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Impacts of reduced *Lepidurus arcticus* availability on brown trout life history traits in a mountain reservoir

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Abstract

Lepidurus arcticus (the Arctic tadpole shrimp) is a vulnerable keystone species in Arctic and alpine water bodies where its occurrence and population size may influence the viability and life history traits of resident salmonids. Using data from a Norwegian mountain hydropower reservoir, Aursjøen, we illustrate how reduced availability of *L. arcticus* as prey resulted in the reduced condition, growth and delayed maturation of resident brown trout (*Salmo trutta*). We further link changes in the relative abundance of *L. arcticus* as prey to changing reservoir conditions, e.g. water level changes in the spring period, thereby establishing an indirect link between reservoir operation regimes and brown trout population traits. While no evidence for decreased brown trout survival was found, the results indicate that alternative brown trout prey resources, i.e. the small chydorid cladoceran *Eury cercus lamellatus*, do not appear to have successfully offset the caloric loss from reduced consumption of large-sized *L. arcticus*. Although the fundamental explanation for the observed *L. arcticus* collapse remains largely unknown, the present findings provide strong evidence that this vulnerable crustacean species can affect the abundance, viability and life history traits of valued resident salmonid populations in oligotrophic alpine lakes and reservoirs exposed to climate- and hydropower-driven changes in water levels and temperature.

Keywords Branchiopoda · crustaceans · hydropower reservoir · keystone species · nutrition · prey availability

Introduction

Improved understanding of relationships between abundance of keystone invertebrate species and life history traits of their predators would facilitate better management and mitigation of biodiversity loss in alpine and high-latitude freshwater ecosystems (Lento et al. 2019). In lakes hosting

salmonid fishes, large-sized crustacean species commonly act as keystone species due to their omnivorous diet and high importance for fish nutrition (Sømme 1934; Borgstrøm et al. 1985; MacNeil et al. 1999). Although large-sized crustaceans are known to be a highly nutritious food (Lien 1978; Dararat et al. 2012) and to affect food-web dynamics in lakes (Primicerio and Klemetsen 1999; Jeppesen et al. 2001; Weidman et al. 2011; Eloranta et al. 2013), there is little research on how differences in their relative abundance may affect the life history traits, such as growth and maturation, of apex salmonid predators.

The Arctic tadpole shrimp (*Lepidurus arcticus* Pallas 1793; Branchiopoda, Notostraca) is a keystone species commonly occurring in freshwater lakes and ponds throughout the circumpolar sub-Arctic to high-Arctic zones, inhabiting areas from 60° N to 80° N (Rogers 2001; Rautio et al. 2011; Lakka 2013; Coulson et al. 2014). *L. arcticus* is an indicator species of environmental change (Lakka 2013) and is a red listed species in Finland and Sweden (Westling 2015; Väinölä et al. 2019). *L. arcticus* is often preyed upon by breeding birds such as Steller's eider (*Polyysticula stelleri*), Arctic tern (*Sterna paradisaea*), purple sandpiper (*Calidris*

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maritima) and dunlin (*Calidris alpina*) (Quakenbush et al. 2004; Lakka 2013). It is an annual species that grows rapidly from emergence in early summer and is an important prey item for many fish species such as brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*), European minnow (*Phoxinus phoxinus*), European whitefish (*Coregonus lavaretus*), broad whitefish (*Coregonus nasus*), and Arctic grayling (*Thymallus arcticus*) (Borgstrøm et al. 1985; Haugen and Rygg 1996a; Moulton et al. 2007; Woods et al. 2013, Lakka et al. 2019). In the absence of fish, *L. arcticus* is commonly among the most abundant benthic invertebrate species in many Arctic ponds and lakes (Christoffersen 2001; Jeppesen et al. 2001), with predation by fishes having been implicated in the marked decline of *L. arcticus* in many instances (Aass 1969; Jeppesen et al. 2001, Heggen et al. 2010). As a consequence, the absence of *L. arcticus* has been noted to negatively affect fish populations, with declines in their abundance having been associated with reduced recruitment and growth of fish (Kristensen et al. 2006).

As with many r-selected, short-lived species (Reznick et al. 2002), *L. arcticus* abundances are variable in time and responsive to predator densities and prevailing environmental conditions. Accordingly, *L. arcticus* often disappears and reappears as fish densities rise and fall (Aass 1969). Furthermore, they can be extremely sensitive to prevailing environmental conditions, often occurring in very low numbers in late, cold summers as well as in cold-water lakes in Norway (Borgstrøm et al. 2018; Qvenild et al. 2018; Qvenild and Hesthagen 2019). However, as a cold-water stenotherm, *L. arcticus* might also be affected by warm temperatures (Lakka 2013), with predicted climate-driven increases in water temperatures likely to have detrimental impacts on their abundance and distribution within Norway (Qvenild et al. 2018). For example, the ecophysiological activity of *L. arcticus* peaks at 10 °C (Lakka 2013; Pasquali et al. 2019) and it has been found in natural waters only as warm as 19 °C (Arnold 1966). Water chemistry, principally pH, also holds implications for the viability of *L. arcticus*, with slight drops in pH below the critical limit of about 6.0 having the potential to locally extirpate populations (Borgstrøm and Hendrey 1976; Fjellheim et al. 2007; Lakka 2013). Furthermore, in hydropower reservoirs, the amplitude, frequency and timing of water level fluctuations can influence the recruitment and abundance of both *L. arcticus* and the predatory brown trout likely through decreased food and habitat availability and increased juvenile mortality associated with drying and freezing of shallow littoral areas (Brabrand 2010; Hirsch et al. 2017; Eloranta et al. 2018).

In Norway, and when available, *L. arcticus* is considered to be one of the most important prey for brown trout populations in alpine lakes and reservoirs (Aass 1969; L'Abée-Lund and Sægrov 1991; Fjellheim et al. 2007). Importance varies

both seasonally and by fish size, tending to peak in brown trout diets in August and to be higher in larger fish (Haugen and Rygg 1996a, b). The strength of the prey selection process, particularly among brown trout (Aass 1969), suggests that their occurrence in fish stomachs is a useful surrogate for benthic sampling programs when attempting to determine overall relative *L. arcticus* abundance within a lake. Indeed, paired fish stomach and benthic sampling studies have shown fish stomach examination to be among the best methods for monitoring low-density populations of prey species such as *L. arcticus* (Fjellheim et al. 2007; Järvinen et al. 2014; Qvenild et al. 2018; Qvenild and Hesthagen 2019). While useful, the method is sensitive to the timing of sampling, particularly for short-lived species such as *L. arcticus* that exhibit short generation time. Nevertheless, *L. arcticus* presence in fish stomachs can be used to study long-term changes in the abundance and occurrence of this keystone species (Einarsson et al. 2004; Fjellheim et al. 2007; Sægrov et al. 2013).

Given the importance of *L. arcticus* as a prey item for brown trout (Borgstrøm et al. 1985), loss of their availability as prey could hold significant implications for brown trout life history traits, reducing growth and/or condition as a result of reduced energy intake (Lien 1978; Haugen and Rygg 1996a, b; Brabrand 2010). Here, we use data collected from standardized sampling of a Norwegian hydroelectric reservoir to examine the consequences of differences in the relative abundance of *L. arcticus*, as inferred from stomach contents analysis, for the condition, growth, maturity and survival of resident brown trout. We compare key environmental variables, such as water level fluctuations and air temperature previously linked to *L. arcticus* population success (Borgstrøm et al. 1985; Lakka 2013; Pasquali et al. 2019). Finally, we compare periods of *L. arcticus* high (1985–1989) and low (1995–1999) relative abundance and test the hypothesis that low relative abundance and dietary use of *L. arcticus* is associated with differences in key biological traits such as reduced body condition, growth rate, maturity and survival of reservoir resident brown trout.

Methods

Study area

The study was carried out in the Aursjoen reservoir (Fig. 1) which is located in the Reinheimen mountain area at 1097 m a.s.l. in southern-central Norway (61.94° N, 8.27° E) and used as a feed reservoir for hydro-electric power generation (115×10^3 MWh). Given the seasonal nature of hydroelectric generation, the reservoir undergoes an up to 12.5 m annual fluctuation in water level surface elevation, typically being lowest in late spring and highest in late autumn

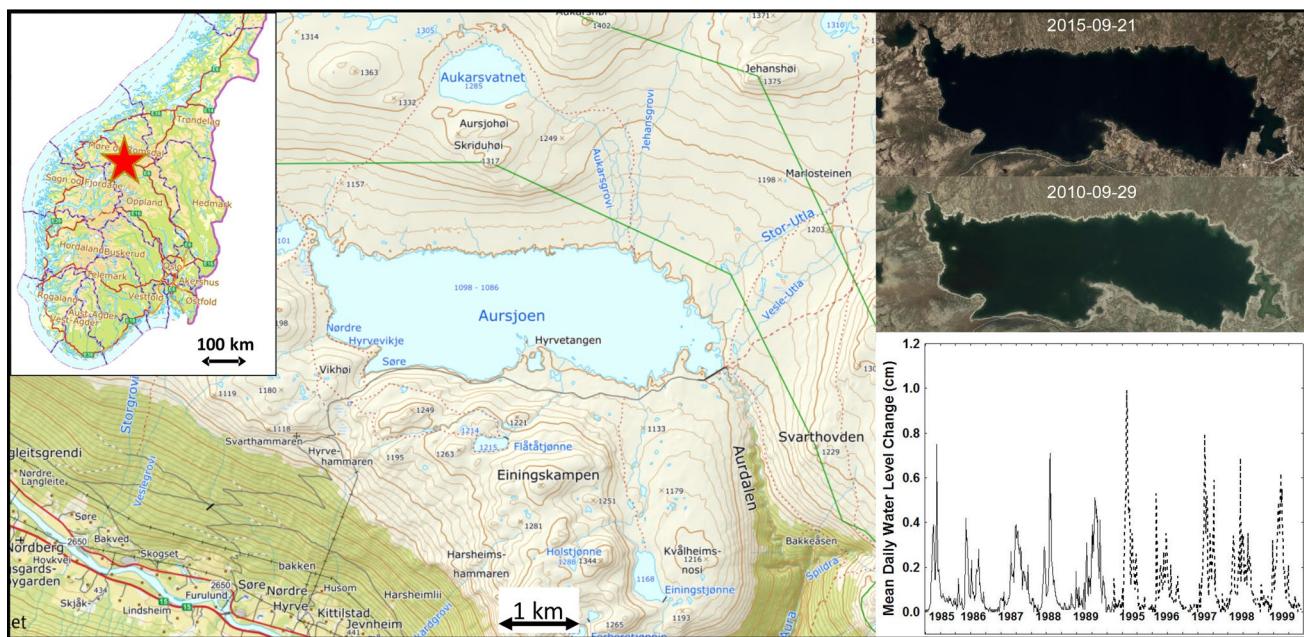


Fig. 1 Map of Aursjoen reservoir depicting location in relation to southern Norway, aerial photographs from 21 September 2015 and 29 September 2010 depicting the extant of exposed shoreline associated with 2 m water level drawdown (1097.7 m versus 1095.7 m a.s.l., respectively), and absolute daily water level changes (cm) during the

study periods 1985–1989 (solid line) and 1995–1999 (broken line). Maps and photos are obtained from www.norgeskart.no and <http://www.norgebilder.no>, respectively. The water level data is obtained from a database managed by the Norwegian Water Resources and Energy Directorate (www.nve.no)

(Online Resource 1). Consequently, the reservoir surface area can vary from 7.4 km² at high water levels to as little as 2.7 km² at low water levels, thereby exposing 64% of the reservoir bottom areas to desiccation (Hesthagen 2018). The highest daily water level changes typically occur during or after ice-off in May to June, coinciding with the critical hatching and juvenile development period of *L. arcticus* (Brabrand 2010; Borgstrøm 2019). The reservoir has a maximum depth of 28 m, mean depth of 7.4 m, is oligotrophic (14 µg L⁻¹ total phosphorus, 48 µg L⁻¹ total nitrogen, 2–5 mg L⁻¹ total organic carbon) with pH in the range 6.2–6.5, and experiences surface temperatures that rarely exceed 15° (Hesthagen 2018, www.vann-nett.no).

Sampling

Brown trout are the only resident fish species in the reservoir. The population has been supplemented annually by hatchery-reared fish (age 0+), with between 2000 and 7000 specimens stocked annually to offset reservoir impoundment effects (Hesthagen 2018). The monitoring of fish stocks has been carried out yearly since 1981 during the late open-water season (August–September) using gillnets (25 × 1.5 m) with knot-to-knot mesh sizes of 39 mm prior to 1999 and 35 mm in subsequent years. The nets were set overnight and randomly distributed throughout the reservoir. All captured fish (n = 3417) were weighed (mass in g), measured

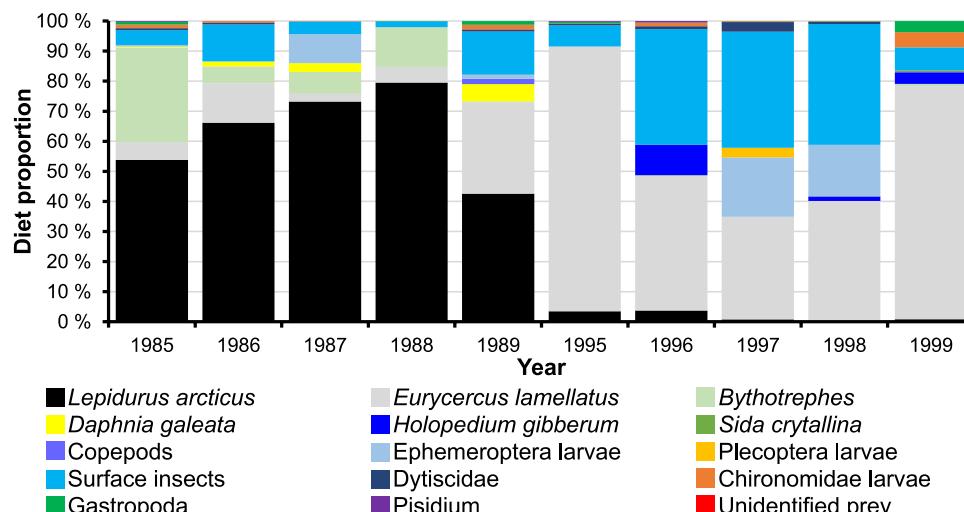
(fork-length in mm), sexed and assessed for maturity using a binary classification (mature, immature) based on the state of gonadal development and the presence of developing ova. Scales were removed for aging purposes. Two study periods were selected for comparison: 1985–1989 with high *L. arcticus* abundance and 1995–1999 with low *L. arcticus* abundance in brown trout diet.

Stomachs were dissected from a sub-sample of fish each year (n = 20–159) and preserved for subsequent examination in the laboratory. All prey items were identified to the lowest practical taxonomic level (Fig. 2), counted, and measured to the nearest 0.01 mm whenever possible prior to calculation of dry weight using the body length–mass regressions described in L'Abée-Lund and Sægrov (1991) and Breistein and Nøst (1997). The relative contributions of each prey taxon to the estimated total mass of all stomach contents (i.e., sum of all estimated dry weights) were calculated for each fish. Finally, these prey proportions (% dry weight) for individual fish were used for calculation of population-level proportions of different prey taxa, including *L. arcticus* and the semi-benthic chydorid cladoceran *Eury cercus lamellatus*, in each year.

Statistical analyses

A before and after statistical design was employed (Smith 2002) to test for an association between *L. arcticus* and

Fig. 2 Proportion of different prey taxa in the stomach contents of brown trout collected from Aursjoen, Norway, in years 1985–1989 and 1995–1999



brown trout condition, growth, maturity and survival characteristics. Periods of high (1985–1989) and low (1995–1999) *L. arcticus* abundances were identified on the basis of gut content analysis (Fig. 2) and separated by a period equivalent to the average historical capture age (5.1 years) to eliminate possible carry-over effects that might bias analyses (Harrison et al. 2011).

Differences in stocking levels between periods were tested using one-way ANOVA to rule out possible confounding effects (Smith 2002) on period-to-period differences in fish life history traits. To account further for the cumulative effects of stocking over the individual lifetimes of fish, stocking was measured as the 5-year average up to the year of capture. Differences in yield (kg ha^{-1}) and catch per unit effort (CPUE), expressed as the number of fish caught per 100 m^2 net area per 12 h, between the two periods were similarly tested using one-way ANOVA.

Early season water levels, water level fluctuations and water temperature are suggested to be important for the hatching and development of *L. arcticus* (Brabrand 2010; Lakka 2013; Pasquali et al. 2019). Therefore, differences between periods in monthly open water season (May through September) daily water level (m a.s.l), absolute daily water level change (absolute water level change from day_t to day_{t+1} regardless of sign) and air temperature were assessed for significant differences in mean using the Kruskal-Wallis (K-W) test after assessment for data normality (Zar 2010). A between period comparison of May through September mean water levels was completed by comparing day of the year (DOY) means calculated as the arithmetic average of the water level for a given DOY across the five years within each period and subtracting the low abundance period mean from the high abundance period mean. The resulting positive and negative values, respectively, thus indicate higher and lower average water levels during the high *L. arcticus* abundance period. The statistical significance of

differences between the periods was tested with a paired *t* test (Zar 2010). Significant differences in fish condition were determined by testing the homogeneity of the estimated weight-length regression slope for the two periods (high and low *L. arcticus* abundance) within a general linear modelling (GLM) framework (Zar 2010) and further via one-way ANOVA using Fulton's condition factor (K). Differences in growth were tested by comparing standard von Bertalanffy growth models (Diana 2004) for each *L. arcticus* abundance period that were estimated using non-linear regression methods (Bates and Watts 1988), with significance established using an analysis of residual sum of squares (Chen et al. 1992; Haddon 2001).

The probability of maturity was modelled as a function of age with logistic regression following methods described in Agresti (2002), with mean age-at-maturity estimated from the model at the 0.5 probability point and significant differences between *L. arcticus* abundance periods established using an analysis of residual sum of squares (Chen et al. 1992; Haddon 2001). Survival was estimated based on the numbers of aged fish captured each year, with annual survival probabilities estimated using Chapman-Robson methods (Chapman and Robson 1960; Robson and Chapman 1961) beginning with the first fully vulnerable age-class in the catch. Chapman-Robson methods have been shown to out-perform regression estimators, yielding the lowest errors and biases (Dunn et al. 2002). All statistical analyses were performed using the Statistica Release 8 statistical software (Statsoft, Tulsa, OK).

Results

Gut contents of sampled brown trout showed a shift from a diet dominated by *L. arcticus* and *Bythotrephes* sp. to one dominated by *E. lamellatus* and surface insects (Fig. 2).

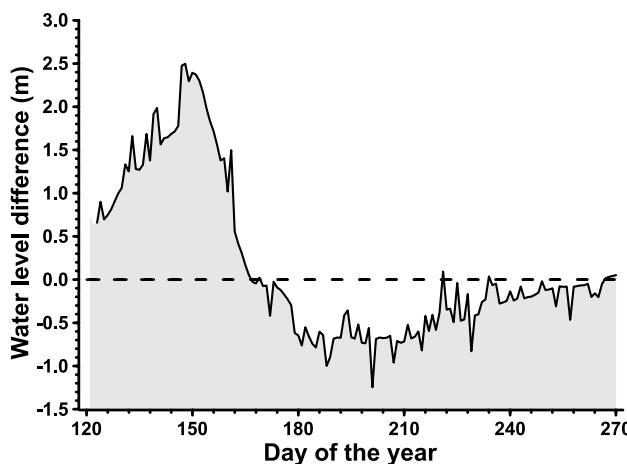


Fig. 3 Average calendar day of the year differences in water level between the high and low *L. arcticus* abundance periods in Aursjoen. Positive values indicate higher average water levels during the high abundance period. Means calculated as the average water level for a given day of the year for all years within each abundance period

Significant differences were observed in the mean annual relative contribution of the two key prey items (*L. arcticus*: ANOVA $F_{1,8} = 190.88, P < 0.001$; *E. lamellatus*: ANOVA $F_{1,8} = 17.544, P = 0.003$) to brown trout stomach contents during the two study periods, with *L. arcticus* declining from 66.1 to 1.8% and *E. lamellatus* increasing from 8.5 to 55% between 1985 and 1989 and 1995–1999, respectively (Fig. 2). There was no significant difference in average fish stocking levels between the two periods characterized by high and low *L. arcticus* abundance (ANOVA $F_{1,8} = 0.013, P = 0.991$), with mean annual values of 5336 and 5264 stocked specimens, respectively.

Between period differences were evident in monthly mean daily reservoir water levels (m a.s.l.), with all monthly comparisons (May through September) showing significant ($P \leq 0.006$ for all K-W tests) but minor

(0.27–1.26 m) differences that equate to approximately 2–10% (0.1–0.5 km²) of the mean wetted area of the reservoir. Absolute mean daily water level changes differed significantly between the high and low *L. arcticus* abundance periods in all months ($P \leq 0.003$ for all K-W tests) except July (K-W $P = 0.495$), with changes ranging from lows of 0.01–0.04 m in the period July through September to highs of 0.16–0.25 m in June (Online Resource 2). Moreover, the pattern of differences between periods was most evident throughout the May to September period, with daily mean water levels in the high *L. arcticus* abundance period being consistently higher in the early May to June period and consistently lower in the later August to September period. Across the May to September period, mean day of the year water levels differed significantly ($t = 2.234, P = 0.0027, df = 149$) between periods (Fig. 3). Air temperatures differed significantly between periods (high abundance – low abundance) in most months, with June (+ 1.62 °C), August (− 2.23 °C) and September (− 2.19 °C) evidencing significant differences ($P \leq 0.006$ for all K-W tests) and May (− 0.29 °C) and July (− 0.55 °C) showing no significant differences ($P \geq 0.091$ for all K-W tests). Across months temperatures varied from lows in the 4 °C range in May to highs in the 10 °C range in July before declining to values in the 4–6 °C range in September.

Period significantly influenced the slope and intercept of the brown trout weight-length regression ($F_{1,3414} = 2550.60, P < 0.001$), with length ($F_{1,3414} = 100428.00, P < 0.001$) being a significant determinant of weight in each period (Table 1, Online Resource 3). Similarly, there was a significant difference in Fulton's condition factor (K) for fish captured in the high and low *L. arcticus* abundance periods ($F_{1,3415} = 2805.6, P < 0.001$), with the mean K value falling from 1.17 to 0.99. Differences in condition were evident at all ages (age-4: $F_{1,1203} = 448.94, P < 0.001$; age-5: $F_{1,1054} = 315.80, P < 0.001$; age-6: $F_{1,423} = 322.87, P < 0.001$),

Table 1 Generalized linear model (GLM) results of homogeneity of slope testing for significant differences in standard weight-length models for brown trout captured in each of the high (1985–1989) and low (1995–1999) *L. arcticus* abundance periods in Aursjoen. The parameter estimates, 95% confidence limits (CI) and percent explained variation (R^2) for the weight-length models in each period are also presented

GLM homogeneity tests

parameter		df	F	P
Intercept		1	44356.00	<0.001
period		1	2550.60	<0.001
length		3414	100428.00	<0.001
Period	n	Slope	Slope CI	Intercept
Weight-Length Regressions				Intercept CI
1985–1990, $R^2 = 0.94$	2421	2.90	2.87, 2.94	− 4.69
1995–1999, $R^2 = 0.98$	996	3.04	3.01, 3.06	− 5.09
				− 4.77, − 46.12
				− 5.16, − 5.033

for which there were a sufficient number of fish captured to complete robust comparative statistical testing.

Brown trout length-at-age differed significantly ($F_{3,3414} = 606.94, P < 0.001$) between the study periods, with the estimated von Bertalanffy model for the high *L. arcticus* abundance period lying wholly above the model estimated for the low abundance period (Table 2; Fig. 4). Consistent with condition and growth, the yield (kg ha^{-1}) of brown trout in the *L. arcticus* high and low abundance periods differed significantly (ANOVA $F_{1,8} = 81.39, P < 0.001$), declining from an average of 1.90 kg ha^{-1} to 0.19 kg ha^{-1} . Similarly, brown trout CPUE (number of fish caught per 100 m^2 per 12 h) also differed significantly between periods (ANOVA $F_{1,8} = 43.38, P < 0.001$), declining from 0.43 in the high abundance period to 0.15 in the low abundance period.

Maturity increased more rapidly with age during the high *L. arcticus* abundance period than in the low abundance period (Fig. 5), with the respective mean age-at-maturity estimates being 5.1 and 7.0 years in the high and low abundance periods. Probability of maturity models differed significantly ($F_{2,12} = 9.568, P < 0.001$) between the study periods.

Within the two study periods, brown trout survival varied among years, ranging from 0.31 to 0.47 at high abundance and 0.28–0.48 at low *L. arcticus* abundance period. However, mean survival did not vary between the periods ($F_{1,8} = 0.089, P = 0.773$), averaging 0.38 and 0.39 in the high and low *L. arcticus* abundance periods, respectively.

Discussion

As hypothesized, reservoir resident brown trout evidenced reduced body condition, growth and maturity in years of low *L. arcticus* abundance, but did not show any significant change in survival. Overall, the results suggest that the effects of reduced *L. arcticus* acted primarily on the life history traits of the brown trout by reducing somatic growth and gonadal development. In a bioenergetics context (Elliott 1976), the results point to an overall decline in energy intake by brown trout associated with the decreased relative abundance and availability of *L. arcticus* as prey, causing reduced condition and growth. Coincident with these changes, brown trout yield also declined by on average 1.7 kg ha^{-1} , falling to 10% of long-term historical catches. While survival did not significantly change between periods, the similarly large reductions noted in CPUE are indicative of declines in abundance between periods (Elliott and Fletcher 2001) that coincided with the noted declines in *L. arcticus*. Observed reductions in growth in all age groups and increases in mean age-at-maturity (here 2 years) would further be expected to reduce overall reproductive potential given the strength of the fecundity–size relationship in brown trout (Elliott 1994; Jonsson and Jonsson 2011).

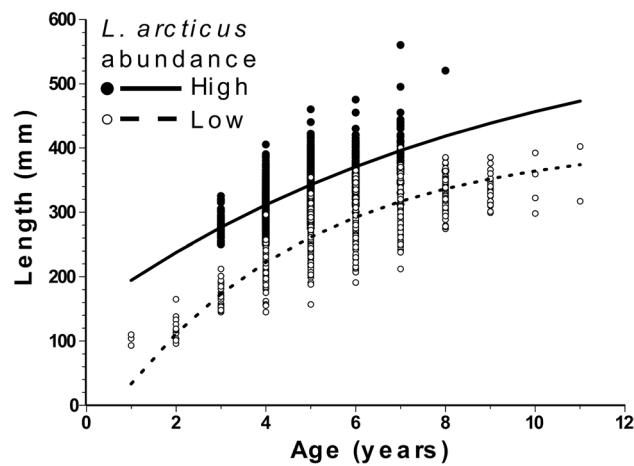


Fig. 4 Estimated von Bertalanffy models for brown trout growth captured in the high (filled circle) and low (circle) *L. arcticus* abundance periods in Aursjoen reservoir. The estimated models for these two periods are plotted as solid and dashed lines, respectively

Table 2 von Bertalanffy model estimates obtained from nonlinear regressions for brown trout captured in the high and low *L. arcticus* abundance periods in Aursjoen. L_{MAX} defines the asymptotic maximal length of the fish, k is the growth coefficient defining the rate at which L_{MAX} is achieved, and t_0 is the theoretical size at age zero

Period	Coefficient	Estimate	T-statistic	P
High abundance (n=2421)	L_{MAX}	614.164	6.295	<0.001
	k	0.109	2.860	0.004
	t_0	-2.491	-3.193	0.001
Low abundance (n=996)	L_{MAX}	343.325	38.807	<0.001
	k	0.768	13.304	<0.001
	t_0	0.633	5.011	<0.001

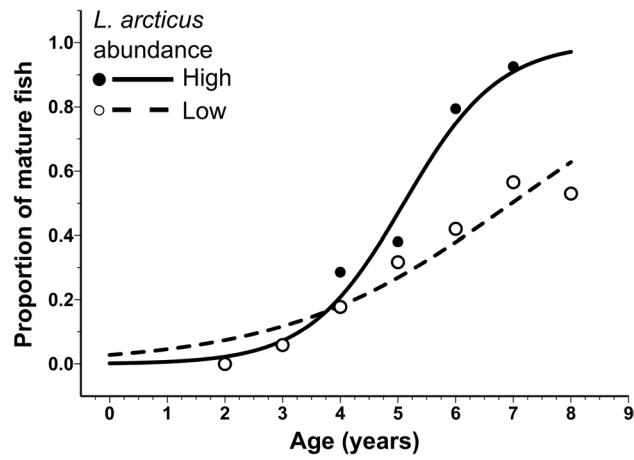


Fig. 5 Proportion of mature brown trout captured in the high (filled circle) and low (circle) *L. arcticus* abundance periods in Aursjoen reservoir. Logistic models estimated from the data are plotted for the high ($R^2 = 0.971$) and low ($R^2 = 0.913$) abundance periods

Our results suggest a link between *L. arcticus* and the environment having implications for brown trout. *L. arcticus* has a 1-year life cycle, but their resting eggs can stay viable for several years and tolerate freezing and desiccation, as observed for other crustaceans (Rogers 2014). The successful recruitment and thus availability of *L. arcticus* as an important summer-time food source for brown trout is highly dependent on successful laying of eggs during the autumn of the previous year, as well as on the successful hatching of eggs and the rapid development of juvenile stages early in the growing season. Water level and temperature during these critical spawning and hatching periods are particularly important for *L. arcticus* recruitment and abundance due to their effect on dewatering or flushing of deposited eggs, accessibility of littoral spawning and nursing areas, and the development time of early life stages (Borgstrøm et al. 1985; Brabrand 2010; Pasquali et al. 2019). Therefore, delayed or insufficient filling of a reservoir and/or rapid water level fluctuations in spring and autumn may impair successful hatching and spawning of *L. arcticus*, potentially reducing food availability for resident fish populations (Borgstrøm et al. 1985; Brabrand 2010). In Aursjoen, the relatively higher water levels in May–June (Fig. 3) during the high abundance period (1985–1989) would have yielded conditions favourable to the successful hatch and juvenile recruitment as compared to the low abundance period (1995–1999) when reservoir water levels were as much as 2.5 m lower. Further, the more limited or incomplete reservoir filling characterizing the low *L. arcticus* abundance period would have reduced availability of important shallow littoral feeding areas for both *L. arcticus* and the resident brown trout, reducing the availability of the prey to its predator.

In Aursjoen, the low *L. arcticus* abundance seems to be associated with lower daily water levels in early summer, i.e. during or soon after the critical hatching period between late May and early July when brown trout also feed actively. Due to their rapid growth rate, *L. arcticus* are preyed upon a few weeks after hatching by brown trout (Borgstrøm 1970) and they provide one of the richest prey energy sources (4.8–5.5 calories mg⁻¹ dry weight) typically found in brown trout stomachs (Lien 1978). The observed heavy reliance by brown trout on *L. arcticus* has been noted by other studies of mountain Norwegian reservoirs where brown trout prey upon *L. arcticus* particularly in the July through September period when the bulk of brown trout growth also occurs (Borgstrøm 1973; Borgstrøm et al. 1985; Jonsson and Jonsson 2011). The effects of the potential loss of this high-quality food resource may not be restricted to the fish populations and aquatic environments, because many avian predators also feed on *L. arcticus* (Quakenbush et al. 2004; Lakka 2013).

Lepidurus arcticus are also sensitive to water level fluctuations (Borgstrøm 1973; Borgstrøm et al. 1985), with

the degree of sensitivity linked to the seasonal timing of the fluctuations. *L. arcticus* lives and hides from predators among mosses and stones in very shallow, < 0.5 m littoral habitats (Lakka 2013) and is likely to be among the first taxa affected by water level fluctuations. Further, higher and more variable water levels may exert greater mechanical action on reservoir ice, thereby promoting earlier break-up and a longer ice-free period (Stander 2006; Gebre et al. 2013). Loss of ice-cover has been linked to greater littoral warming (Vincent 2009; Brown and Duguay 2010), particularly when associated with warmer spring air temperatures as occurred in the 1985–1989 June period at Aursjoen. In turn, warmer temperatures have been correlated with higher *L. arcticus* growth in the High Arctic (Lakka 2013), while lower temperatures and reduced ice-free periods have been correlated with lower abundance in southern Norway (Qvenild et al. 2018). Indeed, temperature, pH and water level fluctuations are the main triggers for controlling *L. arcticus* presence in brown trout diet in reservoirs. Thus, water level fluctuations promoting earlier ice-break up, when followed by increased air temperatures and reduced water level fluctuations during the critical period of *L. arcticus* emergence and growth, would seem to favour *L. arcticus* and promote both greater abundance and better feeding conditions for reservoir resident brown trout.

In contrast, periods of reduced water levels in spring, coupled with reduced air temperatures and coincident increases in water level fluctuations during the critical period of *L. arcticus* emergence and growth, as happened in the 1995–1999 period in Aursjoen, would appear to have the opposite effect and work to reduce *L. arcticus* abundance and prey availability for brown trout. Even though *L. arcticus* eggs tolerate drying (Longhurst 1955), they do not hatch on dry land. Therefore, for successful recruitment, the shallow littoral spawning and hatching areas of *L. arcticus* should be watered in August to September and the following spring when the water temperature is optimal for hatching (5–10 °C). The combination of intensive water level fluctuation during the hatching time and high temperatures in late summer, as observed during the low abundance period, would seem to limit *L. arcticus* recruitment and survival and its subsequent availability as an optimal food source for brown trout in Aursjoen reservoir. Extended and more variable water levels through the summer foraging period may also have acted to increase reservoir turbidity (Bonalumi et al. 2012) and affected fish foraging efficiency (Borgstrøm et al. 1992; Stuart-Smith et al. 2004) and use of *L. arcticus* as prey.

Laboratory studies have demonstrated that fish show a clear preference for large prey items (Ringler 1979; Wetterer 1989), which are normally thought to be the most energetically profitable. The feeding strategy of brown trout is flexible and influenced by the size frequency distribution of

potential prey. Thus, brown trout will tend to feed on either small numbers of large prey or large numbers of small prey (Sánchez-Hernández and Cobo 2015). In Aursjoen, the loss of the larger *L. arcticus* as a key prey item was offset by increased consumption of the smaller *E. lamellatus*, although the utilization of this species does not appear to have successfully offset the caloric loss from reduced consumption of *L. arcticus*. Using data on the mean dry weight equivalence of *L. arcticus* obtained from brown trout stomachs multiplied by the caloric value of *L. arcticus* as prey (Lien 1978) suggests the average caloric value of *L. arcticus* in sampled brown trout stomachs declined from 368.5 calories in 1985–1989 to 10.9 calories in 1995–1999. The average loss of 357.6 calories was only partially offset by increased use of *E. lamellatus* whose mean dry weight equivalence in calorie terms equalled 296.7 over the 1995–1999 period. The resulting 16.5% net calorie loss is sufficient to reduce the achievable scope for growth (Elliott 1994) when cumulated over the entire growing season. The ultimate effect of a reduction in calorie intake can be moderated by differences in water temperatures as a result of the noted interaction between temperature and ration (calories consumed) in the determination of brown trout growth (Elliott 1994), with increases in temperature at a given ration tending to reduce the realized growth rate (Elliott 1976).

Further affecting brown trout condition and growth may have been the ecological characteristics of *E. lamellatus* as the alternative for *L. arcticus*. Although *E. lamellatus* is known as brown trout prey and can account for between 31 and 41% of age-1+ brown trout diet, consumption tends to fall in fish larger than 150 mm (Hesthagen et al. 1992). In lakes at the Hardangervidda mountain area in Norway, *E. lamellatus* is the main prey for small brown trout and is consumed by larger individuals (>400 mm) if large-sized crustaceans (*Lepidurus arcticus* and *Gammarus lacustris*) are absent or scarce (Qvenild and Hesthagen 2020). However, the highest *E. lamellatus* abundances occur later in the growing season, e.g. September to October (Koksvik 1995) than is observed for *L. arcticus* that peak as brown trout prey in August–September (Qvenild et al. 2018). Declines in the use of smaller prey with size relates to the energetic advantage obtained by feeding on larger prey (Wankowski and Thorpe 1979), with salmonids tending to grow larger when feeding on larger, more energetically valuable prey (Mittelbach and Persson 1998). A lack of suitably large prey and overall prey availability are thought to constrain fish growth (Kerr 1971; Dodrill et al. 2016), particularly as time spent foraging tends to increase with fish size (Ware 1972). Thus, the foraging gain-cost ratio of *E. lamellatus* appears to have limited the brown trout scope for growth in the low *L. arcticus* abundance period in Aursjoen.

Variations in seasonal availability may also act to limit the overall energetic gains obtained by heavy reliance on

E. lamellatus. In Norwegian lakes, *E. lamellatus* has its highest abundance in autumn, e.g. September–October, with the increase in biomass occurring later than the seasonal increases in the water temperatures (Koksvik 1995) that would drive increasing metabolic energy demands in brown trout (Elliott 1976). The abundance of *E. lamellatus* appears to be connected to the development of littoral zone vegetation used as preferred habitat (Smirnov 1962). In hydro-electric reservoirs where the littoral zone has been degraded by water level regulation (Eloranta et al. 2017; Hirsch et al. 2017), the strong link between the development of littoral zone vegetation and *E. lamellatus* abundance may limit further their value as replacement prey, particularly as *L. arcticus* emerge early in spring, grow quickly (Borgstrøm et al. 1985) and can provide suitable energy sources to brown trout early in the growing season.

Lepidurus arcticus is known to be susceptible to environmental changes, having been adversely affected throughout much of its natural range, e.g. by acid rain in southern Norway (Fjellheim et al. 2001). The species is also temperature sensitive (Lakka 2013). Indeed, the timing of ice break-up and the rate of spring warming and water levels have been shown to be significant determinants of the growth and development of *L. arcticus* (Brabrand 2010; Borgstrøm 2019). Current climate change predictions forecast significant increases in both air temperature and precipitation in Norway (IPCC 2014), with a potential consequence being the localized extinction of cold-adapted crustacean species (Lindholm et al. 2012), including *L. arcticus* (Lakka 2013; Qvenild et al. 2018; Qvenild and Hesthagen 2019). Localized extinctions will have significant consequences for resident fish species, such as brown trout. Based on the documented experiences of the Aursjoen reservoir, reduction of *L. arcticus* in other lakes and regulated reservoirs is likely to be associated with lower brown trout growth rates, reduced condition and delayed maturation, which will reduce the fish production and recreational value of the affected water bodies.

Conclusions

Findings here provide further evidence that *L. arcticus* can act as a keystone species in Arctic and alpine water bodies, with its occurrence and availability as prey having marked impacts on the body condition, growth and maturity of resident fish species such as brown trout. Monitoring and evaluation of potential climate change, acidification, water level regulation and other anthropogenic impacts on *L. arcticus* populations may therefore serve as an appropriate indicator of ecosystem disturbance, with changes likely to impact fish populations. Moreover, such monitoring would provide

valuable information useful for management actions aimed at sustaining the biodiversity and natural ecosystem processes in oligotrophic waterbodies and would help with the preservation of key ecosystem services such as recreational fishing and maintenance of drinking water quality. Our study suggests a high importance of early-season water levels for recruitment and availability of *L. arcticus* as a nutritious prey for reservoir resident brown trout. Hence, instead of compensatory fish stockings, more holistic, ecosystem-based management actions, such as altered water level regulation patterns and habitat restorations, could better improve and protect the ecological status of the unique invertebrate and fish fauna found in alpine hydropower reservoirs.

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