supported the highest number of *G. lacustris* in all years (Table 2). There has been a reduction in the total *G. lacustris* population in the shallow waters of the lake between 1972 and 2000 (Figs 4, 5; Table 2), despite an apparent increase in the frequency of 0^+ juveniles. In 1972 no 0^+ juveniles were found in July, possibly because the samples were taken early in the month and the young had not yet hatched, although only 4 0^+ juveniles were taken at st. 14 during the whole summer. In contrast, juveniles of the year formed a large part of the total *G. lacustris* population in the shallow littoral in all the years 1985, 1986 and 2000. In 1972 the juvenile generation from the previous year was the largest group in June at station 14, while in 1985 and 1986 this group was almost absent. In 2000 there was an increase of this group again (Fig. 5).

In 1972 there were significantly more females than males at both investigated stations (st.14: χ^2=5.24, p<0.05; st. 15: χ^2=21.34, p<0.01). However, by 1976 this had changed, and there were significantly more males than females (χ^2=58.78, p<0.01). There was also a significant excess of males in 1985 and 1986 (p<0.01). This excess continued up to and including 2000, although the difference in 2000 was not significant (p<0.269). The highest number of juveniles from the year's recruitment was found in July 2000. However, numbers declined rapidly, and 72 % of the juveniles had disappeared by August. From August to September an additional 52 % decline was recorded. Sampling in deeper waters revealed no indications of downward migration of juveniles.

Discussion

There has been a marked change in the composition of the benthic macroinvertebrate fauna of Øvre Heimdalsvatn since 1972. Chironomidae and Oligochaeta have shown a substantial increase at the same time as other groups have decreased in relative abundance. This is due to a major increase in densities of Chironomidae and Oligochaeta. Surprisingly, other taxa like Ephemeroptera, Trichoptera and Plecoptera have also increased in numbers, contradictory to what one might expect with an increasing minnow population during the study period. One explanation of this increase could be innate natural population fluctuation. There was a threefold reduction in insect emergence in 1972 compared with 1971in Øvre Heimdalsvatn (Brittain & Lillehammer 1978), and 1972 may therefore have been a year with low benthic production. The time of sampling relative to emergence is also an important factor, especially for Ephemeroptera and Plecoptera, as they are concentrated in shallow water prior to emergence and mostly have univoltine life cycles (Brittain, 1978b; Lillehammer, 1978a).

The higher numbers of some insect taxa may also be the result of the introduction of minnows to Øvre Heimdalsvatn and their increasingly high densities in the littoral. Many fishes are visual predators and search for large prey that are easy to see (Brooks & Dodson 1965; Crowder &

Cooper 1982), thus reducing the number of large invertebrate predators and herbivores, resulting in reduced predation and competition on smaller species (Crowder and Cooper 1982). Gilinsky (1984) reported an increase of a herbivorous chironomid after predation from bluegill on a carnivorous chironomid. A shift towards smaller invertebrates has been reported from several studies following fish introduction or from comparative studies of lakes with and without fish (Broooks & Dodson 1965; Conlan 1994; Crowder & Cooper 1982; McNaught et al. 1999; Tate & Hershey 2003). In 1971-72 the large invertebrate carnivore, *Diura bicaudata,* was the most abundant plecopteran in the littoral of Øvre Heimdalsvatn (Lillehammer 1978a) and 20 % in weight of the trichopteran fauna were carnivorous/omnivorous (Lillehammer 1978b). However, since no consistent species identification has been carried out in subsequent years, it was not possible to determine whether the increase in frequency of some groups was due to a reduction of invertebrate carnivores.

There has been a marked decline in the population of *G. lacustris* during the study period. *Gammarus lacustris* is omnivorous (Kortelainen 1990; MacNeil et al. 1997; McNaught et al. 1999; Wilhelm & Schindler 1999), and *Gammarus* species can be an important structuring factor in benthic communities (Conlan 1994). However, if *G. lacustris* was an important structuring factor of the benthic community in Øvre Heimdalsvatn one might expect greater differences in the benthic fauna between sampling stations, since densities of *G. lacustris* vary considerably around the lake. However the diet of the *G. lacustris* population in Øvre Heimdalsvatn consists largely of macrophyte fragments, epiphytic algae and small crustaceans (R. Borgstrøm unpublished data) and a positive relationship between the abundance of *Gammarus* and the amount of substrate detritus has been demonstrated (Aarefjord et al., 1978).

There have been some changes over the last 30 years in the grazing of domestic animals during the summer (Brittain & Borgstrøm 2009), but insufficient to have any impact on the nutrient status of the lake or modify allochthonous inputs. However, a possible effect of the minnow population is altered nutrient flow within the lake. Fish are recognized as an important part of nutrient cycling in lakes. Several studies report an increase in primary production in lakes after fish stocking (Leavitt et al. 1994; McNaught et al. 1999; Parker et al. 2001; Zimmer et al. 2001). This is explained by the fact that fish make nutrients from terrestrial and benthic sources available for the pelagic community (Brabrand et al. 1990; Tatrai 1987). This is probably of less importance in Øvre Heimdalsvatn where minnow is predominantly restricted to the shallower parts of the lake (Museth et al. 2002). Consequently most of the excretion from minnow is deposited in the littoral, where they also feed. Minnows have their most active period during summer, when primary production is high. In contrast, many of the insects in Øvre Heimdalsvatn have most of their growth during wintertime, utilising the supply of allochthonous material from the catchment (Larsson et al., 1978). Nevertheless, by altering the nutrient flow in the lake, minnows may have increased primary production, and indirectly increased food availability to the benthos. Minnows may also increase food availability directly by passage through their gut (Tatrai 1987). Benthic invertebrates like Plecoptera, Chironomidae and Oligochaetae has been found to ingest faecal deposits in laboratory (unpublished data cited in Larsson et al., 1978). In Utah a higher abundance of *Lumbriculus* (Oligochaeta) was found in lakes with fish, compared with fishless lakes (Carlisle & Hawkins, 1998), showing the important cascading effects of fish on benthic invertebrates.

Aquatic insects and other benthos in Øvre Heimdalsvatn may have a refuge in time by having most of their growth during winter, a period when minnows are much less active (Brittain et al. 1988). They may also occupy small interstitial spaces that cannot be reached by minnows, and thus escaping predation. Substrate complexity is an important factor structuring predation in aquatic communities, and interstitial spaces serve as a refuge from predation (Crowder & Cooper 1982; Gilinsky 1984; Luecke, 1990; Power 1992).

The decline in the population of *G. lacustris* in Ø. Heimdalsvatn is reflected in the diet of the brown trout. *Gammarus lacustris* was an important part of the diet for brown trout population in the period 1969-1972, especially during autumn and winter (Lien 1978). By 1975-1977 the amount of *G. lacustris* in the trout diet had declined considerably, and the amount of Chironomidae had increased. This is also observed in the changes in the benthos samples from 1976, with an increase of Chironomidae and a decline of *G. lacustris*. A study in 1985 showed a further decline of *G. lacustris* in trout diet (Bruun 1988). Subsequently, there was a slight increase in 1994 and 1996 (Hasle & Skjølås 1995; Markhus & Meland 1997), followed by a reduction again in 1999 (Hame & Holen 2001; Herberg & Naalsund 1999). Thus, it is likely that predation pressure by brown trout on *Gammarus* varies between years and fluctuates with their respective populations. Annual recruitment of brown trout has declined significantly since the introduction of minnows, although lower exploitation rates have led to no major changes in total trout biomass (Borgstrøm et al. 2009).

In 1972, data on the length distribution of *G. lacustris* is only available for two stations (14 and 15). Nevertheless the low catch of young of (0^+) juveniles in 1972 is remarkable. This could be explained in part by the fact that sampling in July was undertaken before the juveniles had hatched. Also in 1985 few juveniles were caught in July, but here the juveniles were present in August and September. In 1986 the July sampling date was as early as in 1972, but the juveniles had already hatched. The hatching of the juveniles is probably temperature dependent, and the rapid rise and high temperature in the shallow waters in 1986 compared to 1972 may explain the differences in time of hatching. In 1972 there was a marked increase of adult *G. lacustris* in the July sample at st. 14, followed by a rapid decline in August. There was also a small increase of adult *G. lacustris* in July 1985, but in 1986 and 2000 there were no marked increases. It is possible that the sampling in 1986 and 2000 was too late to catch the part of the population migrating from deeper water to spawn. They might have migrated back to deeper water, and therefore the number of adults was underestimated. Even though there was an increase of adults in July 1985, the amount of increase was considerably less than in 1972. In 1986 there was a marked increase in number of 2^+ male adults in September at st. 14, although this movement of 2^+ males was not found in other years. The pattern of migration is less clear in the later years. This may be due to limited sampling or predator avoidance may also play an important role in structuring the migration.

In 1986 the highest number of adults at st.14 was found in September, consisting largely of males from final year generation. In 2000 the largest number of adults was found in August, after the hatch of the juveniles. Thus, no consistent pattern was apparent. Nevertheless the number of adult (1 and 2 year old) *G. lacustris* declined from 1972 to 1985 and declined further by 2000. Females showed the greatest decline, resulting in the altered sex ratio from 1972 onwards. Females may be more vulnerable to predation from minnows, because they grow slower and are smaller than males (Mehli 1973). Allan & Malmqvist (1992) documented selective feeding on smaller *G. pulex* by the bullhead, *Cottus gobio*, and this selectivity towards smaller prey increased with decreasing size of the fish. Newmann & Waters (1984) also found size selectivity for small *G. pseudolimnaus* by the slimy sculpin, *Cottus cognatus,* and 0^+ trout. The amount of *G. lacustris* in the diet of minnows increased around the time that juveniles appeared (Herberg & Naalsund 1999; Lien 1981). This may explain the rapid decline found for juveniles in 2000. Juveniles may be preferred because they are weaker swimmers and have weaker armour than adults (Conlan 1994). They are also a preferable size for minnows.

In conclusion, there have been major changes in the benthos of Øvre Heimdalsvatn over the 28 years from 1972 to 2000. These changes have occurred at the same time as the European minnow has been introduced to the lake and increased substantially in numbers. The effect of the introduction of minnows on the benthic macroinvertebrates of the lake littoral can be clearly seen in the major reduction in the population of *G. lacustris* and the increased proportions of smaller forms, especially chironomids and oligochaetes in relation to the EPT taxa, Ephemeroptera and Trichoptera.

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Table 1 - Table 1 – Benthos sampling dates in the lake ;Øvre Heimdalsvatn, for the years 1972, 1976, 1985, 1986 and 2000

1972	1976	1985	1986	2000
6-13 June	13 June	14-15 June	15 June	23 June
6-9 July	4 and 30 July	17-18 July	9 July	22 July
23-25 August	28 August	28-29 August	26 August	27 August
18-20 September	6 October	25-26 September	24 September	30 September

Table 2 - Results from Wilcoxon signed rank test (Z-values presented with p-values in brackets) of differences between years in benthos numbers pr minute from kick samples at five sampling stations in Øvre Heimdalsvatn

Taxa	**1972-1985**	**1972-2000**	**1985-2000**
Trichoptera	1.75 (0.080)	2.02 (0.043)	0.40 (0.68)
Plecoptera	2.02 (0.043)	2.02 (0.043)	- 0.40 (0.68)
Oligochaeta	2.02 (0.043)	2.02 (0.043)	-2.02 (0.043)
Gammarus lacustris	-1.75 (0.080)	-2.02 (0.043)	1.21 (0.22)
Ephemeroptera	1.21 (0.22)	2.02 (0.043)	2.02 (0.043)
Chironomidae	2.02 (0.043)	2.02 (0.043)	0.67 (0.50)

Figure legends

Fig. 1. Map of the lake, Øvre Heimdalsvatn, with the location of the sampling stations for the shallow littoral benthos

Fig. 2. The percentage composition of the total macroinvertebrate fauna in the shallow littoral of Øvre Heimdalsvatn during 1972, 1976, 1985 and 2000. Values are based on monthly kick samples at five sampling stations in 1972, 1985 and 2000 and at a single station (st. 15) in 1976.

Fig. 3. Relative frequency of the most important groups of benthos in Øvre Heimdalsvatn in 1972, 1985 and 2000. The frequency is based on the average number per year divided by the total average for each group over all years. Thus a group with no increase or decrease would get an index number of 1.

Fig. 4. Mean (± S.E.) numbers of *Gammarus lacustris* per 1 min. kick sample in Øvre Heimdalsvatn at the same five stations in the years 1972, 1985 and 2000.

Fig. 5. Numbers of juveniles, males and females of *Gammarus lacustris* in samples taken at st. 14 in Øvre Heimdalsvatn during June, July, August and September in 1972, 1985, 1986 and 2000. The numbers from 1972 are transformed to 4 min. kick samples.

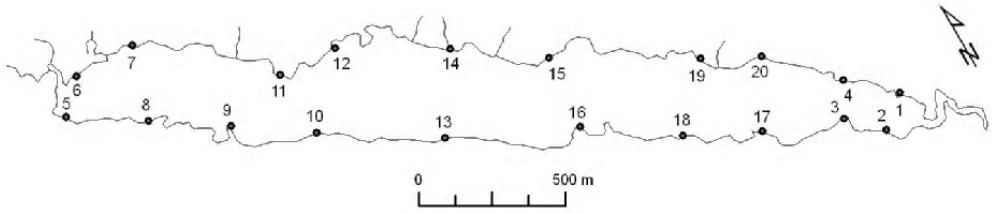


Fig. 1

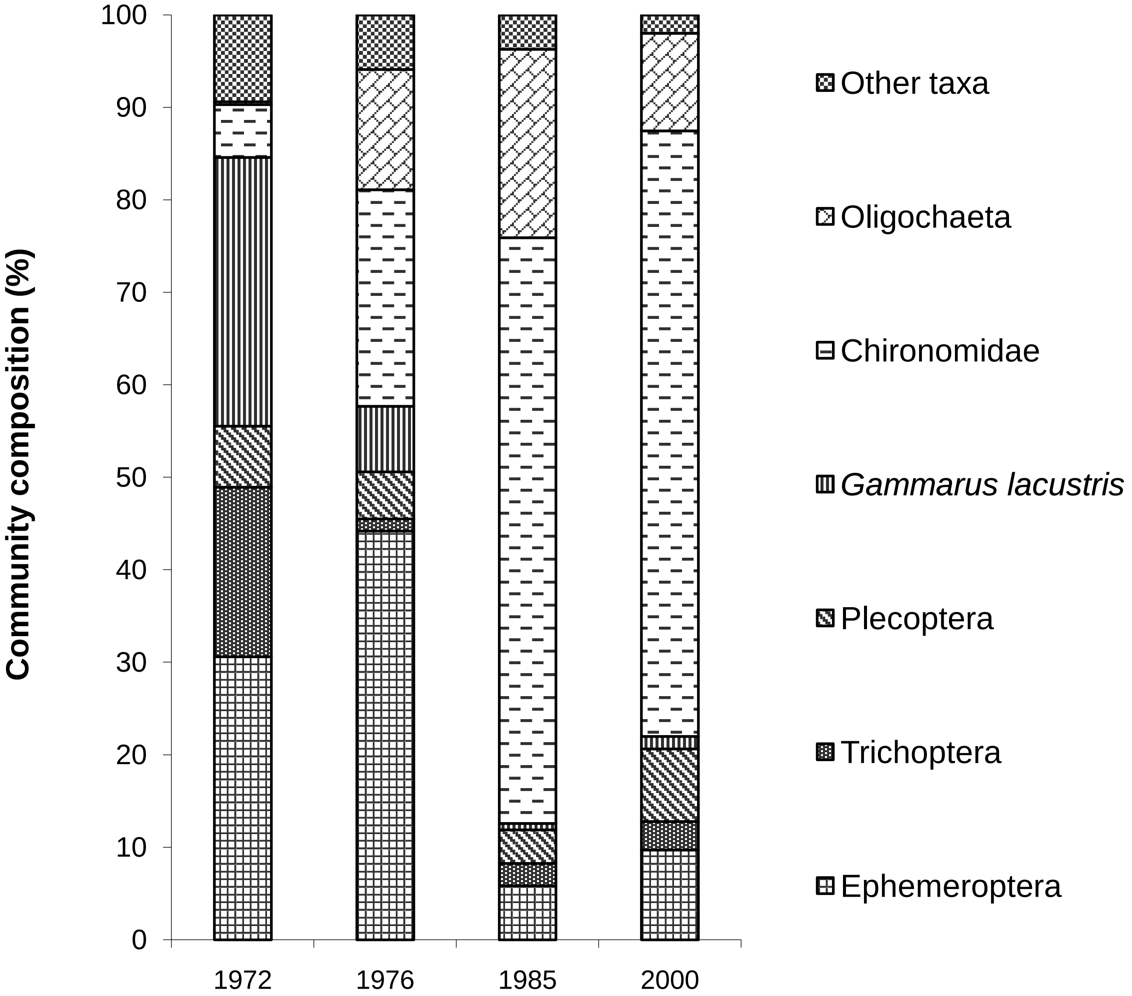

Community composition (%)
100
90
80
70
60
50
40
30
20
10
0
1972
1976
1985
2000
Other taxa
Oligochaeta
Chironomidae
Gammarus lacustris
Plecoptera
Trichoptera
Ephemeroptera

Fig 2

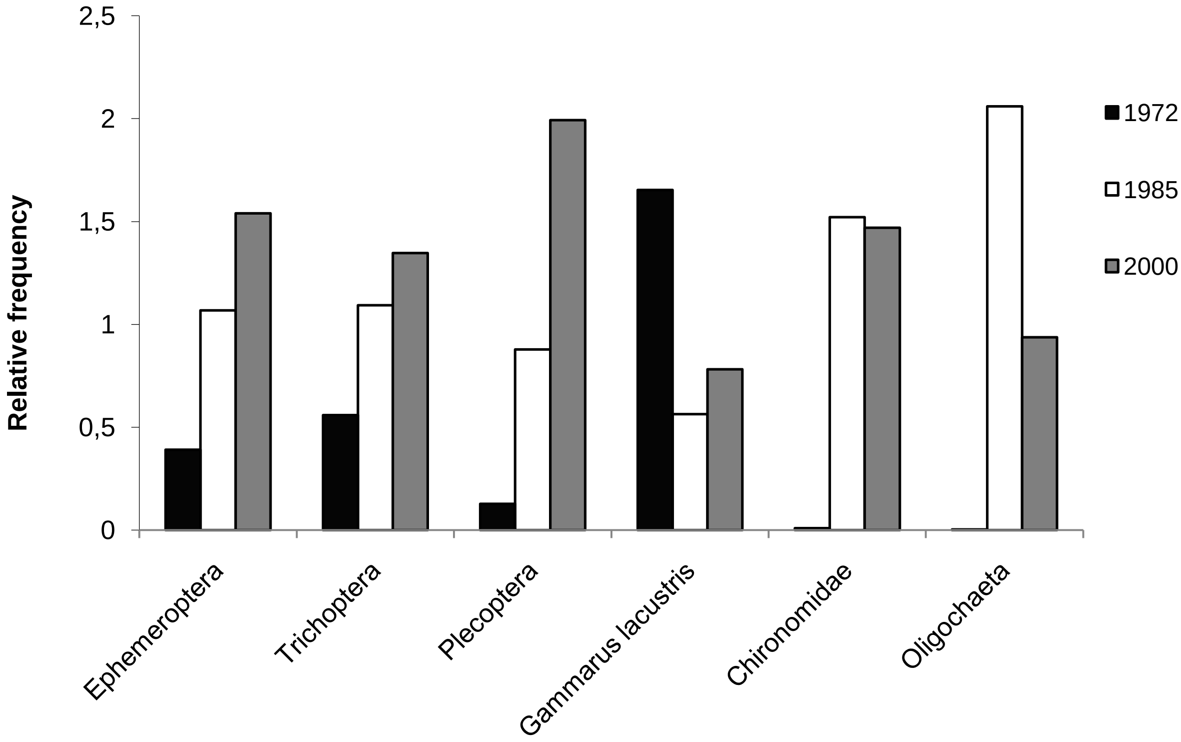
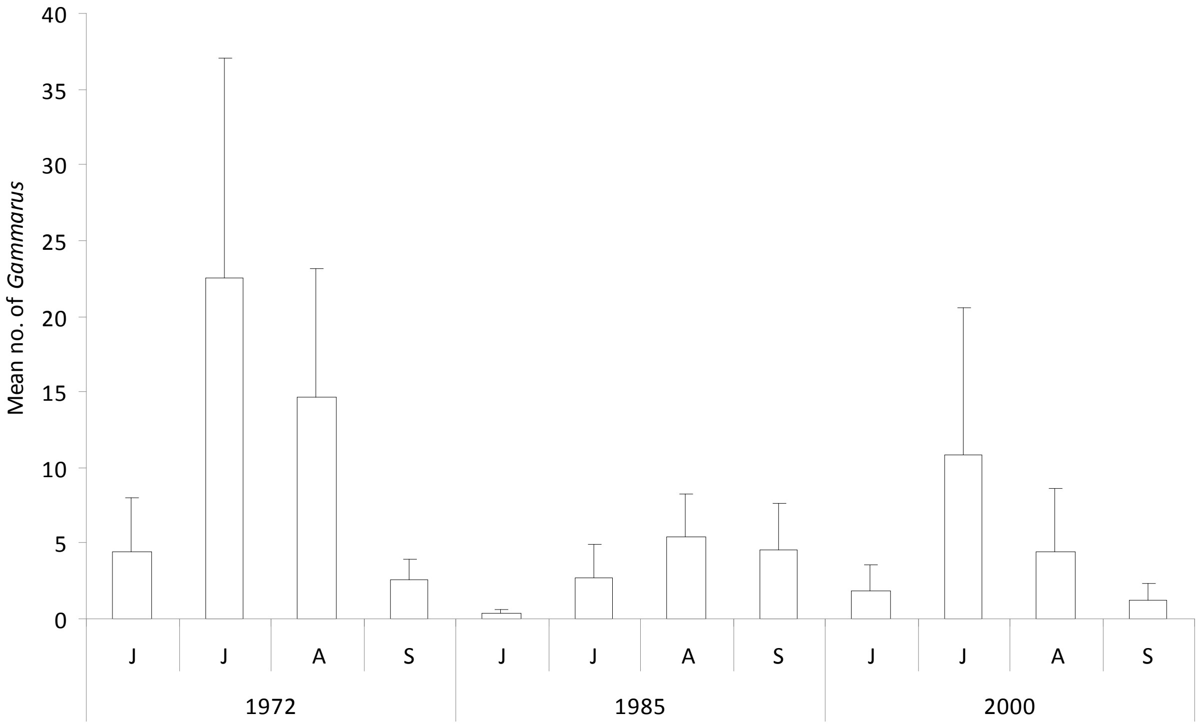
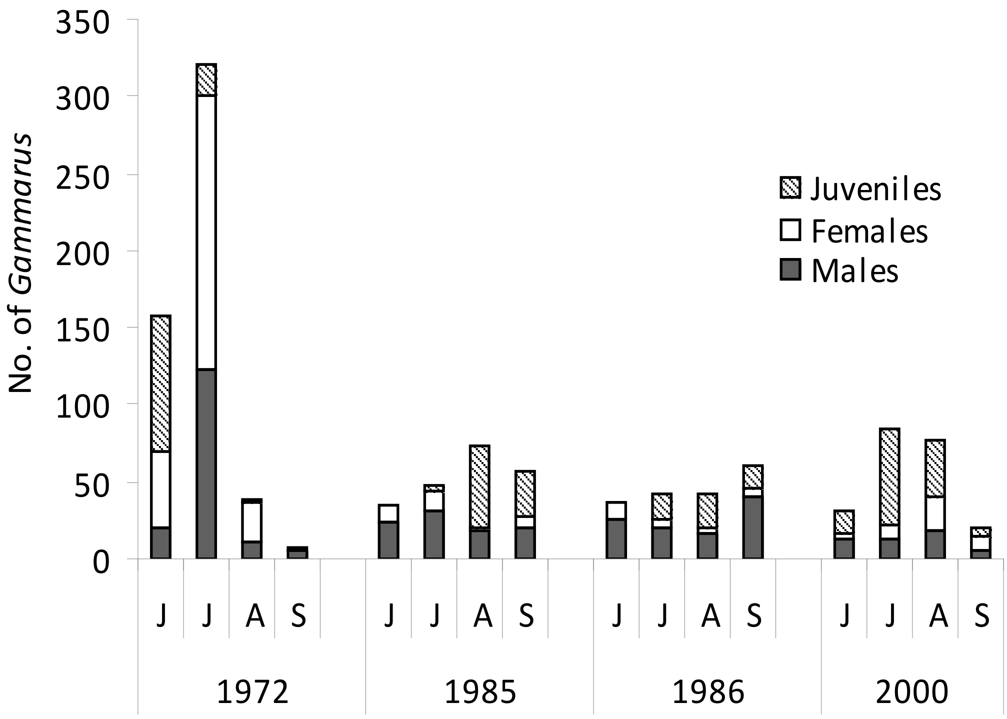

2,5
2
1,5
1
0,5
0
Relative frequency
1972
1985
2000
Ephemeroptera
Trichoptera
Plecoptera
Gammarus lacustris
Chironomidae
Oligochaeta

Fig. 3



40
35
30
25
20
15
10
5
0
Mean no. of *Gammarus*
J
J
A
S
J
J
A
S
J
J
A
S
1972
1985
2000

Fig. 4



No. of Gammarus
350
300
250
200
150
100
50
0
Juveniles
Females
Males
J
J
A
S
1972
1985
1986
2000

Fig. 5