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# Long-term variation in the population structure of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*

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**Abstract** The effects of induced water level fluctuations and introduction of the mysid *Mysis relicta* Lovén on population structure of brown trout, *Salmo trutta* L., and Arctic charr, *Salvelinus alpinus* (L.), were studied during 1953–1995 in Limingen hydroelectric reservoir, Norway. The main response was a marked reduction in catch-per-unit-effort (CPUE) for trout and charr, probably caused by reduced recruitment following increased variation in water level. For both species, mean length decreased until 1967 and increased thereafter, whereas mean mass-at-length increased for the whole period. Both length and mass-at-length were negatively correlated with CPUE. The increases in mean length and mass-at-length were probably because of reduced competition following the reduced recruitment. *Mysis relicta* has become an important food item for charr but not for brown trout, but the increases in mean length and mass-at-length of charr started prior to the appearance of *M. relicta* in the charr diet.

**KEYWORDS:** Arctic charr, brown trout, catch-per-unit-effort, hydropower, *Mysis relicta*, time-series.

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## Introduction

Long-term data series often demonstrate considerable temporal variation in the abundance and composition of fish populations. Most published time series are for marine fishes (e.g. Rothschild 1986; Stenseth, Bjørnstad, Falck, Fromentin, Gjørseter & Gray 1999), or for anadromous salmonids (e.g. Groot & Margolis 1991; Summers 1995; Hilborn, Quinn, Schindler & Rogers 2003). The observed variation is often complex, and anthropogenic impacts (especially exploitation; Pauly,

Christensen, Guénette, Pitcher, Sumaila, Walters, Watson & Zeller 2002) together with climatic variation (Gates 1993) are important in driving this variation. Freshwater fish often have a low commercial value; therefore long-term catch statistics seldom exist. On the contrary, as the freshwater environment is easier to study than the marine environment and the fish populations are more clearly delineated, it may be possible to identify the factors that are important for producing variation in population abundance and structure.

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Fish populations are strongly affected by man, not only because of different kinds of technical encroachments, but also by harvesting and introduction of alien species. In the northern, temperate zone, the use of water for hydropower production has significantly altered the environment for aquatic organisms (Thornton, Kimmel & Payne 1990). Establishment of reservoirs leads to significant changes in the annual run-off regime. Water is usually stored in reservoirs during the snow melt and used to produce electricity in cold periods when precipitation is low. The annual fluctuation in water level causes severe changes in the affected shoreline areas, from being dry and frozen during winter to being submerged, in some cases, with turbid water in summer. The short-term effects of hydropower development on fish are reasonably well understood (O'Brien 1990). However, although hydropower development started in the beginning of the 20th century, very little information exists about the long-term effect on fish communities within reservoirs. This is unfortunate because the fish species affected, especially in the northern, temperate zone, have a long life span. The studies that do exist, often focus on the variation in feeding behaviour and growth and document significant diet shifts in brown trout, *Salmo trutta* L., after the establishment of a reservoir and the increased change in water level following the diversion and reallocation of water (Aass, Nielsen & Brabrand 1989; L'Abée-Lund, Aass & Sægrov 2002). Usually a large number of prey species are utilised prior to the encroachment, but after some decades of reservoir management, the diet is usually dominated by a few species. In some Scandinavian lakes, and also in USA and Canada, there was an attempt to ameliorate the effect of hydropower development on fish production by stocking lakes with large-sized crustaceans such as *Mysis relicta* Lovén (Lasenby, Northcote & Fürst 1986). This species is omnivorous, feeding on detritus, phyto- and zooplankton (Grossnickle 1982), usually in the profundal zone during the day and in the pelagic zone at night (Moen & Langeland 1989). After the introduction of *M. relicta* in Norwegian reservoirs, marked changes in both zooplankton density and composition, and in the diet of Arctic charr, *Salvelinus alpinus* (L.), were documented (Langeland 1981, 1988; Garnås 1986; Gregersen 1998). However, few studies have addressed how the Arctic charr population structure may vary after such changes. Long-term records are necessary, as short-term estimates of the effect of the changes may be confounded by temporal variability unrelated to the undertaken regulation.

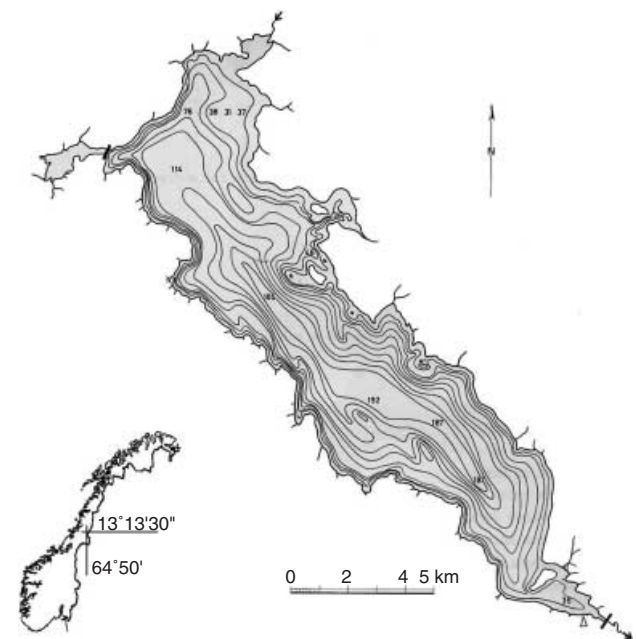
In this paper, long-term data (>40 years) are presented for the population structure of Arctic charr

and brown trout in Lake Limingen, Mid-Norway (hereafter Limingen). The data made it possible to evaluate the effects of hydropower development in 1953 and 1963 and the introduction of *M. relicta* in 1969. In particular, long-term catch-per-unit-effort (CPUE), length and mass data were analysed to understand the effects of these encroachments.

### Study system

Lake Limingen, 418 m above sea level, with a surface area of 95.7 km<sup>2</sup> is among the largest lakes in Norway (Fig. 1). The lake is deep (mean depth 87 m, maximum depth 192 m), with a steep littoral zone. The catchment is dominated by Cambro-Silurian bedrock, and only a few farms and a small village are situated along the lake shores. The lake is oligotrophic with a Secchi depth of 9–14 m during late summer, wind exposed and thermally stratified only during short summer periods (Langeland, Reinertsen & Olsen 1982). There are no indications of changes in water chemistry or nutrient content during the period of study. Furthermore, air temperature data from a nearby meteorological station (supplied by the Norwegian Meteorological Institute) showed that there was no long-term trend in temperature ( $r = 0.005$ ,  $P = 0.98$ ).

Limingen has been developed for hydropower production. No damming has taken place, but the lake can

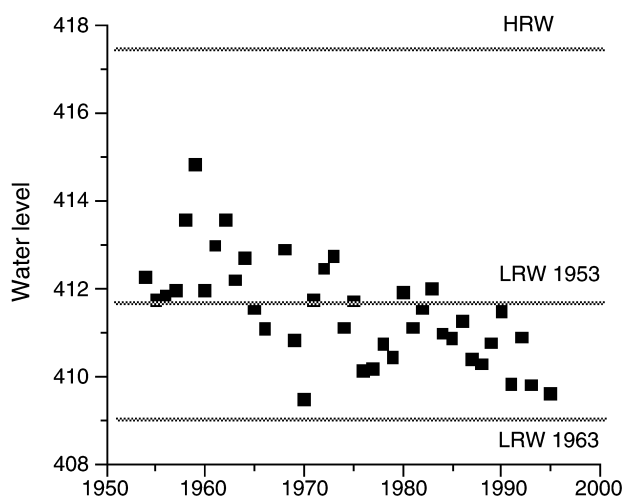


**Figure 1.** Lake Limingen with depth contours and location in Norway is shown in the inset. The main inlet, Røyrvikelv, the outlet, and the dams at the outlet and between Limingen and Gjersvika are indicated.

be lowered 8.7 m by two tunnels. The first tunnel, put into operation in 1953, allowed the water level to be lowered by 6 m and a second tunnel built in 1963 made it possible to reduce the water level by an additional 2.7 m. In addition, hydropower developments on the largest tributary, River Rørvikelv, have left an almost dry river channel that is unsuitable for charr and trout spawning. Low lake water levels generally occur during April to May, and the lake is usually filled to the upper permissible water level by July to August. This water level is usually maintained until December, after which a reduction in water level starts. The observed minimum water level during summer has decreased significantly with time (Fig. 2;  $r^2 = 0.430$ ,  $n = 40$ ,  $P < 0.001$ ). Because of the large difference in water level, the organic material in the littoral zone has been transported down to the deeper parts of the lake. The littoral zone, down to 8.7 m below maximum water level, now comprises rocks and gravel.

The shallow part of Limingen in north-west, Gjersvika, has not been affected by the construction of a dam at the point of connection with Limingen. Thus, data on fish species in Gjersvika are not included in the analysis.

The main fish species in the lake is Arctic charr, which usually utilises the littoral habitat as well as the pelagic and deeper epibenthic areas (Langeland, L'Abée-Lund, Jonsson & Jonsson 1991b). In addition, brown trout and minnow, *Phoxinus phoxinus* (L.), occur in the lake. Brown trout is native, but has also been stocked from 1960 onwards to compensate for a reduction in yield. The stocking programme was discontinued in 1982. Minnow invaded the lake during the 1970s, but their density is still very low.



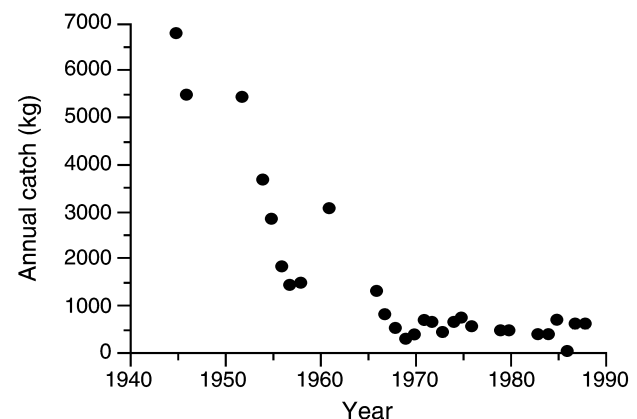
**Figure 2.** The annual lowest recorded water level in Limingen, 1953–1995. HRW, highest regulated water level; LRW, lowest regulated water according to licences granted in 1953 and 1963.

Three morphotypes of Arctic charr (called locally small, large and grey) are recognised in Limingen (Nyman 1972; Nyman, Hammar & Gydemo 1981), but their relationship is not clear. Large charr reach sizes of about 60 cm, and mature individuals are usually colourful (red to orange). Small charr rarely reach a size of 20 cm. Sexually mature individuals of this morph (4–6 years old) have visible parr marks and large eyes. The third morph is grey in colour, usually large in size and often with a heavy parasite load. Annual surveys of the catch of locals fishing for Arctic charr were conducted to estimate total yield. The number of locals fishing in this area is low (usually approximately 30). Two scientists (Sven Sømme 1945–1952 and Per Aass 1954–1967) and technicians from one institution (Faxälvens Vattenregleringsföretag 1968–1988) undertook the surveys. The yield estimates are therefore probably robust, although previously unpublished. The surveys demonstrate a significant decline from an annual catch of Arctic charr of about 6000 kg prior to the encroachment to about 500 kg in the period after 1970 (Fig. 3).

During 1969, the mysid *M. relicta* was introduced into Limingen as a food source for the charr to supplement the reduced benthic fauna community. *Mysis relicta* reproduction was documented in 1970 and charr started feeding on *M. relicta* in 1974 (Aass 1986). During recent years, *M. relicta* has become one of the most important food items for the charr during autumn (Gregersen 1998).

## Materials and methods

The benthic fish community was sampled using sets of standardised gill nets during late July to early August.



**Figure 3.** Annual yield (kg) of Arctic charr in Limingen during 1945–1988.

Systematic sampling began in 1953 coinciding with the implementation of the first tunnel. Thereafter the fish community was sampled annually until 1961. From 1961 to 1988, sampling was usually performed every second year. After 1988, only one sampling (1995) was performed.

Continuity in fish sampling has been an aim. Each summer, the same mesh size nets were set at 180 fixed stations around the lake. The nets were set perpendicular to the shore, and fished from the late evening until early next morning. The exact number of hours each net fished is not known, so it has been assumed that each net fished one full night at each station. The total effort each year was 360 net-nights. The same personnel were responsible for the sampling programme during most of this time.

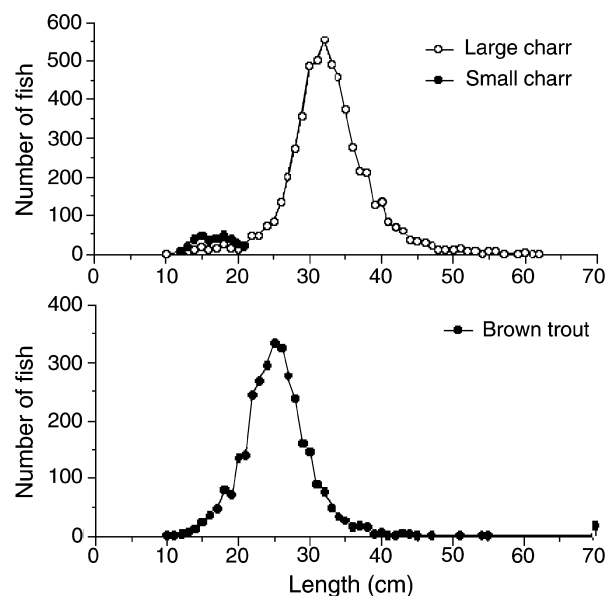
The nets used were 25 by 1.5 m sinking benthic gill nets. Mesh sizes varied from 26 to 45 mm (bar mesh). Each night, a set of 30 nets of varying mesh sizes were set [45 mm (three nets), 39 mm (three nets), 35 mm (nine nets), 31 mm (nine nets), 28.5 mm (three nets) and 26 mm (three nets)]. Such a set of gill nets will not catch a representative sample of the fish community in the lake (Jensen 1995). However, as the same set of nets have been used each year at the same locations and at the same time, the catches are considered comparable.

Until 1978, all the nets were of cotton. In 1980, monofilament nylon were used in 50% of the nets and from 1982 onwards all nets were made of monofilament nylon. It is well known that the material used influences the catching efficiency of nets (Hamley 1975). The catching efficiency is much higher for monofilament nets than cotton nets. Earlier studies indicated that nets made of monofilament catch two to three times more fish than nets made of cotton (Lawler 1950; Hamley 1975). Based on the 1980 results (own unpublished data) when monofilament nets captured 2.6–2.8 times more fish per net than cotton nets, it was assumed that the monofilament nets were three times more efficient than cotton nets. Total annual catch post-1978 was adjusted to what would have been expected if cotton nets had been used throughout the study period.

Each fish was weighed (nearest 1 g), measured (total length, TL, to the nearest 0.5 cm), sexed and classified as sexually mature or immature. The information about sexual maturity and length was used to classify individuals into morphs (small and large). In this way grey charr are classified as large charr. In 1995 only, charr were classified in the field based on body morphology and colour. Less than 1% of the Arctic charr sampled that year could be classified as grey

charr. Some additional fishing (data not presented) indicated that this morph was more prevalent at depths not normally sampled. Thus, the number of grey charr in the material was probably limited. The length distribution of the Arctic charr was bimodal, with one group of fish smaller than 22 cm (Fig. 4). These small fish were smaller than the sizes normally retained in the nets used, and are only captured when caught by the teeth. A relatively large number of these small Arctic charr were sexually mature and relatively old (P. Aass, unpublished data). All these small, sexually mature charr were classified as small, whereas the sexually immature charr <22 cm were classified as large. The number of small charr was low, and are excluded when analysing for temporal variation in length and mass.

Variation in mean length between years was analysed using General Linear Model (GLM) methods. In the models, uneven capture rates in the different mesh sizes were adjusted by including mesh size as a covariate in the model. ANCOVA was chosen to analyse for variation in mass-at-length (condition), using ln-transformed mass as the dependent variable, ln-transformed length and mesh size as covariates, and the presence or absence of *M. relicta* as treatment variable. Year 1970 was fixed as the first year when *M. relicta* was present, even if the density in the first year was low. In some models, to test for possible density effects, CPUE was used as the measure of total fish density. Furthermore, year was included as a covariate



**Figure 4.** Total length distribution of Arctic charr (small and large) and brown trout captured in Limingen, 1953–1995.

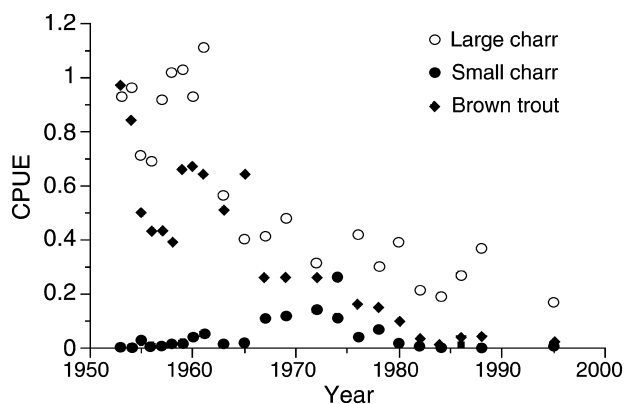
in some models. When necessary, traits were ln-transformed to normalise variance. The hypothesis that the data are better represented by two linear segments, rather than a single linear segment, was tested using linear stepwise regression (for an application see Post & Parkinson 2001). The linear stepwise regression model provides an independent estimation of the slopes of the two linear segments and of the inflection points (with associated standard errors). Stepwise linear regressions were fitted to the data using the computer program JMP (SAS institute Inc.):

$$Y = \begin{cases} b_0 + b_1X & \text{if } X \leq \text{Break} \\ b_0 + b_1X + b_2(X - \text{Break}) & \text{if } X > \text{Break} \end{cases}$$

where  $Y$  is either mean annual length (cm), or estimated mass-at-length (ln g, estimated from the ANCOVA of ln-mass on ln-length),  $X$  is year,  $b_0$  is the intercept of the first segment,  $b_1$  is the slope of the first segment,  $b_2$  is the difference in slope between the first and second segments, and Break (year) is the inflection between the first and the second segments. The slope of the second segment is calculated as  $b_1 + b_2$ .

## Results

The CPUE of large Arctic charr and brown trout decreased with time (Fig. 5). The CPUE for both species decreased from more than 1 fish net<sup>-1</sup> night<sup>-1</sup>, to about 0.2 fish net<sup>-1</sup> night<sup>-1</sup> for large Arctic charr and to almost 0 for brown trout. The CPUE of large Arctic charr was significantly positively correlated with CPUE for brown trout ( $r^2 = 0.66$ ,  $n = 23$ ,

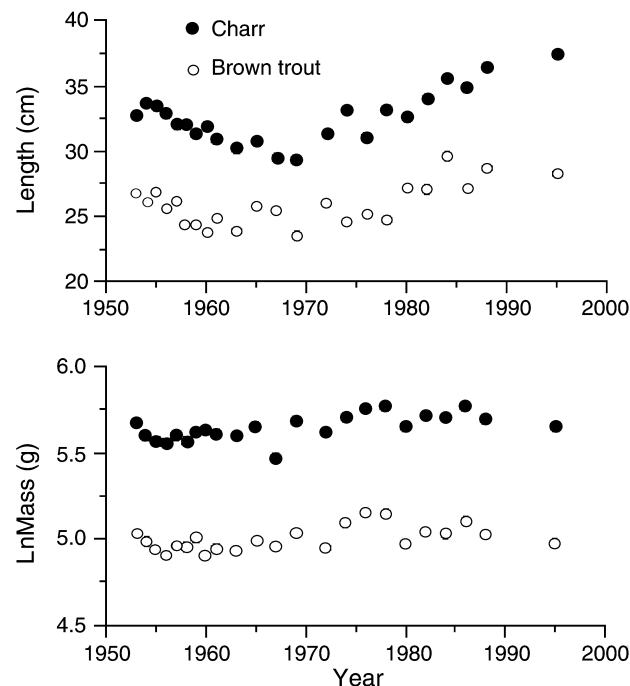


**Figure 5.** Temporal variation in catch-per-unit-effort of Arctic charr (small and large) and brown trout in Limingen during 1953–1995. Nets made of cotton were used until 1978 and replaced with net of nylon in 1982. In 1980 nets consisted of 50% of each material. The total annual catch has been adjusted to their respective catchability (see text).

$P < 0.001$ ). The CPUE for small charr was always low (mean  $\pm$  SD;  $0.036 \pm 0.044$  fish net<sup>-1</sup> night<sup>-1</sup>), with a peak during the late 1960s and early 1970s. The CPUE of large and small Arctic charr was not correlated ( $r^2 = 0.05$ ,  $n = 23$ ,  $P = 0.290$ ). For brown trout ( $F_{1,21} = 38.66$ ,  $P < 0.001$ ) and large Arctic charr ( $F_{1,21} = 34.81$ ,  $P < 0.001$ ), but not for Small Arctic charr ( $F_{1,21} = 0.25$ ,  $P = 0.625$ ), the mean CPUE was lower after *M. relicta* became established.

Arctic charr length varied from 10.5 to 62.0 cm, with a mean length of  $31.9 \pm 6.6$  cm, and brown trout length varied from 10.5 to 70.5 cm, with a mean of  $25.5 \pm 4.7$  cm (Fig. 4). Mean length varied strongly between years for both species. During the period from 1953 up to c. 1970, mean length of both Arctic charr and brown trout decreased significantly; thereafter, mean length increased (Fig. 6). For both species a stepwise linear regression could be fitted to the data, with the estimated inflection year being  $1966 \pm 3$  for brown trout and  $1967 \pm 1$  for Arctic charr. The temporal variation in mean length of the two species was positively correlated ( $r^2 = 0.636$ ,  $n = 23$ ,  $P < 0.001$ ).

The least square mean (LSM) mass-at-size (a proxy for condition, estimated using ANCOVA) varied significantly between years for both species. Both species



**Figure 6.** Temporal variation in mean length and least square mean mass-at-length (ln-transformed) of brown trout and large Arctic charr in Limingen during 1953–1995.

**Table 1.** Summary results for ANCOVA on annual mean length or least square mean (LSM) mass-at-length of Arctic charr and brown trout in Limingen. Treatment was presence or absence of *Mysis relicta* (d.f. = 1), and catch-per-unit-effort (CPUE) for trout and charr combined was used as a covariate (d.f. = 1). LSM mass-at-length are from ANCOVA with ln-mass as dependent variable, ln-length as covariate and year as treatment effect

Dependent variable	<i>Mysis relicta</i> CPUE (ln-transformed)			
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Arctic charr				
Length	0.65	0.360	0.65	0.437
Mass-at-length	8.73	0.008	0.78	0.388
Brown trout				
Length	0.003	0.955	2.72	0.115
Mass-at-length	5.23	0.033	0.45	0.504

became 'fatter' with time (Fig. 6; Arctic charr;  $r^2 = 0.361$ ,  $n = 23$ ,  $P = 0.002$ ; brown trout,  $r^2 = 0.230$ ,  $n = 23$ ,  $P = 0.018$ ). It was not possible to fit stepwise linear regressions to these data, indicating that a simple linear regression represented the trend better. For both brown trout ( $F_{1,21} = 11.62$ ,  $P = 0.002$ ) and large Arctic charr ( $F_{1,21} = 19.06$ ,  $P < 0.001$ ), LSM mass-at-size was larger after *M. relicta* was established than before. The temporal variation in mean mass-at-length of the two species was positively correlated ( $r^2 = 0.706$ ,  $n = 23$ ,  $P < 0.001$ ).

The linear regression indicated that mean length was negatively correlated with pooled CPUE (ln-transformed) for the two species (Arctic charr;  $r^2 = 0.335$ ,  $n = 23$ ,  $P = 0.004$ ; brown trout,  $r^2 = 0.361$ ,  $n = 23$ ,  $P = 0.002$ ). When introducing the presence or absence of *M. relicta* as a factor in the analysis, neither treatment nor covariate was significant (Table 1). Mean LSM mass-at-length was significantly negatively correlated with total CPUE for both species (Arctic charr;  $r^2 = 0.275$ ,  $n = 23$ ,  $P = 0.010$ ; brown trout,  $r^2 = 0.206$ ,  $n = 23$ ,  $P = 0.030$ ). However, only the presence or absence of *M. relicta* was significant in an ANCOVA model containing total CPUE as a covariate (Table 1). For both species, mean LSM mass-at-length was larger in the presence of *M. relicta* than when it was absent.

## Discussion

The epibenthic population of brown trout and Arctic charr responded in the same way to the water level changes and the introduction of *M. relicta* in Lake Limingen. The main responses were a strong reduction in CPUE, indicative of a reduction in population size,

and concurrent changes in mass-at-length (condition). As both species responded in the same way, despite differences in their biology, this suggests a common explanation for the observed changes.

For both species, CPUE and probably density decreased with time. Simultaneously, estimated yield of Arctic charr by local fishermen fell from about 1 kg ha<sup>-1</sup> before hydropower development to 0.3 kg ha<sup>-1</sup> in the next 10 years and to 0.05–0.1 kg ha<sup>-1</sup> in 1983–1985. The total annual yield of brown trout by local fishermen in 1983–1986 has been estimated to be < 10 kg (P. Aass, unpublished data). The smaller population may be because of either a reduction in recruitment or an increase in mortality. Following the development of the hydropower facility, erosion leading to increased turbidity may have temporarily had a negative effect on the fish populations (Waters 1995). Water turbidity would only have a short (a few years) initial effect. As the effect was long-lasting, turbidity cannot explain this trend.

The two species spawn during the autumn, but in very different habitats. In general, brown trout spawn in rivers and streams (Klemetsen, Amundsen, Dempson, Jonsson, Jonsson, O'Connell & Mortensen 2003) while Arctic charr usually spawn in the epibenthic zone in lakes (Klemetsen *et al.* 2003). In Limingen, the large charr spawned at 2–8 m depth, and the small charr at 10–15 m (P. Aass, unpublished data). Prior to the hydropower development, major Arctic charr spawning areas also existed in the main inlet, Røyrvikelv (P. Aass, unpublished data). The inlets and the outlet from the lake were the major recruitment areas for the brown trout. The small tributaries have not been influenced by the encroachment, but they are of minor importance as spawning areas for the brown trout. The hydropower development in Røyrvikelv and the water level variation in Limingen totally destroyed the spawning habitat in the Røyrvikelv and the outlet. The natural high water level obtained in Limingen through autumn and early winter (usually through December) secured access to the tributaries for the brown trout. Brown trout spawning in the littoral zone cannot be ruled out (Brabrand, Koestler & Borgström 2002), but has never been reported in Limingen. Thus, reduced access to and the destruction of the major spawning habitats have intuitively led to a dramatic reduction in the recruitment of both the Arctic charr and the brown trout.

Both Arctic charr and brown trout spawn during late autumn, when the water level is high and all spawning areas are accessible. Water level is reduced during winter and spring, and reaches its lowest level during late spring. As a consequence, the eggs and

embryos may dry out and also be exposed to ice and frost during late winter. However, the draw down has increased over time. Aass (1973) documented that the annual variation in the lowest water level in reservoirs may give pronounced fluctuations in year class strength of Arctic charr. Thus, the intensity of any mortality on the egg stage because of water level fluctuation may have increased with time. This fits the observed reduction in CPUE over time. The hypothesis is supported by some preliminary analyses using incomplete data on the Arctic charr in Limingen that indicates a significant negative relationship between the variation of observed minimum and maximum water level and year class strength.

Both species reacted rapidly to the new conditions in the reservoir. However, the temporary increase in Arctic charr CPUE in 1960  $\pm$  2 years was probably the result of the strong year class that hatched in 1953 (P. Aass, unpublished data). This cohort grew into catchable size in 1958 and dominated the population for 5 years. Afterwards the decline continued for both species.

The observed reduction in CPUE with time for both species may also be explained if survival rates of either juveniles or adults have decreased with time. However, the current observations do not support this hypothesis. If feeding opportunities were reduced for both species such that survival was reduced, either through interspecific competition or reduced food availability, the mass-at-length and growth rate would have decreased with time. However, mass-at-length (condition) increased with time, especially in the period when the CPUE for both species was low. This is a strong argument against the effects of competition. Furthermore, data on length-at-age for the Arctic charr did not suggest that growth rate had been reduced (C.S. Jensen, unpublished data). Both species are rather flexible in their diet (Lien 1978, 1981; Hindar & Jonsson 1982; Langeland *et al.* 1991b), enabling them to cope with reduced food organism diversity by changing feeding behaviour (Nilsson 1961; L'Abée-Lund *et al.* 2002). Moreover, brown trout have maintained their growth over seven decades in a regulated reservoir despite significant changes in the food categories eaten (L'Abée-Lund *et al.* 2002).

*Mysis relicta* can restrict growth in juvenile (0+, 1+) Arctic charr because of similarities in habitat use and food choice (Langeland & Moen 1992). Similar effects were observed in *Coregonus* species (Hammar 1988; Tohtz 1993). However, the most marked decrease in Arctic charr CPUE in Limingen occurred before *M. relicta* was released and became established.

Furthermore, the presence of *M. relicta* does not explain the increased juvenile brown trout mortality, as the habitat use and food selection are very different. *Mysis relicta* is a phyto- and zooplankton feeder (Lasenby 1991), whereas brown trout feed mostly on larger organisms such as benthic insects and littoral crustaceans (Langeland *et al.* 1991b).

During the first period after the encroachment the mean length of both brown trout and Arctic charr decreased. This was probably because of the negative effect of the increased amplitude of water level fluctuations on the benthic invertebrates that are the most important food source for both species. This is a common response to this kind of encroachment (Grimås 1961, 1962, 1964). However, after a period of decrease, the mean length of both brown trout and Arctic charr began to increase. The turning point came in 1966 for charr and in 1967 for trout. The estimated inflection points are prior to the introduction of *M. relicta*, even allowing for some error in the inflection point estimates. There is only one possible explanation for this trend, which has independently been observed in two species. Reduced overall density, as shown by the markedly reduced CPUE for both species, probably led to decreased intraspecific competition for both species. The second hydropower development in 1963 may have resulted in a critical reduction in Arctic charr spawning areas. The resultant reduced recruitment may have led to reduced intraspecific competition immediately following the changes in water level in 1963. However, the later build-up of a large *M. relicta* population may have introduced a novel source of energy that led to increased growth. *Mysis relicta* was not found in the stomachs of Arctic charr caught in 1972, but appeared in the diet in 1974, and from 1976 was the major food organism in summer (Gregersen 1998). However, the Arctic charr may have started feeding on *M. relicta* in winter earlier than the summer observations suggest. Næsje, Jensen, Moen & Saksgård (1991) showed that Arctic charr undergo significant seasonal changes in Mysid feeding. During the ice covered period *M. relicta* made up more than 80% of weight of prey items found in stomachs, and <10% during July to August. This seasonal change in *M. relicta* in the diet was attributed to significant habitat overlap between the two species in winter, but not in summer. The active feeding on *M. relicta* performed by Arctic charr during winter may, however, have a limited effect on growth because of low temperatures. The brown trout situation was somewhat different, as *M. relicta* can contribute about 30% to the trout's diet in July to August (Langeland,



Koksvik & Nydal 1991a). However, no information about the brown trout diet was available.

A strong association between CPUE and both mean length and mean mass-at-length indicated that density-dependent processes are important. Experimental studies showed that brown trout and Arctic charr may compete strongly (Forseth, Ugedal, Jonsson & Fleming 2003), and production of either species is lower in sympatry than in allopatry (Nilsson 1963). Intraspecific competition may also be important, leading to reduced growth rates (Bohlin 1977). Thus, the present findings may be the result of competitive release, where both inter- and intraspecific competition may be important. The presence of a new and useful food source for the Arctic charr may have led to the increase in mean length and mean mass-at-length. L'Abée-Lund, Langeland, Jonsson & Ugedal (1993) showed that Arctic charr are able to evaluate food availability in various habitats. After 1974, *M. relicta* was the most important food source for the Arctic charr in Limingen. No data on the diet of the brown trout in Limingen are available, but *M. relicta* seems to be of minor importance as a food item for brown trout in lakes where they co-occur (Langeland *et al.* 1991a; Næsje, Jensen, Moen & Saksgård 1991). The increase in the mean length and mass-at-length started a few years prior to the appearance of *M. relicta* in the diet of the Arctic charr, and in brown trout several years before *M. relicta* was introduced. Based on this scenario, the most likely explanation for the increases in length and mass-at-length observed in brown trout and Arctic charr was decreased competition.

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