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RESEARCH ARTICLE

Contrasting responses of Arctic charr and brown trout to compensatory nutrient enrichment in an oligotrophicated reservoir

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ABSTRACT

Many large lakes in northern Scandinavia have become oligotrophicated due to hydroelectric water regulation in the twentieth century, causing a loss of littoral habitat and negative consequences for ecosystem productivity, fish populations, and fisheries. Compensatory nutrient enrichment is a potential remediation method that has successfully been carried out in Canada and the US. Here we assessed the response of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) to nutrient addition in a whole lake experiment in Stor-Mjölkvattnet, Sweden, with nearby Burvattnet as a reference. Nitrate and phosphate were added for eight consecutive years. The study also included sampling the seventh year after discontinuation of nutrient addition, which allowed us to investigate how long nutrient enrichment would be effective on fish growth. Populations of Arctic charr and brown trout responded quickly and vigorously to the treatment, with approximately a doubling of the catch per unit effort. Nutrient addition had a consistent positive effect on charr length, weight, and condition at a given age, with a median response to nutrient addition (as measured by Shapley values) of 32 mm, 45 g, and 0.087 g cm^{-3} × 100. The response in length and weight was strongest in the age classes 4+ and 5+. The corresponding responses of trout were 13 mm, 32 g, and 0.044 g cm^{-3} × 100, respectively. Seven years after the enrichment had ended, charr at ages ≤6+ years were back to their previous state before treatment, i.e. slow growing and in bad condition. The older age-classes of charr (≥7+), however, were in good condition, suggesting that those fish, as young had experienced the excellent conditions prevailing in the last years of nutrient enrichment and largely kept this advantage. We conclude that compensatory nutrient addition is a useful method for restoring charr populations and reversible.

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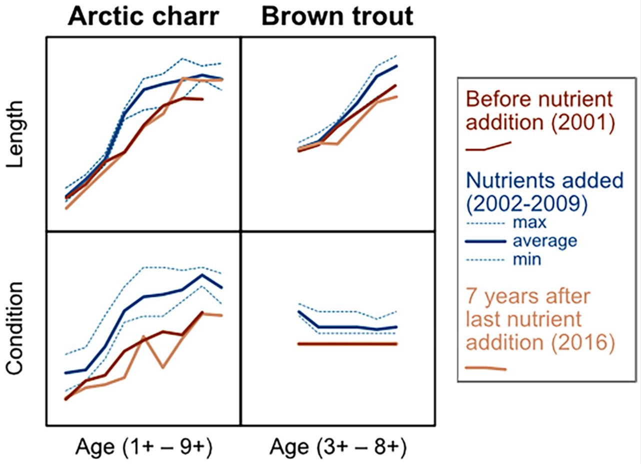
GRAPHICAL ABSTRACT



KEY POLICY HIGHLIGHTS

- Large water level fluctuations in northern hydropower reservoirs cause severe damage to littoral habitats, eventually causing lowered biological productivity including lowered growth rate and lower abundance of Arctic charr.
- Compensatory nutrient enrichment can mitigate the damage on native populations of Arctic charr by increasing plankton production and thereby restore charr growth to levels similar to before impoundment.
- After discontinuation of nutrient addition, the fish growth returns to low levels.
- Compensatory nutrient enrichment is thus an effective, yet reversible, management method for restoring charr fisheries in heavily damaged reservoirs.

Introduction

Ecosystems in northern lakes, including food webs and fish populations, have been directly or indirectly affected by several, partly interdependent, environmental pressures, e.g. acidification (Appelberg et al. 1993; Rosseland 2021), climate change (Creed et al. 2018; Muhlfeld et al. 2024), oligotrophication (Stockner et al. 2000; Huser et al. 2018) and hydropower expansion (Renöfält et al. 2010; Eloranta et al. 2018).

Many rivers and lakes in Scandinavia and North America have been impounded for hydroelectric energy production. In northern Sweden, eight of the eleven largest rivers have been regulated and most of the large lakes in these catchments are regulated (Supplementary Figure S1). Particularly the reservoirs in the upper parts of the catchments have a large annual variation of the water level, with a difference between highest and lowest permitted water level usually exceeding 3 m and in the most extreme cases as much as 35 m. The drawdown typically occurs during winter and spring, and the reservoirs are recharged by snow melting as well as summer and autumn rain.

Hydropower regulation initially leads to a period of trophic upsurge directly after dam construction when nutrients are leaked from areas that have become inundated, which causes an increase in fish growth (Nilsson 1961; Aass 1970; Grimard and Jones 1982; Milbrink et al. 2011). However, the trophic upsurge declines and is followed by oligotrophication (Aass 1973; Milbrink et al. 2011). One explanation for the oligotrophication is that winter drawdown is a strong disturbance of the littoral habitats, which results in loss of fine sediments, as well as reduced abundances and changed community composition of macrophytes and benthic macroinvertebrates (Carmignani and Roy 2017; Trottier et al. 2019). This loss of habitat and damage to the food web alters nutrient cycling and lowers ecosystem productivity. Another explanation for the oligotrophication of reservoirs is that an increase in water residence time due to the increase of lake volume results in lower nutrient concentrations according to the Vollenweider model (Vollenweider and Kerekes 1982). The effects of the habitat loss and the oligotrophication cascades through the food webs and eventually results in a very strong long-term decline of fish abundance, growth and condition (Aass et al. 2004; Milbrink et al. 2011). However, the response of the fish communities to water level regulation is complex and depends upon the magnitude of the water level regulation as well as its interaction with lake morphometry and whether there are other fish species present or not (Eloranta et al. 2018).

Compensatory nutrient enrichment has been successfully ordained to mitigate the negative effects of oligotrophication on fish populations both in North America (Stockner and Ashley 2001; Pieters et al. 2003; Perrin et al. 2006; Wilson et al. 2018; Schindler et al. 2020) and Scandinavia (Milbrink and Holmgren 1987, 1999; Rydin et al. 2008). Careful addition of nutrients (phosphorus and nitrogen) during the summer season stimulates phytoplankton production (Rydin et al. 2008; Wilson et al. 2018). The phytoplankton community composition does not change to taxa with low food quality, and the increased resource availability thus results in an increase in zooplankton production (Persson et al. 2008). This eventually results in an increase in the growth rates of Arctic charr (*Salvelinus alpinus*), which reaches levels similar to pre-impoundment conditions (Milbrink et al. 2011). Whereas the response of the pelagic food web during the initial years of compensatory nutrient addition has been documented in several cases, less is known about the long-term response across age-classes of sympatric Arctic charr and brown trout (*Salmo trutta*), and there is very little knowledge on the response of the fish communities upon termination of compensatory nutrient enrichment.

In small subarctic lakes, where no or few other fish species are present, charr rely heavily upon littoral food resources, whereas in larger subarctic lakes with sympatric populations of brown trout, charr characteristically use a more pelagic niche (Karlsson and Byström 2005; Eloranta et al. 2013). This can be explained by a relatively high pelagic production alongside with strong interspecific competition for littoral resources (Nilsson 1963; Eloranta et al. 2015). In large and heavily regulated lakes with reduced littoral production and limited availability of macroinvertebrate prey, Arctic charr is thus expected to shift towards a pelagic and/or profundal niche, particularly in reservoirs with sympatric populations of Arctic charr and brown trout. This shift, in combination with the constrained pelagic productivity due to oligotrophication causes increased intraspecific competition that results in decreased growth, condition and abundance of Arctic charr (Milbrink et al. 2011). Although brown trout has been considered to be more sensitive to hydropower development than Arctic charr due to its dependence on spawning habitats in rivers and littoral food sources (Nilsson 1961; Eloranta et al. 2013), the oligotrophication will further constrain pelagic primary production and food resources also for Arctic charr.

The objective of this study was to evaluate the response of sympatric populations of Arctic charr and brown trout to compensatory nutrient enrichment and re-oligotrophication after discontinuation of nutrient addition. We hypothesize that:

1. Arctic charr, which is predominantly using pelagic habitat, responds positively across age-classes to the stimulation of the pelagic primary production caused by nutrient addition.
2. Brown trout, which is predominantly using littoral habitats, will respond less strongly to nutrient addition than charr.
3. Compensatory nutrient enrichment is a reversible mitigation method and re-oligotrophication results in a return of the fish populations to a state similar to before nutrient addition.

Material and methods

Study sites and nutrient addition

The impounded lake Stor-Mjölkvattnet (outlet coordinate 63.8502°N, 13.3767°E) in the upper reaches of the river Indalsälven in Sweden was the target lake for compensatory nutrient enrichment, and the nearby upstream lake Burvattnet (outlet coordinate 63.9558°N, 13.3343°E) was the reference lake (Supplementary Figure S1). Stor-Mjölkvattnet and Burvattnet have surface areas of 13.6 and 13.2 km^2, maximum depths of 97 and 139 m, and mean depths of 31 m and 43 m, respectively. Both lakes are naturally oligotrophic subalpine clearwater lakes that were impounded in the 1940s to become hydropower reservoirs. The minimum and maximum permitted water levels are 543-554 m above sea level in Stor-Mjölkvattnet and 559–566 m in Burvattnet, and the realised water levels are close to the permitted levels each year, with the highest water levels occurring in the fall and the lowest occurring in April. A vertical-slot fish ladder is connecting the two lakes (Supplementary Figure S2). The fish community is dominated by naturally occurring Arctic charr, *Salvelinus alpinus* (Linnaeus, 1758) and brown trout, *Salmo trutta* Linnaeus, 1758. In addition, there is a small population of naturally occurring burbot, *Lota lota* (Linnaeus, 1758).

Nutrients were added to Stor-Mjölkvattnet following a protocol for compensatory nutrient enrichment of oligotrophicated inland waters similar to what has been used in North America (Stockner and Hyatt 1984; Ashley and Stockner 2001; Wilson et al. 2018) and Scandinavia (Milbrink and Holmgren 1987, 1999). Nitrogen [$Ca(NO_3)_2$] and phosphorus (H_3PO_4) were added annually in June–July 2002–2009

(Table 1) by pumping aqueous solution into the wake of a tugboat that was travelling back and forth in the lake, with most of the nutrients distributed in the deeper northern part of Stor-Mjölkvattnet, which is most distant from the outlet. The average total phosphorus concentrations were 4.1 μgP L^{-1} in Stor-Mjölkvattnet and 4.3 μgP L^{-1} in Burvattnet in 2001 (before nutrient amendment), and the mean for the years with nutrient amendment in Stor-Mjölkvattnet (i.e. 2002–2009) were 5.2 μgP L^{-1} in Stor-Mjölkvattnet and 3.1 μgP L^{-1} in Burvattnet. Additional information on lake and catchment morphometry, water chemistry, nutrient budgets, and planktonic biota have been presented in Rydin et al. (2008) and Persson et al. (2008).

Fish sampling and analysis

Standardised test-fishing were performed from mid-August to early September in 2001–2009 and 2016 with 30×1.5 m nylon nets of the Nordic type with 12 predetermined sections of different mesh sizes ranging from 5 to 55 mm knot to knot (Appelberg 2000; Swedish Institute for Standards 2005). Eight stations in each lake were randomly chosen largely covering the different depth zones of Stor-Mjölkvattnet and Burvattnet. The sampling intensity was 64 net nights in each lake each year. In total, 1874 Arctic charr and 814 brown trout specimens were captured (Supplementary Table S1, S2). Each fish was identified to species, weighed, and measured (fork length) as described in Milbrink et al. (2011). Almost 90% of all captured specimens were age determined based on otolith readings (Filipsson 1967; Milbrink et al. 2011). The Fulton coefficient (K) was used as an estimate of condition of the fish, and was calculated as:

$$K = \frac{W}{L^3} \times 100,$$

where W is the weight (g) and L is the length (cm) (Ricker 1975).

Statistical analyses

To illustrate population level temporal patterns in catch per unit effort, smoothing spline fits were used (Eubank 1999). Since these population level patterns can be difficult to interpret due to potential differences between lakes and years in the age structures of the populations, we accounted for this by including age in the analysis of the response of Arctic charr and brown trout length, weight and condition (independent variables, fitted separately). Furthermore, we analysed the response of charr

Table 1. Nutrient additions to Stor-Mjölkvattnet.

Year	Phosphorus (ton/year)	Nitrogen (ton/year)
2002	1.2	9.4
2003	1.2	7.1
2004	0.6	4.7
2005	1.0	5.7
2006	1.0	5.7
2007	1.0	5.7
2008	1.0	5.7
2009	1.0	5.7

and trout using two fundamentally different statistical methods, i.e. ANOVA and Random Forest. The analyses were made on identical data sets that were limited to age-classes with at most six missing values per lake and age class. This resulted in the inclusion of the age-classes 1+ to 9+ for charr ($N = 1610$) and from 3+ to 8+ ($N = 711$) for trout (Supplementary Table S1, S2). All statistical analyses were made using JMP Pro 18.0.2.

The ANOVA included the independent variables Lake, Year, the interaction Lake × Year (nominal scale) and Age (ordinal scale). Weight and length were Box-Cox transformed to homogenize the variances (Box and Cox 1964). The ANOVAs were followed by Tukey HSD post hoc tests at $\alpha = 0.05$ (Zar 1984).

The Random Forest analysis (Breiman 2001; Akselrud 2024) was made using the Bootstrap Forest platform in JMP. Random Forest is a machine learning method that constructs several decision trees after random selection of explanatory terms and bootstrap samples from the training data set. The predicted value of each instance (observation) is the average of the predictions for that instance of all decision trees. The model was run for charr and trout separately and using the terms (independent variables) Year, Age and Nutrient addition. All three terms were nominal, and the nutrient addition term was binary (nutrients added/not added). The data sets for charr and trout were split in training sets (70% of the observations of each species) and validation sets (30%). The maximum number of trees was set to 200, but calculations were restricted to stop using the Early Stopping function, which stops the construction of new trees when there is no further increase in R^2 (i.e. no further decrease in the root mean square error, RMSE). For each dependent variable (length, weight and condition), 100 runs were made to find the optimal setup of the hyperparameters Number of terms sampled per split (1–2 terms) and Minimum size of split (2–20 observations). The hyperparameters were uniformly distributed. The model results were interpreted using Shapley values calculated with the SHAP algorithm (Lundberg and Lee 2017; Molnar 2025). The SHAP values explain the prediction of an observation by calculating the contribution of each term to the prediction. The baseline of the comparison is the mean of all observations.

Results

Arctic charr

Arctic charr in Stor-Mjölkvattnet responded positively on the population level to compensatory nutrient enrichment, but the timing differed between catch per unit effort in abundance ($CPUE_N$) and weight ($CPUE_W$) (Figure 1). Initially, there was a rapid increase in $CPUE_W$ from 147 g/net in 2001 to a maximum of 447 g/net in 2006, after which it declined but remained higher than before nutrient addition during the rest of the period with nutrient amendment. Seven years after the last nutrient addition, $CPUE_W$ had decreased to 122 g/net. $CPUE_N$ increased from 1.5 individuals/net in 2001 up to a maximum of 2.7 individuals/net in 2009, after which it declined to 1.3 individuals/net in 2016. In Burvattnet, the largest $CPUE_W$ and $CPUE_N$ of Arctic charr were observed in 2001, with 218 individuals/net and 1.7 g/net (Figure 1). During the years 2002–2016 both $CPUE_W$ and $CPUE_N$ were lower

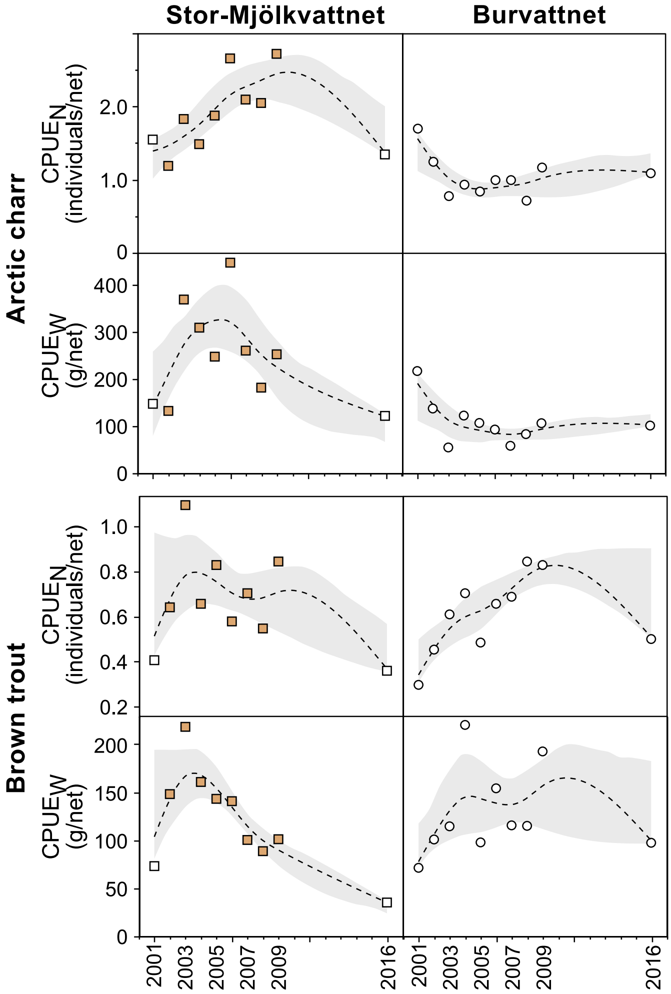


Figure 1. Catch per unit effort of Arctic charr and brown trout in number of individuals, CPUE$_N$ (individuals/net) and wet weight CPUE$_W$ (g/net) in Burvattnet (open circles: no nutrients added) and Stor-Mjölkvattnet (open squares: without nutrient addition, yellow squares: with nutrient addition). Hatched lines: spline fits ($\lambda = 0.05$), grey area: 95% confidence intervals of spline fits.

but showed no consistent trends and were on average 97 ± 27 g/net, and 1.0 ± 0.2 individuals/net (mean ± standard deviation), respectively.

Both the ANOVA and the Random Forest analyses explained a large fraction of the variation in charr length (85–87%), weight (77–85%) and condition (47–48%) (Table 2, 3). The predictions of the two methods were highly correlated ($r = 0.91 - 0.97$) and thus yielded quantitatively similar predictions (Figure 2).

The ANOVAs of Arctic charr showed that weight, length and condition of the age-classes 1+ to 9+ varied significantly (Table 2, Figure 2). Most of the variation was accounted for by Age but there were also highly significant effects of Lake, Year, and the interaction Lake × Year. Comparisons between years in Stor-Mjölkvattnet showed that charr length was significantly larger in 2003, 2004, 2006 and 2007 than in the control year 2001, and that there was no difference

Table 2. ANOVAs of Arctic charr at age 1+ to 9+ in Stor-Mjölkvattnet and Burvattnet with length, weight and condition as dependent variables (fitted separately). Length and weight were Box-Cox-transformed (λ=−0.185 and −0.050, respectively) prior to analysis to obtain homogeneity of variance. The effects Lake and Year are nominal, and Age is ordinal. $N = 1610$, degrees of freedom: 17, 1582 in all models.

Whole model	Length	Weight	Condition
r^2_{adj}	0.851	0.851	0.471
RMSE	30.4	28.3	0.100
F	341	341	54.1
P	<0.0001	<0.0001	<0.0001
Residual SS	1462536	1263356	15.96
Total SS	9971013	8619662	30.70

	Length			Weight			Condition		
Effect tests	SS	F	*p*	SS	F	*p*	SS	F	*p*
Lake	376240	407	<0.0001	393718	493	<0.0001	2.37	235	<0.0001
Year	4330	5.2	<0.0001	49801	6.9	<0.0001	0.82	9.0	<0.0001
Lake × Year	90928	10.9	<0.0001	80495	11.2	<0.0001	0.45	5.0	<0.0001
Age	7307783	988	<0.0001	6225987	974	<0.0001	9.73	121	<0.0001

Table 3. Random Forest analysis of Arctic charr (age 1+ to 9+) with length, weight and condition as dependent variables (fitted separately) and the independent terms Year, Age and Nutrient addition. $N_{training} = 1127$, $N_{validation} = 483$ in all models.

	Length	Weight	Condition
Number of terms sampled per split	2	2	2
Minimum size of split	2	6	2
Number of trees	18	10	11
RMSE training	30.2	67.4	0.090
RMSE validation	30.2	68.0	0.107
R^2 training	0.874	0.792	0.549
R^2 validation	0.874	0.771	0.477
Variable importance (%)			
Age	90	85	66
Year	4	7	15
Nutrient addition	5	7	19

between 2001 and 2016 (Supplementary Figure S3). In Burvattnet, there was a tendency towards lower length 2003–2009, with significantly lower length in 2007 and 2008 than in 2001. A comparison between the lakes showed that length was significantly higher in Stor-Mjölkvattnet than in Burvattnet in 2003–2009 but did not differ between the lakes during the control year 2001 or in 2016. The charr weight responded in a similar way as the length, but with significantly higher weight in 2002, 2003, 2006 and 2007 than in 2001 in Stor-Mjölkvattnet (Supplementary Figure S3). The weight decreased over time in Burvattnet with significantly lower weight in 2007 and 2008 than in 2001. A comparison between the lakes show that length was significantly higher in Stor-Mjölkvattnet than in Burvattnet in 2002–2009 but did not differ between the lakes during the control year 2001 or in 2016. The condition of charr was significantly higher in 2002 and 2003 (i.e. the first years with nutrient amendment) than all other years except 2007 (Supplementary Figure S3). The condition did not differ among years in Burvattnet, and the condition was higher in Stor-Mjölkvattnet than in Burvattnet all years except in 2001 and 2016.

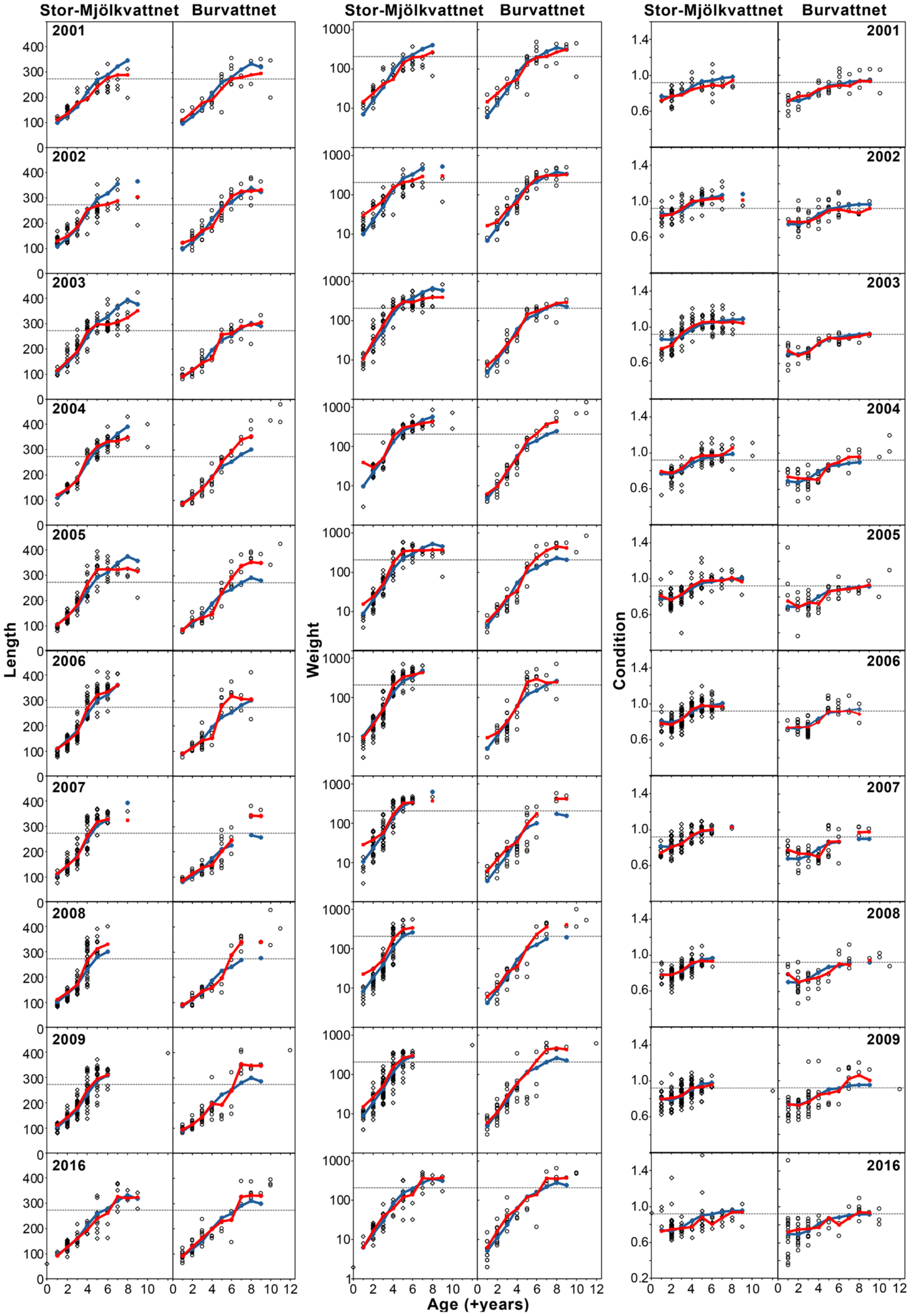


Figure 2. Length (mm), wet weight (g) and condition (g cm^{-3} × 100) vs. age of Arctic charr in Stor-Mjölkvattnet and Burvattnet. Blue lines and crosses: ANOVA predictions for age-classes 1+ to 9+. Red lines and crosses: Random Forest predictions for age-classes 1+ to 9+. Horizontal lines are reference lines calculated as the weighted mean of both lakes in 2001 of individuals ≥6+ years old.

In the Random Forest analysis, Age was the most important term in explaining charr length, weight and condition, with a variable importance range of 66–90% (Table 3). The variable importance of the terms Nutrient addition and Year ranged between 5 and 19% and 5–15%, respectively. Nutrient addition had a consistent positive effect on length, weight and condition, as indicated by the Shapley values (Figure 3). The median of the Shapley values for individual predictions of length, weight and condition were 32 mm, 45 g and 0.087 g $cm^{-3} \times 100$ higher with nutrient addition than without nutrient addition. The strongest responses of charr to nutrient addition in Stor-Mjölkvattnet, were in the age classes 4+ and 5+, which had median Shapley values 60 mm, and 97 g higher with nutrient addition than without nutrient addition (data not shown).

Brown trout

For brown trout, the catch per unit effort showed largely similar hump shaped patterns in Stor-Mjölkvattnet and Burvattnet, but with a more rapid increase in Stor-Mjölkvattnet during the first years of nutrient amendment (Figure 1). The $CPUE_W$ and $CPUE_N$ in Stor-Mjölkvattnet were 0.4 individuals/net and 73 g/net in 2001, peaked in 2003 at 1.1 individuals/net and 218 g/net, after which it decreased to at 0.7 ± 0.1 individuals/net and 123 ± 29 g/net during 2004–2009. In 2016, $CPUE_W$ and $CPUE_N$ were 0.4 individuals/net and 35 g/net. In Burvattnet, the smallest catch of trout occurred in 2001 with 0.3 individuals/net and 71 g/net, after which $CPUE_N$ increased gradually to 0.8 individuals/net in 2008 (Figure 1). $CPUE_W$ also increased, but was more variable, with a mean of 139 ± 46 g/net during 2002–2009. In 2016, $CPUE_W$ and $CPUE_N$ had decreased to 0.5 individuals/net and 98 g/net.

Both the ANOVA and the Random Forest analyses explained much of the variation in length (44–54%) and weight (38–54%) but less of the variation in condition (13–14%) (Tables 4, 5). The methods yielded quantitatively similar predictions ($r = 0.86 - 0.95$), but there was a tendency towards higher predictions of the Random Forest analysis than the ANOVA for weight and especially in 2016 (Figure 4).

The ANOVAs of brown trout showed that weight, length and condition of the age-classes 3+ to 8+ varied significantly (Table 3, Figure 4). Most of the variation in length and weight was accounted for by Age but there were also significant effects of Lake, Year and the interaction Lake × Year. Comparisons between years in Stor-Mjölkvattnet showed that there was no difference in length or weight between 2001 and the nutrient amendment years 2002–2009, but both length and weight were higher 2002–2009 than in 2016 (Supplementary Figure S3). The length and weight of charr in Burvattnet did not differ between 2001 and any of the years 2002–2209, but was lower in 2016 than in 2001, 2003, 2007 (weight only) and 2009 than in 2016. Both length and weight were significantly higher in Stor-Mjölkvattnet than in Burvattnet. Most of the variation in condition of trout was explained by Year, but also Lake and Lake × Year, while Age only had a weak effect (Table 4). In Stor-Mjölkvattnet, the condition of trout did not differ between 2001 and any other year, but trout had a higher condition during all years with nutrient amendment (2002–2009) than in 2016 (Supplementary Figure S3). The condition did not differ

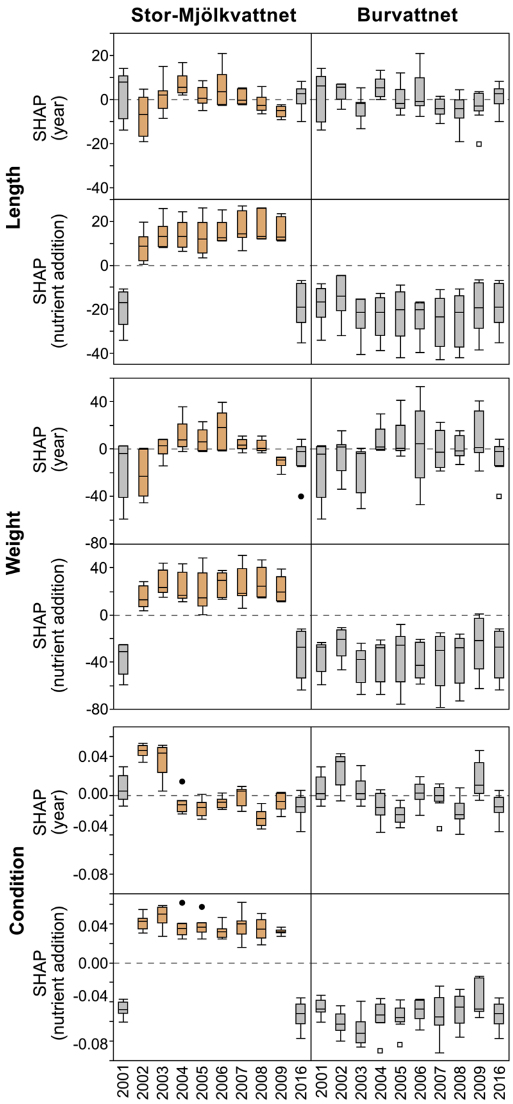


Figure 3. Shapley values (SHAP) from the Random Forest models for Arctic charr showing the contribution of the terms Year and Nutrient addition to the predictions of length, wet weight and condition. The reference lines indicate the average predicted contribution of the term across all observations.

between years in Burvattnet, and the condition was significantly higher in Stor-Mjölkvattnet than in Burvattnet in 2003 and 2008.

In the Random Forest analysis, Age was the most important term in explaining trout length, weight and condition, with a variable importance range of 65–86% (Table 5). The variable importance of the terms Nutrient addition and Year were 2–18% and 12–18%, respectively. Nutrient addition had a consistently positive effect on length, weight and condition, as indicated by the Shapley values (Figure 5). The median of the Shapley values for individual predictions of length, weight and condition were 13 mm, 32 g and 0.044 g cm^{-3} × 100 higher with nutrient addition than

Table 4. ANOVAs of brown trout at age 3+ to 8+ in Stor-Mjölkvattnet and Burvattnet with length, weight and condition as dependent variables (fitted separately). Length and weight were Box-Cox-transformed ($\lambda=-0.307$ and -0.160, respectively) prior to analysis to obtain homogeneity of variance. The effects Lake and Year are nominal, and Age is ordinal. $N=711$, degrees of freedom: 24, 686 in all models.

Whole model	Length	Weight	Condition
r^2_{adj}	0.543	0.536	0.133
RMSE	42.6	60.1	0.085
F	36.1	35.2	5.53
P	<0.0001	<0.0001	<0.0001
Residual SS	1244881	2197851	4.943
Total SS	2819230	5525834	5.900

	Length			Weight			Condition		
Effect tests	SS	F	*p*	SS	F	*p*	SS	F	*p*
Lake	34809	19.2	<0.0001	98091	27.2	<0.0001	0.1571	21.8	<0.0001
Year	88869	5.44	<0.0001	227841	7.02	<0.0001	0.4122	6.36	<0.0001
Lake × Year	51144	3.13	0.0010	100047	3.08	0.0012	0.1934	2.98	0.0017
Age	1277414	141	<0.0001	2438053	135	<0.0001	0.0960	2.66	0.021

Table 5. Random Forest analysis of brown trout (age 3+ to 8+) with length, weight and condition as dependent variables (fitted separately) and the independent terms Year, Age and Nutrient addition. $N_{training} = 498$, $N_{validation} = 213$ in all models.

	Length	Weight	Condition
Number of terms sampled per split	1	1	1
Minimum size of split	5	4	13
Number of trees	3	3	2
RMSE training	45.0	104.8	0.071
RMSE validation	49.9	125.7	0.111
R^2 training	0.534	0.511	0.118
R^2 validation	0.445	0.380	0.139
Variable importance (%)			
Age	83	86	65
Year	13	12	18
Nutrient addition	4	2	18

without nutrient addition. For the term Year, both lakes had lower Shapley values for length and weight in the latter part of the time series.

Discussion

Our results showed that compensatory nutrient enrichment increased the growth rate and condition of a naturally occurring local Arctic charr population. The increase reached levels similar to what is encountered in comparable unregulated lakes and before impoundment (Supplementary Figure S4). This is in line with our first hypothesis, that Arctic charr, which is a predominantly a pelagic zooplankton feeder especially in regulated lakes, would respond positively when the pelagic primary production is stimulated by nutrient enrichment. Similar results have been obtained from whole lake experiments on salmonid populations in oligotrophicated ecosystems in North America (Stockner and Ashley 2001; Pieters et al. 2003; Perrin et al. 2006; Schindler et al. 2020) even though the scale and the biota may be totally different, and the results would thus seem to be more or less generally applicable. We also hypothesized that brown trout in sympatry with charr would respond less

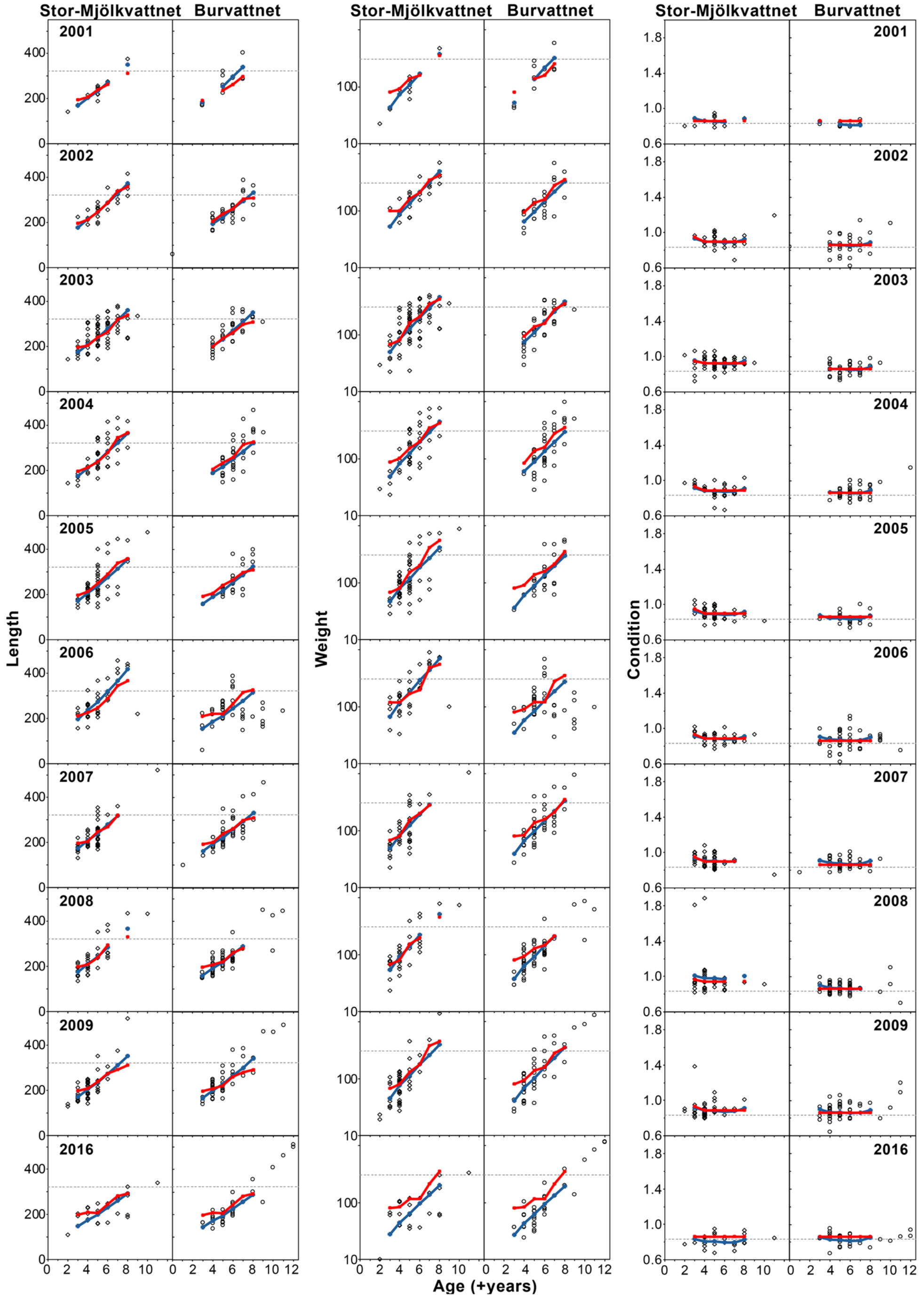


Figure 4. Length (mm), wet weight (g) and condition (g cm^{-3} × 100) vs. age of brown trout in Stor-Mjölkvattnet and Burvattnet. Blue lines and crosses: ANOVA predictions for age-classes 3+ to 8+. red lines and crosses: Random Forest predictions for age-classes 3+ to 8+. Horizontal lines are reference lines calculated as the weighted mean of both lakes in 2001 of individuals ≥6+ years old.

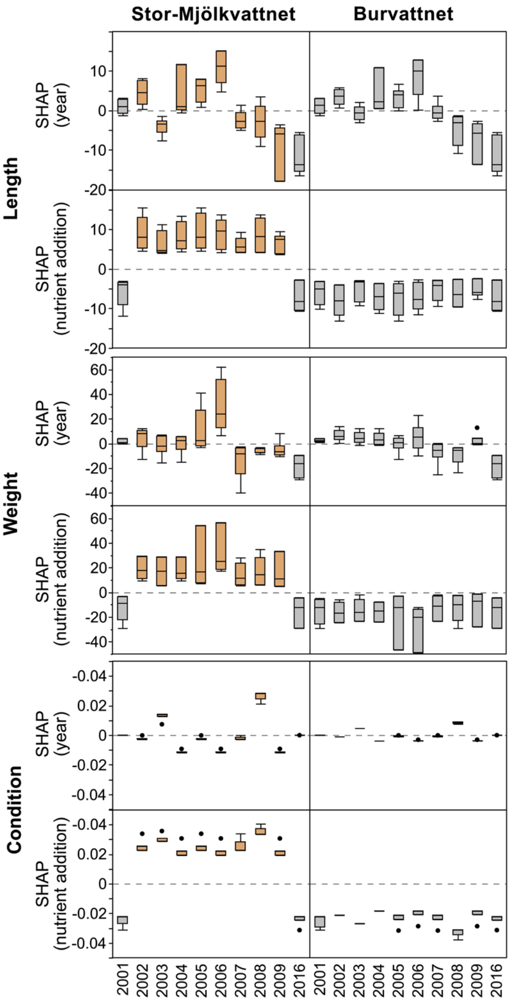


Figure 5. Shapley values (SHAP) from the Random Forest models for brown trout showing the contribution of the terms Year and Nutrient addition to the predictions of length, wet weight and condition. The reference lines indicate the average predicted contribution of the term across all observations.

strongly to nutrient addition because trout is more tightly bound to the littoral zone, which is impoverished because of habitat destruction, and still experience low availability of benthic prey despite the stimulation of the pelagic food web. A positive response in trout growth and condition to nutrient amendment was observed, but it was not consistent over the study period, and it was considerably weaker than the response of charr.

Our results also showed that compensatory nutrient enrichment is a reversible mitigation method. After the discontinuation of the nutrient enrichment, the catch per unit effort and condition of the charr returned to levels similar to before the treatment was applied. Also, when the comparison was made with 4+ char (one of the most vigorously responding age-classes) from other regulated lakes, this reversibility was evident (Supplement Figure S4). An exception to this return to a smaller and slow-growing population was that older specimens of Arctic charr (7+ and older) having been caught in Lake Stor-Mjölkvattnet in 2016 were larger and in particularly good condition than younger conspecifics. These fish would have been born during the last years of nutrient enrichment, and their shape is likely to be an effect of the good resource availability then and a few years after.

Hydropower regulation of lake ecosystems changes the hydrology from natural water level fluctuations to a regulated water regime, and this change has profound effects on both the abiotic environment and the food web. The regulation often differs from natural fluctuations in terms of amplitude, rate of change, frequency and timing, and it is an important stressor on the ecosystem (Hirsch et al. 2017). Directly after the dam construction, previously terrestrial areas are inundated, which results in an initial trophic upsurge. Nutrients and organic matter leaking from the newly submerged soils stimulate the primary production in the littoral and pelagic food webs (Baxter 1977). This increased basal productivity propagates through the food web and results in increased growth of fish (Milbrink et al. 2011) (Supplementary Figure S4). The duration of the positive inundation effect may vary considerably depending upon the size and quality of the flooded land, the speed of erosion and effects of silting (Nilsson 1963). According to Aass (1973), the positive effects decreased after four years in the Norwegian lake Pålsbufjord, and the effect is of similar duration, i.e. around 5 years, in the few Swedish hydropower reservoirs from which there are data on fish growth (Milbrink et al. 2011) (Supplementary Figure S4). The trophic upsurge is then followed by several decades with successively decreasing fish productivity. Heavy ice and wave erosion results in an almost total loss of fine sediments and organic matter from the zone between highest and lowest allowed water levels, thus transforming the littoral zone to an unproductive stony impediment (Supplementary Figure S5). The effect on biota is reduced abundance and diversity of the littoral fauna (Grimås 1964; Aroviita and Hämäläinen 2008). Species associated with block bottoms or capable of withstanding freezing or being particularly mobile may be favoured, but otherwise fish food organisms become increasingly scarce and fish populations therefore decline (Nilsson 1963; Aass 1973; 1984). Sixty years after the regulation of Stor-Mjölkvattnet and Burvattnet, the mean size of charr had declined to ca. 200 mm and 100 g, which correspond to ca. 50% decrease in length and ca 60% decrease in weight compared with the mean size of char in unregulated lakes.

In contrast to the littoral habitat, which sustains heavy damage from water regulation, the pelagic habitat may not be physically altered to the same extent. However, oligotrophication due to water regulation of these already oligotrophic systems is expected to reduce the productivity at the base of the planktonic food web. Previous studies in regulated and unregulated lakes in the Scandinavian mountain range have shown that phytoplankton are heavily nutrient limited, primarily by P in the Jämtland region (64°N) and by N in the Abisko region (67°N), but NP co-limitation is common and Fe may be primarily limiting in lakes with extremely low dissolved organic content (Vrede and Tranvik 2006; Bergström et al. 2020). The low phytoplankton standing stocks in the most nutrient poor lakes (total $p < 4$ μgP L^{-1}) has been predicted to result in strong food quantity limitation of somatic growth of crustacean zooplankton (Persson et al. 2007). Since zooplankton fecundity is even more sensitive to starvation than somatic growth (Wenzel et al. 2012), exacerbated nutrient limitation would reduce the population growth rates of zooplankton. The resources in the pelagic would therefore not be sufficient to sustain the growth of the planktivorous Arctic charr at a natural level in oligotrophicated hydropower reservoirs, and the regulation results in dwindling growth rates and low condition of Arctic charr, with no prospect for recovery (Milbrink et al. 2011). There are, however, exceptions to the decreased fish growth and condition. In a comparison between charr populations of a heavily regulated alpine lake and a comparable unregulated lake, Eloranta et al. (2017) found that there was a lower relative abundance (catch per unit effort) as well as a larger use of pelagic food resources in the regulated lake, but neither growth rates nor condition of charr were lower in the regulated lake. A tentative explanation for the latter observations could be that the investigation took place 32 years after dam construction, and the full extent of the ecological effects of water regulation may not yet have been manifested. Another explanation could be differences among reservoirs in terms of biotic communities, morphometric complexity, and the magnitude and frequency of the water level regulation (Eloranta et al. 2018).

We suggest that any negative effects of hydropower regulations on charr populations may become even more severe in the future for at least two reasons. First, there is a large scale oligotrophication going on in northern Sweden, with a dramatic decrease of phosphorus concentrations during the last four decades, both in lakes and rivers (Huser et al. 2018; Nilsson et al. 2024). Similar decreases of lake water phosphorus concentrations have been observed also in northern Norway (de Wit et al. 2023) and in Canada (Eimers et al. 2009). The sparsely populated northern Scandinavian catchments have not experienced substantial anthropogenic eutrophication from urban developments or agriculture (Stockner et al. 2000), and decreased anthropogenic input is thus not a good explanation of the negative trend. The decline is particularly strong in low nutrient environments, such as in alpine and subalpine lakes and streams, and phosphorus concentrations are negatively correlated with forest growth, temperature, pH and alkalinity (Nilsson et al. 2024). The oligotrophication may thus be understood as a combined effect of, e.g. climate change and recovery or lag phase from acidification (Huser and Rydin 2005). Looking at the results from the reference lake Burvattnet, this large scale oligotrophication could potentially explain the decreasing abundance, growth and condition of charr during the experiment. This is corroborated by the observations that both total phosphorus concentration and phytoplankton biomass also declined during the period 2001–2005 in Burvattnet (Persson et al. 2008). Secondly, the global warming is particularly rapid in northern ecosystems (IPCC. 2021). The increasing temperature is predicted to have a strong negative effect on Arctic charr, which is a cold adapted species, eventually resulting in its extinction from many Scandinavia lakes (Muhlfeld et al. 2024). This is both a direct temperature effect and an indirect effect of pike colonisation in lakes that are beyond its present distribution. We anticipate that the combined effects of the loss of the littoral habitat and oligotrophication caused by hydropower regulation, the large-scale oligotrophication and the stress on charr inflicted by increasing temperature will aggravate the situation even further for Arctic charr, eventually resulting in a further decline or even extinction of charr in more lakes than can be predicted from either of these factors alone.

To understand the different responses of charr and trout to compensatory nutrient enrichment, we need to address the differences in life history and feeding ecology of these salmonids. Due to historically much similar invasion routes, Arctic charr and brown trout quite often coexist in oligotrophic lakes in northern Scandinavia although only charr is present in the northernmost and coldest lacustrine environments, such as in the archipelago of Svalbard (Klemetsen 2010; Hammar 2014). There is a more or less fragile balance between Arctic charr and brown trout, charr dominating in lakes and rivers further north and at higher altitude, whereas brown trout increases in dominance in lakes and rivers further south in Scandinavia and elsewhere in Europe (Aass 1970). This delicate balance between Arctic charr and brown trout can shift on a local scale, as was illustrated in an experiment in the lake Takvatn in northern Norway, in which charr were successively and selectively removed by selective fishing to the advantage of brown trout (Klemetsen et al. 2002). As a result of the charr removal, both charr and trout grew faster and the size structure of the charr population changed from a stunted size distribution to a bimodal distribution that included large piscivorous individuals that preyed upon small charr.

Allopatric Arctic charr and brown trout populations are feeding in a similar manner, preferably on shallow bottoms in the littoral zone and their food intake is thus much the same (Nilsson 1965; Aass 1970; Langeland et al. 1991). In contrast, sympatric populations of the two species are generally segregated, with trout mainly feeding in the littoral and charr in the pelagic and in the profundal zone (Gregersen et al. 2006), where chironomid larvae may constitute a major part of the diet (Kangosjärvi et al. 2024). However, this habitat segregation can be broken during winter, and Arctic charr are frequently found in the littoral thanks to its ability to tolerate low temperatures and maintain high activity (Langeland et al. 1991). In heavily regulated hydropower reservoirs with sympatric charr and trout, the adaptive niche use of Arctic charr thus results in an almost exclusively pelagic and profundal diet. When the planktonic food web becomes more productive due to nutrient enrichment, the charr responds rapidly and vigorously. Nutrient enrichment started in late June 2002, and it was obvious already in the field, when the fishing took place in mid-August the same year, that the charr had changed their abdominal proportions. The abdomen became bulkier, and the head appeared relatively small, the back was broad and the neck higher after the nutrient addition started than before (Supplementary Figure S6). Stomach analyses revealed a very high abundance of *Bythotrephes longimanus* in a majority of the Arctic charr caught (Rydin et al. 2008).

Brown trout has been considered to be more sensitive to hydropower regulation than charr due to its reliance on benthic habitats and its requirement for running waters for spawning and rearing of young trout (Nilsson 1961; Gregersen et al. 2006). Comparing the catch per unit effort and condition of trout vs. charr in Stor-Mjölkvattnet and Burvattnet during the control year, we noticed that the catch per unit effort was larger for charr, but the condition was on a similar level. Although we do not have information on the trout populations in these lakes before the dams were built, the state of the populations immediately before nutrient addition does not suggest that trout has been more severely affected by the hydropower development. During the nutrient addition period, there was only a limited response of brown trout. An obvious explanation for this lack of response is that the littoral habitat has been degraded to such an extent that there cannot be any substantial increase in the productivity in the littoral food web despite the increased nutrient availability. The trout, which presumably stayed feeding in the littoral on the remnants of the bottom fauna and surface insects, therefore responded weakly. Another explanation for the weak response is that trout usually hatch and spend their first years in smaller waters in the catchment, and these waters were not affected by the nutrient amendment. This is corroborated by the fact that we only caught very few specimens of brown trout younger than 3+ years in any of the lakes. Thus, the recruitment and growth of trout largely depended on the resource availability. An exception to the generally weak response of trout was that very large specimens occurred more frequently during the later years of nutrient addition. This suggests that these older and presumably piscivorous individuals benefitted from the increased abundance of smaller size charr.

One apprehension before the onset of the experiment was that the charr population would retain the stunted size structure it had before nutrient addition. Instead, the growth became faster and continued both to a larger size and to a higher age. Stunted population size structure is a phenomenon of foremost Arctic charr, Eurasian perch (*Perca fluviatilis*) and yellow perch (*Perca flavescens*) occurring in thousands or even millions of conspecifics of the same small size irrespective of age. It has been shown that young and small individuals of Arctic charr are superior in exploiting common resources, which is a normal consequence of size-dependent competition favouring small charr (Byström 2006). The occurrence of stunted populations is not a question of lack of predation on small fish and cannibalism is actually not a driving force (Byström 2006). A prerequisite for cannibalism is clearly that the availability of small prey is high. On the other hand, the number of cannibals must not be too high and the growth rate of the cannibals not too high either, thus allowing enough of new recruits to develop. It seems likely that for stunted populations to form, pulses of recruitment, however erratic, are behind (Persson et al. 2000; Byström 2006; Persson et al. 2007). In a modelling study, Ylikarjula et al. (1999) showed that resource limitation of fish growth is sufficient to explain the occurrence of stunted growth. This is in line with our observations that charr growth apparently became less resource limited and the charr grew both faster and to a bigger maximum size.

In 2003 to 2009 a big share of the oldest charr (age from 7+ and older) in Burvattnet were relatively large and heavy and thus appeared to be in very good condition. A possible explanation is that the presence of a fish ladder (Supplementary Figure S2) enabled migration between Burvattnet and Stor-Mjölkvattnet, thus allowing them to feed on an abundance of food items in Stor-Mjölkvattnet and then return the same way. Food migration is not an unknown phenomenon in Arctic charr (Aass 1970). Downstream spring and summer food emigrations may involve a considerable part of the charr population, Aass (1970) reflecting upon the situation in Lakes Pålsbufjord and Tunhovdfjord in Norway. It is also recognized that young Arctic charr (age 2+ to 3+) start exploratory migration for food in inlet brooks and rivers however small in the spring (Näslund et al. 1993). Charr migrations in both directions *via* a fish ladder and the mechanism behind is so far little known.

Another possibility for Burvattnet charr to gain weight would have been to utilize the shallow southern basin of Burvattnet (Lill-Burvattnet, area 2 km^2, max depth 24 m) in the proximity of the outlet and the fish ladder. The benthic productivity can be assumed to be relatively high in this shallow and warm basin where light penetrates to bottoms below the draw down limit, and these favourable conditions may attract fish of good size. These explanations are not mutually exclusive and may work in concert.

While our results showed that compensatory nutrient enrichment is a mitigation method that works for charr, it must be recognized that there may be negative effects on ecosystems connected with the application of nutrients. One potential problem is that excessive nutrient addition results in eutrophication. However, the nutrient dose in the present experiment was sufficiently small to keep the system in an oligotrophic state, half of the added phosphorus sedimented as organic matter to deep bottoms, and approximately one third of was lost downstream (Rydin et al. 2008). Given the oligotrophic state, large depth and volume, and short water renewal time of Stor-Mjölkvattnet, it is evident that the P load we applied did not change the trophic state of the lake and it did not approach the critical limit for the P load *sensu* Vollenweider and Kerekes (1982). The plankton community responded with a moderate increase in the biomasses of phytoplankton and zooplankton, the species composition of the phytoplankton community remained largely unchanged but with an increase of edible Cryptophytes, and the food quality of phytoplankton increased both in terms of P:C ratio and fatty acid composition (Persson et al. 2008). The well-known negative effects of eutrophication, e.g. a decline in water transparency, occurrence of algal blooms that include shifts to inedible and potentially toxic cyanobacteria, anoxic hypolimnion, anoxic sediments with high internal loading, and winter fish kills (Lampert and Sommer 1997) were thus avoided. The effect of downstream transport of nutrients is expected to gradually attenuate downstream because of retention in downstream reservoirs and lakes. For comparison, we added on average 1 ton P annually, of which one third was lost downstream. This translates into an annual downstream P load of approximately 0.3 ton P year^{-1}. Even without taking any further retention between Stor-Mjölkvattnet and the river mouth at the Baltic Sea into account, this constitutes less than 5‰ of the annual P load of Indalsälven to the Bothnian sea. These findings show that the nutrients added in the whole lake experiment did not cause undesired effects neither locally nor downstream. But to avoid adverse ecosystem effects whenever compensatory nutrient addition is applied, the composition and dosage of nutrients must be based on thorough knowledge about specific local properties of the water such as catchment characteristics, hydrology, water renewal time, and lake morphometry. It is also of paramount importance that a proper monitoring of nutrient concentrations, nutrient transport and biota is carried out to enable the detection of potentially occurring adverse effects.

In conclusion, we have shown that it would be quite possible to transfer the method of compensatory nutrient enrichment into general practice in carefully selected lakes, like has taken place in Canada and the US. The total costs for adding nutrients and for monitoring may, however, be relatively high although sports fishing organizations and the local communities would have the necessary capacity in terms of manpower to keep costs on a more modest level. Compensatory nutrient enrichment is thus an effective method of restoring natural fish populations in waters regulated for hydroelectric purposes, but it must always be kept in mind that nutrient enrichment cannot replace naturally functioning undisturbed ecosystems in unregulated lakes.

Authors’ contributions

GM, ER and TV conceived the work. GM planned and supervised the fishing and made field measurements and age determinations. TV and GM made the data analysis. All authors contributed to the writing of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Declaration of interests

The authors have no competing interests to declare that are relevant to the content of this article.

Data availability statement

The data that support the findings of this study are openly available in Swedish National Data Service at https://doi.org/10.5878/eyp9-2k93.

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