Plankton development in Lake Jonsvatn, Norway, after introduction of *Mysis relicta*: a long-term study

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ABSTRACT: Quantitative sampling of phyto- and zooplankton has been carried out for 25 yr in Lake Jonsvatn, Norway, in order to assess changes after the introduction of *Mysis relicta*. In Lille Jonsvatn, the outlet basin, the cladoceran populations collapsed 7 yr after the mysid introduction. The mean cladoceran biomass was reduced by 95 to 99% for a decade before *Bosmina longispina*, *Holopedium gibberum* and *Daphnia galeata* developed new populations. *B. longispina* and *H. gibberum* almost disappeared again after a few years, while *D. galeata* was replaced by *D. longispina*, which unexpectedly maintained a relatively dense population in the presence of high mysid abundance. Rotifers declined significantly in Lille Jonsvatn after the mysid establishment, whereas copepod biomass did not change. Phytoplankton biomass increased during the first years after the cladoceran collapse, but declined later to levels lower than in pre-mysid years. The changes were probably a combined effect of reduced nutrient loads and grazing pressure. In the main basin, Store Jonsvatn, there were no detectable effects on the zooplankton community during the first 10 to 15 yr after the introduction, in spite of development to common densities of mysids within 8 yr. Over time, cladocerans decreased significantly, however, and mean biomass for the last 5 yr showed a 60% reduction compared with the first 10 yr. No significant long-term changes were detected in copepods, rotifers or phytoplankton biomass in Store Jonsvatn. Differences in temperature, stratification, light transmission and depth may partly explain the different plankton development in the 2 basins.

KEY WORDS: *Mysis relicta* · Long-term study · Phytoplankton biomass · Zooplankton biomass

INTRODUCTION

From 1954 to 1975 the opossum shrimp *Mysis relicta* was introduced in many lakes in Scandinavia in order to serve as a supplementary food for fish. In Sweden, introductions took place in 61 lakes (Fürst et al. 1984), and in Norway in 9 lakes. The Norwegian introductions all took place between 1968 and 1974, and through downstream dispersal *M. relicta* established populations in 6 additional lakes. The introductions in Scandinavia were specifically performed in lakes that were regulated for hydroelectric power production, where production of fish food organisms was reduced because of large fluctuations in water level. Before and

concurrently with the Scandinavian introductions, the species was also introduced to a large number of North American lakes (Lasenby et al. 1986, Nesler & Bergersen 1991).

Mysis relicta was assumed to feed mainly on dead organic matter from the bottom in the deeper parts of the lakes, and through extensive diurnal vertical migrations it would act as an energy elevator by serving as fish food in the upper water layers (Fürst et al. 1984). The dietary habits of *M. relicta* turned out to be quite complex, however. Grossnickle (1982) showed in an overview that *M. relicta* is capable of both filter-feeding and raptorial feeding, eating phytoplankton, zooplankton, benthos, detritus and sediments. More re-

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cent studies have added nuanced information to the omnivorous feeding habits of *M. relicta* (Branstrator et al. 2000, Johannsson et al. 2001, Lasenby & Shi 2004, Ikonen et al. 2005, Scharf & Koschel 2005). After introductions both in North America and Scandinavia, it gradually became evident that *M. relicta* had the ability to reduce zooplankton abundance and change species composition through its predatory behavior (Lasenby & Langford 1973, Threlkeld et al. 1980, Kinsten & Olsén 1981, Lasenby et al. 1986, Nero & Sprules 1986a, Langeland et al. 1991, Spencer et al. 1999). In many of the target lakes, *M. relicta* turned out to be an effective competitor with planktivorous fish for zooplankton prey. Because of its diurnal migratory behaviour, *M. relicta* avoided, to a large extent, predation by pelagic fish that search visually for food (Næsje et al. 1991).

The knowledge of effects from mysid introductions in Scandinavia is mainly restricted to oligotrophic regulated lakes (Fürst et al. 1984, Langeland et al. 1991). Lake Jonsvatn is unregulated and consists of basins that differ with respect to morphometry and water quality. Some studies indicate that increased lake productivity may reduce the adverse effects of *Mysis relicta* on the plankton populations (Nesler & Bergersen 1991). In the present study, special attention was given to the basin called Lille Jonsvatn, which had a higher nutrient level than typical lakes with introduced mysids in Norway, and was therefore hypothesized to be less negatively affected.

The introduction of *Mysis relicta* to Lake Jonsvatn was due to a water diversion tunnel from the neighbouring Lake Selbusjøen where mysid introduction took place in 1973. Most probably, *M. relicta* was swept into Lake Jonsvatn when the tunnel was opened for the first time in 1978. The tunnel is normally closed. An investigation in 1981 showed that *M. relicta* was by then established in Store Jonsvatn. As water flows from Store Jonsvatn through Lille Jonsvatn into the outlet river, *M. relicta* most likely developed populations almost simultaneously in the 2 basins.

The present study deals with the long-term development of phyto- and zooplankton in Lake Jonsvatn after introduction of *Mysis relicta*. It is based on data from 1980 to 2006. The Lake Jonsvatn study represents the longest continuous data series in Scandinavia on the development of the plankton communities after introduction of *M. relicta*. It has been classified by the Norwegian Research Council as especially valuable to maintain.

MATERIALS AND METHODS

Study site. Lake Jonsvatn (63° 22' N, 10° 37' E) is located 150 m above sea level in central Norway (Fig. 1). It is an oligotrophic lake that serves as a drinking water
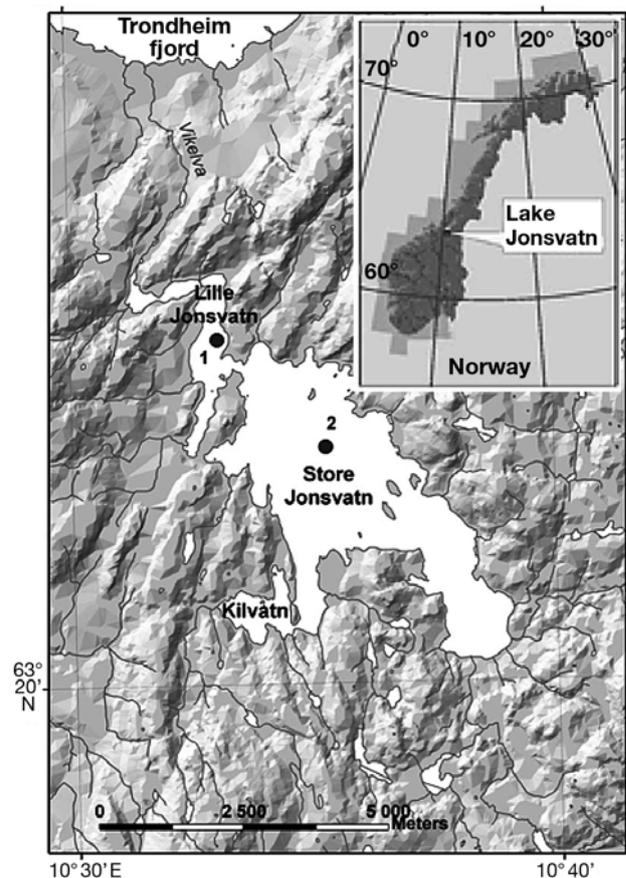

Fig. 1. Lake Jonsvatn, Norway, and sampling stations in Lille Jonsvatn (1) and Store Jonsvatn (2)

reservoir for the city of Trondheim (160 000 inhabitants). The surface area is 15 km^2, maximum depth 97 m and mean depth 37 m. In addition to the main basin—Store Jonsvatn (12.4 km^2)—the lake has 2 nearly disconnected basins, Lille Jonsvatn (1.6 km^2) and Kilvatn (0.8 km^2). There are narrow sounds with depths of 1 to 3 m between the main lake and the embayments. The maximum depth in Lille Jonsvatn is 37 m and in Kilvatn 34 m.

The chemical data of Lille Jonsvatn and Store Jonsvatn are characteristic for oligotrophic conditions (Table 1). However, both total P (Mann-Whitney *U*-test,

Table 1. Physical and chemical characteristics (range of annual means) of surface waters (0 to 5 m) of Lille Jonsvatn and Store Jonsvatn between 1989 and 2006. Data provided by the Environmental Division, Municipality of Trondheim

| | Annual mean range | |
	Lille Jonsvatn	Store Jonsvatn
pH	7.1–7.5	7.2–7.4
Conductivity (µS cm^{-1})	64–74	51–64
Total P (µg l^{-1})	4.6–10.6	2.4–7.4
Total N (µg l^{-1})	311–428	297–419

p = 0.001) and total N (p = 0.045) are significantly higher in Lille Jonsvatn. The P content (average of mixed samples from 0 to 5 m from all seasons) has significantly decreased in both Store Jonsvatn and Lille Jonsvatn during the investigation period (Fig. 2).

Epilimnetic summer temperatures normally reach 15 to 20°C in both basins, whereas temperatures at 20 m depth reach 5 to 7°C (Fig. 3). Temperatures closer to the bottom stay at 4 to 6°C throughout the summer. Due to a higher degree of wind exposure, the thermocline lies deeper in Store Jonsvatn than in Lille Jonsvatn (Fig. 3). Secchi depth observations show that light transmission is highest in Store Jonsvatn (Table 2).

The drainage area mainly consists of coniferous forests and some cultivated farmland, especially around Lille Jonsvatn. Restrictions on farming and development have been imposed since the early 1990s in order to reduce the runoff of nutrients from human activities.

Arctic char *Salvelinus alpinus*, brown trout *Salmo trutta*, northern pike *Esox lucius* and three-spined stickleback *Gasterosteus aculeatus* are the only fish species that occur in Lake Jonsvatn. Brown trout, northern pike and three-spined stickleback occurred only in the littoral zone in Store Jonsvatn, whereas Arctic char utilized both the littoral and the pelagic
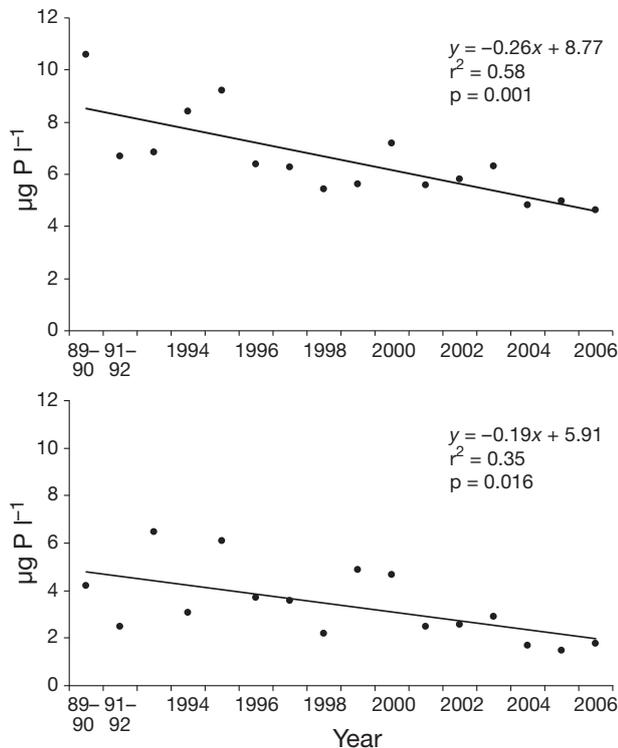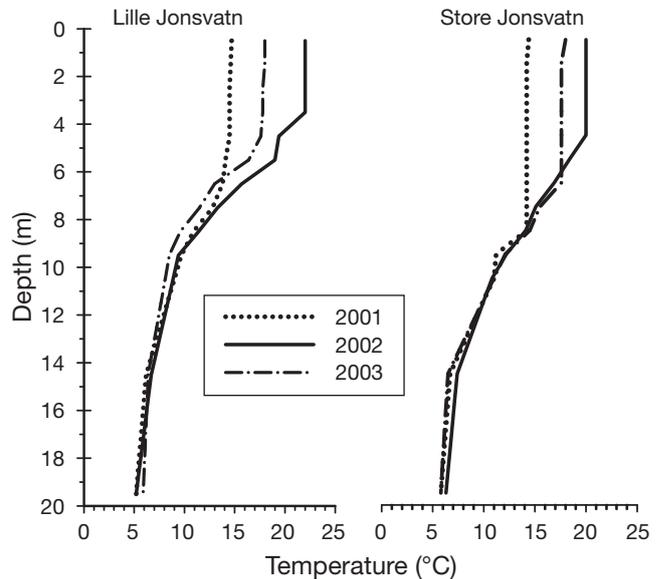

Fig. 3. Temperature profiles in Lille Jonsvatn and Store Jonsvatn. Early August data from 3 subsequent years with different summer temperatures

zones (Næsje et al. 1991). An investigation of the fish populations in Lille Jonsvatn in 1999 gave an extremely low yield of Arctic char and brown trout both in the littoral zone, along the bottom in deeper areas and in the pelagic zone, whereas northern pike were exclusively caught along the bottom (Koksvik 2000). We have observed three-spined stickleback only along the shore. In Store Jonsvatn, the catch per unit effort (CPUE, 24 h fishing, 0 to 10 m depth) in floating gillnets was <1 to 5 Arctic char per 100 m^2 net area in the pelagic zone (Næsje et al. 1991), while the corresponding yield (0 to 6 m depth) was 0.4 Arctic char and 0.2 brown trout in Lille Jonsvatn (Koksvik 2000). According to local fishermen, the populations of Arctic char and brown trout have been very small for several decades in Lille Jonsvatn.

Fig. 2. Regression of total P (μg l^{-1}) versus sampling year in Lille Jonsvatn (top) and Store Jonsvatn (bottom). Only pooled data were available for the years 1989–1990 and 1991–1992. Data provided by the Environmental Division, Municipality of Trondheim

Table 2. Secchi depths (m) in Lille Jonsvatn and Store Jonsvatn. Data are June–September averages for 2001 to 2006

| Year | Secchi depth (m) | |
	Lille Jonsvatn	Store Jonsvatn
2001	4.3	5.5
2002	5.5	6.7
2003	5.4	6.8
2004	5.0	6.8
2005	5.3	6.9
2006	5.3	6.2
Mean	5.1	6.5

Plankton sampling. Plankton was sampled at Stns 1 & 2 (Fig. 1). Zooplankton was sampled with a 1 m long plexiglass tube sampler. Each sample contained 5 l of water. A vertical column extending from 0 to 20 m depth was consistently sampled every 1 m. Samples from 5 m layers were mixed and treated as one sample. Additional zooplankton sampling was carried out by vertical net hauls (90 µm mesh) to secure sufficient material for length measurements and biomass calculations. The net was hauled vertically from 20 m to the surface. Zooplankton samples were preserved with Lugol's solution in the field and later transferred to 70 % ethanol for permanent storage.

All zooplankton samples were identified to species and enumerated. Counts were carried out on the total samples or subsamples containing $\frac{1}{10}$ of the total sample. On each sampling date, length measurements were made on 30 to 50 individuals of each cladoceran species from each station. Copepods were distinguished to the instar level when counted. Biomass calculations for cladocerans and copepods (with fixed individual weights for different instars) were made according to length/weight regressions from Bottrell et al. (1976) and Langeland (1982). Rotifer biomass was calculated using individual weights given in Bottrell et al. (1976). The zooplankton material has been incorporated into the collections of the Museum of Natural History and Archaeology at the Norwegian University of Science and Technology.

Integrated phytoplankton samples from 0 to 5 and 5 to 10 m were collected in Lille and Store Jonsvatn with a plexiglass water sampler (volume = 1.6 l). Phytoplankton samples of 200 ml were taken from the pooled samples and preserved with Lugol's solution. The samples were analysed according to the Utermöhl settling technique. For each sample a minimum of 200 cells or colonies was counted and identified to genus or species. Volume of counted cells was calculated using simple geometric models, and the biovolume was converted to wet weight assuming a specific gravity of 1.0 mg mm^{-3}. Wet weights for algal groups and total algal biomass are given as means of biomass of the 2 integrated samples, i.e. mean biomass of 0 to 10 m.

Mysis relicta was sampled by vertical net hauls in Lille Jonsvatn in 1996 and 1999–2006. The net had a frame opening of 1 m^2, a mesh size of 500 µm and was equipped with a lead weight at its mouth, sinking upside down before being hauled up again vertically. Each sample thus consisted of 2 vertical hauls, between 1 m above the bottom (30 m) and the surface. Sampling was performed on the plankton station in the dark in October–November, which is within the period when *M. relicta* is most abundant in the pelagic zone in Lake Jonsvatn (Næsje et al. 1991, 2003); 3 replicate hauls were performed on every sampling occasion.

The present study did not include sampling of mysids in Store Jonsvatn.

In 1980, zooplankton was sampled on 3 occasions within the June–September period, and in 1983 to 1987, monthly from June to September. From 1988 onwards, zooplankton samples were collected 6 times per year (monthly sampling in June and September, twice monthly in July and August). Both plankton stations were always sampled simultaneously. Phytoplankton was sampled at the same stations and dates as zooplankton in Lille Jonsvatn in 1980, 1983, 1985, 1986 and 1988–2006, and in Store Jonsvatn in 1980, 1983, 1985, 1987, 1994 and 1996–2006. Biomass means of both phytoplankton and zooplankton are given as estimated averages of all samples in the particular year. The change in sampling intensity from 1988 onwards might have led to a slight increase of mean zooplankton biomass and for some years a decrease in mean phytoplankton biomass, but not to an extent that has influenced the trends of development in either group.

RESULTS

Zooplankton

In Lille Jonsvatn, a mean biomass (June–September) of 1100 to 1650 mg m^{-2} (dry weight) was recorded until 1985, when a dramatic decline took place (Fig. 4). The cladoceran biomass was then reduced to less than 5 % of the mean for 1980–1984, and in 1986–1987 the cladocerans had become virtually extinct (mean biomass = 2 and 9 mg m^{-2}, respectively). Extremely low biomasses of cladocerans were recorded for 10 yr. The previously dominant species, *Bosmina longispina*, had a mean biomass in 1985–1994 that was less than 1 % compared with the estimates for years prior to 1985, and the other common species, *Daphnia galeata* and *Holopedium gibberum*, were irregularly found in low numbers throughout this period. In 1995, a moderate recovery of *B. longispina* was recorded (140 mg m^{-2}). In 1996, the mean biomass of *B. longispina* increased to almost 600 mg m^{-2}, and *D. galeata* and *H. gibberum* also developed populations with mean biomasses of 170 and 320 mg m^{-2}, respectively (Fig. 5). Total cladoceran biomass was again on the level recorded before the collapse in 1985. After 1996, the mean biomass of cladocerans has varied between 230 and 540 mg m^{-2}. Since 1998, *B. longispina* has been virtually absent, and *H. gibberum* has also been recorded in extremely low numbers except for a moderate abundance in 2000. The daphnids continued to increase until 2000, and have afterwards fluctuated in abundance. The highest daphnid biomass (540 mg m^{-2}) in the entire investigation period was recorded in 2006. *D. galeata*
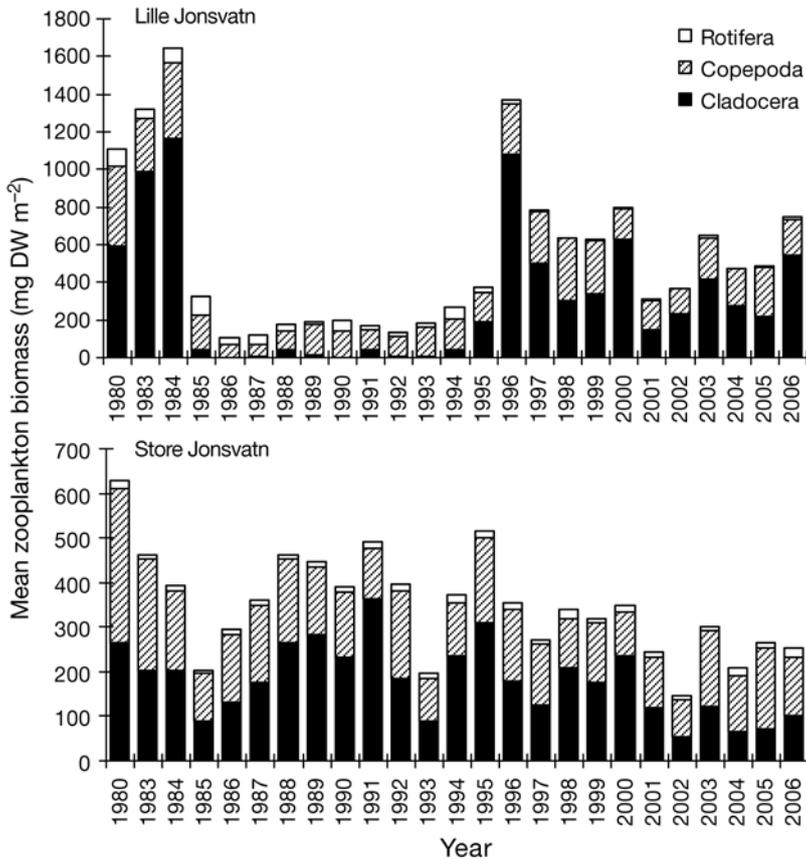
Fig. 4. Mean June–September biomass (mg dry weight m^{-2} over 20 m) of zooplankton in Lille Jonsvatn (top) and Store Jonsvatn (bottom) in the period 1980–2006. The lake was not sampled in 1981 and 1982
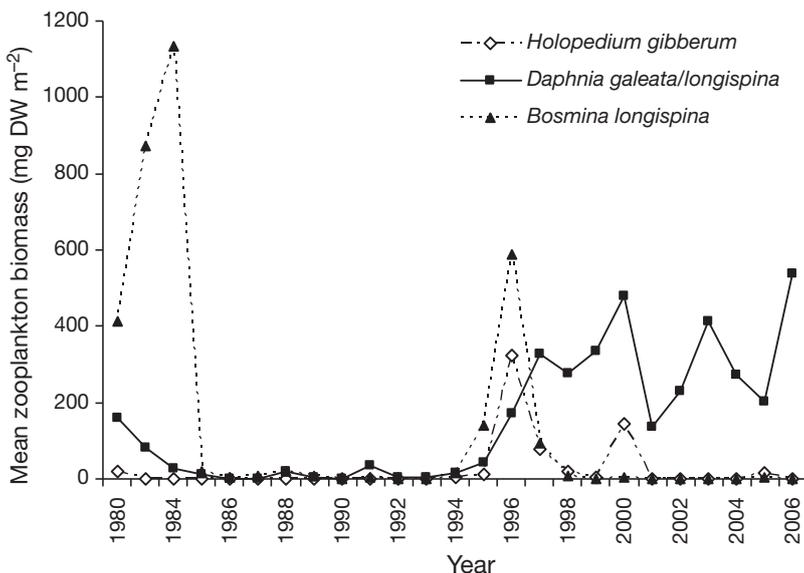

Fig. 5. *Holopedium gibberum*, *Daphnia galeata/longispina* and *Bosmina longispina*. Development of zooplankton biomass (mg dry weight m^{-2} over 20 m) in Lille Jonsvatn over the period 1980–2006. The lake was not sampled in 1981 and 1982

was the only daphnid in the samples until 1998, when *Daphnia longispina* turned up, and became the dominant species from 1999 onwards. The biomass of *D. galeata* after the appearance of *D. longispina* was extremely low (<1 to 6 mg m^{-2} in 2004–2006).

Total biomass of copepods also declined in Lille Jonsvatn after 1984 (Fig. 4), but not to the same extent as cladocerans. Mean biomass for the years 1985–1995 was 129 ± 12 (SE) mg m^{-2}, compared to 369 ± 43 mg m^{-2} for the years prior to 1985; copepod biomass was significantly different in the 2 periods (Mann-Whitney *U*-test, p < 0.01). The biomass reduction in copepods was mainly due to the dominant species *Cyclops scutifer*. The other copepods in question, *Heterocope appendiculata*, *Arctodiaptomus laticeps* and *Mesocyclops leuckarti*, showed no clear trend in biomass between 1985 and 1995. In 1996, copepods developed the highest biomass since 1984, and a level of 270 to 330 mg m^{-2} was maintained until 2000. Mean biomass for the period 1996–2006 was 224 ± 18 mg m^{-2}, which is 73% higher than for 1985–1995. The difference in biomasses between the 2 periods was highly significant (p < 0.001). *C. scutifer* was the dominant species through the entire period. *Acanthodiaptomus denticornis* turned up as a new copepod species in 1999, and maintained the second highest biomass for all but one year afterwards, closely followed by *A. laticeps*.

Rotifer biomass was relatively high (55 to 95 mg m^{-2}) in 1980–1984 and dominated by the colony forming *Conochilus* sp. that made up 50 to 75% of the total. *Asplanchna priodonta*, *Polyarthra* sp., *Keratella cochlearis* and *Kellicottia longispina* also made up a significant share of the biomass. After 1984, *Conochilus* sp. biomass dropped to almost zero for a 10 yr period; after that, it varied at very low levels. *Kellicottia longispina* was also strongly decimated after 1984. From 1996 on, all species had very low biomass, and total rotifer biomass averaged 2 to 12 mg m^{-2} in 1997–2006. *Keratella cochlearis* had the highest biomass most years during this period. The development of rotifers through the entire investigation period fits an exponential regression (Fig. 6).

In Store Jonsvatn, zooplankton biomass decreased between 1980 and 1985, but then increased again until 1988 (Fig. 4). The changes were caused by the cladocerans *Bosmina*
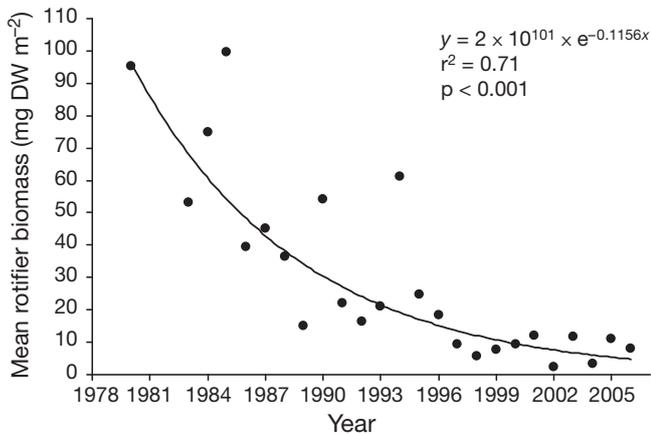
Fig. 6. Regression of mean rotifer biomass (mg dry weight m^{-2} over 20 m) versus sampling year (1980–2006) in Lille Jonsvatn. The lake was not sampled in 1981 and 1982

longispina and *Daphnia galeata* and the copepods *Cyclops scutifer* and *Heterocope appendiculata*. After 1988 there was a long-term decrease in cladoceran biomass (Fig. 7). The change fits a linear regression. The most pronounced decline was found in *B. longispina* and *D. galeata.* Mean biomass of cladocerans in 1998–2006 was 128 ± 22 mg m^{-2} compared to 226 ± 27 mg m^{-2} in 1988–1997. The difference in biomass was highly significant (Mann-Whitney U-test, p < 0.01), and 4 of the last 5 years studied represent the lowest biomasses of Cladocera in the entire investigation period.

A corresponding decline in copepod biomass was not detected in Store Jonsvatn. Mean biomass in 1998–2006 was 127 ± 11 mg m^{-2} compared to 150 ± 11 mg m^{-2} in 1988–1997 (not significant; Mann-Whitney U-test, p = 0.14). *Cyclops scutifer* was the dominant species in most years, constituting a mean of 55% of the total copepod biomass in 1988–2006. *Heterocope*
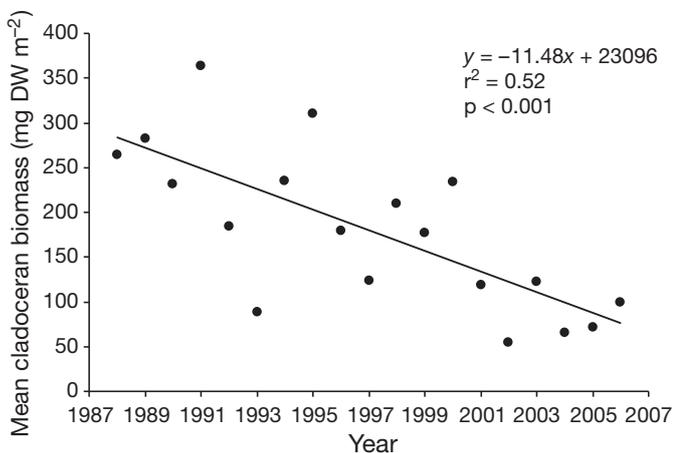

Fig. 7. Regression of mean cladoceran biomass (mg dry weight m^{-2} over 20 m) versus sampling year (1988–2006) in Store Jonsvatn

appendiculata and *Arctodiaptomus laticeps* were present with moderate abundance in all years and did not show any significant trend in biomass. As in Lille Jonsvatn, *Acanthodiaptomus denticornis* was recorded as a new species in Store Jonsvatn in 1999, and was found in very low numbers most years afterwards.

Rotifer biomass was low in Store Jonsvatn throughout the entire investigation period. Yearly means varied between 7 and 20 mg m^{-2} and there was no long-term trend in biomass change. *Conochilus* sp. was the dominant rotifer most years and constituted an average of 61% of the total rotifer biomass. The next most abundant rotifers were *Polyarthra* sp. with 20% and *Asplanchna priodonta* with 8% of the total rotifer biomass.

Phytoplankton

In Lille Jonsvatn, the maximum annual peak biomass reached 2020 and 2150 mg m^{-3} (wet weight) in 1989 and 1994, respectively, and values >1000 mg m^{-3} were recorded in 1980–1989 (Fig. 8). Except for 1994, the spring peak biomass gradually declined from 1989 onwards, to maximum values near 300 mg m^{-3} at the end of the investigated period. Diatoms constituted 60 to 90% of the recorded maximum biomass in 1980–1990 and 1994, and *Asterionella formosa* and *Synedra* spp. were the dominant species.

The mean June–September biomass showed a significant decline from 1000 to 1100 mg m^{-3} in 1985, 1986 and 1989 to about 200 mg m^{-3} at the end of the investigation (Fig. 9). Diatom biomass declined from 293 mg m^{-3} or 41% of the mean total biomass in 1985–1995 to 73 mg m^{-3} or 23% of the mean biomass in 1995–2006. The diatoms made up a significantly lower proportion of the total algal biomass in the latter period (Mann-Whitney U-test, p = 0.02). *Asterionella formosa* and *Synedra* spp. were also recorded in the summer samples, and in the later phase of the investigation *Rhizosolenia eriensis*, *R. longiseta* and a small *Cyclotella* species (5 μm diameter) became more frequent diatom species.

The biomass of cryptophytes, the second most important algal group, changed from a mean of 170 mg m^{-3} in 1985–1995 to 110 mg m^{-3} in 1996–2006. However, their proportion of the total biomass increased significantly (Mann-Whitney U-test, p = 0.007), from about 23 to 36% from the former to the latter period, respectively, and cryptophytes constituted in 1996–2006 up to 60% of the biomass during summer and autumn samples. *Rhodomonas lacustris* was the most frequent cryptophyte species.

Chrysophytes constituted close to 24% of the mean biomass in all investigated years. *Dinobryon sociale* var. *americanum* was the dominant species during the
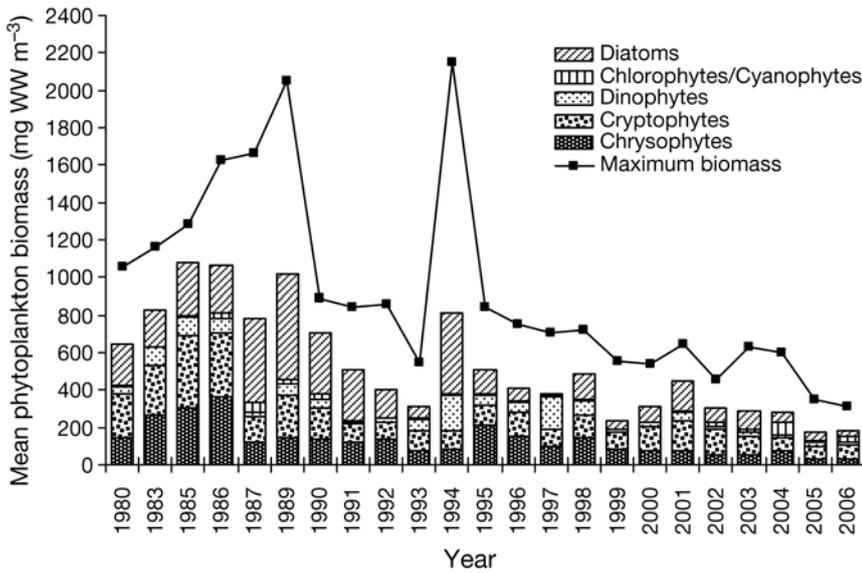
Fig. 8. Mean (mg wet weight m^{-3} over 10 m) and maximum biomasses of phytoplankton groups in Lille Jonsvatn over the period 1980–2006. There are no data from 1981, 1982, 1984 or 1988

and a maximum biomass was recorded in August 2004, when gelatinous chlorophytes constituted 22% of the total biomass. The colony-forming cyanophyte *Coelosphaerium kuetzingianum* was recorded in the late summer samples from 1996, and it was sufficiently abundant to be included in the biomass estimates from 2003 onwards. In 2004 this species constituted close to 60% of the recorded biomass in August samples. However, on an annual (June–September) basis the species never exceeded 12% of the biomass, and for the investigated period cyanophytes did not exceed 1% of the total biomass.

In Store Jonsvatn, a maximum phytoplankton biomass of 450 to 500 mg m^{-3} was recorded in June 2001 and 2002, and diatoms constituted 30 and 45% of the biomass, respectively. The highest mean seasonal biomass, 370 and 270 mg m^{-3}, were recorded in the same years. In all other years, mean seasonal biomasses varied from 130 to 230 mg m^{-3}, and no specific trend in biomass development was recorded during the investigated period. The mean biomass for 1980–2006 was 190 mg m^{-3}, or about one-fourth of the mean biomass recorded for Lille Jonsvatn in the same period. However, in 2005 and 2006 the mean June–September biomass was similar in the 2 lakes.

Cryptophytes and chrysophytes each constituted about 30% of the mean June–September biomass in Store Jonsvatn, whereas the biomass shares of diatoms and dinophytes were close to 19 and 16%, respectively. Chlorophytes accounted for 3% of this biomass. The taxa mentioned for Lille Jonsvatn were also the most frequent ones in Store Jonsvatn, except for gelatinous chlorophytes and cyanophytes that were present in very low numbers and not included in the biomass estimates in the latter basin.

spring period and was also frequently recorded in the summer and autumn periods together with other *Dinobryon* species and individuals of *Bitrichia chodati*, *Pseudochephyrion entchii*, *Chrysoikos skujai*, *Mallomonas crassisquamma*, *M. akrokomos* and *Chrysochromulina parva*.

Three dinophyte species, *Gymnodinium lacustre*, *Peridinium inconspicuum* and *Ceratium hirundinella*, constituted about 10% of the total biomass in all years. Chlorophytes, usually *Scenedesmus* sp., *Monoraphidium dybowskii*, and *M. griffithii*, were recorded in low numbers. However, from 2002 on, gelatinous chlorophytes such as *Sphaerocystis schroeteri* and *Willea irregularis* were also included in the biomass estimates,
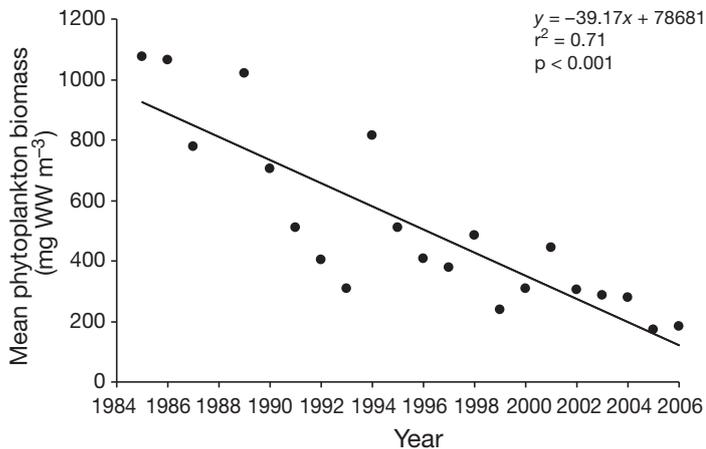
Phytoplankton–zooplankton relationships

Biomass relationships between phytoplankton (0 to 10 m) and herbivorous zooplankton (0 to 20 m) have changed significantly in Lille Jonsvatn (Fig. 10). In the first years of the investigation, 1980 and 1983, the mean biomass of herbivorous zooplankton was larger than that of phytoplankton (1.6 and 1.4 times, respectively). This situation changed to an inverse relationship after 1984, with a phytoplankton biomass that was 4 to 12 times larger than that of zooplankton in 1986–1990. From 1996 onwards, the biomass of herbi-
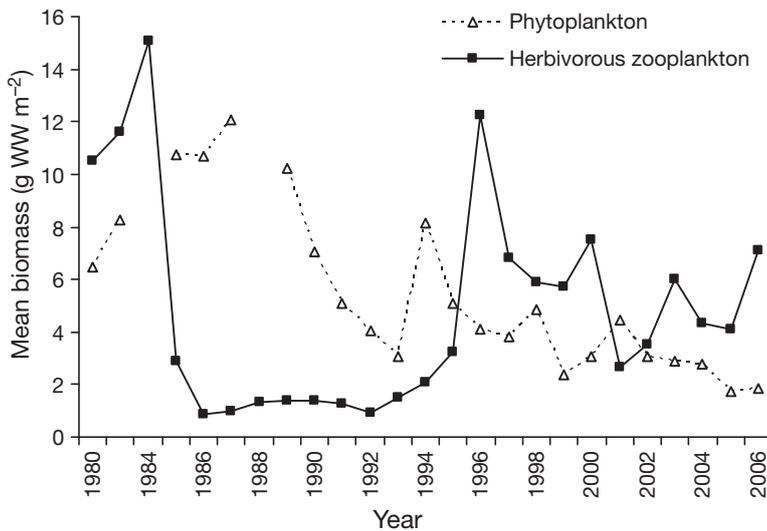

$y = -39.17x + 78681$
$r^2 = 0.71$
$p < 0.001$

Fig. 9. Regression of mean phytoplankton biomass (mg wet weight m^{-3} over 10 m) versus sampling year (1985–2006) in Lille Jonsvatn. There are no data from 1988

Fig. 10. Comparison of phytoplankton and herbivorous zooplankton biomass (g wet weight m^{-2}) development in Lille Jonsvatn from 1980 to 2006. There are no data from 1981 or 1982 and only zooplankton data from 1984 and 1988

vorous zooplankton was on average 2.2 times higher than that of phytoplankton (except for 2001) for the period 1996–2006. In Store Jonsvatn, the mean biomass of herbivorous zooplankton was on average 1.8 times higher than that of phytoplankton in all years, except for 2001 and 2002.

Mysis relicta

Mysid data from Lille Jonsvatn in 1996 and yearly from 1999 to 2006 indicate 2.5 to 4.5 times higher abundance in 2003–2006 compared to 2000–2002 and 1996 (Fig. 11). The highest abundance was recorded in 2003 with 252 ind. m^{-2}. In 1999, *Mysis relicta* was very scarce, with an abundance of only 3 ind. m^{-2}. The first attempt to collect mysids in Store Jonsvatn was in
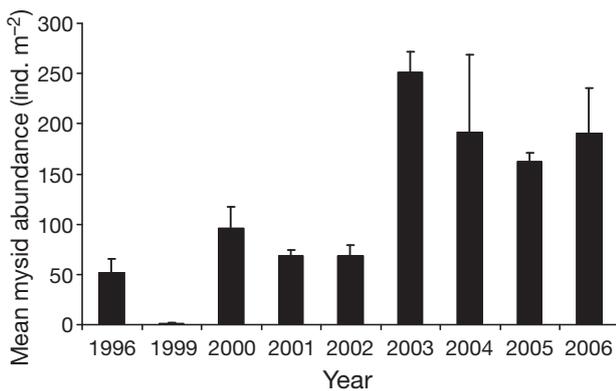

Fig. 11. *Mysis relicta*. Abundance (ind. m^{-2}; mean ± SD) in Lille Jonsvatn in 1996 and 1999–2006

November 1981, when the mean abundance was estimated at 2.7 ind. m^{-2} in vertical hauls from 50 to 0 m (Koksvik et al. 1991). Næsje et al. (1991) recorded 50 to 110 ind. m^{-2} in Store Jonsvatn in 1986–1987 (August–December samples), and in 2000, the average of 3 vertical hauls (50 to 0 m) in November was 31 ind. m^{-2} (J. I. Koksvik unpubl. data).

DISCUSSION

The results of the present long-term study reveal large differences in the plankton development in 2 basins of Lake Jonsvatn after introduction of *Mysis relicta*. In Lille Jonsvatn, the cladoceran populations collapsed about 7 yr after the introduction that likely took place in 1978 in another basin of the lake, about 6 km from Lille Jonsvatn. *Bosmina longispina* was the strongly dominating cladoceran in Lille Jonsvatn before the collapse, followed by *Daphnia galeata*. The preference for cladocerans in the diet of *Mysis* spp. is well documented (Lasenby & Langford 1973, Richards et al. 1975, Kinsten & Olsén 1981, Langeland 1981, 1988, Bowers and Vanderploeg 1982). In Lake Tahoe, the dominant zooplankters *Bosmina* and 2 species of *Daphnia* virtually disappeared after the introduction of *M. diluviana* (formerly *M. relicta*) (Richards et al. 1975), and *Bosmina* and *Daphnia* were the preferred prey in Flathead Lake (Spencer et al. 1999). In Lake Selbusjøen, the source lake for mysids in Lake Jonsvaten, cladocerans were reduced to a very low biomass 5 to 6 yr after the introduction of *M. relicta* in 1973. The mysids had then developed an abundance of 200 to 600 ind. m^{-2} based on vertical haul samples. *B. longispina*, *Holopedium gibberum* and *D. longispina* were the most severely decimated cladoceran species (Langeland 1981, Langeland et al. 1991).

In another lake in the same region, Lake Stugusjøen, a similar development took place (Langeland 1981, 1988). *Mysis relicta* was introduced in 1973, and from 1978 the 3 most abundant planktonic cladocerans, *Bosmina longispina*, *Daphnia galeata* and *Holopedium gibberum*, were almost absent in the samples. From 1980, vertical hauls showed a mysid abundance of 30 to 100 ind. m^{-2}. In 2 mysid-free neighbouring lakes, Lakes Møsjøen and Grønsjøen, no significant decrease in the zooplankton populations was recorded for the same period. These lakes have similar environmental conditions as Lake Stugusjøen, and the only fish species in all 3 lakes were Arctic char and brown trout.

The cladoceran numbers decreased dramatically for a period of 10 yr in Lille Jonsvatn, and the low abundance was considered permanent until the numbers again began to increase in 1995. In 1996, the mean biomass of cladocerans very surprisingly developed to the same level as before the collapse. *Bosmina longispina* was again the dominant species, followed by *Holopedium gibberum* and *Daphnia galeata*. The causes for the sudden return of cladocerans are unclear. Threlkeld et al. (1980) reported a reappearance of *Bosmina* in Lake Tahoe for a short period with low *Mysis diluviana* density. In the present study, mysid density in Lille Jonsvatn was low in 1996 and considerably lower than the 4 last years of the investigation (2003 to 2006). Unfortunately, *M. relicta* was not sampled in Lille Jonsvatn prior to 1996; however, from frequent occurrence in the plankton samples, the existence of the species in this part of the lake was well known. The new collapse of *B. longispina* and *H. gibberum* in 1998–1999 did not coincide with a recorded increase in *M. relicta* abundance, as the mysid density was extremely low in 1999. Interspecific competition with the rapidly increasing *Daphnia* populations may have played an important role for the reduction of *B. longispina* and *H. gibberum.* The *Daphnia* populations continued to increase until 2000, and afterwards varied considerably, with the highest mean density occurring in 2006, when the second highest density of *M. relicta* was recorded.

There is no coincidental long-term study of the development of planktivorous fish in Lake Jonsvatn. In 1999, however, a survey of the fish populations in Lille Jonsvatn, performed by series of floating and bottom-set gill nets (10 to 45 mm mesh size), revealed that the population of Arctic char, the only planktivorous fish species, was very small (Koksvik 2000). Gut analysis showed that *Mysis relicta*, *Daphnia galeata* and *D. longispina* were the most important food items. Arctic char has also been found to prey extensively on *M. relicta* and cladocerans in Store Jonsvatn (Næsje et al. 1991). However, since Arctic char was reported by local fishermen to have been scarce in Lille Jonsvatn from pre-mysid years and up to the present, it is unlikely that this species was an important agent in the development of zooplankton and *M. relicta* in Lille Jonsvatn.

In 1998–1999, *Daphnia galeata* was replaced by *D. longispina.* This development is the opposite of what Rieman & Falter (1981) reported from a study in Pend Oreille Lake in Idaho, where only the round-headed *D. thorata* was present before the introduction of mysids, whereas a pointed-helmet form, *D. galeata mendotae*, gained numerical dominance after the introduction. Summer forms of *D. galeata* in Lake Jonsvatn typically have pointed helmets, whereas *D. longispina* is round-headed. Protuberances such as spines and pointed helmets may be important in preventing predation from other invertebrates, and was discussed as a defence against mysid attacks in Pend Oreille Lake.

The ability of *Daphnia longispina* to develop and sustain a population at a relatively high biomass level in Lille Jonsvatn in the presence of the dense *Mysis relicta* population recorded in 2003–2006 is puzzling. Both *D. longispina* and *D. galeata* mainly inhabited the upper 10 m of the water column and the size of the 2 species was about equal. It is difficult to see what anti-predator strategies *D. longispina* might have developed that made it more competitive and viable than *D. galeata*, and why Store Jonsvatnet or other mysid lakes in the same district have not experienced an equivalent development. In Store Jonsvatn, *D. galeata* was the strongly dominating daphnid through the entire investigation. In Lake Selbusjøen, *D. longispina* was more negatively affected than *D. galeata* (Langeland et al. 1991), and in Lake Stugusjøen *D. galeata*, the only daphnid in the lake, completely disappeared 5 yr after the introduction of *M. relicta* (Langeland 1981).

In Lille Jonsvatn, the 10 yr period with extremely low cladoceran biomass may also have affected the dominant copepod species, *Cyclops scutifer*, which showed a significant biomass decrease. It is reasonable that the predation pressure by *Mysis relicta* became stronger on copepods when cladocerans were scarce or absent. When cladoceran abundance increased again from 1995 to 1996, *C. scutifer* did as well. The assumption that the decrease in *C. scutifer* was caused by mysid predation is supported by a study of Canadian lakes by Nero & Sprules (1986b), where *C. scutifer* abundance was found to be much lower in 2 mysid lakes than in 2 similar lakes without mysids. *Heterocope appendiculata* and *Arctodiaptomus laticeps* decreased after *M. relicta* introduction in the nearby Lakes Selbusjøen (Langeland et al. 1991) and Stugusjøen (Langeland 1988), but in Lake Jonsvatn no such long-term trend was found, although both species have varied considerably within periods of a few years. Rybock (1978) reported a consistently negative selection for the copepod *Diaptomus* in Lake Tahoe.

Among the rotifers, *Conochilus* sp. strongly dominated the biomass in Lille Jonsvatn for the first years of the present study; however, it collapsed concurrently with the cladocerans and did not recover again. An equivalent development did not take place in Store Jonsvatn, where *Conochilus* sp. also was the dominant rotifer. It is plausible that *Conochilus* sp. was decimated by *Mysis relicta* predation in Lille Jonsvatn, although it might be a difficult prey as it forms colonies of considerable size. Rotifers have been paid less attention than cladocerans and copepods, but in some studies are reported to be part of the mysid diet

(Lasenby & Langford 1973, Bowers & Grossnickle 1978, Johannsson et al. 2001, Ikonen et al. 2005). Lasenby & Langford (1973) reported *Kellicottia* to be an important prey in Stony Lake, Ontario. Additionally, after the disappearance of *Daphnia* and *Bosmina* in Lake Tahoe in 1970–1971, densities of *Kellicottia longispina* varied inversely with estimates of *M. diluviana*, and gut analysis showed intensive use of *Kellicottia* as prey (Threlkeld et al. 1980). Rybock (1978) found positive selection for *Kellicottia* in Lake Tahoe and showed in an experiment that large *M. diluviana* were able to eat 3.5 *K. longispina* per hour. Based on these studies, it seems reasonable that the decrease in *K. longispina* density in Lille Jonsvatn after 1984 also was a result of increased predation by *M. relicta* after the cladoceran collapse. The very low rotifer biomass in Lille Jonsvatn for the 10 last years of the investigation could be a combined effect of *M. relicta* predation and interspecific competition among the herbivorous zooplankton. An increase in abundance of large daphnids has led to a decrease in rotifers in other lakes in the region (Reinertsen et al. 1990, 1997), and is in accordance with the much debated size efficiency hypothesis (Brooks & Dodson 1965).

The recorded cladoceran collapse in Lille Jonsvatn in 1985 was not clearly reflected in the development of algal biomass and composition during the grazing-free period 1985–1994. High maximum and mean annual algal biomasses were recorded in the years following 1985, but the decline in peak biomasses started from 1989 onwards, and mean biomass showed a significant decline from the late 1980s, i.e. before the reappearance of the cladocerans in 1995–1996. Although phytoplankton may be an important part of the *Mysis* spp. diet (Grossnickle 1982, Johannsson et al. 2001), it has not been shown that *M. relicta* by its herbivory has influenced phytoplankton biomass in lakes. As the total P content in Lille Jonsvatn showed a significant decrease from ~11 µg l^{-1} in 1989–1990 to 5 µg l^{-1} in 2006 (Fig. 2), this may have been a major reason for the phytoplankton biomass decline. When comparing data from a large number of north temperate lake ecosystems, Mazumder (1994) found a strong positive response of algal biomass to total phosphorus in ecosystems where grazers are controlled by planktivores (odd-link ecosystems). The extremely low abundance of large cladocerans, the most important grazers, in Lille Jonsvatn from 1985 to 1995, indicates very strong planktivore control. It is also obvious that a change in grazing pressure after 1995, as indicated by the higher zooplankton (than phytoplankton) biomass (Fig. 10), affected the phytoplankton development in Lille Jonsvatn for the last 10 yr of the present study. The ratio of herbivorous zooplankton to phytoplankton in most years after 1995 reflects an intensive grazing

pressure, which is also shown by the significant increase in cryptophytes in the biomass share of rapidly growing algae, i.e. *Rhodomonas lacustris* (Fott 1975, Cronberg 1980, Reinertsen et al. 1990). Due to increased turnover rate of the phytoplankton, less biomass is produced per unit P, as the P:C ratio of algae increases with increasing growth rate (Olsen et al. 1983). The presence of gelatinous chlorophytes and cyanophytes also confirms a high grazing pressure (Porter 1977, Reinertsen 1982). A significant decrease in total P was also found in Store Jonsvatn in 1989–2006 (Fig. 2), but no change in total algal biomass or algal composition was recorded.

The sudden collapse in cladoceran populations recorded in Lille Jonsvatn did not take place in Store Jonsvatn, where attractive prey and mysids have coexisted for many years; however, there has been a long-term, slow decline in the density of the most attractive cladocerans. The decrease in cladoceran biomass in Store Jonsvatn has been less dramatic and taken considerably longer than in other lakes with introduced *Mysis relicta* in the same area. In Lakes Selbusjøen and Stugusjøen, the cladoceran populations were strongly reduced 5 to 6 yr after the mysid introduction (Langeland 1988, Langeland et al. 1991). No long-term trends in biomass change in copepod or rotifer species were detected in Store Jonsvatn.

The large differences in zooplankton development in the 2 basins of Lake Jonsvatn may be explained by differences in temperature and light conditions. In controlled laboratory experiments, Boscarino et al. (2007) found that *Mysis diluviana* preferred temperatures between 6 and 8°C and had limited movement into water of 12°C or higher. Martinez & Bergersen (1991) found that temperatures above 14°C excluded *M. diluviana* from the epilimnion of Lake Granby, Colorado, and Rudstam et al. (1999) stated that mysids seldom occur in temperatures above 15°C. Summer temperatures in the epilimnion normally exceed 14 to 15°C in all parts of Lake Jonsvatn. Due to a higher degree of wind exposure, the thermocline is often 1 to 2 m deeper in Store Jonsvatn than in Lille Jonsvatn. This might give the zooplankton a greater vertical refuge for population development in Store Jonsvatn. The duration of egg development in Daphniidae at 15°C is 5 to 7 d (Bottrell et al. 1976) and post-embryonic development (the time from hatching to attaining maturity) was, in an *in situ* experiment in Lake Haugatjern, not far from Lake Jonsvatn, 6 d at 13°C (Langeland et al. 1985). The period with sufficiently high temperatures to establish zooplankton refuges will normally last 1 to 2 mo in Lake Jonsvatn and provide enough time for development of several new generations. The larger refuge in Store Jonsvatn may be an important factor in explaining the differences in zooplankton development between the 2 basins.

Differences in Secchi disc transparencies of 1 to 2 m show lower light transmission in Lille Jonsvatn than in Store Jonsvatn. This might result in acceptable light conditions for *Mysis relicta* to feed in the upper water layers for longer time periods at night in Lille Jonsvatn than in Store Jonsvatn in periods with acceptable temperatures (<14 to 15°C), and it may also contribute to a more sheltered environment for the zooplankton populations in the productive layers in Store Jonsvatn. Næsje et al. (2003) found that 90% of adult *M. relicta* stayed deeper than 49 to 53 m during light hours in May–September in Store Jonsvatn in a cool summer (maximum temperature 15°C at 1 m depth). Some juveniles (<8 mm) stayed 10 to 20 m higher up. During dark hours, both adults and juveniles performed vertical migrations and were found in all layers up to the surface. However, from mid-May to mid-July the nights are short at the high latitude of Lake Jonsvatn, and the period with acceptable light conditions for mysids to feed near the surface is quite limited. The shorter distance of vertical migration in Lille Jonsvatn (the maximum depth is 37 m and there are large areas with depths ≤30 m) might also contribute to easier access for *M. relicta* to the zooplankton in the upper layers in this part of the lake.

The present long-term study in Lake Jonsvatn revealed an unexpected plankton development in both investigated basins. In Store Jonsvatn, the zooplankton biomass was unaffected for a longer time than in other regional lakes with introduced *Mysis relicta*, and the eventual decline in cladocerans was less pronounced. In Lille Jonsvatn, the mysid introduction was expected to give reduced negative effects due to the higher nutrient level in this part of the lake. However, the cladocerans collapsed almost totally in this basin. The most diverging result from earlier documentation of mysid impacts was the development of *Daphnia longispina* in Lille Jonsvatn after a depletion of cladocerans that had lasted for 10 yr. The documented ability of a large daphnid to develop and sustain a relatively high population density for years in the presence of a relatively high mysid abundance adds new knowledge to interactions in mysid lakes, and shows the importance of long-term studies.

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