



Marine diets of anadromous Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) in Svalbard, Norway

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Abstract

During summer, native anadromous Arctic char (*Salvelinus alpinus*) and the alien species pink salmon (*Oncorhynchus gorbuscha*) now coexist in marine environments in Svalbard, following the introduction of the latter in the Barents Region. To investigate potential dietary competition between these two salmonid species, stomach contents from Arctic char ($n = 301$) and pink salmon ($n = 28$) were sampled from different areas within the archipelago. The most important prey in terms of biomass for both salmonid species were amphipods; *Themisto libellula* ($B = 26.0\%$) for Arctic char and *Onisimus littoralis* ($B = 35.0\%$) for pink salmon. Pianka's niche overlap revealed that dietary overlap between the two species was moderately high ($O_{\text{obs}} = 0.59$); both species had strong associations with intertidal invertebrates in areas where direct comparisons were possible (Kongsfjorden/Krossfjorden). However, both salmonid species did also eat some fish, with Arctic char consuming more offshore pelagic fish, while the small number of fish eaten by pink salmon were primarily coastal demersal fish species. Arctic char was a more generalist feeder, while pink salmon was more of a dietary specialist. Furthermore, the diet composition of the Arctic char consisted of 32.9% Atlantic prey while the pink salmon, surprisingly, ate only Arctic species, likely due to their tightly coastal feeding habits. Even though the sample size for pink salmon was low, this study contributes new insights into salmonid diets in Svalbard and the potential for introduced species to compete with native Arctic endemics, particularly in the expected warmer Arctic of the future.

Keywords Salmonid · Alien species · Diet overlap · Climate change · Barents Sea · Stomach contents

Introduction

The High Arctic Svalbard Archipelago is situated in the northern part of the Barents Sea (Fig. 1). Relative to other areas at the same latitude, the climate in Svalbard is mild, in large part because of heat transported by the West Spitsbergen Current (WSC), an extension of the North Atlantic Current (Beszczynska-Möller et al. 2012; Smedsrud et al. 2013). The freshwater systems in Svalbard cover no more

than 400 km² (0.6%) of its land area and are characterized by low precipitation, low primary production, low biodiversity, long seasonal ice cover, and cold water (von Quillfeldt and Øseth 2016). Arctic char (*Salvelinus alpinus*) is the only limnic vertebrate known to reproduce successfully in Svalbard (Gulseth and Nilssen 2000; Johnsen et al. 2021). This salmonid fish has a circumpolar distribution in the Arctic (Johnson 1980). It is the northernmost freshwater fish species, with a natural range stretching from Ireland and the British Isles to Svalbard and Severnaya Zemlya on the Eurasian Continent, and from Maine to Ellesmere Island on the North American Continent, (Johnson 1980; Ferguson et al. 2019; Svenning et al. 2020; Chernova et al. 2021). Arctic char usually occupies cold lakes, often as the sole fish species (Klemetsen et al. 2003; Ferguson et al. 2019), but there are also purely riverine populations (Jensen and Rikardsen 2008). This species exhibits remarkable life cycle variability in different populations; many populations are stationary in one waterbody and exhibit polymorphic body sizes with a large and a small (dwarf) morphotype (Hindar and

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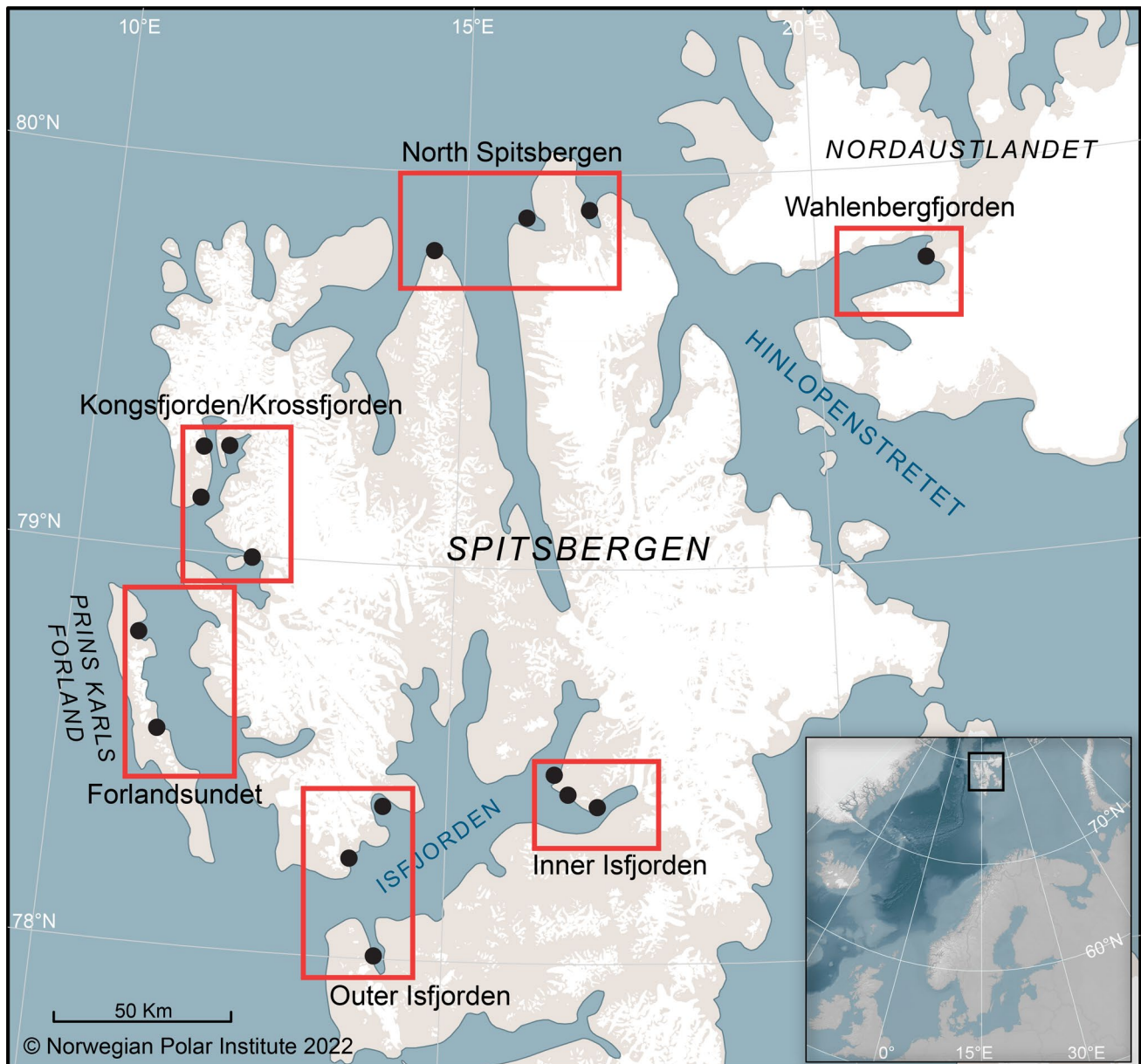


Fig. 1 Map of the Svalbard Archipelago, identifying locations (and areas) where Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) were collected for dietary studies during 2015–2018

Jonsson 1993; Tallman et al. 1996), while in other populations, some individuals perform seasonal migrations to the sea (i.e., anadromy).

Anadromy in Arctic char is complex and takes place only in populations in the northern part of the species range. Seaward migrations are undertaken by both juvenile and mature fish (Rikardsen and Elliott 2000; Klemetsen et al. 2003). Stationary and anadromous Arctic char exist sympatrically and belong to the same gene pool; individuals may even shift from one form to the other during their lifetime (Nordeng 1983; Hindar et al. 1986). In Svalbard, Arctic char occupy some 100–150 lakes, but only about 20 of these are home

to anadromous Arctic char (Svenning 2010). Stationary fish are mainly small individuals that feed on insects and zooplankton. These fish do not get longer than 15 cm. However, some stationary fish shift to cannibalism and can grow to be 70 cm long (Gullestad 1975; Gulseth and Nilssen 2001; Johnsen et al. 2021). In lakes connected to the sea, some individuals become anadromous and can grow to large size (Svenning and Borgstrøm 1995; Gulseth and Nilssen 2001; Svenning et al. 2007). In Svalbard, Arctic char normally migrate to the sea as soon as the rivers thaw in late spring/early summer and return to the lakes in the late summer or autumn (Gulseth and Nilssen 2000; Svenning et al. 2020).

In recent years, there have been early (April–May) migrations to the sea, followed by early returns, although small Arctic char have been caught at sea as late as October (Christensen, unpubl. data). Svalbard Arctic char undertake their first migration when they are 4–8 years old, i.e., 3–4 years before they spawn for the first time (Dahl 1926; Gullestad 1975; Gulseth and Nilssen 2001). During the relatively short period spent at sea, anadromous Arctic char grow rapidly (Gulseth and Nilssen 2001; Klemetsen et al. 2003). However, migration comes with extreme risk, return rates range between ~33% for the smallest fish (< 20 cm) and ~70% for the largest fish (> 35 cm; Gulseth and Nilssen 2000). Mortality at sea is not well studied for Svalbard Arctic char but it is attributed to predation by seals or piscivorous fish, e.g., Atlantic cod (*Gadus morhua*) or not being able to survive the winter at sea after failing to migrate upstream before rivers freeze/dry up (Gulseth and Nilssen 2000; Svenning and Gullestad 2002). In addition, local citizens in Svalbard actively fish for anadromous Arctic char with gillnets and rods, which has reduced some local Arctic char populations (Svenning et al. 2020; Johnsen et al. 2021).

The marine diet of Arctic char in Svalbard has been the subject of several studies. Pelagic, intertidal, and demersal fish as well as crustaceans were reported to be prey for char by Dahl (1926). More recent studies report similar results, with some variation; the char diet includes capelin (*Mallotus villosus*), juvenile Cottidae and Liparidae, *Mysis oculata*, *Gammarus* spp. and euphausiids—mainly *Thysanoessa* spp. (Skogstad and Skogstad 2006; Ebne 2009; Bergane 2018). Euphausiids appear to be especially important for small Arctic char (< 40 cm), while fish becomes more prevalent in larger individuals (Ebne 2009; Bergane 2018).

Pink salmon (*Oncorhynchus gorbuscha*) is a native Pacific salmonid species that has a wide distribution around the North Pacific Ocean (Heard 1991; Hard et al. 1996). From 1956 until the end of the century, fertilized eggs and pink salmon fry were released in rivers in northwest Russia, which has led to pink salmon occurring in both Russian and mainland Norwegian rivers (Gordeeva et al. 2015; Niemelä et al. 2016; Sandlund et al. 2019), where it spawns successfully in some rivers in both countries (Hesthagen and Sandlund 2015; Mo et al. 2018). Unlike the iteroparous Arctic char, pink salmon are semelparous and spend most of their life at sea, having a life cycle of only two-years. Fry hatch during spring from eggs laid the previous year and migrate downstream to the sea almost as soon as they have emerged from the riverbed (Quinn 2018). Pink salmon remain at sea for one winter and return to spawn in rivers during summer/fall and die shortly thereafter (Heard 1991; Sandlund et al. 2019). Pink salmon was first caught in Svalbard in 1961 and now occurs regularly in the archipelago, both in freshwater and in the sea (Gullestad 1968; Witkowski and Głowacki 2010; Gjelland and Sandlund 2012).

Currently, there is no threat of pink salmon reproducing successfully in Svalbard rivers since they freeze or dry up during fall and winter. However, this might change in the future with continued warming of the climate and increasing levels of precipitation. Their presence in freshwater systems suggests that they are already attempting to spawn, and pink salmon have been documented to aggressively protect their spawning redds (Mo et al. 2018; Sandlund et al. 2019). This could potentially affect Arctic char. A more pressing issue is potential dietary competition between the species when foraging at sea. Pink salmon in its natural range feed on many of the same prey types as Arctic char, e.g., euphausiids, amphipods, and small fish, but also on pteropods, squid, and copepods (Hard et al. 1996; Kaeriyama et al. 2000, 2004), which is also true for pink salmon off the coast of mainland Norway (Diaz Pauli et al. 2023). During years with large spawning stocks of pink salmon in the Pacific, zooplankton biomass can be significantly reduced, which affects zooplankton consumption by competing salmonids (Shiomoto et al. 1997; Ruggerone and Nielsen 2004). High abundance of pink salmon has been shown to have negative effects on recruitment, growth, and survival in sockeye salmon (*Oncorhynchus nerka*) in the North Pacific (Ruggerone and Connors 2015).

During recent decades, both the volume and the temperature of Atlantic Water (AW) transported to the Barents Sea has increased markedly (Lind et al. 2018; Pörtner et al. 2019). This has resulted in large reductions in sea ice extent and volume (Tverberg et al. 2014; Lind et al. 2018) and “Atlantification” of the marine ecosystem (Renaud et al. 2012; Fossheim et al. 2015; Weydmann-Zwolicka et al. 2021). These system changes are likely to impact the diet of anadromous char and potentially also alter predator pressure with increases in the presence of piscivorous Atlantic gadids, e.g., Atlantic cod, haddock (*Melanogrammus aeglefinus*), and saithe (*Pollachius virens*; Renaud et al. 2012). The local harbor seal (*Phoca vitulina*) population is also increasing in number and expanding their distribution within the archipelago (Bengtsson et al. 2021). Furthermore, Atlantification of the ecosystem might increase competition with the alien species pink salmon, especially if it successfully spawns in the archipelago.

The purpose of this study was to increase knowledge regarding the marine diet of Arctic char and pink salmon in Svalbard, and to investigate potential dietary overlap between these species. In addition, community structure of the salmonids in terms of size, sex and maturity were analyzed. Such knowledge will be needed by environmental authorities in the years to come to manage salmonids in a new climate regime.

Materials and methods

Study area

Arctic char and pink salmon were collected between mid-July and mid-August from 2015 to 2018 at six different coastal areas in Svalbard: (1) inner Isfjorden; (2) outer Isfjorden; (3) Forlandsundet; (4), Kongsfjorden/Krossfjorden; (5) North Spitsbergen; and (6) Wahlenbergfjorden (Fig. 1). Isfjorden, Kongsfjorden/Krossfjorden and Forlandsundet are all greatly influenced by AW brought up the west coast of Spitsbergen by the WSC (Nilsen et al. 2016; Tverberg et al. 2019; Skogseth et al. 2020). North Spitsbergen is also influenced by AW from the WSC, but usually has a more pronounced surface layer of Arctic Water (ArW) due to its proximity to the Arctic Ocean (Cokelet et al. 2008; Geoffroy et al. 2017). Wahlenbergfjorden is mixed, with influences from both AW and ArW from Hinlopen Strait in its outer parts, while the inner parts of the fjord are characterized by locally produced meltwater from glaciers and sea ice (Bartels et al. 2018; Menze et al. 2020).

Field and laboratory methods

Fish were caught using 27 m long and 1.8 m high gillnets with mixed mesh size ranging from 35 to 63 mm (knot to knot). The nets were attached to the shore and stretched through the littoral and sublittoral zones. Immediately after capture, fish were killed and fork length to the closest mm and body mass to the closest g were measured. Sex and reproductive status (juvenile, mature spawning in the year of capture or mature not spawning in the year of capture) were determined based on the state of the gonads (Dahl 1917). Mature fish that would not spawn this year had undeveloped gonads, but well-developed blood vessels to the gonads. Mature females that would not spawn this year additionally had a mix of residual eggs and undeveloped eggs. Otoliths were removed and put in 70% ethanol mixed with glycerol and stomachs were taken out and stored at $-20\text{ }^{\circ}\text{C}$ until analyzed.

In the lab, otoliths were put on a black Petri dish with a few drops of glycerol and age was determined by counting opaque zones under a stereo microscope (Barber and McFarlane 1987). Stomachs were thawed in lukewarm water and opened with a pair of scissors and their contents were washed with tap water over a sieve with a 0.5 mm^2 mesh size. All remaining hard parts were placed in a Petri dish and all elements were identified to the lowest possible taxonomic level using identification guides by Klekowski and Węśławski (1992) and Vassilenko and Petryashov (2009). When possible, the size of prey organisms or

identifying body parts (otolith, carapax) were measured. Biomass of consumed prey was reconstructed by using data on size-weight relationships of relevant organisms collected along the west coast of Svalbard (1990–2000) by the Institute of Oceanology of the Polish Academy of Sciences (IO PAN).

Statistical analysis

All statistical analyses were performed with R version 4.1.2 in RStudio (R Core Team 2021), and significance level was set at $\alpha < 0.05$. Potential differences in length and age between juveniles, sexually mature females and sexually mature males of Arctic char were tested using Kruskal–Wallis rank-sum tests (Hollander et al. 2013), followed by Dunn’s test of multiple comparisons (Dunn 1964), using Holm’s method for adjusted p values (Holm 1979). A Student’s T test was used to test difference in length between males and females of pink salmon. Assumptions of homogeneity of variance and normal distribution were tested using Levene’s test (Levene 1960) and Shapiro–Wilk’s normality test (Shapiro and Wilk 1965). Length was used instead of body mass to compare sizes between the groups to avoid the influence of body condition, which might be more affected by the timing of descent/ascent to/from sea.

The contribution of different prey types to the diet of Arctic char and pink salmon was explored at the population level by calculating the frequency of occurrence (FO_i ; the percentage of all individuals that had consumed prey type i), relative frequency (N_i ; the percentage of prey type i to the total number of prey) and relative percentage of (reconstructed) biomass (B_i ; the percentage biomass of prey type i to the total prey biomass; Hyslop 1980; Chipps and Garvey 2007).

Dietary patterns of Arctic char and pink salmon were explored by grouping prey in ecologically relevant classes; pelagic invertebrates, demersal invertebrates, intertidal invertebrates, pelagic fish, demersal fish and “other”. The “other” class consisted of prey which could not be identified to taxonomic groups lower than to order, e.g., fragments of fish and invertebrates, and hence were excluded from further analysis along with individual Arctic char and pink salmon which only had prey items of this class in their stomachs. Relative importance of prey and feeding strategy (generalized vs specialized) were evaluated visually by plotting FO against B of the different prey classes in a modified “Costello plot” (Costello 1990; Amundsen et al. 1996).

Prey associated with AW (*Thysanoessa inermis*, *Themisto abyssorum*, capelin and Atlantic herring (*Clupea harren-gus*)) were grouped together as “Atlantic prey” and the rest were classified as “Arctic prey” when comparing the contribution of prey associated with AW vs prey associated with ArW to diet composition.

Dietary overlap of co-occurring Arctic char and pink salmon populations, based on reconstructed biomasses of the five different prey classes described above, was estimated by calculating Pianka’s niche overlap index (O_{obs}) and comparing it with a null expectation (O_{exp}) using the *ra3* algorithm (1000 replications) in the EcoSimR package in R (Pianka 1974; Gotelli et al. 2015). Levels of overlap were set to low (< 0.4), intermediate (0.4–0.6) and high (> 0.6; Grossman 1986).

To visualize differences in diet composition between sampling areas and the two salmonid fishes, non-metric multidimensional scaling (NMDS) was applied with the R package *vegan* (Oksanen et al. 2013), using Euclidean distance and center log ratio transformed biomass proportions (0:1) of the five prey classes at the individual predator scale, accounting for zeroes by replacing them with pseudo-counts of 0.001 (Sisk-Hackworth and Kelley 2020). Ellipses showing 95% confidence interval of the mean position for each group (area/species) were drawn to visualize potential overlap. To test if diet composition differed between species/areas, permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used with 1000 permutations to test if group centroids differed significantly from each other, followed by pairwise comparisons with Holm’s adjusted *p* values. Assumption of multivariate homogeneity of groups dispersions was tested prior to performing PERMANOVA (Anderson 2006). Due to patchiness in the data—e.g., some areas were not sampled during certain years and

some sex/maturity classes were missing from some years/areas—all individuals, regardless of year of sampling and sex/maturity class were pooled for each area when comparing diet composition of Arctic char between areas.

Results

In total, 301 Arctic char and 28 pink salmon were collected in Svalbard between 2015 and 2018. 272 char and 17 pink salmon had identifiable prey items in their stomachs (Table 1). Most Arctic char were caught during 2017 ($n = 103$) and 2018 ($n = 116$), in North Spitsbergen ($n = 94$) and Forlandsundet ($n = 73$, Table 1). Most pink salmon were caught in 2017 in Kongsfjorden/Krossfjorden ($n = 21$). Among the Arctic char, 41 (13.6%) were sexually mature males, 80 (26.6%) juvenile males, 71 (23.6%) sexually mature females, 108 (35.9%) juvenile females and 1 (0.3%) juvenile of undetermined sex. Of the sexually mature Arctic char, only 7 of the males and 1 of the females had gonadal development suggesting that they would breed in the season of capture. The mean length and body mass of the Arctic char were 45.3 cm (range 22.5–72.0 cm) and 1160 g (range 110–4900 g, and the mean age was 11 years (range 5–20 years, Table 2). Eight of the Arctic char could not be successfully aged. Juvenile, mature female and mature male Arctic char overlapped in terms of age/length (Fig. 2), however there were significant differences

Table 1 Number of Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) collected from 6 different areas in Svalbard 2015–2018

	Arctic char					Pink salmon			
	2015	2016	2017	2018	All years	2015	2016	2017	All years
Inner Isfjorden	28 (27)	2	2	–	32 (31)	2	–	–	2
Outer Isfjorden	–	1	7 (5)	20 (19)	28 (25)	–	–	–	–
Forlandsundet	7 (6)	20	14 (5)	32 (29)	73 (60)	–	2	–	2
Kongsfjorden/Krossfjorden	6	18 (16)	23 (15)	–	47 (37)	2	1	21 (10)	24 (13)
North Spitsbergen	–	–	57 (55)	37	94 (92)	–	–	–	–
Wahlenbergfjorden	–	–	–	27	27	–	–	–	–
Total	41 (39)	41 (39)	103 (82)	116 (112)	301 (272)	4	3	21 (10)	28 (17)

For areas and years when fish with empty stomachs were present, the number of individual fish with identifiable stomach contents are presented in parentheses

Table 2 Length, body mass and age of Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) caught in Svalbard during 2015 to 2018

Species	<i>n</i>	Length (cm)		Body mass (g)		Estimated age	
		Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Arctic char	301 ^a	45.3 (8.8)	22.5–72.0	1160 (677)	110–4900	11 (3)	5–20
Pink salmon	28 ^b	46.1 (2.5)	42.0–52.0	1395 (324)	920–2230	1	1

^aOnly 293 Arctic char could be successfully aged

^bOnly 26 pink salmon were weighed

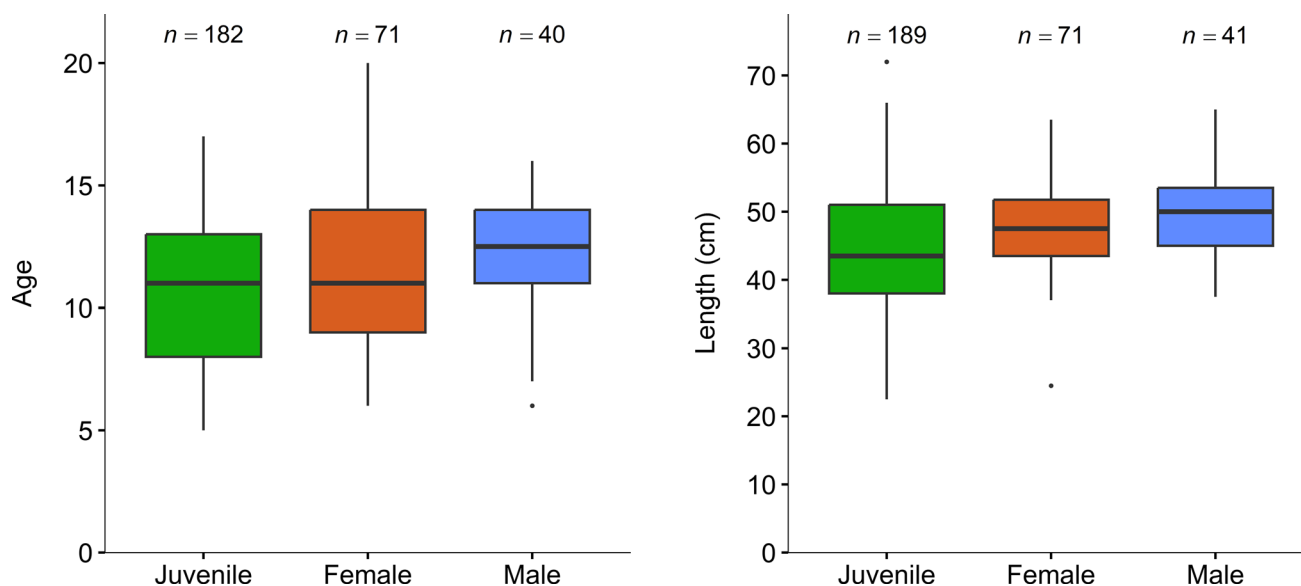


Fig. 2 Length and age of Arctic char (*Salvelinus alpinus*) grouped as juvenile, mature female and mature male based on gonadal development. Boxes contain 25th, 50th (median line) and 75th percentiles,

and whiskers stretch between the minimum and the maximum values (excluding outliers). Outliers ($>1.5 \times$ higher or lower than upper or lower quartile) are represented by dots

between the groups (Kruskal–Wallis test: age, $H_2 = 16.73$, $p = 0.0002$; length, $H_2 = 21.80$, $p < 0.0001$). Pairwise testing revealed that juveniles were on average significantly younger (10.3 ± 2.91 years, $n = 182$) and shorter (43.6 ± 9.5 cm, $n = 189$) than both mature females (age, 11.6 ± 3.09 years, $n = 71$, $p_{\text{adj}} = 0.01$; length, 47.6 ± 6.3 cm, $n = 71$, $p_{\text{adj}} = 0.002$) and mature males (age, 12.0 ± 2.73 years, $n = 40$, $p_{\text{adj}} = 0.001$; length, 49.7 ± 7.09 cm, $n = 41$, $p_{\text{adj}} = 0.0003$). Arctic char from North Spitsbergen were longer than fish at all other locations, and Arctic char from Outer Isfjorden were on average shorter (Online Resource 1). The proportion of invertebrates (both demersal and intertidal) decreased and the proportion of fish increased in the diet of Arctic char with increasing length of the predator (Online Resource 2). No sex differences were apparent (Online Resource 3).

All pink salmon were one year old with gonads developed for spawning (Table 2)—nine were males and 19 were females. Average length and body mass of pink salmon were 46.1 cm (range 42.0–52.0 cm) and 1395 g (range 920–2230 g; Table 2), respectively. There was no significant difference in length between male and female pink salmon.

Dietary analyses showed that Arctic char had consumed 34 different, identifiable prey species/genera (hereafter only referred to as prey species) in addition to 11 different prey types which could not be identified lower than to order (Table 3). The most numerous prey species of Arctic char was the pelagic invertebrate *Themisto libellula* ($n = 7424$, $N_i = 37.2\%$), which was also the species with the highest B_i (26.0%) and second highest FO_i (35.7%; Table 3). Juvenile Cottidae (demersal fish) was the most commonly

consumed fish species ($n = 1019$, $N_i = 5.1\%$) and the prey with the second highest B_i (17.8%) and third highest FO_i (30.0%; Table 3). Other important prey species included the pelagic crustacean *T. inermis* ($FO_i = 40.7\%$; $N_i = 16.5\%$; $B_i = 14.5\%$), the intertidal amphipod *Gammarus setosus* ($FO_i = 17.1\%$; $N_i = 5.9\%$; $B_i = 10.3\%$) and the pelagic (fish) capelin ($FO_i = 13.2\%$; $N_i = 0.4\%$; $B_i = 13.7\%$; Table 3). The most important demersal invertebrate was *M. oculata* ($FO_i = 20.4\%$; $N_i = 8.4\%$; $B_i = 4.4\%$; Table 3). Pelagic invertebrates were the prey class that made up the largest proportion of the Arctic char diet in terms of biomass (41.5%), followed by pelagic fish and demersal fish which made up 18.9% and 18%, respectively (Fig. 3). The Costello plot for Arctic char revealed that it was a generalist feeder—most prey classes had a FO between 16.8 and 37.5%, and B between 5.1 and 18.9%—with pelagic invertebrates as most important prey class ($FO = 61.4\%$, $B = 41.5\%$; Fig. 4). Eight of the Arctic char had only consumed prey of the “other” class (i.e., prey which could not be identified lower than to order).

Pink salmon had consumed 12 different, identifiable prey species in addition to 5 prey types which could not be identified lower than to order (Table 3). The most numerous prey species of pink salmon were juvenile *Gammarus* spp. ($n = 139$; $N_i = 32.6\%$) and *Onisimus litoralis* ($n = 138$, $N_i = 32.4\%$), which are both intertidal invertebrates (Table 3). *O. litoralis* was also the species with the highest B_i (35.0%), followed by *G. setosus* (26.0%), while juvenile *Gammarus* spp. had the highest FO_i (52.9%). Juvenile Cottidae had the second highest FO_i (41.1%) and the (shared) third highest

Table 3 Prey class, species, body size measures, number of individuals and dietary indices of Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) caught in Svalbard 2015–2018

Prey class	Species	Size (mm)	Reconstructed weight (g)	Arctic char			Pink salmon					
				n	FO _i (%)	N _i (%)	B _i (%)	n	FO _i (%)	N _i (%)	B _i (%)	
Pelagic invertebrate	<i>Themisto libellula</i>	10–15	0.2	7424	35.7	37.2	26.0	26	23.5	6.1	6.6	
	<i>The abyssorum</i>	<10	0.1	4	1.4	0.02	0.007	–	–	–	–	
	<i>Thysanoessa inermis</i>	15–25	0.25	3305	40.7	16.5	14.5	40	17.6	9.4	12.7	
	<i>Thy. longicaudata</i>	10–15	0.1	501	8.6	2.5	0.9	2	5.9	0.5	0.3	
	<i>Pagurus zoea</i>	6	0.1	19	1.4	0.1	0.03	–	–	–	–	
	<i>P. juvenile</i>	–	0.002	1	0.4	0.005	<0.001	–	–	–	–	
	<i>Calanus</i> spp.	5	0.002	93	2.9	0.47	0.003	–	–	–	–	
	<i>Hyas megalopa</i>	–	0.002	1	0.4	0.005	<0.001	–	–	–	–	
	<i>Nereis pelagica</i>	20–30	0.2	2	0.4	0.01	0.007	–	–	–	–	
	<i>Gonatus fabricii</i>	30–40	1.0	1	0.4	0.005	0.02	–	–	–	–	
	Demersal invertebrate	<i>Mysis oculata</i>	10–15	0.15	1673	20.4	8.4	4.4	–	–	–	–
		<i>Weyprechtia pinguis</i>	10	0.5	28	0.7	0.1	0.25	–	–	–	–
		<i>Ischyrocerus</i> spp.	10	0.1	131	5.0	0.7	0.2	–	–	–	–
		<i>Gammarillus homari</i>	10–15	0.2	24	3.9	0.1	0.08	4	5.8	0.9	1.0
<i>Atylus carinatus</i>		10–15	0.2	1	0.4	0.005	0.004	–	–	–	–	
<i>Lebbeus polaris</i>		30	1.0	1	0.4	0.005	0.02	–	–	–	–	
Lysianassidae sp.		7	0.2	4	1.1	0.02	0.01	1	5.8	0.2	0.3	
<i>Anonyx sarsi</i>		10–15	0.15	2	0.4	0.01	0.005	–	–	–	–	
<i>Calippus laeviusculus</i>		5–10	0.1	2	0.7	0.01	0.004	–	–	–	–	
<i>Lepidopcreum umbo</i>		7	0.1	–	–	–	–	1	5.8	0.2	0.1	
Ostracoda sp.		–	0.1	1	0.4	0.005	<0.001	–	–	–	–	
<i>Anatides groenlandica</i>		30–50	1.0	6	0.4	0.03	0.1	1	5.8	0.2	1.3	
Intertidal invertebrate		<i>Gammarus setosus</i>	10–30	0.5	1177	17.14	5.9	10.3	41	17.6	9.6	26.0
		<i>Gammarus oceanicus</i>	10–15	0.2	132	20	7.1	0.66	13	17.6	3.1	3.3
	<i>Gammarus</i> spp. juvenile	<10	0.004	2431	23.9	12.2	0.2	139	52.9	32.6	0.7	
	<i>Onisimus litoralis</i>	15	0.2	1573	7.5	7.9	5.5	138	17.6	32.4	35.0	
	<i>Orchomenella minuta</i>	5	0.1	4	0.4	0.02	0.007	–	–	–	–	
	Capelin (<i>Mallotus villosus</i>)	100–150	10.0	78	13.2	0.4	13.7	–	–	–	–	
Pelagic fish	Atlantic herring (<i>Clupea harengus</i>)	100–150	10.0	18	0.4	0.09	3.2	–	–	–	–	
	Polar cod (<i>Boreogadus saida</i>)	100–150	12.0	10	3.2	0.05	2.1	–	–	–	–	
	Cottidae juvenile	30–50	1.0	1019	30.0	5.1	17.8	10	41.1	2.3	12.7	
	<i>Anisarchus medius</i>	50–100	5.0	1	0.4	0.005	0.09	–	–	–	–	
Demersal fish	Lumpenidae sp.	50	0.5	–	–	–	–	–	–	–	–	
	<i>Eumicrotremus</i> sp.	30–50	1.0	5	1.07	0.03	0.09	–	–	–	–	

Table 3 (continued)

Prey class	Species	Size (mm)	Reconstructed weight (g)	Arctic char			Pink salmon				
				n	FO_i (%)	N_i (%)	B_i (%)	n	FO_i (%)	N_i (%)	B_i (%)
Other	Unidentifiable fish	< 10	-	51	11.4	0.3	-	-	-	-	-
	Fish bones	-	-	54	15.7	0.3	-	-	-	-	-
	Fish egg	3–5	0.05	169	2.5	0.8	0.1	-	-	-	-
	Amphiod fragments	< 10	-	9	3.2	0.05	-	1	5.9	0.2	-
	Decapod fragments	-	-	2	0.7	0.01	-	-	-	-	-
	Bivalve fragments	10–15	-	-	-	-	-	1	5.9	0.2	-
	Insect	6.0	0.1	1	0.4	0.005	0.002	-	-	-	-
	Polychaeta setae	20–40	-	12	3.9	0.06	-	3	11.8	0.7	-
	Ascidiae	30–50	-	-	-	-	-	1	5.9	0.2	-
	Macroalgae fragments	-	-	1	0.4	0.05	-	-	-	-	-
	Terrestrial plant fragments	-	-	-	-	-	-	1	5.9	0.2	-

FO_i frequency of occurrence, N_i relative frequency, B_i relative percentage of biomass

B_i (12.7%) together with *T. inermis* (Table 3). Intertidal invertebrates dominated other prey classes in terms of the proportion of biomass (65.1%; Fig. 3) and FO (76.5%). The Costello plot further revealed that pink salmon specialized on this same prey class (Fig. 4).

Dietary niche overlap between Arctic char and pink salmon was investigated only for fish from Kongsfjorden/Krossfjorden (2017), where there was both temporal and spatial overlap between the two species (Arctic char, $n = 15$, pink salmon, $n = 10$). Diet composition of Arctic char in this subset, was dominated by pelagic fish ($B = 62.6\%$) and intertidal invertebrates ($B = 34.9\%$) in terms of biomass. The diet of pink salmon was dominated by intertidal invertebrates ($B = 77.5\%$) and demersal fish ($B = 21.9\%$; Fig. 5). Dietary niche overlap was at the high end of the intermediate interval ($O_{\text{obs}} = 0.59$, $O_{\text{exp}} = 0.45$, $p = 0.25$), though the diet composition of the two salmonids was significantly different (PERMANOVA: $F_1 = 3.81$, $p = 0.025$, stress = 0.04). Both salmonids in this subset consumed a lot of intertidal invertebrates. However, Arctic char ate more pelagic fish, while the fish prey targeted by pink salmon were mostly demersal fish (Fig. 6). Further, the diet composition of the Arctic char in this subset consisted of 32.9% Atlantic prey while pink salmon consumed only Arctic prey (Online Resource 4).

Regional dietary comparisons were only possible for Arctic char ($n = 272$, excluding individuals without identifiable prey in their stomachs), because the sample sizes by location for pink salmon were too low. Pelagic invertebrates dominated the diet of Arctic char in North Spitsbergen ($B = 65.4\%$) and made up almost half of their diet in Outer Isfjorden ($B = 49.3\%$, Fig. 7). Intertidal invertebrates dominated the diet composition in Inner Isfjorden ($B = 66.1\%$) and Wahlenbergfjorden ($B = 51.9\%$), and demersal fish was the dominant prey class in Forlandsundet ($B = 64.8\%$, Fig. 7). The highest proportion of demersal invertebrates was in Wahlenbergfjorden ($B = 28.2\%$) and the highest contribution of pelagic fish was in North Spitsbergen ($B = 27.7\%$, Fig. 7). There was overlap in diet composition between all areas, except North Spitsbergen (Fig. 8), which was significantly different from the other areas (PERMANOVA: $F_5 = 18.96$, $p = 0.0001$, stress = 0.17). Pairwise comparisons revealed that the diet of Arctic char was significantly different in each area ($p_{\text{adj}} = 0.15$). In North Spitsbergen Atlantic prey made up the highest proportion in the diet ($B = 46.3\%$), followed by Outer Isfjorden ($B = 29.8\%$), while Arctic prey species dominated at all other locations (Online Resource 5).

Discussion

This study presents novel information about the diet of Arctic char and pink salmon in Svalbard as well as assessing dietary overlap between these two salmonids. It confirmed

Fig. 3 Diet composition of Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) in Svalbard (2015–2018) presented as reconstructed biomass (proportions) of five different prey classes

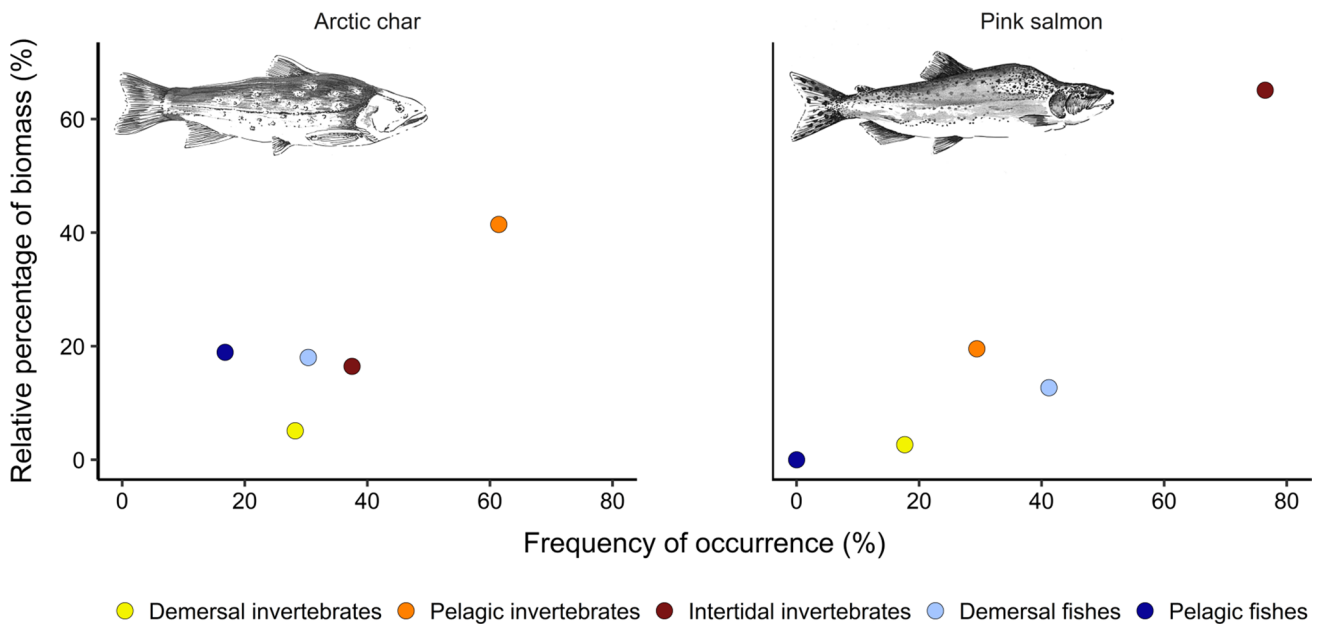
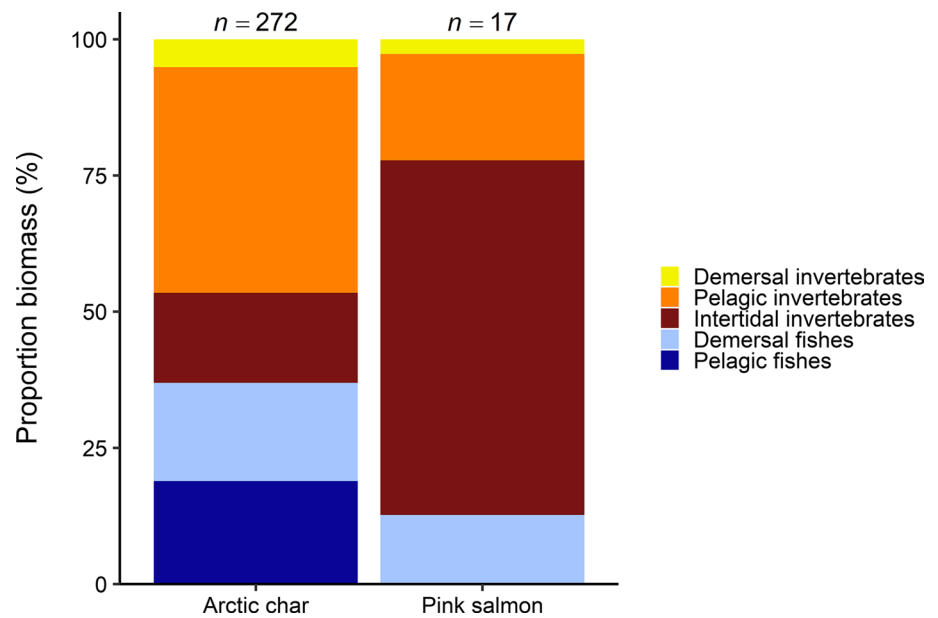


Fig. 4 Frequency of occurrence and relative percentage of reconstructed biomass of five different prey classes in the diet of Arctic char (*Salvelinus alpinus*; n=272) and pink salmon (*Oncorhynchus gorbuscha*; n=17), caught in Svalbard (2015–2018). Illustrations by Milena Sontowska

previous findings that anadromous Arctic char in Svalbard are generalist feeders that exhibit a slight preference for pelagic invertebrates, with amphipods, euphausiids, and small marine fish species being their most important prey (Skogstad and Skogstad 2006; Ebne 2009; Bergane 2018). It also revealed that pink salmon in Svalbard feed on many of the same species as Arctic char, but have a more specialized diet, comprised mainly of intertidal invertebrates, with the amphipods *G. setosus* and *O. littoralis* being especially important in terms of biomass. Pink salmon in its native

range in the North Pacific, as well as in the Norwegian Sea have a varied diet, consisting of amphipods, euphausiids, small fish, copepods, pteropods, and squid (Heard 1991; Kaeriyama et al. 2004; Diaz Pauli et al. 2023). This species is generally considered to be a dietary generalist (Radchenko et al. 2018). The apparent contrast in feeding mode between North Pacific pink salmon and pink salmon in this study (generalist vs specialist), is likely explained by study “scale”. All pink salmon in this study were caught close to the coast, which might limit the number of prey classes recorded; in

Fig. 5 Diet composition of Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) in Kongsfjorden and Krossfjorden, Svalbard during 2017, presented as reconstructed biomass proportions of five different prey classes

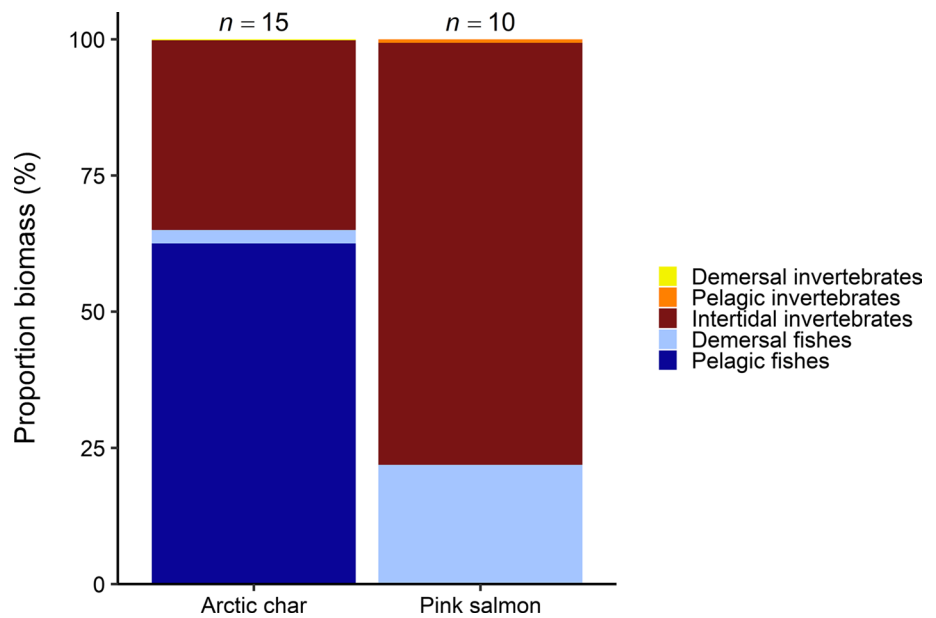
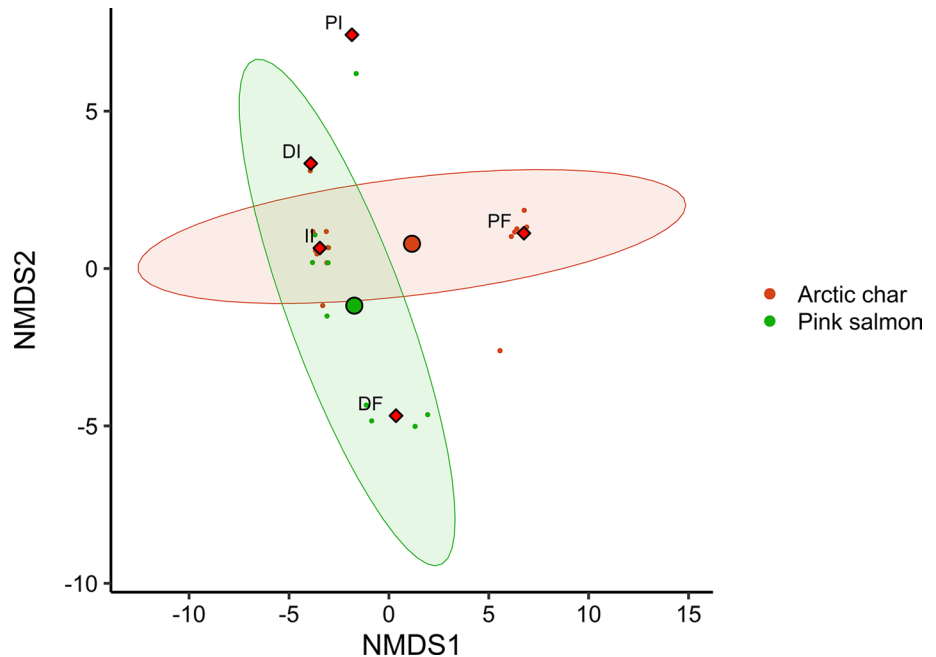


Fig. 6 Non-metric multidimensional scaling (NMDS) of diet composition based on reconstructed biomass proportions of Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) from Kongsfjorden/Krossfjorden, Svalbard 2017. Large points with black borders represent group centroids (Arctic char/pink salmon) and ellipses show 95% confidence area for mean position of each group. Rhombi with black borders show (prey) species; demersal invertebrates (DI), pelagic invertebrates (PI), intertidal invertebrates (II), demersal fish (DF) and pelagic fish (PF)



the Norwegian Sea, the diet for the whole population was varied, but areas tended to be dominated by one type of prey (Diaz Pauli et al. 2023). In Svalbard, *G. setosus* is found in inner fjord basins and *O. littoralis* is almost exclusively associated with soft bottom, tidal flats in front of rivers and glaciers (Węśławski 1994; Węśławski et al. 2000), strongly indicating that pink salmon in Svalbard feed in these areas. This would also explain the absence of prey associated with AW—which are more pelagic—in the pink salmon diet.

All of the pink salmon in this study were mature 1-year-olds, with well-developed gonads. It is well known that as pink salmon prepare to spawn, most of their energy is

allocated towards gonad maturation and feeding rates decline (Heard 1991), so it was perhaps not surprising that a large proportion of the pink salmon caught in this study had empty stomachs (11 of 28). Both their empty stomachs and their gonad development state suggest that they were preparing to migrate upstream to spawn. This fact might bias their distribution toward the intertidal zone. Prey from this zone dominated the stomach contents ($B = 65.1\%$) of the pink salmon that were still feeding.

Interestingly, *T. abyssorum*, was rare in the diet of Arctic char in this study and completely absent in the diet of pink salmon, while both species had consumed relatively

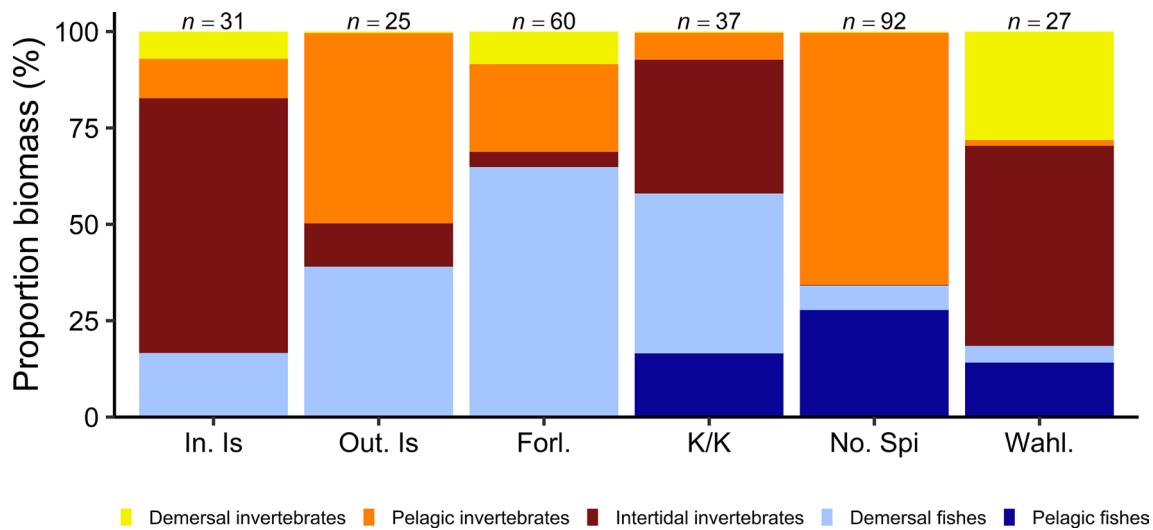
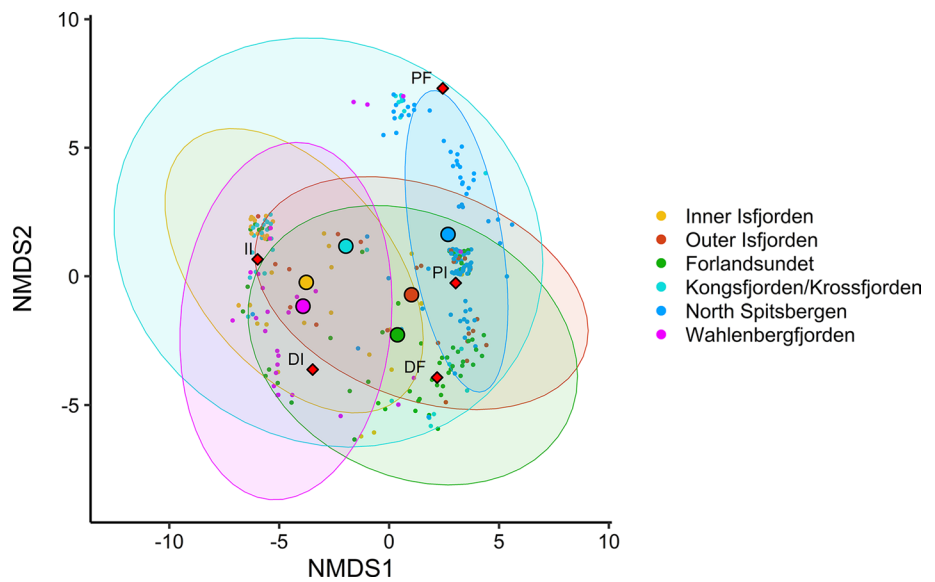


Fig. 7 Diet composition of Arctic char (*Salvelinus alpinus*) from different areas in Svalbard (2015–2018), presented as reconstructed biomass (proportions) of five different prey classes. Isfjorden (In. Is),

Outer Isfjorden (Out. Is), Forlandsundet (Forl.), Kongsfjorden/Krossfjorden (K/K), North Spitsbergen (No. Spi.), and Wahlenbergfjorden (Wahl.)

Fig. 8 Non-metric multidimensional scaling (NMDS) of diet composition based on reconstructed biomass proportions of Arctic char (*Salvelinus alpinus*) and pink salmon (*Oncorhynchus gorbuscha*) from six areas in Svalbard (2015–2018). Large points represent group centroids and ellipses show 95% confidence areas for each area. Rhombi show (prey) species; demersal invertebrates (DI), pelagic invertebrates (PI), intertidal invertebrates (II), demersal fish (DF), and pelagic fish (PF)



high proportions of *T. libellula*. This is despite the high abundance of *T. abyssorum* in Svalbard fjords, especially in areas with large volumes of AW (Dalpadado et al. 2016; Hop et al. 2019). This suggests that both salmonids have a strong preference for *T. libellula* over *T. abyssorum*. This is also known to be the case for polar cod (*Boreogadus saida*) in Svalbard (Cusa et al. 2019). *T. libellula* is generally larger than *T. abyssorum*, which could explain this preference, though the two amphipods have similar energy/lipid content per biomass (Percy and Fife 1981; Auel et al. 2002; Węśławski et al. 2006). It could also suggest that the two salmonids feed in areas with relatively high

abundances of *T. libellula*, e.g., inner fjord basins, as seen in Kongsfjorden (Dalpadado et al. 2016; Hop et al. 2019).

Dietary niche overlap was relatively high between Arctic char and pink salmon ($O_{obs} = 0.59$) in Svalbard when the two species co-occurred in the same fjord system, with both species consuming high proportions of intertidal invertebrates (pink salmon: $B = 77.5\%$, Arctic char: $B = 34.9\%$). What separated the diets of the two salmonids was the dominance of pelagic fish in the diet of Arctic char ($B = 62.6\%$). Fish comprised a smaller portion of the pink salmon diet ($B = 21.9\%$) and the fish they did eat were demersal species. This suggests that Arctic char and pink salmon feed in

different areas and in different parts of the water column at least some of the time. Pink salmon feed mainly in intertidal areas on bottom-dwelling prey, while Arctic char feed both in pelagic areas further offshore and in the intertidal zone. Pink salmon in the North Pacific are known to compete with other salmonid species via intense consumption of shared resources, mainly zooplankton, during years with high abundances of pink salmon (Shiomoto et al. 1997; Ruggerone and Nielsen 2004). In 2017, there was a record number of pink salmon in rivers in mainland Norway (Sandlund et al. 2019), which corresponds well with the relatively high numbers of pink salmon caught in Svalbard during this year compared to the other years in this study. Interestingly, zooplankton were practically absent in the diet of both Arctic char and pink salmon (< 1% in pink salmon) in Kongsfjorden/Krossfjorden in 2017. The limited sample size, especially for pink salmon, and time scope of this study do not allow any firm conclusions to be drawn but suggest that there is strong potential for competition for resources between Arctic char and pink salmon in Svalbard if pink salmon become more abundant in the archipelago.

Intertidal invertebrates were an important part of the diet for Arctic char in Inner Isfjorden and Wahlenbergfjorden, and to a degree, also in Kongsfjorden/Krossfjorden. These three areas are within fjords, where locally produced water likely makes up a relatively large proportion of the water column, especially deep within the fjords and close to glacier fronts (Bartels et al. 2018; Tverberg et al. 2019; Skogseth et al. 2020). Pelagic invertebrates were more common in the diet of Arctic char sampled in Outer Isfjorden, Forland-sundet and North Spitsbergen, which are less sheltered and more exposed to inflowing water masses which transport zooplankton (Hop et al. 2006; Geoffroy et al. 2017; Skogseth et al. 2020). Outer Isfjorden and North Spitsbergen were also the areas where Atlantic prey contributed most to the Arctic char's diet. Interestingly, demersal fish were eaten by Arctic char in the areas on the west coast, but not in the north and east, where pelagic fish were more prevalent in the diet compared to demersal fish. Body size might play a role given that the Arctic char from North Spitsbergen were on average larger than from the other areas, making it possible for them to consume pelagic fish, which were larger on average than the demersal fish eaten by either salmonid. However, interannual variation in the diet (prey community) cannot be ruled out, given that Arctic char from North Spitsbergen and Wahlenbergfjorden were only caught in 2017 and 2018, which were the years with the highest relative proportion of pelagic fish in the diet. Likewise, most Arctic char from Inner Isfjorden, where the diet was dominated by intertidal invertebrates, were caught in 2015. There appeared to be a size dependent trend in the diet of Arctic char as previously shown by Ebne (2009) and Bergane (2018). However, due to inconsistencies in the data in terms of year and area

where different sized fish were caught—this trend was not investigated further.

Arctic char that were not sexually mature (juveniles) were significantly younger and smaller than adult males and females, but the differences in mean age and length were not great between juveniles of the two sexes (1.3 years and 4.3 cm compared to adult females, and 1.7 years and 6.1 cm compared to adult males). There was considerable variation in size at a given age. Considering that the age at first migration can vary between 4 and > 10 years for Arctic char in Svalbard (Gulseth and Nilssen 2001; Ebne 2009; Johnsen et al. 2021), this overlap was not unexpected. However, the relatively high average age and large size of juveniles in this study indicates that most were not first-time migrators. Mortality of anadromous Arctic char is high while at sea, especially for small individuals (< 25 cm), and only 10–50% of first-time migrators survive to return (Finstad and Heggberget 1993; Gulseth and Nilssen 2000). It is likely that smaller Arctic char are disproportionately eaten by seals and predatory fish. Atlantic cod in mainland Norway are known to eat salmonid smolts (Hvidsten and Møkkelgjerd 1987; Hvidsten and Lund 1988) and Arctic char with bitemarks, that probably come from seals, have been observed in Svalbard (Svenning et al. 2020). With continued increases in the volume and temperature of AW and increasing abundances of predators associated with AW, such as Atlantic cod, haddock, saithe and harbor seals, all of which are increasing in Svalbard fjords (Renaud et al. 2012; Bengtsson et al. 2021), the predatory pressure of Arctic char is also likely to increase. This could have negative effects on the local Arctic char population, especially for small, first-time migrators.

Stomach content analysis has inherent biases that are important to address when studying diet (Trites and Spitz 2018; Amundsen and Sánchez-Hernández 2019). Differences in degradation and evacuation rates due to fat content, particle size and digestibility of different prey items can lead to an overrepresentation of large prey with easily identifiable hard parts, and an underrepresentation of small and/or soft bodied prey (Elliott 1972; Hyslop 1980; Legler et al. 2010; Baker et al. 2014). The diet of both Arctic char and pink salmon in this study consisted of relatively large crustaceans and fish, while smaller crustaceans (e.g., copepods and decapod larvae) and gelatinous organisms (e.g., pteropods) were absent or only made up a tiny proportion of the diet despite being abundant in Svalbard waters (Weydmann et al. 2014; Gluchowska et al. 2016). Neither copepods nor pteropods have been reported to be particularly important as food for Arctic char in Svalbard, but copepods are consumed by Arctic char in mainland Norway (Rikardsen et al. 2000), and both copepods and pteropods are important prey for pink salmon in the North Pacific (Heard 1991; Kaeriyama et al. 2004). Further, methods for quantitative estimation of diet, e.g., through

reconstruction of biomass contribution of prey items introduces potential bias by making assumptions of prey condition and length to body mass relationships (Baker et al. 2014; Amundsen and Sánchez-Hernández 2019). Due to the state of digestion of prey in the stomachs, this method was chosen over the more robust gravimetric method (Amundsen and Sánchez-Hernández 2019) when analyzing differences in diet composition. It is important to note that all fish in this study were caught relatively close to shore, which might discriminate against any potential individuals feeding further out in the fjords. There might also have been an underrepresentation of small individuals, which would be especially relevant for (juvenile) Arctic char, due to the mixed mesh size of the gillnets (smallest mesh size 35 mm).

Further studies should focus on a limited number of areas sampled during the same time intervals and include methods that can determine diet over longer periods, e.g., stable isotope and fatty acid analyses to estimate the diet during periods when Arctic char and high numbers of pink salmon coexist in the marine environment compared to periods without high numbers of pink salmon. Parallel sampling of the local potential prey community should also be considered to investigate possible selectivity by the salmonids.

Conclusions

Novel findings of the pink salmon's diet in Svalbard revealed that they share important prey species with the native Arctic char population. Differences in the proportions of different prey classes indicated that dietary overlap was moderately high, but also that the two salmonid species likely use different areas and different parts of the water column for at least some of their foraging. High proportions of empty stomachs in the pink salmon that were mature indicate that they were preparing to migrate to freshwater to spawn. Although the Arctic char in this study showed a preference for the Arctic pelagic amphipod *T. libellula* over its Atlantic counterpart *T. abyssorum*, the Arctic char did consume other species associated with AW, e.g., *T. inermis*, capelin, and Atlantic herring. With continued Atlantification of the marine environment in Svalbard, it is likely that the diet of the native Arctic char population will resemble that of the population in mainland Norway, which consists of herring, euphausiids, copepods, gadids, and other Atlantic fish species (Rikardsen et al. 2000, 2007; Rikardsen and Amundsen 2005). Continued warming of the Arctic is also likely to increase the level of competition between the salmonid species, to the detriment of the Arctic char. If pink salmon start to spawn in the Svalbard Archipelago it is likely that they will have negative

impacts on the anadromous char populations from lakes that have access to the sea.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-023-03196-8>.

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Author contribution All authors have agreed to be listed and have approved the submitted version of the manuscript. The following authors contributed to study design: GC, OB, KMK and CL; fieldwork: GC, CL, KMK and OB; labwork: JMW and GC; statistical analyses: OB; manuscript preparation: all authors.

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Data availability The data are available via contact with the corresponding author.

Declarations

Competing interests The authors have no competing interests to declare.

Ethical approval No ethics approval was needed for this study, but all national and institutional guidelines and regulations were fulfilled during capture and handling of the animals used in the study – most importantly, the Ethical Guidelines for the Use of Animals in Research issued by the (Norwegian) National Committee for Research Ethics in Science and Technology (NENT), 2018.

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