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Has climate change altered Jan Mayen Island Arctic Charr life-history traits and feeding ecology?

Jan G. Davidsen

jan.davidsen@ntnu.no

NTNU University Museum, Norwegian University of Science and Technology

Aslak D. Sjursen

NTNU University Museum, Norwegian University of Science and Technology

Samantha Crowley

Dalhousie University

Stig Skreslet

Nord University

Margrét Thorsteinsson

Westfjords Iceland Nature Research Centre

Gaute Kjaerstad

NTNU University Museum, Norwegian University of Science and Technology

Eiliv Larsen

Geological Survey of Norway

Astrid Lysså

Geological Survey of Norway

Ian Bradbury

Fisheries and Oceans Canada

Michael Power

University of Waterloo

Research Article

Keywords: Salvelinus alpinus, Feeding ecology, Landlocked populations, Life-history complex, Niche overlap, Stable isotope analyses

Posted Date: November 2nd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11308270/v1

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Additional Declarations: No competing interests reported.

Abstract

The population of Arctic charr in Lake Nordlaguna on the Arctic island of Jan Mayen became landlocked by a volcanic eruption in AD 1732 that caused a coastal uplift closing the lake off from the sea. Although considered as a relatively productive lake in terms of planktonic primary production, the lake is relatively species poor in comparison to lakes in other parts of the Arctic. Jan Mayen has already undergone significant shifts in temperature, with mean open-water season temperatures having risen from 3.8 ^{o}C in the early 1960s (1960-65) to 5.6 ^{o}C in the 2015–2020 period. To assess how rising temperatures may have influenced Arctic charr life-history traits and feeding ecology, we conducted a test fishery in Lake Nordlaguna to evaluate whether current life-history strategies and trophic niche use of the resident population has shifted from the early 1960s as the climate has warmed. The results showed that smaller Arctic charr were larger and age-at maturity younger than in 1963–1965, however trophic niches appear to have remained stable. It is, therefore, suggested that the increased temperature over the last six decades at Jan Mayen has changed the Arctic charr life-history strategy to mature at younger ages due to a limited food supply. Additional genetic analyses did not show differentiation of trophic morph types, however, the Jan Mayen population as a whole is shown to be highly genetically distinct from Arctic charr in other North Atlantic locations.

INTRODUCTION

The Arctic island of Jan Mayen (71°00N, 08°47W) is located along the Mid-Atlantic Ridge almost equidistant from the coasts of Greenland and Iceland in the eastern Greenland Sea. The island is small, with a total area of approximately 373 km^2. Given its size and geographic position between the cold East Greenland and Jan Mayen currents and the warm North Atlantic current, the island climate is sensitive to climate change driven shifts in the surrounding currents (Björck et al., 2022). The dominant features of the island include the Beerenberg volcano, the world's most northerly active subaerial volcano. which last erupted in 1985 and has a single lake, Nordlaguna, situated at the base of Beerenberg. The lake basin was formed over the last 560.000 years by a series of volcanic eruptions (Larsen et al., 2022) and during the last 3000 years the basin has undergone a number of key biological changes having been varying influenced by marine and freshwater as a result of sea-level changes (Björck et al., 2022). Currently, the lake is inhabited by a single species of fish, Arctic charr (*Salvelinus alpinus*), whose population is thought to have originated from migratory anadromous charr of unknown origin (Skreslet, 1973). While their arrival date on the island is unknown, geological studies have been able to show the population became landlocked by a volcanic eruption AD 1732 that caused a coastal uplift that closed the lake off from the sea (Larsen et al., 2021).

Nordlaguna experiences a polar climate influenced by the mixing of its surrounding marine currents (Syse, 1968). The narrow annual range of temperatures, and generally strong winds, inhibit thermal stratification (Skreslet, 1969). Although considered as a relatively productive lake in terms of planktonic primary production, the lake is relatively species poor in comparison to lakes in other parts of the Arctic (Skreslet & Foged, 1970). For example, while 60 and 32 Dipteran species, respectively, are known to

inhabit Svalbard and Bear Island, only eight are known to inhabit Jan Mayen (Stur & Ekrem, 2020). Lack of zooplankton and poorly developed and small benthic faunal assemblages appear to limit Arctic charr growth, making cannibalism the only pathway for a few individual fish to attain large size (Skreslet, 1973). Bi-modal Arctic charr populations are common in higher latitude fish populations and are considered to have reached an equilibrium state with their environment (Johnson, 1976). When closely associated with cannibalism in more northerly environments, bi-modality is believed to have largely arisen as a consequence of increased seasonality in the food supply (Griffiths, 1994) or to have resulted from the interplay of reduced post-maturity growth and mortality to yield populations containing many small, few intermediate, and a limited number of large fish (Power, 1978).

The occurring and predicted rapid rates of climate warming in the Arctic (Meredith et al., 2019) are likely to have significant consequences for freshwater fishes (e.g., Campana et al., 2020). Arctic charr, in particular, are predicted to experience localized extirpations due to their adaptation to colder water (e.g., Winfield et al., 2010; Hein et al., 2012) or to undergo life-history adaptations, including changes in anadromy patterns (Finstad & Hein, 2012). A warmer and wetter climate will increase rates of mineral weathering, the decomposition of soil organic matter, erosion and sedimentation, and is likely to lead to higher concentrations of organic matter, minerals, and nutrients in lakes such as Nordlaguna (Prowse et al., 2006). Such changes in the key drivers of the freshwater environment have the potential to affect large-scale lake and river ecosystem processes (e.g., brownification, nutrient enrichment, sedimentation) leading to changes in ecosystem alpha and beta diversity and/or productivity (Lento et al., 2019). For example, fertilization experiments in Arctic lakes have been associated with increased primary productivity, changes in pelagic and benthic food webs, increases in the biomass of plankton and benthic invertebrate biomass and the growth and size of resident fish (Bettez et al., 2002; Lienesch et al., 2005; O'Brien et al., 2005).

Changes have already been observed on Jan Mayen. For example, since the 1960's sea ice around Jan Mayen has been greatly reduced and has been totally absent since the 1990's. Loss of sea ice has resulted in winter storms having greater impacts in terms of beach barrier erosion and wave wash-over, thereby increasing marine influences on the lake (Björck et al., 2022). Long-term sampling of marine fishes proximate to Jan Mayen have shown increases in marine fish species, with the increase in part being attributable to species' range expansions and the displacement of boreal species into Arctic regions as a consequence of climate-driven ocean warming (Wienerroither et al., 2011). Similarly, the effects of climate change are evident in longer growing seasons, altered soil moisture conditions and increased nutrient availability that have contributed to changes in the observed diversity and composition of vegetation on the island (Kapfer et al., 2012). Such changes are predicted to affect the flow of energy and nutrients through food webs (Ruiter et al., 2005) and are likely to have consequences for keystone species on the island, such as Arctic charr.

Although temperature was fluctuating over the 1960–2020 period, observed 2-m air temperatures on Jan Mayen indicate substantial warming, with mean open-water temperatures having increased at the rate of 0.04°C per year and open-water seasonal means having increased from 3.8°C (1960–65) to 5.6°C

(2015–2020) between the sampling periods (Fig. 1). Increases in temperature are expected to accelerate somatic growth in high latitude populations of Arctic charr, resulting in larger size-at-age and increased stock biomass (e.g. Smalås et al., 2020). The increases in temperature that have occurred may already have elicited changes in the resident Nordlaguna Arctic charr population, given the strong connections between temperature and lake productivity (O'Beirne et al., 2017; Woelders et al., 2018) and the expectations for temperature driven changes in Arctic freshwater fish populations (e.g., Reist et al., 2006). Thus, in 2019 a test fishery of Lake Nordlaguna was undertaken to determine if warming trends were reflected in observable changes in the biological characteristics of resident Arctic charr and whether such changes could be considered as significant when compared to similar data collected in the early 1960s (Skreslet, 1973). To that end, we compare diets, condition, and rates of maturation and growth between the samples obtained in 2019 and those obtained from the 1963-65 period to determine the significance of any differences between the periods. We predicted that observed changes in lake temperatures would be manifest in: (1) dietary shifts, i.e. significant differences in prey use as a result of nutrient driven increases in algal production (Gough et al., 2016), (2) increased condition and rates of maturation, and (3) growth in the 2019 sampling as compared to the 1963-65 period. Finally to evaluate the trophic niche of the population we: apply stable isotope methods as recommended (e.g., Hobson, 2006) to advance understanding of the ecology of the Jan Mayen population and contextualize the Jan Mayen population with respect to literature reported data from other insular landlocked populations in northern Europe, and use genetic methods to describe genetic relationships within the Nordlaguna population and between the Jan Mayen population and other North Atlantic populations of Arctic charr.

MATERIAL AND METHODS

Study area

The island of Jan Mayen (Fig. 2) lies between 70–72 °N and 08–09 °W, 550 km northeast of Iceland and 500 km east of Greenland. The island is situated in the sub-Arctic transitional zone and surrounded by the Greenland, Iceland and Norwegian seas (Skreslet, 2004). The north part of the island is dominated by the stratovolcano Beerenberg that reaches an elevation of 2272 m a.s.l. The volcano is the world's northernmost active volcano above sea level, and it is part of the surface expression of a large sub-sea volcanic province (Elkins et al., 2016). Situated at the base of Beerenberg is the only lake on the island that does not dry out in the summer, Lake Nordlaguna. The lake is 1.5 km long, 1 km wide (approximately 1.02 km^2), and lies between 1–2 m a.s.l. (Bang & Skreslet, 1965). Most of the lake is > 25 m deep with a maximum depth 36 of m in the SW part (Björck et al., 2022). The lake is supplied by intermittent rivers active during the snow melt period (Skreslet, 1969) and is bounded on the east by steep mountain slopes. To the west the lake is separated from the ocean by an approx. 5 m high and 150–240 m broad beach barrier composed of sand to boulder-sized material and with no outlet to the sea. The outlet prior to AD 1732 was towards the SE, south of Fugleberget Domen (Larsen et al., 2021).

Water temperatures in Lake Nordlaguna over the 2019–2020 period have varied from a high of 8°C in August to a low of 0°C over the December to April period. Conductivity during the same period varied

from 1000–3500 µS/cm, declining significantly in June as spring freshet waters began to enter the lake. Water samples collected during the fish sampling were analysed for water chemistry by SGS Analytics Norway AS. Phosphorous and nitrogen were measured as < 1 µg L^{-1} and 43 µg L^{-1}, respectively, indicating an ultra-oligotrophic lake (Istvánovics, 2009). Total organic carbon was measured at 1.6 mg L^{-1}, chloride at 1670 mg L^{-1}, pH at 7.4 and color at (410 nm) < 1.

Arctic charr, benthic invertebrates and zooplankton sampling

Sampling of Arctic charr was completed 15–16 August 2019, using four overnight sets of sinking benthic multi-mesh gillnets (10.0, 12.5, 15.5, 21.0 mm mesh). The care and use of fish complied with the Government of Norway's animal welfare laws, guidelines and policies

and was approved by the County Governor of Nordland (Permission nr. 2014/1086). Based on surveys from the 1960s, it was expected that the Arctic charr population would contain only a small number of larger cannibalistic individuals. Thus, for permit imposed conservation reasons, fishing was restricted to sampling mainly smaller fish so as to avoid significantly reducing the reproductive potential or stability of the population (Le Bris et al., 2015).

The total length (TL, mm), mass (g), sex, maturity stage, flesh colour, parasite infestation and stomach fullness of each fish were determined in the field immediately after capture. Sagittal otoliths were removed and stored in envelopes for later age determination, with age determined following methods described in Grainger (1953). For analytical purposes, and following size groupings initially described in (Skreslet, 1973), captured fish were divided into size-groups based on the threshold (40 cm) above which cannibalism becomes predominant as has been reported in previous studies of isolated lacustrine Arctic charr populations in the Canadian Arctic (Hobson & Welch, 1995; Guiguer et al., 2002). Previously, for Jan Mayen, regular cannibals measured > 37 cm, but small Arctic charr were probably recruited to cannibalism at sizes below 27 cm in Lake Nordlaguna (Skreslet, 1973).

From each fish a 1g piece of dorsal muscle tissue was excised from posterior to the dorsal fin and above the lateral line (Guiguer et al., 2002; Davidsen et al., 2020) and frozen for use in stable isotope analyses. A random sample of fish were also sampled for genetic analysis, with a portion of the excised muscle tissues preserved in ethanol. Coincident with fishing, sampling for benthic invertebrates and zooplankton was completed opportunistically using standardized benthic invertebrate sampling methods (e.g., Eloranta et al., 2017) and a 90 µm zooplankton net towed manually behind a boat. A water sample was collected at 0.5 m depth and later analysed at Analysesentret AS (Norway).

Between-year Comparisons

Data collected from the 2019 sampling were compared to data reported by Skreslet (1973), with comparisons restricted to the category of small Arctic charr owing to the limitations of the large Arctic charr sample sizes obtained in both the 1960s and 2019. For 2019 a standard weight-length relationship

(e.g., Wootton, 1998) for each sex were estimated using ordinary least squares and tested for significant differences following procedures outlined in Zar (2010). Estimated slope coefficients were further tested for significant deviation from 3, the value indicating isometric growth, following procedures also described in Zar (2010). For comparative purposes condition was computed using Fulton's condition factor (Skreslet, 1973) and compared between sexes in 2019 using one way-ANOVA and between sampling periods using Fisher's exact test Zar (2010) to test for significant differences between the proportions of fish with higher and lower condition.

Mean age at maturation for the 2019 sampling data was determined using data pooled for both sexes after testing for differences in the proportion of mature individuals between the sexes using Fisher's exact test (two-tailed, $p = 0.618$). The probability of maturity was modelled as a function of age using logistic regression following methods described in Agresti (2002), with mean age-at-maturity estimated at the 0.5 probability point. Proportions of mature and immature fish ≤ 40 cm were compared between sampling dates using Fisher's exact test.

Comparisons of size-at-age were completed using one-way ANOVA where sufficient sample sizes at the common age existed. Plots of size-at-age were completed for visual comparison of growth-related patterns, although detailed data from the 1960s were not available and its absence ruled out completion of formal statistical testing. An instantaneous rate of mortality (M) for the small size-classes (≤ 40 cm) from the 2019 sampling was estimated based on the numbers of aged fish captured, beginning with the first fully vulnerable age-class, using Chapman–Robson methods (Chapman & Robson, 1960; Robson & Chapman, 1961). The method is known to yield low errors and biases in comparison to other available methods (Dunn et al., 2002). The validity of the underlying geometric model used in the Chapman–Robson procedure was verified following methods described in Seber (1982).

A volumetric analysis of stomach filling rate was conducted following Hyslop (1980). Stomach contents from the upper end of the oesophagus to the pyloric sphincter were identified to the lowest practical taxonomic level (typically order or family) under a stereoscopic microscope. The relative importance of each prey category was evaluated as % volume for each stomach and the total volume of the food category taken by all sampled fish with stomach contents was expressed as a percentage of the total volume of each stomach content item (Hyslop, 1980). Obtained data from the 2019 sampling were then compared to published historical data (e.g., Skreslet, 1973). Between period similarity in diets was determined by computing Morisita's measure and Horn's index which are both known to minimize biases in the assessment of niche overlap (Krebs, 1999). Dietary data were also used to compute Levin's standardized measure of niche breadth following methods described in Krebs (1999).

Stable Isotope Analyses

For stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$) a sample of dorsal muscle tissue from the 2019 fish was used, as muscle tissue is commonly used to determine long-term dietary reliances (e.g., Fry, 2002). For slow growing northern fish, muscle tissue represents the long-term average of ingested prey (Hesslein et al.,

1993), typically the summer period during which most somatic growth occurs (Eloranta et al., 2010). Dorsal muscle samples were dried at 50°C for 24 hours and shipped to the University of Waterloo where the samples were ground with mortar and pestle to a fine homogenate powder for analyses. Stable isotope analyses were completed using methods described in Knudsen et al. (2019), Davidsen et al. (2020) and Eldøy *et al.* (2021). Briefly, analyses were performed using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a 4010 Elemental Analyser (CNSO 4010, Costech Analytical Technologies Inc., Valencia, USA). All analytical results were expressed in standard per mil (‰) notation and reported relative to the relevant international standard. Working internal laboratory standards were calibrated against the International Atomic Energy Agency standards CH3 and CH6 for carbon and N1 and N2 for nitrogen, and were run as controls at the beginning, middle and end of each analysis to ensure the continued accuracy of all measurements (± 0.2‰ for carbon and ± 0.3‰ for nitrogen). Analytical precision was assessed using mean differences of one in ten duplicate samples, where the mean ± standard error was 0.1 ± 0.1‰ for $\delta^{13}C$ and 0.1 ± 0.2‰ for $\delta^{15}N$.

For analysis, stable isotope data ($\delta^{13}C$, $\delta^{15}N$) were used to compute metrics of trophic structure as described by Layman et al. (2007) including: carbon and nitrogen ranges (CR, NR), mean distance to centroid (CD) and mean nearest neighbour (NND). Data were further used to construct standard stable isotope cross-plots (mean ± standard deviation). For purposes of contextualization, the isotopic data obtained from Jan Mayen Arctic charr were compared to the limited data available for similar landlocked Arctic island populations from the North Atlantic, notably Bear Island (Lake Ellasjøen and Øyungen: Evenset et al., 2005; Hawley et al., 2016) and Svalbard (Arresjoen: Rognerud et al., 2002).

Genetic analyses

A subset of 32 samples from the 2019 Jan Mayen sampling were used for genomic analyses to investigate the potential for within-population genetic structure corresponding to identified trophic groups. Also investigated was the genetic admixture between Jan Mayen Arctic charr and a sub-sampling of other North Atlantic Arctic charr populations. The majority of the Jan Mayen charr used for genetic analyses were aged 2–3 years, small in size, and encompassed a range of feeding strategies along the pelagic-benthic continuum. Four were large (> 40 cm), estimated to be 16–19 years old, and were classified as piscivorous. Trophic assignments for the genetic analyses were based on the corresponding stable isotope analysis completed for each fish. Thirteen of the 32 samples were identified as males, five as females, and 14 were of unknown sex. The majority of the 32 individuals used for analyses were immature. The eight other North Atlantic locations from which Arctic charr samples for genetic comparisons were obtained were located in Bear Island, northern Norway, Greenland and Iceland (Table 1).

Table 1
Samples of Arctic charr from northern Atlantic Arctic charr populations used for genetic analyses

Country	Sample location	Coordinate (DD)	*n*
Jan Mayen (Norway)	Nordlaguna	N71.00312, W8.46934	32
Bear island (Norway)	Lake Trestikkelen	N74.47203, E19.08772	31
Norway, Northern	Laken Botnvatnet	N67.10000, E15.51670	21
Greenland, Mideast	Scoresbysund Fjord	N71.29834, W25.02528	23
Greenland, Southwest	Lake Tasersuaq	N60.26670, W44.63330	19
Iceland, Northwest	Sugandafjördur	N66.08557, W23.36668	8
Iceland, Northwest	Patreksfjördur	N65.53622, W23.78811	6
Iceland, Mideast	Eskifjördur	N65.07407, W14.03906	6
Iceland, Northwest	Leirufjördur	N66.22650, W22.58136	3

We conducted low-coverage whole genome sequencing of the samples. DNA was extracted using the DNeasy 96 Blood and Tissue Kit (Qiagen) following the manufacturer protocols. DNA quality was assessed on a 1% agarose gel, and concentration was measured using the Qubit HS dsDNA quantification kit (ThermoFisher). Samples were normalized to equimolar concentrations and then prepared using DNA Prep kits (Illumina). Individual libraries were pooled and had their size quantified on a 2100 Bioanalyzer (Agilent Technologies). Libraries were then sequenced on an Illumina NovaSeq6000 S4 at the Génome Québec Centre d'Expertise et de Services.

Bioinformatic Processing

Adapter content was trimmed from raw sequence reads with fastp (Chen et al., 2018) using default parameters. The trimmed reads were aligned to an *S. alpinus* reference genome (Crowley *et al*., pers com) using BwaMem2 (version 2.2.1; Li, 2013). Following alignment, duplicated reads were identified and removed using the MarkDuplicates function from the Genome Analysis Toolkit (GATK version 4.4.0.0; Van der Auwera & O'Connor, 2020), and then the RealignerTargetCreator and IndelRealigner functions (GATK v.3.7) were used to realign reads around insertions and deletions. We also used the SAMtools coverage function (version 1.22.1; Danecek et al., 2021) to determine the mean read depth and coverage for each individual on a per-chromosome basis. We used ANGSD (Analysis of Next Generation Sequencing Data, v0.941; Korneliussen et al., 2014) to calculate genotype likelihoods. We used the SAMtools method of calculating likelihoods (-gl 1), with minimum mapping and base quality score cutoffs of 20 (-minQ and -minMapQ 20), and a minor allele frequency cutoff of 0.05. We discarded reads that did not map uniquely (-uniqueOnly 1) or whose mates did not map (-only_proper_pairs 1), and limited genotype likelihood calculation for sites where at least 80% of individuals had data, and where

total depth across all samples was equal to two times the number of samples. We used these methods to generate genotype likelihoods for SNPs in: (a) only the Jan Mayen samples to assess potential within-population structure, and (b) with the Jan Mayen samples alongside samples from eight other North Atlantic locations (Table 1) to assess admixture among populations.

We used PCAngsd (v1.35; Meisner & Albrechtsen, 2018) to visualize (a) the general genomic landscape of the Jan Mayen population on its own, and (b) the genomic landscape alongside Arctic charr from the eight other North Atlantic locations. To maximize efficiency of computational resources, we down-sampled the genotype likelihood files to every tenth SNP for input into PCAngsd.

We also used ngsadmix (version 32; Skotte et al., 2013) to investigate genetic admixture amongst Arctic charr from the nine North Atlantic locations. Prior to running ngsadmix, we identified and excluded potentially paralogous loci and pruned loci for linkage disequilibrium, to avoid biasing admixture analyses. Briefly, we generated a list of likely "deviant" (i.e. paralogous) sites by running ngsParalog (v.3; Linderoth, 2018) on a larger dataset which included the nine North Atlantic populations described here, and filtered out these potentially-deviant SNPs from the ANGSD-generated Beagle files. We subsequently pruned loci for linkage disequilibrium using ngsLD (v1.2.0, Fox et al., 2019), calculating LD between SNPs in 200 kb windows (-max_kb_dist 200), and pruning with an r^2 threshold of 0.1 using the -prune_graph function. With ngsLD, we tested values of K from 1–10, by running ten replicates for each value of K and subsequently estimating the best value using the method described by Evanno et al. (2005), implementing in the CLUMPAK program (Kopelman et al., 2015).

Lastly, we calculated genome-wide F_{ST} between Jan Mayen, mideast Greenland, southwest Greenland, Iceland (combining samples across the four locations therein), Bear Island, and northern Norway (Table 1). We masked the reference genome for previously-identified paralogs and 150 bp on either side of them, using the bedtools maskfasta tool (Quinlan & Hall, 2010) as described in Dallaire et al. (2025). Next, we used ANGSD to calculate the sample allele frequency (SAF) for each location using the -doSAF function, polarizing using the reference genome to maintain consistent major/minor alleles across locations. We then used winSFS (v.0.7.0; Rasmussen et al., 2022) to generate the joint site frequency spectra (SFS) for each pair of locations. Lastly, we used the SAF files alongside the joint SFS files to calculate per-site F_{ST} between pairs of populations using the realSFS F_{ST} function, as well as the global weighted F_{ST} across the full genome for each comparison.

RESULTS

In total, 116 fish with a mean total length of 159 mm (SD = 106; range 104–700 mm) were captured, with the majority (93%) being ≤ 40 cm as a result of the required use of smaller (< 21 mm) mesh sizes. A bimodality in the length-frequency distribution of the catch was observed (Fig. 3) and replicated the bimodality in capture sizes reported by Skreslet (1973).

Of the n = 110 fish successfully aged, ages ranged from 2 to 19 years and were numerically dominated by the younger age classes (90% < 8 years). Further biological details of the sample are given in Table 2.

Table 2
Summary of biological characteristics and stable isotope values (mean±standard deviation) for Arctic charr captured in Lake Nordlaguna in 2019. Small Arctic charr ≤ 40 cm. Condition is given as Fulton's K.

Length (cm)	***n***	**Small Arctic charr**	***n***	**Large Arctic charr**
	109	**13.3 ± 1.6**	**7**	**56.6 ± 8.2**
Mass (g)	95	16.7 ± 6.8	7	1951.6 ± 906.1
Age (years)	104	4.7 ± 1.1	6	16.5 ± 2.5
Condition (K)	95	0.7 ± 0.1	7	1.0 ± 0.1
$\delta^{13}C$	105	-22.6 ± 1.7	7	-24.3 ± 1.5
$\delta^{15}N$	105	9.7 ± 0.8	7	13.4 ± 0.4
C:N ratio	105	3.7 ± 0.3	7	4.3 ± 1.0

Estimated weight-length relationships for male and female small Arctic charr did not differ significantly (common slope t-test=-0.312, $P = 0.756$; common intercept t-test = 1.904, $P = 0.061$). Thus, the data for the sexes were pooled to estimate a common weight-length relationship (ln mass(g) = -4.391 + 2.776 * ln length (cm), r2 = 0.925, regression $P < 0.001$) that indicated allometric growth (t-test = 2.744, $P = 0.007$) in small Jan Mayen Arctic charr. Condition differed significantly by size (ANOVA $F_{1,100}=107.615$, $P < 0.001$), with small Arctic charr being in poorer condition than larger Arctic charr. Among small Arctic charr condition also differed significantly by sex (ANOVA $F_{1,73}=7.688$, $P = 0.007$), with males being in better condition (mean ± S.D: 0.72 ± 0.07) than females (0.68 ± 0.07). A similar result was obtained using the stable isotope C:N ratio as a proxy for condition (higher C:N = better condition) when testing differences in condition among size groups (ANOVA $F_{1,110}=15.704$, $P < 0.001$) or within the small fish group by sex (ANOVA $F_{1,73}=10.130$, $P = 0.002$). When compared to the 1960s, the 2019 fish were generally in better condition, with the proportion of those having a Fulton's K < 0.5 being significantly lower than those having similar values in the 1960s (Fisher's exact two-tailed $P = 0.001$).

Of 89 individuals for which sex and maturity could be determined, 45% were males and 55% females. Most fish were sexually mature (males, 83%, females 94%), with no significant difference in the proportion of immature and mature individuals observed between the sexes (Fisher's exact two-tailed $P = 0.107$). Mean age-at-maturity in the 2019 samples was estimated at 3.2 years (males 2.7, females 3.8). Across the two sampling years in the 1960s, a similar sex ratio (males 45%, females 55%) was observed. In contrast to the 2019 data, the percentage of sexually mature individuals differed significantly (Fisher's exact two-tailed $P < 0.001$) among the sexes (males 19%, females 95%).

Comparisons of mean size-at-age were completed for fish in the age-3 and age-4 categories where sufficient numbers of fish (n ≥ 4) existed. At age-3, fish captured in 2019 (mean±standard deviation:11.9 ± 0.9) were significantly larger (ANOVA $F_{1,41}$=50.947, $P < 0.001$) than those captured in the 1960s (10.0 ± 0.4). Similarly, age-4 fish captured in 2019 (13.6 ± 0.8) were significantly larger (ANOVA $F_{1,41}$=45.584, $P < 0.001$) than those captured in the 1960s (10.8 ± 0.5). Comparative plots of the length-at-age data indicate that by age-5, the apparent growth advantage of the 2019 samples has disappeared (Fig. 4). The Chapman-Robson estimated mortality rate for fish ≤ 40 cm was 0.434 (range: 0.369–0.498). The z-based test of the validity of the geometric model underlying the Chapman-Robson estimate substantiated its validity ($p > 0.05$).

Prey Resources and Stomach Contents

No zooplankton were collected in the zooplankton tows. A single benthic species of Cladocera (*Macrothrix hirsuticornis*) was found in the benthic kick samples in addition to Nematoda, Chironomidae, Oligochaeta and Ostracoda.

From the sampled fish, the stomach contents of n = 112 stomachs were analysed, of which n = 20 were empty. From the remaining 82 fish, all items in the stomach contents of 32 individuals could be identified. Stomach content data indicated feeding mainly on small crustaceans (74%), with Chironomidae (1%), Amphipoda (1%), fish (1%), terrestrial insects (< 1%) and other invertebrates (< 1%) constituting minor portions of the diet. The remaining 21% of the stomach contents could not be identified. Size-related differences were evident, with smaller fish feeding mainly on small crustaceans and the larger fish (> 40 cm; n = 7) feeding largely on fish. Comparison with data collected in 1965 indicated a significant shift in diet, with neither Morisita's measure nor Horn's index indicating significant dietary overlap between the periods (Morisita's measure = 0.165, Horn's Index = 0.378). The most notable shift in diet was the large increase in the consumption of Cladocera in 2019 versus 1965 (Fig. 5). Dietary data were also used to compute Levin's standardized measure of niche breadth and indicated a decline in breadth from the 1965 sampling (B_A=0.492) to the 2019 sampling (B_A=0.238) reflective of the reduced diversity of prey items found in the 2019 stomachs (see Fig. 5).

Stable Isotope Analysis

Stable isotope ($\delta^{13}C$, $\delta^{15}N$) analysis indicated clear trophic separation on the basis of size (Fig. 6), with the larger fish occupying a trophic niche consistent with piscivory, as similarly observed in the stomach contents from the same size spectra. Layman metrics indicated that fish ≤ 40 cm displayed both a greater degree of niche diversification ($\delta^{13}C$ range 9.21 *vs* 4.64) and trophic diversity ($\delta^{15}N$ range 4.97 *vs* 0.93) than larger fish. Smaller fish also displayed a greater average degree of trophic diversity within their feeding niche (mean distance to centroid 1.158 *vs* 0.896) but were less divergent among individuals in terms of their individual niches (mean nearest neighbour 0.247 *vs* 0.768) and more evenly distributed across their trophic niches (Standard deviation of nearest neighbour distance 0.264 *vs* 0.538).

For smaller fish there was a significant relationship between $\delta^{15}N$ and $\delta^{13}C$ ($\delta^{15}N = 3.088$; $\delta^{13}C = -0.29$, $r^2 = 0.444$). When corrected for baseline differences using zooplankton and Arctic charr data collected from the literature, data for Jan Mayen Arctic charr fall mid-range in the reported range of $\delta^{13}C$ values (Fig. 7). Jan Mayen small Arctic charr are similarly placed in the mid-range of reported $\delta^{15}N$ values, whereas Jan Mayen large Arctic charr exhibit the highest observed $\delta^{15}N$ values.

Genetic analyses

We generated genotype likelihoods for 4852994 single nucleotide polymorphisms (SNPs) for the 32 Jan Mayen samples selected for genomic analyses. The mean read depth for these samples was 2.81X across all chromosomes, with a mean base quality score of 35.3, and a mean alignment mapping score of 39.3. Visualization of the overall genomic variation using PCAngsd for the Jan Mayen samples on their own (down-sampled to 485299 SNPs) showed no obvious clustering of samples by inferred trophic group (i.e. piscivorous *vs*. omnivorous), nor any other obvious grouping of samples in terms of their scores on the first two principal components of the PCA (Fig. 8A), which explained ~ 5.9% and ~ 3.5% of the variation in the SNP data, respectively.

Across the Jan Mayen samples and those from the five other geographic groupings across the North Atlantic, we generated genotype likelihoods for 9918835 SNPs. A PCA done on a subset of these (991870 SNPs) revealed strong clustering of samples by location (Fig. 8B), with Jan Mayen the most separated from the other populations on PC1 (which explained ~ 9.6% of the variation in the SNP data), and closest to Bear Island on the PC2 axis (explaining ~ 6.9% of the variation). The best-supported number of clusters/groups of samples (K value) from the ngsadmix results was four (Fig. 8C, bottom panel), with Jan Mayen, northern Norway, Bear Island, and western Greenland as distinct genetic groups, and eastern Greenland and Iceland comprised of a mixture of these four groups. The second-best supported value of K was two (Fig. 8C, top panel), illustrating the same main split between Jan Mayen and the other North Atlantic populations as seen in the PCA biplot in Fig. 8B. For both of these values of K, Jan Mayen shared some admixture with the Iceland and Greenland populations, but none/negligible amounts with the northern Norway and Bear Island populations.

Lastly, population genetic differentiation as measured by global weighted F_{ST} was greatest between Jan Mayen and western Greenland (0.258), followed by Jan Mayen and northern Norway (0.241), Jan Mayen and eastern Greenland (0.219), and Jan Mayen and Iceland (0.209). These four pairwise comparisons with Jan Mayen had greater global weighted F_{ST} values than those between the other North Atlantic populations. The lowest value of F_{ST} for a Jan Mayen comparison was with Bear Island (0.137), which was nonetheless greater than pairwise comparisons for all other North Atlantic populations (including other Bear Island comparisons) except those involving western Greenland. The lowest global F_{ST} values among all of the compared North Atlantic populations were for eastern Greenland *vs.* Bear Island (0.104), eastern Greenland *vs.* Iceland (0.105), and Iceland *vs.* Bear Island (0.107).

DISCUSSION

Temperature has been shown to have a strong influence on habitat selection, growth rate, maturation and survival of many fish species, including Arctic charr (Lyytikäinen et al., 1997; Kristensen et al., 2006; Elliott & Elliott, 2010; Killen, 2014). As the mean air summer temperature (June – August) at Jan Mayen has increased over the almost six decades between samplings, it can be expected that Arctic charr in Lake Nordlaguna will evidence differences in both their biological and dietary characteristics. Here, we noted that small-sized Arctic charr were larger in 2019 than in the 1960s, and that there has been a shift to earlier maturation and improved body condition in terms of a significantly lower percentage of poorly conditioned individuals. Shifts in diet were evident in the dominance of Cladocera and a decline in Oligochaeta in examined stomach contents of recently sampled Arctic charr as compared to those sampled in the 1960s. Dietary overlap indices further showed no significant overlap between periods. The transition of a limited number of individuals toward piscivory was evident in the samples from both periods, with the larger fish capture in 2019 having a significantly narrower trophic niche than smaller conspecifics that used a broad range of resources obtained from both the pelagic and littoral zones. Thus, while climate-driven changes are evident when comparing samples obtained some 54 years apart, the changes are subtle and suggestive of the capacity of populations to adapt in the near term. Finally, as compared to other northern populations, Jan Mayen small Arctic charr appear to be less reliant on pelagic energy sources than Bear Island Arctic charr populations, possibly as a result of the limited abundance of zooplankton available for consumption as indicated by zooplankton sampling in 2019. Genetically, the Jan Mayen population displays no within-population separation related to trophic groups, and is strongly differentiated from other North Atlantic populations despite some genetic admixture with populations from eastern Greenland and Iceland.

Age of maturation

In the 2019 sampling, the vast majority (73%) of small Arctic charr (≤ 40 cm) were sexually mature (mean age 3.2 years), at ages younger than those reported by Skreslet (1973). Based on the 1963 and 1965 samples, Skreslet noted that most fish in the 136–272 mm size range began to mature at ages 3–7 years, that no fish in the smallest size group (≤ 114 mm) were mature, and that only few individuals from the 1955–57 cohorts initiated maturation before age 5. In contrast, in the 2019 sampling, of those that could be reliably aged and assessed for sexual maturity, 12.5% of fish < 11.4 cm were mature and 76% of all fish five years or younger were mature. The reduced age and size at maturation observed in Jan Mayen Arctic charr as a result of warming accords with general predictions that warmer climates will lead to decreased adult body size and younger age-at-maturity in salmonid fishes (Jonsson, 2023). It supports the more general temperature–size rule (TSR) for ectotherms where individuals maintained at lower temperatures grow more slowly and mature at larger sizes (later ages) than conspecifics living at higher temperatures (Atkinson, 1994). For example, the long-term warming of Canadian Shield lakes has resulted in similar changes in lake trout (*S. namaycush*) age-at-maturity, with a < 2^{o}C change in mean air temperature yielding a 5-year decline in age-at-maturity (Guzzo et al., 2025). The results as noted here for

Jan Mayen, therefore, accord well with both theory and observation and are not an unexpected outcome of warming climates.

Individual growth

The TSR also notes that individuals living in warmer waters when they are young will grow more quickly (Atkinson, 1994), which was reflected in the noted increases in size-at-age in the 2019 sampling from the warmer waters. Temperature driven differences in the patterns of maturation and juvenile growth observed in Jan Mayen, therefore, correspond well with TSR meta-analyses which have shown observed patterns of juvenile growth rate and age-at-maturity in freshwater fishes typically align with TSR predictions (Brooks et al., 2025). Similarly, a detailed analysis of 26 Arctic charr populations along the environmental gradient inherent in 32.5^{o} of latitude demonstrated significant variation in life-history traits with temperature, notably earlier maturation and faster juvenile growth in warmer environments (Smith et al., 2026). The effects of temperature on growth observed here were subtle, with effects detectable only at younger ages where sample sizes allowed, but absent after age-5 when a large proportion of the dominant small (< 40cm) size-classes would have reached sexual maturity. Long-term studies elsewhere have indicated more persistent effects of temperature on growth. For instance, a sclerochronological analysis of Arctic charr sagittal otoliths from Lake Takvatnet, Norway, showed that long-term warming (1983–2016) was positively correlated with the growth of juveniles aged1-4 years, suggesting climate change impacts (Kotowych et al., 2023). The limitation of growth effects to younger age classes may reflect changes in population size structure. For brown trout (*Salmo trutta*), downscaled climate impact scenarios suggest that growth rates may increase in young fish but decline with age, resulting in a larger proportion of smaller individuals as population growth rates change (Bærum et al., 2021). Warming may also increase lake productivity through increased nutrient loading (e.g., Huser et al., 2022). In addition, temperature can affect growth trajectories independently of its direct effects on metabolism, particularly in fish that are not feeding at maximum ration (e.g., Elliott, 1975). This may be relevant in oligotrophic Arctic lakes, where food availability can limit growth. As growth is an integrative measure combining both the positive and negative influences of a given environment, changes in growth observed coincident with warming climates may be, in whole or in part, attributable to changes in productivity rather than temperature. Nevertheless, whether changes in growth are driven by direct temperature effects, the indirect effects of nutrient increases, or a combination of both, climate warming appears to have had a clear effect on Jan Mayen Arctic charr.

Diet and trophic niches

Despite differences in how the feeding habits are presented, trophic niches of Arctic charr sampled in 1934 (Bird, 1935), 1963-65 (Skreslet, 1973) and in the current study in 2019 seem to be similar. According to the analyses of stable isotopes and Layman metrics, smaller Arctic charr sampled in 2019 used a wider variety of food resources and were more omnivorous than the larger fish, which could be expected if the larger fish were largely piscivorous specialists (i.e. cannibals). That means that the piscivorous individuals occupied a smaller trophic niche, as seen in the $\delta^{13}C$, $\delta^{15}N$ biplot. Further, it was

found that the larger fish were more widely disbersed in their niche space than smaller fish. In the material from 1963-65, Skreslet (1973) also found two size groups of adults, mature small charr and large cannibals. Most of the mature smaller charr were non-selective deposit feeders, while small younger and immature charr feeding on small benthic species. Similarly, the dominant stomach contents noted in the 2019 sample were benthic species of Cladocera. In comparison, Bird's 1934 sampling of ten Jan Mayen Arctic charr caught in a gillnet (Bird, 1935) noted that smaller fish (seven averaging 15 cm and 85 g) fed primarily on the larvae and pupae of the chironomid *Cricotopus basalis* and moss, while the larger fish (three ranging from 0.9–1.14 kg) were cannibalistic.

Shifts in diet were evident in the dominance of Cladocera and decline in Oligochaeta in examined stomach contents of recently sampled Arctic charr as compared to those sampled in the 1960s. Dietary overlap indices showed no significant overlap between periods. The transition of a limited number of individuals toward piscivory was evident in the samples of both periods, with the larger fish captured in 2019 having a significantly narrower trophic niche than smaller conspecifics that used a broad range of resources obtained from both the pelagic and littoral zones.

The optimum temperature for Arctic charr growth in body mass and length is near 14°C (Beuvard et al., 2022; and references here in), however, the definition of optimum temperature for growth is only valid under the assumption that there is no food limitation (Jobling, 1981). An increase in ambient temperature leads to an increase in metabolic rate, which in turn leads to increased energy demand. If the increased metabolic demand is not matched by a corresponding increase in food supply, the net outcome is likely to be a reduction in fitness and the growth rate of the fish (Elliott, 1975; Russell et al., 1996). In Nordlaguna, the current study did not reveal any qualitative changes in food supply since the surveys in 1963 and 1965 (Skreslet & Foged, 1970). There are still no zooplankton and the benthic macrofauna is very poor, mainly consisting of the benthic Cladocera *Macrothrix hirsuticornis.* It is therefore suggested that the increased temperatures over the last six decades at Jan Mayen have shifted the Arctic charr life-history strategy toward maturation at younger ages due to the limited food supply. For example, Kristensen et al. (2006) reported that climatic changes over a two decade period similarly affected short term and inter-annual growth and influenced long term shifts in age-specific growth patterns in a lacustrine population of Greenland Arctic charr.

Ecological and genomic divergence

The genomic analyses provided important context for understanding the evolutionary history of the landlocked Arctic charr in Lake Nordlaguna. Despite the presence of distinct trophic morphs in the lake, we found no evidence of genetic differentiation between the larger piscivores and the smaller omnivores, suggesting that the observed ecological divergence results from phenotypic plasticity or is a very recent niche specialization that has not been reinforced by reproductive isolation. The result is consistent with predictions of the phenotypic plasticity model whereby environmentally regulated alternative and discrete traits emerge and are subsequently promoted by genetic differences (Skúlason et al., 1999; Adams & Huntingford, 2004). In the case of Nordlaguna, within lake selection pressures have only had a

limited time to operate since the AD 1732 impoundment of the lake (Larsen et al., 2021). Nevertheless, differences in trophic ecology can emerge quickly as translocation studies have noted in Maine (e.g., Michaud et al., 2008).

When placed in a broader North Atlantic context, the Jan Mayen population appears genetically distinct from all other sampled regions. The admixture analyses consistently positioned Jan Mayen as the most divergent group, with negligible affinities to northern Norway or Bear Island and only limited admixture with Iceland and eastern Greenland. Pairwise F_{ST} comparisons with Greenland, Iceland, and northern Norway yielded similar results. On the other hand, though the admixture analyses showed Jan Mayen to have a lower admixture with Bear Island than with east Greenland or Iceland, the PCA results showed Jan Mayen clustering closest to Bear Island on the second axis, and the Jan Mayen/Bear Island F_{ST} value was the lowest of all the Jan Mayen comparisons. Nonetheless, the F_{ST} between Jan Mayen and Bear Island was higher than for the other North Atlantic population comparisons, including Bear Island compared with eastern Greenland, Iceland, and northern Norway. Taking the results of these analyses together, we might speculate that both the Jan Mayen and Bear Island populations may have originated from common source(s) in Iceland or eastern Greenland, and that these populations have since diverged both from each other and their source(s). The hypothesis, however, requires further investigation with additional phylogenetic or demographic reconstruction analyses to provide a clearer picture of the genetic history of the Jan Mayen and Bear Island populations. In any case, these results do indicate that the Jan Mayen charr represent a long-isolated and evolutionarily unique population, likely shaped by strong genetic drift due to the island's geographic isolation and the absence of contemporary gene flow. The combination of ecological divergence, without evidence of genetic structuring within the lake, paired with the strong genetic distinctiveness at the regional scale, highlights Jan Mayen as an important ecosystem for understanding the mechanisms and effects of rapid ecological differentiation and long-term population isolation in Arctic charr.

Conclusions

Across six decades of warming, the Arctic charr of Lake Nordlaguna have undergone measurable yet nuanced ecological change. Earlier maturation, faster juvenile growth, and altered dietary composition indicate a population responding rapidly to rising temperatures and persistent food limitation. Despite clear trophic divergence between omnivorous and piscivorous individuals, genomic analyses revealed only a single population maintained by phenotypic plasticity rather than reproductive isolation. At the broader North Atlantic scale, however, the Jan Mayen Arctic charr stand out as an evolutionarily unique and long-isolated population with high genetic differentiation. Together, these findings highlight Nordlaguna as a rare natural laboratory where rapid ecological adjustment coexists with evolutionary isolation and which may offer valuable insights into how Arctic freshwater fishes might navigate accelerating climate change.

Declarations

Funding declaration

JGD, ADS and GK were funded by the NTNU University Museum. Stable isotope analyses were supported by an NSERC Discovery Grant awarded to MP. SC was funded by Dalhousie University. EL and AL were supported by the Geological Survey of Norway.

Author Contribution

Author contributions J.G.D, E.L and A.L. conceived the project; JGD, S.C. and M.P. wrote the manuscript; J.G.D, A.D.S and E.L. conducted field activities at Jan Mayen; J.G.D., A.D.S, S.C, M.T., G.K. and M.P. performed laboratory work and data analyses. All authors effectively contributed to read, edit and approve the final version of the manuscript.

Acknowledgement

The County Governor of Nordland, CYFOR CTO NORD and the staff at the Jan Mayen station gave permission and logistical support. Lars Rønning at the NTNU University Museum is thanked for aging the Arctic charr and analysing stomach contents and M. Daverdin at the NTNU University Museum for drawing the map.

Data Availability

The data are generated in the project are available upon reasonable request to the corresponding author.

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Figures

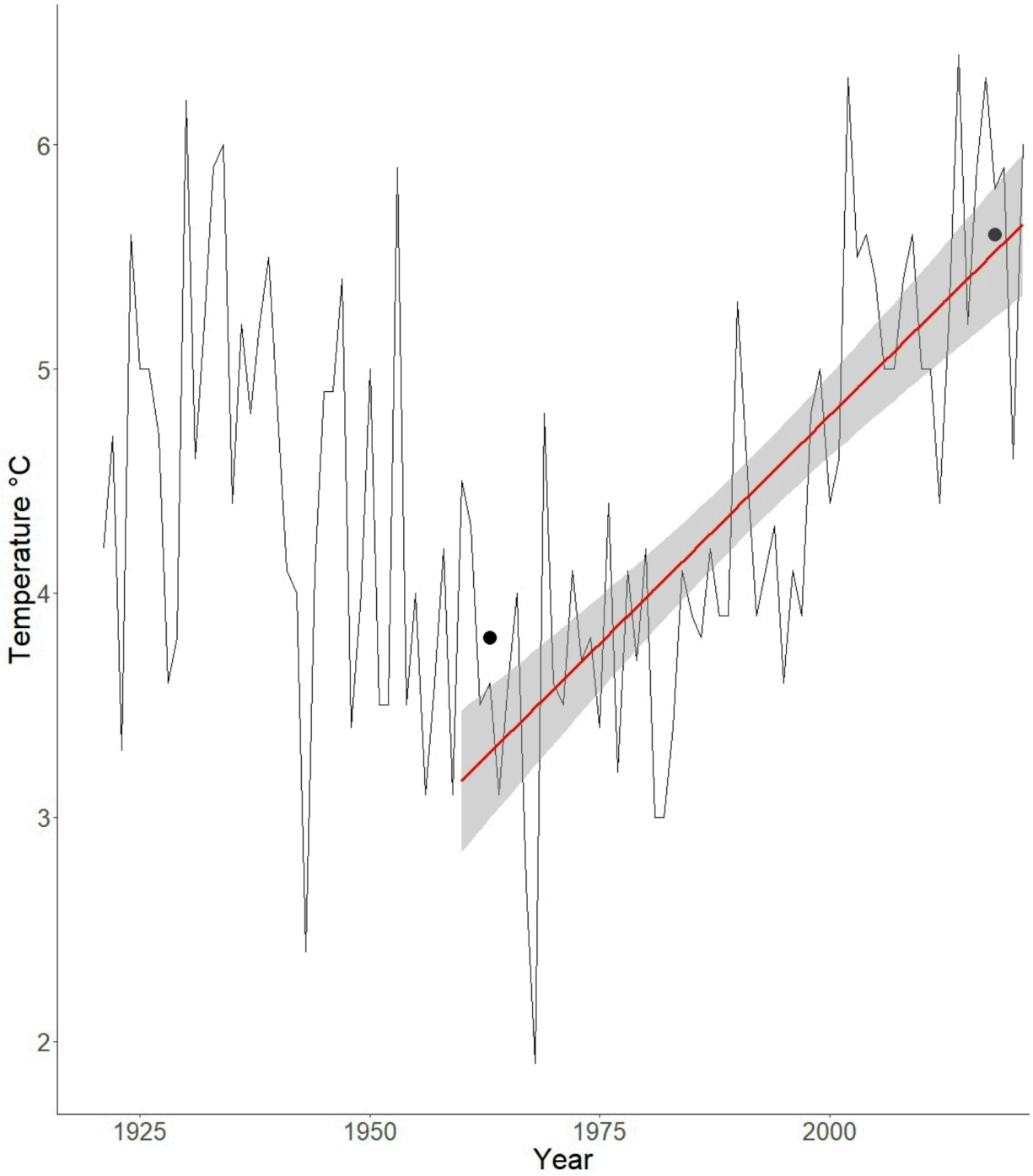


Figure 1

Annual observed 2-m air mean temperatures for the open-water summer season (June-August) from 1960 – 2020 on Jan Mayen. Means for the 1960-65 and 2015-20 periods are plotted as filled circles. The red line plots the linear trend in increasing open-water temperatures for the period 1960-2020 and the grey shadow gives the 95% confidence interval. (CC BY 4.0; Norwegian Meteorological Institute (MET))

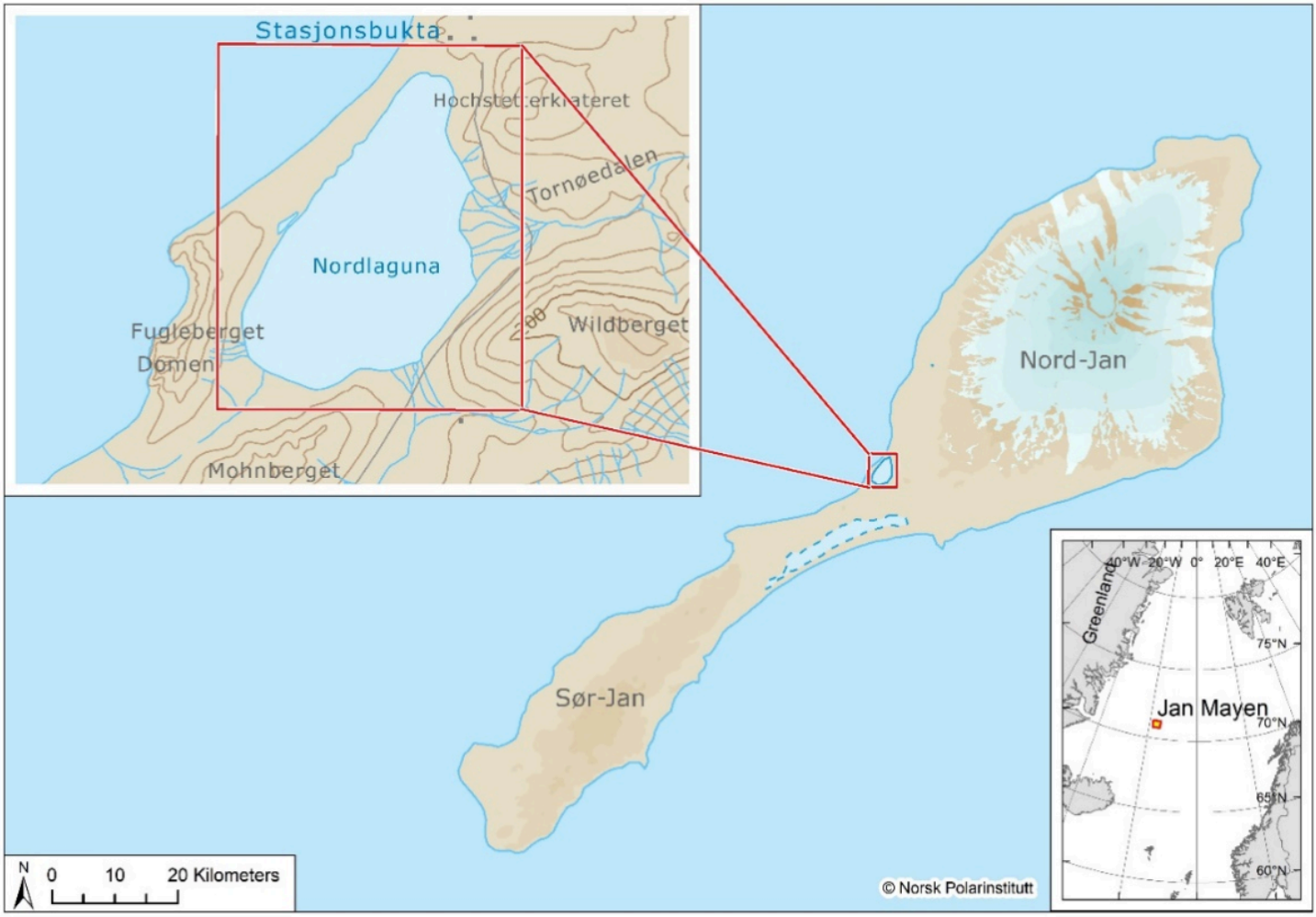


Figure 2

Map showing Nordlaguna in the context of Jan Mayen and Jan Mayen in the context of the North Atlantic Ocean. The historical outlet from the lake followed the river draining SW between Fugleberget Domen and Mohnberget on the upper left magnified inset of the lake.

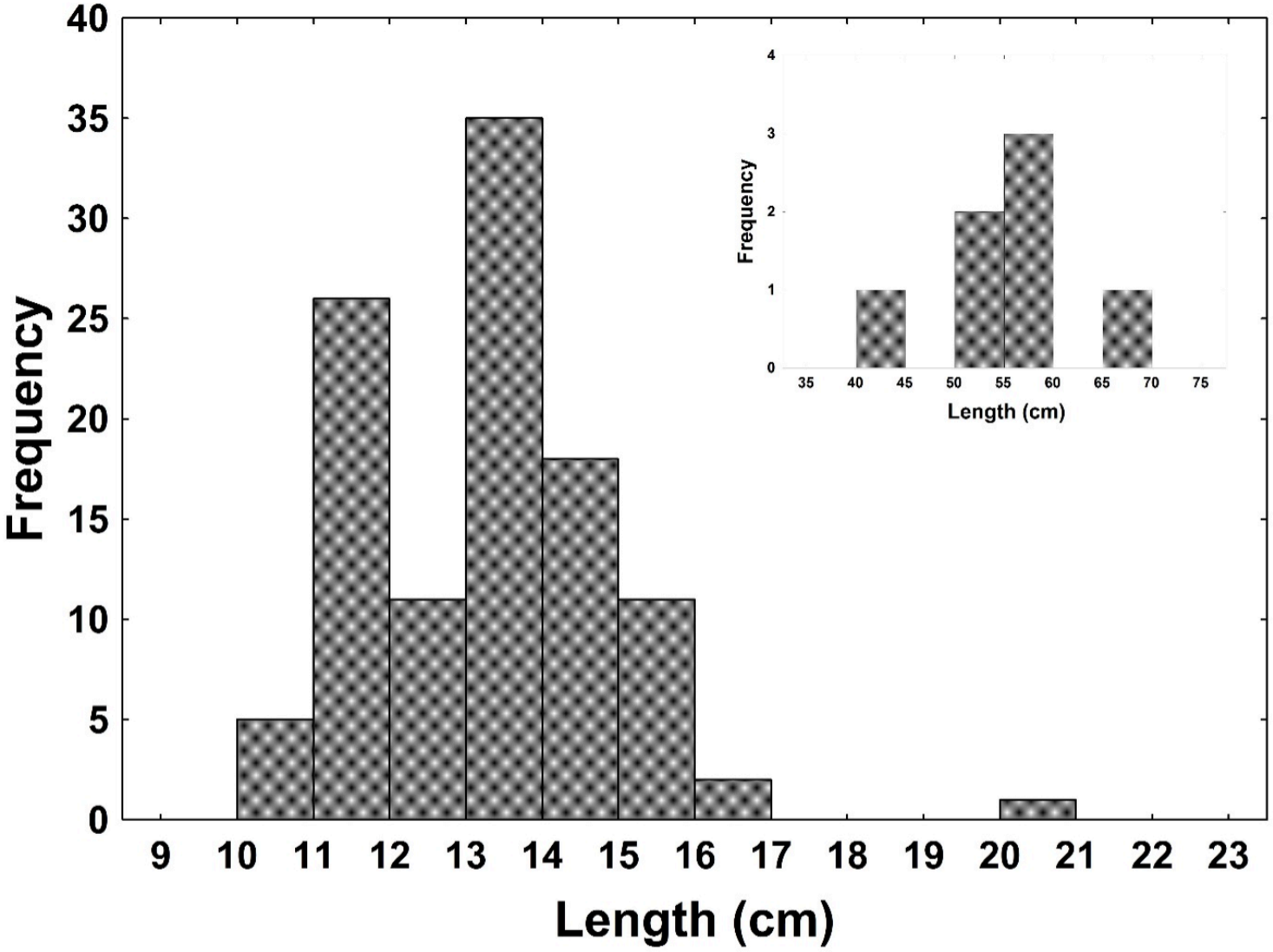


Figure 3

Length-frequencies of the of Arctic charr sampled from Nordlaguna in 2019. The main panel gives the length-frequency distribution of the small Arctic charr (≤ 40 cm). Inset gives the length-frequency distribution of the larger Arctic charr.

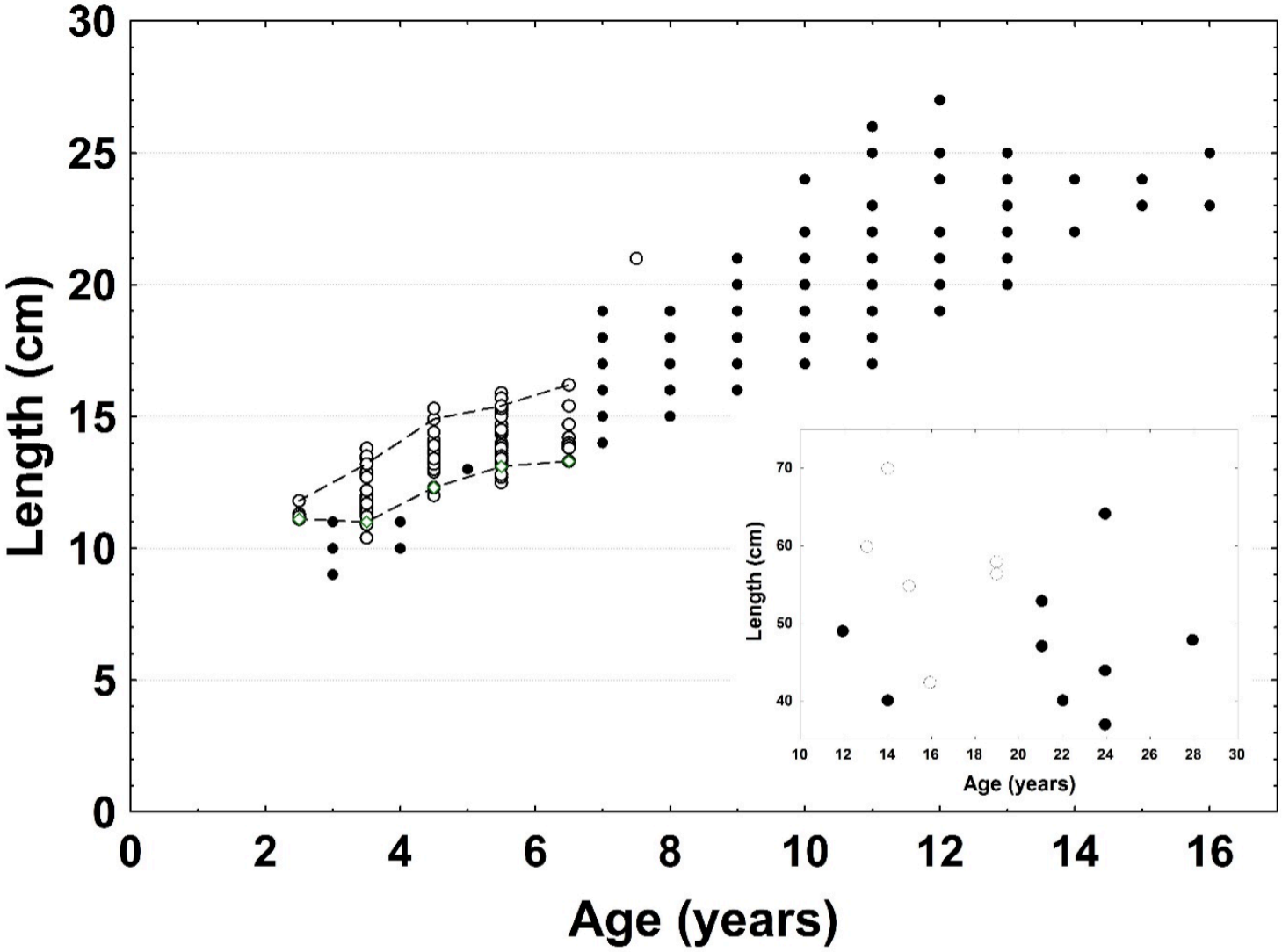


Figure 4

Length-at-age for Arctic charr from Lake Nordlaguna, Jan Mayen Island, captured in August 2019 (open circles) and in the 1960s (filled circles). Fish from 2019 were measured to the nearest mm while fish from the 1960s were reported to the nearest cm. Dashed lines plot the 10th and 90th percentiles for the 2019 data. Data from 2019 have been jittered on the X-axis to improve plot clarity. The inset plots the small number of large Arctic charr captured in each sampling period where Skreslet (1973) define large as any individual > 37cm.

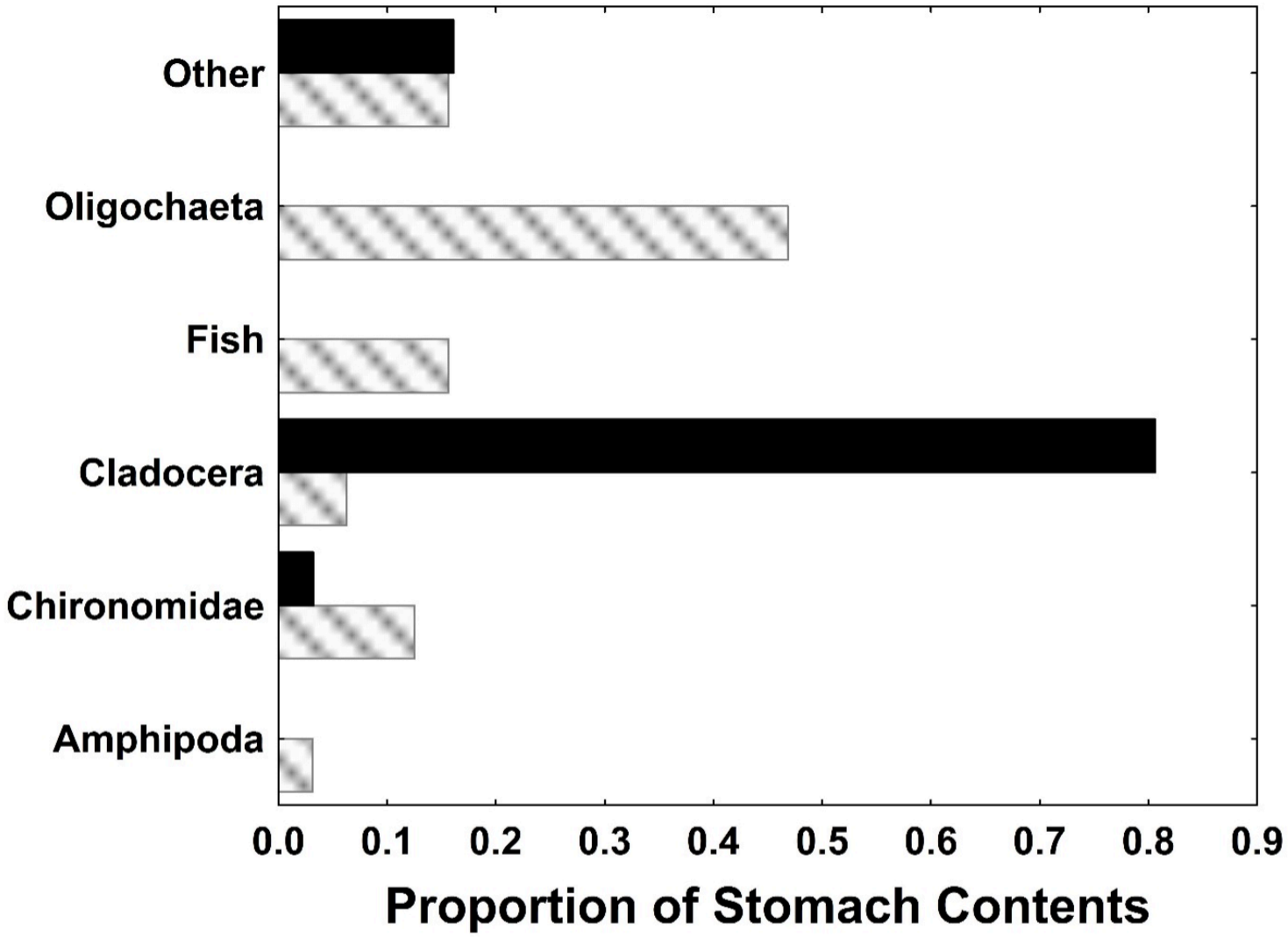


Figure 5

Proportional importance of dietary items found in the stomachs of small Arctic charr (≤ 40 cm) sampled in 1965 (gray bars) and 2019 (black bars) based on the analyses of stomachs containing prey items.

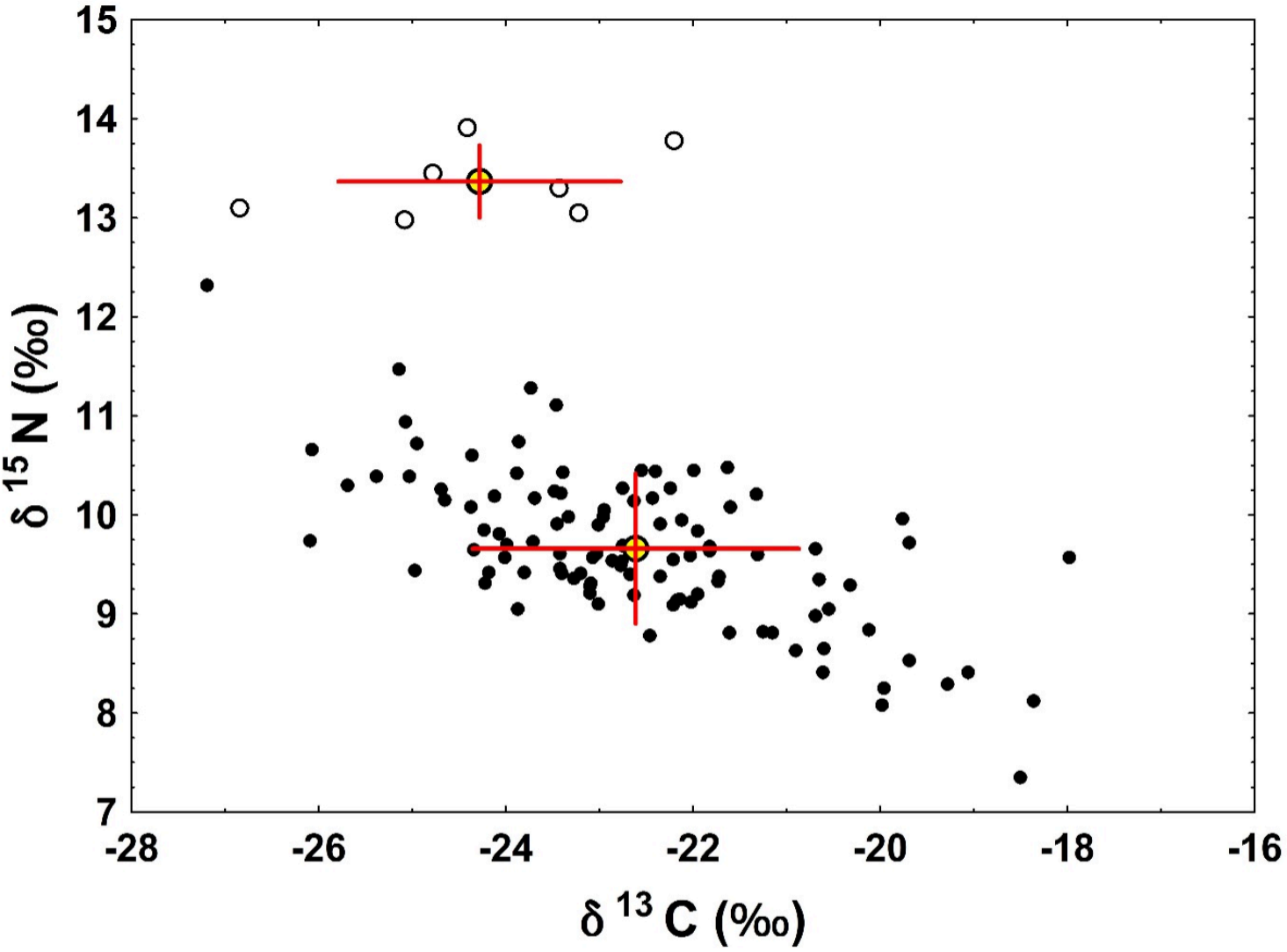


Figure 6

Stable isotopes and stable isotope bi-plot for Arctic charr *S. alpinus* from Lake Nordlaguna, Jan Mayen. Open circles: Putative piscivorous Arctic charr > 40cm total length. Black dots: Putative benthic feeding Arctic charr ≤ 40cm total length. Red horizontal and vertical lines plot mean±standard deviation of the group data, with group mean given as the large black and yellow dot.

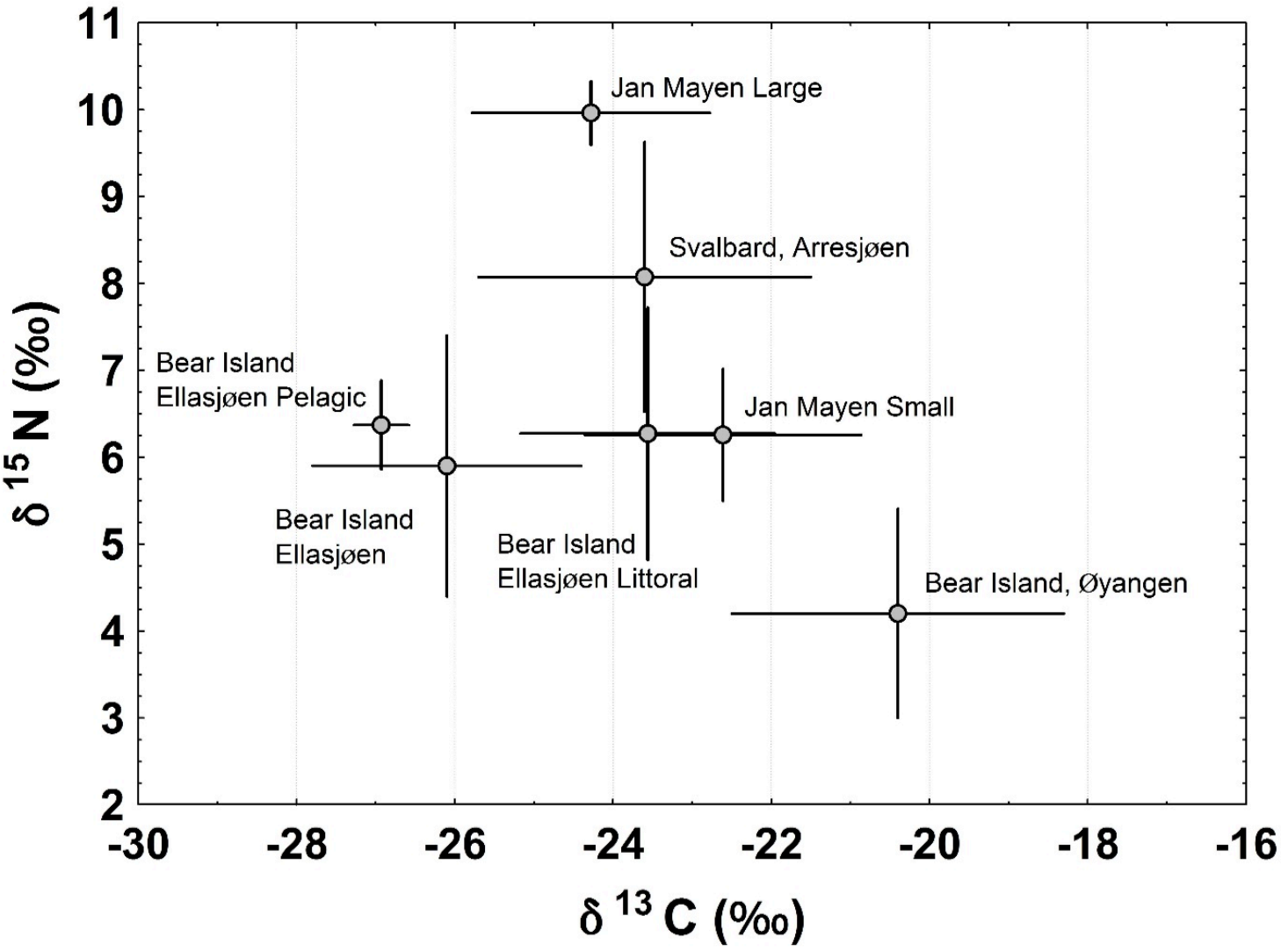


Figure 7

Stable isotope data ($\delta^{13}C$, $\delta^{15}N$) for Arctic charr from Lake Nordlaguna (Jan Mayen), Lake Arresjøen, Svalbard (Rognerud *et al.*, 2002), Lake Øyangen, Bear Island (Evenset *et al.*, 2004) and Lake Ellasjøen, Bear Island, (Evenset *et al.*, 2004; Hawley *et al.*, 2016). Values are plotted as mean±one standard deviation.

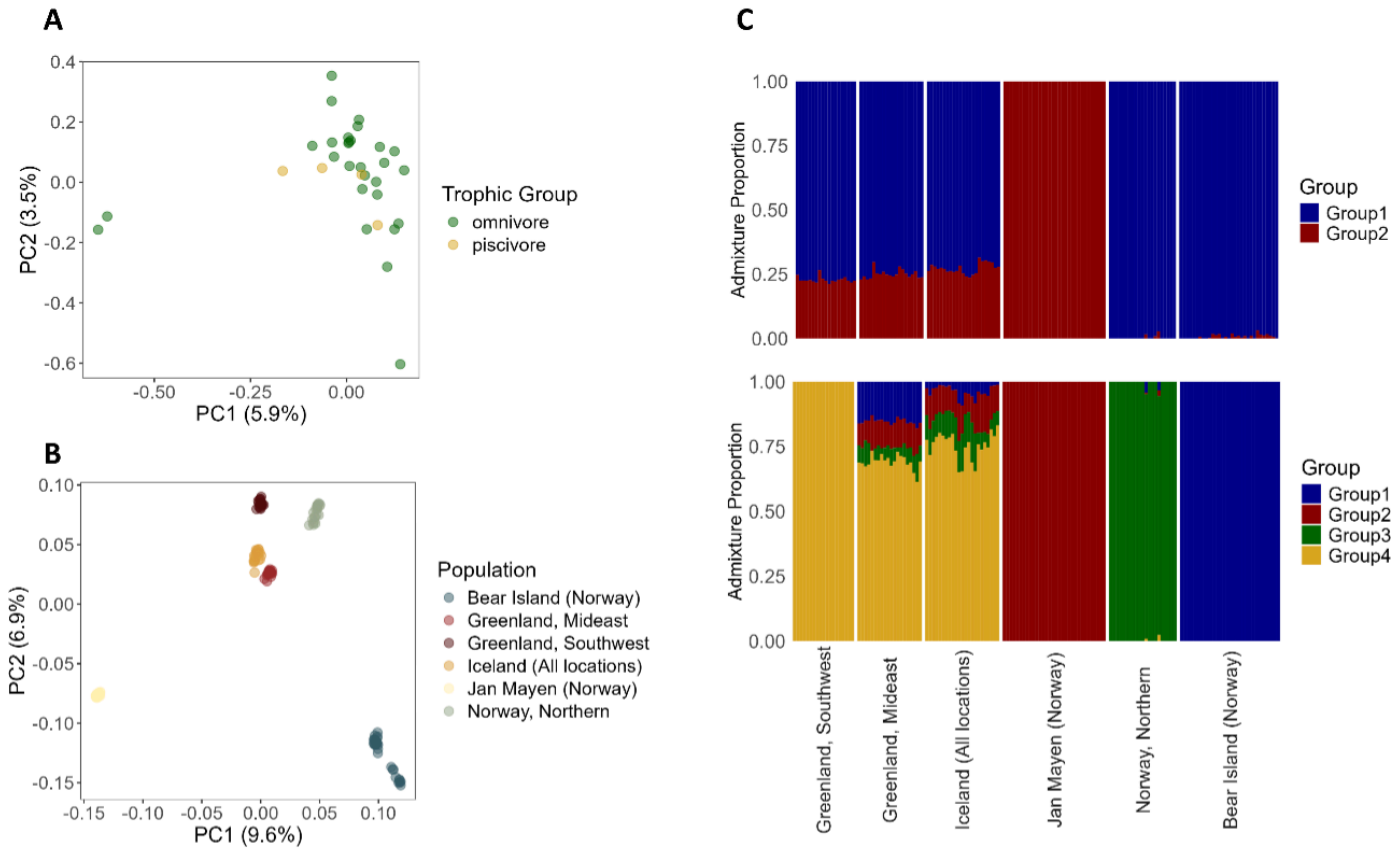


Figure 8

A) Biplot of first two principal components from a PCA generated using PCAngsd on 32 Arctic charr samples from Jan Mayen (485299 SNPs), with samples trophically grouped using stable isotopes as piscivorous *vs* omnivorous; B) Biplot of first two principal components from PCAngsd on Arctic charr Jan Mayen samples as well as Arctic charr samples from five other locations in the North Atlantic (991870 SNPs); C) Admixture proportions for individuals from the six locations in panel B, as generated by NGSadmix, using K=2 groups (top) and K=4 groups (bottom).