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Lepidurus arcticus (Crustacea : Notostraca); an unexpected prey of Arctic charr (*Salvelinus alpinus*) in a High Arctic river

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The phyllopod *Lepidurus arcticus,* commonly called the arctic tadpole shrimp, is an important food item of both Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* in lakes in Iceland and Scandinavia, especially at low fish densities. In the High Arctic, the tadpole shrimp is abundant in fishless localities, but absent or rare in most lakes where fish are present. We studied the diet of Arctic charr in the Straumsjøen watercourse on Spitsbergen, the main island of Svalbard. The outlet river is dry nine months of the year, and all Arctic charr present during summer have descended from the lake. We found that tadpole shrimp contributed substantially to the diet of charr in the outlet river, while it was not found in charr caught in the lake. Low fish density combined with low discharge after hatching of tadpole shrimp eggs may have favoured the co-occurrence of this lacustrine crustacean and Arctic charr in a running water locality. The potential effect of climate change on the occurrence of riverine tadpole shrimp is still uncertain. Retreat of glaciers and decreased turbidity may promote tadpole shrimp, but a predicted increase in precipitation may also have adverse impacts by increasing the risk of flushing tadpole shrimp out of the streams, and thus affecting the Arctic charr diet in running waters on Svalbard.

Introduction

In alpine and subalpine lakes in both northern and southern mainland Norway, and in lakes on Iceland, the notostracan phyllopod *Lepidurus arcticus,* commonly called the arctic tadpole shrimp, is frequently an important summer food item of brown trout *Salmo trutta* (Aass 1969, Borgstrøm 1973, Lien 1978) and Arctic charr *Salvelinus alpinus* (Adalsteinsson 1979, Svenning *et al*. 2013, Woods *et al*. 2013). Non-piscivorous fish feeding on the crustaceans *Gammarus lacustris* and the tadpole shrimp may attain weights of several kg (Borgstrøm 2016). The prerequisite is low fish density, indicated by the disappearance of the tadpole shrimp when

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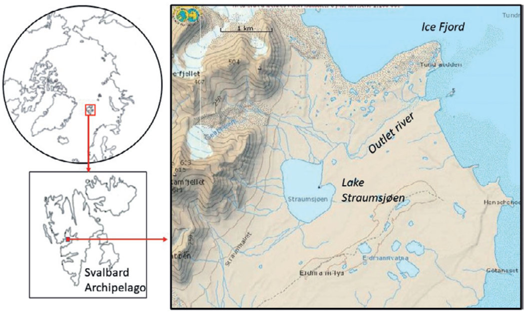

Fig. 1. The Svalbard Archipelago with location of Straumsjøen and its outlet river to the Ice Fjord. The detailed map has been copied from TopoSvalbard, with permission from Norwegian Polar Institute.

fish densities are high, and with subsequent reappearance when fish density declines, as observed in reservoirs in Norway with fluctuating brown trout and Arctic charr densities (Aass 1969).

The arctic tadpole shrimp has a circumpolar distribution, occurring in Siberia, arctic North America, Greenland, Iceland, Svalbard and other High Arctic islands, as well as in alpine and subalpine areas of Scandinavia (Poulsen 1940, Vekhoff 1997, Hessen *et al*. 2004). It is common in fishless localities in the High Arctic, but rare or absent in lakes in this area where Arctic charr are present (Miller 1980, Røen 1981, Jeppesen *et al*. 2001, 2017, Borgstrøm *et al*. 2015). The effect of fish density is apparent in lakes on Bear Island, the southernmost island in the Svalbard Archipelago, where the tadpole shrimp is an important prey item of Arctic charr in shallow lakes with low fish densities, while in deeper lakes with high densities of charr, the tadpole shrimp is either rare or absent from the diet (Klemetsen *et al*. 1985, Christensen *et al*. 2004). In Spitsbergen, the main island of the Svalbard Archipelago, the tadpole shrimp is common in ponds and fishless lakes (Olofsson 1918, Jørgensen and Eie 1993, Lakka 2013), but hitherto not found in localities with charr present, nor has it ever been reported as a food item of charr (e.g. Svenning 1992, 1993, Jørgensen and Eie 1993, Hammar 1998, Svenning *et al*. 2007).

Arctic charr is so far the only reproducing fish species in Svalbard freshwaters (Svenning *et al*. 2015). Streams on Svalbard are dry or completely frozen for approximately nine months of the year (Svenning and Gullestad 2002), but a fraction of the lake residents of juvenile charr may migrate from lakes to streams during the short summer period (Gulseth and Nilssen 1999, Godiksen *et al*. 2011). The diet of charr, however, has never been studied in streams on Svalbard islands, and accordingly, in this study we explore the summer diet of riverine charr in the Straumsjøen watercourse, on Spitsbergen, and contrast this with the diet of the lake-resident charr. We did not expect to find the tadpole shrimp as a food item of riverine charr, because the early instars of this crustacean are planktonic and therefore most probably unable to inhabit running waters.

Material and methods

Study area

The study lake, Straumsjøen (78°19´N, 14°07´E), is situated 15 m above sea level on Spitsbergen, the largest of the Svalbard islands (Fig. 1). The lake is shallow, with maximum depth less than 6 m, and less than 30% of the 0.9 km^2 lake area is deeper than two meters. At depths below 0.8–1 m, the bottom substrate consists of fine sand and gyttja. The lake has several small inlet streams with clear water entering from south and west, but at the northern part, streams coming from the glacier Geabreen may periodically transport silt from the glacier. The glacier has, however, retreated considerably over the past decades, and the inflow of cold melt water has decreased. The Secchi depth in Straumsjøen varied from 1.2 to 2.8 m between early July and late August in 2006.

The outlet river runs for 2.3 km towards the northeast to the Ice Fjord (Fig. 1). Its width varies between 5 and 25 m, with most of the river having a depth < 20 cm during summer, with several slow-flowing riffles and shallow pools, having a substrate dominated by sand and gravel (Fig. 2). During the period 1 July–21 August 2006, discharge from the lake (measured by water height in the lake outlet) reached a maximum on 3–4 July, and thereafter fell gradually until 8 August, when rainfall led to a small increase that lasted about one week. The outlet river is fed by several small tributaries (Fig. 1), some originating from shallow ponds which freeze to the bottom or are dry during winter.

Fig. 2. Section of the outlet river from Straumsjøen. In the foreground, one of the many more or less closed pools in the riverbed at low discharge (Photo: M. Aas),

Olofsson (1918) recorded *L. arcticus* in ponds nearby Straumsjøen in 1910, and in August 2006 we observed high numbers of tadpole shrimp in ponds and their small outlet streams forming tributaries to the outlet river from Straumsjøen. Tadpole shrimps were also observed in isolated pools in the river itself during latter half of July and in August 2006. These pools were connected to the river after periods with rain.

The climate around the Ice Fjord is dry and cold. At Svalbard airport, 40 km from the lake, the average air temperature in June and September is just above freezing, while in July and August (the warmest months), the average is around 5 °C. The average annual precipitation in Svalbard is low, with a mean less than 200 mm per year at Svalbard airport (Data from the Norwegian Meteorological Institute). In 2006, the monthly mean precipitation for July–August was 50.4 mm, and the average air temperature was 7.1 °C. Ice break-up in Straumsjøen occurred 3–5 July in 2006, and the water temperature in the outlet river increased from around 3 °C in early July to a maximum of 13 °C on 25 July, and then decreased to 8 °C on 23 August. Straumsjøen is probably one of the warmest lakes with Arctic charr on Svalbard, where most other lakes seldom achieve summer water temperatures above 6–7 °C (Svenning 2015).

Sampling

A total of 89 and 135 juvenile Arctic charr for stomach content analyses were captured by electrofishing in two river stretches and two sites in the shallow part of the littoral zone in the lake, respectively, on three different occasions: 10–11 July, 23–25 July, and 9–10 August, denoted as period P1, P2, and P3 (Table 1). Mean fork length of juveniles with stomach contents captured in the river and lake, was 9.9 cm (± SD 2.4 cm, and range 5.6–16.0 cm) and 8.4 cm (± SD 2.2 cm, and range 5.0–17.2 cm), respectively. Stomach contents were also sampled from six ascending anadromous charr captured by a trap in the upper

Table 1. Number of Arctic charr (age classes 1–3) captured by electrofishing in Straumsjøen and the outlet river, and examined for stomach contents during the three periods 10–11 July (P1), 23–25 July (P2), and 9–10 August (P3) in 2006. The value in parenthesis indicates the number of stomachs that contained food items.

Period	Lake	River	Total
10–11 July (P1)	38 (10)	29 (10)	67 (20)
23–25 July (P2)	50 (22)	24 (13)	74 (35)
9–10 August (P3)	47 (13)	36 (20)	83 (33)
Total	135 (45)	89 (43)	224 (88)

part of the river in August, as well as from four anadromous charr captured by 1.5 m deep and 40 m long multimesh gillnets with mesh sizes from 8 to 45 mm (bar mesh), set on the bottom both in nearshore area and in the deepest part of the lake, and with 3 m deep multimesh gillnets set from the surface, also at the deepest part. Further, 65 and 100 charr were captured by gillnetting in the lake on 19–22 July and 17–21 August, respectively. Of these, 57 (88%) and 41 (41%) fish had stomach contents. Fork length of all captured fish was measured in mm. The stomach and oesophagus were removed and opened shortly after fish capture, and the percentage degree of fullness was recorded according to Amundsen (1989). The contents were preserved in ethanol for subsequent analyses in laboratory, where the food items were identified and grouped in the following categories: chironomids (larvae and pupae), caddisfly larvae (*Apatania zonella*), Ostracoda, *L. arcticus*, marine prey (gammarids, mysids, fish), terrestrial insects, and a group consisting of various items (plant material, and undetermined contents). The relative contribution of these categories was estimated, following Amundsen *et al*. (1996), with the abundance of prey category *i* presented both as percentage abundance ($\%A_i = (\Sigma S_i/\Sigma S_{tot}) \times 100$) and as frequency of occurrence ($\%F_i = (N_i/N) \times 100$). S_i is the stomach volume comprised by prey category *i*, S_{tot} is the total prey volume of all sampled stomachs, and N_i is the number of stomachs with prey *i* in the total sample, *N*. Otoliths were taken from all sampled fish for use in age determination.

Ethical statement

Sampled fish for further analysis were killed by a hard blow to the head immediately after capture. The Governor of Svalbard had issued permission to catch fish in the Straumsjøen and its outlet river.

Results

Diet of Arctic charr

In both 10–11 and 23–25 July (P1 and P2), larvae and pupae of chironomids had a high frequency of occurrence and high specific abundance in stomachs of juvenile Arctic charr captured in the outlet river (Fig. 3a). Other prey items, including the caddisfly larvae and marine gammarids had a low occurrence, but with a high specific abundance in early July. The tadpole shrimp was present in stomach samples from 23–25 July, but in low frequency and low specific abundance (Fig. 3b). On 10–11 August (P3), however, tadpole shrimps were more common, and had also the highest specific abundance compared to the other prey categories (Fig. 3c). Chironomids were found in most charr caught in August, but with a much lower specific occurrence than in July (Fig. 3c). Five of six anadromous charr captured in the stream in August, had eaten marine prey items, dominated by marine fish, mysids and amphipods, and one had tadpole shrimp as the only food item, with 100% stomach fullness.

Tadpole shrimps were absent in stomachs of resident charr juveniles captured in the littoral zone in all three periods (P1, P2, and P3). In general, chironomids had the highest frequency of occurrence and abundance in stomachs of juvenile charr from the lake (Fig. 3d, e, f). Caddisfly larvae were of much greater importance in diet of juvenile charr from the lake compared to the river, and occurred in high frequency and high specific abundance, especially in August (Fig. 3f). Also, the four anadromous charr captured in the lake (in August) had mainly eaten chironomids, and tadpole shrimps were missing in these fish, as well. Shrimps were neither found in 98 gillnetted resident charr in length range 8.3–47.2 cm. Stomach contents of these fish were dominated by chironomids both in July and August, while caddisfly larvae had been eaten by some fish larger than 20 cm in length.

Discussion

The occurrence of the arctic tadpole shrimp in ponds and tributary streams to the outlet river from Straumsjøen, and in shallow pools in the outlet river, as well as in stomachs of riverine juvenile charr and ascending anadromous charr, represent the first record of this species in running waters and as a food item of charr on Spits-

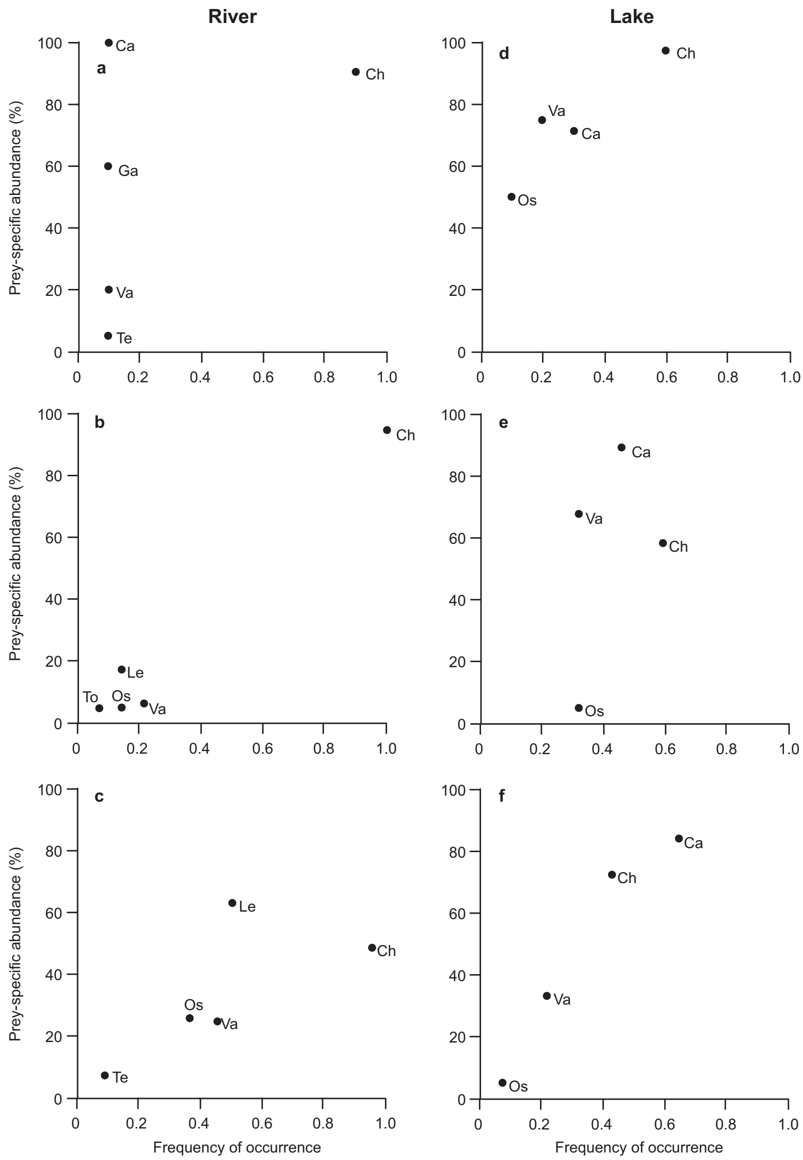

Fig. 3. Prey-specific abundance and frequency of occurrence of prey species in the stomach contents of Arctic charr sampled in Straumsjøen and the outlet river during the three periods: (**a**, **d**) 10–11 July, (**b**, **e**) 23–25 July, and (**c**, **f**) 9–10 August in 2006. Ca = Caddiesflies, Ch = chironomids, Ga = gammarids, Te = terrestrial insects, Os = ostracods, Le = *Lepidurus*, Va =various unidentified items.

bergen, although tadpole shrimp has never been found in a high number of Svalbard lakes previously studied (Svenning 1992, Hammar 2000, Svenning *et al*. 2007, Borgstrøm *et al*. 2015, and references therein). The occurrence of the tadpole shrimp in a lotic habitat was unexpected because the second and third instars of this crustacean species are planktonic (Borgstrøm and Larsson 1974, Hobbie 1980), and therefore not adapted to ordinary stream conditions.

Since juvenile charr also used the small tributaries to the main river, charr sampled in the river with tadpole shrimps in their stomach might have returned after feeding on tadpole shrimps in both the small tributaries and connected ponds. Such feeding migration of charr to tributaries, both from main streams and from lakes is common (Näslund 1990, Sinnatamby *et al*. 2012). However, since large anadromous ascending charr captured in the river had eaten tadpole shrimps, it is likely that these shrimps had been consumed in the river, where shrimps had also been observed. The occurrence of tadpole shrimps in the river still does not preclude its presence as a result of drift from the surrounding ponds. Drifting of early instars of tadpole shrimp has been recorded in a small stream from a headwater lake on Valdresflya, southern Norway, at the beginning of July (Brabrand 2010). However, with the high importance of the tadpole shrimp in the diet of riverine Arctic charr, it seems unlikely that the occurrence is mainly based on drift from tributaries or due to return of juveniles from the tributaries. Regardless of origin, these findings demonstrate that tadpole shrimps both co-occur with charr and contribute to the diet of charr, even in a High Arctic stream system.

Eggs of tadpole shrimp are adhesive, and attach to stones and gravel, and also resist freezing and drying (Borgstrøm and Larsson 1974). Olofsson (1918) sampled planktonic stages of tadpole shrimp in ponds nearby Straumsjøen in late July 1910, indicating newly hatching. With similar hatching time in 2006, several weeks after the culmination of the river discharge, the free-swimming larvae may be able to hold position in the shallow pools formed in the riverbed at low water flow. The older stages, which are mainly bottom-living (Sømme 1934, Borgstrøm 1997), may also be able to hold their position, as has been observed in the fishless river Engelskelva on Bear Island (Klemetsen *et al*. 1985).

Because all streams on Svalbard are dry or completely frozen for about nine months of the year (Svenning and Gullestad 2002, Svenning *et al*. 2007), the outlet stream from Straumsjøen can be inhabited by Arctic charr only a few months during summer. Juvenile charr migrate from the lake as soon as the stream is open in early summer (Aas 2007), but in order to survive the winter, they have to return to the lake before the stream completely freezes or dries up in the autumn. Similar migratory behavior is observed in Arctic charr, with seasonal habitat shifts to streams reported both from other watercourses on Spitsbergen (Gulseth and Nilssen 1999, Godiksen *et al*. 2011) and northernmost Canada (Sinnatamby *et al*. 2012), as well as localities at lower latitudes (Craig and Poulin 1975, Näslund 1990). The tadpole shrimp does not likely trigger the migration of young charrs to the outlet river, since the migration starts weeks before shrimps contribute to the diet. During most of July, chironomid larvae and pupae had a dominant occurrence in the diet of juveniles, as also found throughout the summer in other running water localities, both in arctic Canada (Sinnatamby *et al.* 2012) and in Svalbard (Hegseth 2007).

All stages of the tadpole shrimp, from the first instars to egg-producing individuals, are predated upon by fish (Aass 1969, Borgstrøm *et al*. 1985), making the species very vulnerable at high fish densities (Aass 1969). The presence of the tadpole shrimp in the outlet river and small tributaries to the river may therefore be suggestive of low fish density, allowing the shrimp to exist, but still provide an important contribution to the total food intake of charr juveniles which have migrated downstream from the lake. By mark-recapture in July and August 2006, the estimated number of charr in length-class 7.0–25.9 cm was ca. 2600 in the outlet river, while in the lake the estimated number was ca. 11 600 in length-class 7.0–47.9 cm (Aas 2007), i.e., indicating a much higher number in the lake. According to these estimates, the density of charr juveniles in the stream in July may have been around 10 individuals 100 m^{-2}, which is low compared to densities of juvenile salmonids in temperate streams (e.g. Elliott 1984, Solomon 1985, Grant and Kramer 1990), but still within the range of densities estimated for salmonids in north Norwegian streams (Power 1973).

Drying out and low temperatures of bottom substrates during winter may act to increase winter survival of eggs of the tadpole shrimp, explaining the increased population density and even establishments of the tadpole shrimp after lake regulations (Dahl 1932, Aass 1969, Brabrand and Saltveit 1980), with eggs of tadpole shrimp deposited in the dry and frozen drawdown zone during winter (Borgstrøm and Larsson 1974). Accordingly, shallow ponds as well as pools in the outlet river from Straumsjøen, with freezing of the bottom during winter, low summer discharge, and low fish density, may be suitable habitats for the tadpole shrimp. Changes in discharge or fish density may on the other hand influence the occurrence of the tadpole shrimp in such habitats. Several streams on Svalbard are fed by meltwater from glaciers, which means that discharge increases tremendously during summer, resulting in low water temperatures, combined with a high silt load. High turbidity caused by mineral particles may alter zooplankton abundance and community structure, as observed in lakes influenced by glacial ooze (Blakar and Jakobsen 1979, Elgmork and Eie 1989), as well as in silted reservoirs, where filtering cladocerans and the tadpole shrimp may be highly affected (Borgstrøm 1973, Borgstrøm *et al*. 1992). The glacier Geabreen that feeds Straumsjøen and the outlet river has retreated considerably during the last decades, and at present is characterized by a reduced discharge of cold and silty meltwater that may have improved the conditions for the tadpole shrimp in the river. Alternatively, climate scenarios for high-latitudes indicate both increased temperatures and increased annual total precipitation, with a precipitation increase being largest in winter (Førland *et al*. 2009). More meltwater or periods with heavy rain may increase the risk for flushing of tadpole shrimps in the tributaries and main outflow river, and thus being clearly negative for the shrimp population, and thereby also affecting the energy surplus of charr during the summer period.

In conclusion, the co-occurrence of the tadpole shrimp and Arctic charr in this High Arctic stream, together with a significant contribution of tadpole shrimps to the charr diet was unexpected. Similar co-occurrences of charr and tadpole shrimp may be found in other High-Arctic river systems with low summer discharges. On the other hand, climate change with increased precipitation may affect the riverine occurrence of the tadpole shrimp, but lack of previous studies in this river as well as in other rivers in Svalbard are nevertheless a weak basis for predictions concerning effects of a future climate on the occurrence of tadpole shrimp and its importance as a food item of Arctic charr.

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