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Marine trophic niche use and life history diversity among Arctic charr *Salvelinus alpinus* in southwestern Greenland

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Abstract

Life history strategies and potential marine niche use of Arctic charr *Salvelinus alpinus* (n = 237, 84–652 mm, total body length, L_T) were determined during the ice-free season (2012) at three different watercourses in south-western Greenland. All Arctic charr were collected from freshwater habitats. Based on stable isotopes of δ^{34}S, the Arctic charr were categorized as either marine- or freshwater-dependent feeders. The use of time-integrated trophic tracers (stable isotopes of δ^{13}C, δ^{15}N, δ^{34}S) suggested that several trophic groups of Arctic charr operate alongside within each fjord system. The groups suggested were one group that specialized in the marine habitat, in addition to two freshwater resident morphs (small-sized resident and/or large-growing cannibalistic individuals). Stomach contents consisted entirely of freshwater and terrestrial prey (*i.e.*, insects), indicating that marine-dependent feeders also fed in freshwater habitats after return from their marine migration. Growth and maturity patterns further supported variable life history strategies within each watercourse. The life history strategy patterns and marine trophic niche use were consistent across the watercourses along several hundred kilometres of coastline. This study represents the first ecological baseline for partially anadromous populations of Greenland Arctic charr.

KEYWORDS

diet similarity, feeding ecology, life history complex, marine migration, stable isotope analyses

1 | INTRODUCTION

Arctic research on Arctic charr (*Salvelinus alpinus* L.) has traditionally covered the major geographical areas of northern Europe, Iceland, northern Canada and the Pacific basin drainages of the Asian and North American coasts (Knudsen *et al*., 2016), with research in Greenland having been typically under-represented. Studies of land-locked resident Arctic charr stocks have pointed to bimodal size distributions differing in feeding habits and vital rates such as growth and age of maturity (*e.g*., Jeppesen *et al*., 2001; Kristensen *et al*.,

2006; Riget *et al*., 2000b; Sparholt, 1985), highlighting the importance of Arctic charr for top-down control of lake invertebrate communities (*e.g*., Jeppesen *et al*., 2001; Kristensen *et al*., 2006; Riget *et al*., 2000b; Sparholt, 1985) and documented mercury levels in anadromous stocks (*e.g*., Riget *et al*., 2000a). Initial suggestions of links between Greenland Arctic charr population structure and lake size (Riget *et al*., 2000b) have recently been confirmed with studies in south-western Greenland that demonstrated clear relationships between within-population diversity and lake size using lake size as a proxy for within-lake habitat diversity (Doenz *et al*., 2019). Given

the sensitivity of Arctic aquatic ecosystems to ongoing climate change (O'Neill et al., 2017), observed changes in climate have also been associated with changing patterns of age-specific growth in Greenland Arctic charr likely to be influenced by local factors, including lake morphometry and trophic behaviour (e.g., Jeppesen et al., 2001; Kristensen et al., 2006; Riget et al., 2000b; Sparholt, 1985).

Complicating any general understanding of Arctic charr within Greenland is the fact that Arctic charr is a polyphenic species that may contain both anadromous and several sympatric resident populations within a single watercourse (e.g., Doenz et al., 2019; Klemetsen et al., 2003). Life history traits that are highly variable within populations of Arctic charr include growth and maturation patterns, which are often strongly coupled with trophic behaviour (Power et al., 2008), ecological opportunity (Doenz et al., 2019) or migratory patterns (Jonsson & Jonsson, 1993). For example, variations in resource availability have the potential to accelerate individual development and change the relative proportions of migratory individuals within populations (Nordeng, 1983). Thus, the degree of anadromy displayed by Arctic charr varies across populations (e.g., Dempson, 1984; Doucett et al., 1999b; Makhrov & Bolotov, 2006; Santaquiteria et al., 2016; Wilson et al., 1996), but is common in the midrange of their geographic distribution where access to productive marine coastal areas is relatively easy (Power et al., 2008).

Where partially anadromous stocks occur, they may display variable individual utilization of marine resources (Swanson et al., 2010), and anadromy may co-occur with nonanadromy within the same watercourse (Knudsen et al., 2016; Nordeng, 1961; Santaquiteria et al., 2016). Partial anadromy in Arctic charr can also have implications for food-web structure, particularly in ecosystems with poor resources, through the competitive effects of Arctic charr on the feeding of other sympatric species (Swanson et al., 2010). The prevalence of residency and anadromy within Arctic char populations may thus be influenced by a variety of factors, including food availability and parasites (Nordeng, 1983), differences in body size (Jonsson & Jonsson, 1993), trade-offs between growth and predation risk (Doucett et al., 1999b), competitive release and/or as a result of trophic polymorphisms (e.g., Chapman et al., 2012 and references therein). Partial anadromy may also be temporally variable, depending on the biotic and abiotic conditions prevailing at any given point in time (Doucett et al., 1999b) and, therefore, is likely to change as the balance between differences in marine, freshwater and terrestrial primary productivity are altered as a result of climate change (Finstad & Hein, 2012).

Changes in the balance of anadromy and residency driven by climate change are likely to hold significant implications for populations of Arctic charr in Greenland and elsewhere (Reist et al., 2006) given that resource availability can influence important reproductive traits in salmonids, including the onset of maturation, ova size and fecundity (Flemming & Gross, 1991). To understand how changing climate may affect the incidence and pattern of partial migration in Greenland, it is necessary to understand the phenomenon as it currently exists. Direct observations of migratory behaviour in remote areas (e.

g., via telemetry) are costly and logistically difficult. Identification of anadromy using indirect molecular methods can also be challenging (Doenz et al., 2019; Santaquiteria et al., 2016). In contrast, chemical analytical methods such as stable isotopes (Chapman et al., 2012) are suited to studies of partial anadromy and the determination of individual migration history (e.g., Gillanders, 2005), particularly at the terrestrial–marine margin (Connolly et al., 2003), because freshwater and marine sulphur stable isotopic signatures are highly divergent (Doucett et al., 1999b; Sharp, 2007; Tsukamoto et al., 1998). Biota habitually resident in one environment, therefore, will have distinctively different stable isotope signatures from biota habitually resident in the other environment and species, like Arctic charr, moving between environments to feed will reflect each individual's relative use of marine or freshwater prey in their own stable isotope signatures given that sulphur stable isotope values change little between trophic levels (Fry, 2013; Fry & Chumchal, 2011; McCutchan et al., 2003).

As part of establishing a baseline for Greenland aquatic ecosystems, this study uses stable isotope measures (δ^{13}C, δ^{15}N, δ^{34}S) of individual Arctic charr captured from three separate watercourses in south-western Greenland to describe within- and among-system trophic behaviour, feeding patterns and dependence on marine resources. Specifically, we use stable isotope, stomach content, body length, age, sex and maturation stage data to test the following hypotheses: (a) that reliance on marine prey increases with Arctic charr length, (b) that, as a result of (a), there will be a significant difference in anadromous and resident Arctic charr stomach contents, and (c) that the degree of reliance on marine prey resources will influence patterns of maturity between watercourses.

2 | MATERIALS AND METHODS

2.1 | Study areas

The study was completed in three coastal drainage systems located along the south-western coast of Greenland (Figure 1). The Kapisillit drainage system (64° 26′ N, 50° 12′ W) is located at the bottom of one of the innermost arms of Nuuk Fjord, about 25 km from the edge of the inland ice and 90 km from the coast. The drainage system (approx. 19 km²) is accessible to anadromous fish and comprises a chain of nine glacially eroded lakes situated in a relatively open U-shaped valley, approximately 29 km long. The first five lakes (lower part) lie within 6 km of the fjord, below 100 m elevation, while the uppermost lake is situated at 240 m elevation. The lake areas vary between 0.02 and 7.40 km². The drainage system has no direct contact with the inland ice cap and receives no surface melt water from the ice. Consequently, the Kapisillit River is a clear-water river. In addition to Arctic charr, the fish community consists of Atlantic salmon (Salmo salar L.) and three-spined stickleback (Gasterosteus aculeatus L.) (Arnekleiv et al., 2018).

The Equalit drainage system (60° 45′ N, 45° 33′ W) is located in the Vatnaverfi area along the outer coast of Igaliko Fjord, about 26 km
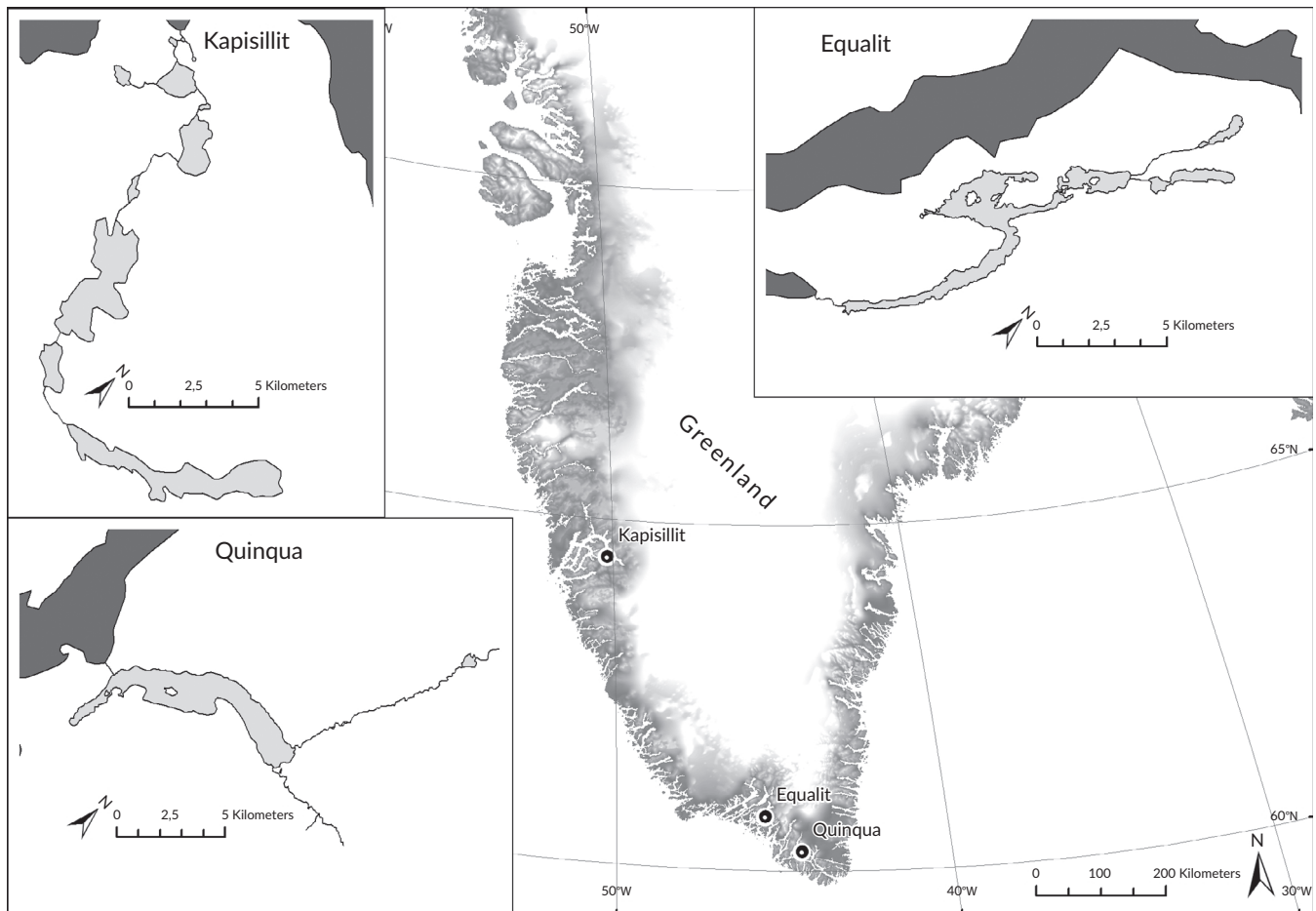
FIGURE 1 Overview of the study areas of Kapisillit, Equalit and Quinqua watercourses in south-western Greenland

east of Qaqortoq. Anadromous fish have access to the approximately 50 km² and 21 km long drainage system. The catchment has four lakes varying in size from 0.7 to 9.5 km², all situated below 100 m elevation. The drainage system has no glacier-fed rivers or lakes. The fish community consists of Arctic charr and three-spined stickleback.

The Quinqua drainage system (60° 16′ N, 44° 38′ W) is located adjacent to the Tasermiut Fjord, about 40 km north-east of Nanortalik. The drainage system (approx. 220 km²) is accessible to anadromous fish and situated 6 km from the fjord in a narrow, approximately 26 km long V-shaped valley. There are two glacially eroded lakes, one 14.9 km² lake at 2 m elevation and one 3.7 km² at approximately 225 m elevation. The area has no contact with the inland ice cap, but receives surface melt water from a number of smaller glaciers. As in Equalit, the fish community consists only of Arctic charr and three-spined stickleback.

2.2 | Arctic charr sampling

The care and use of experimental animals complied with the Government of Greenland animal welfare laws, guidelines and policies as approved by the Government of Greenland, permit reference number G12-008.

In total, 237 Arctic charr were collected in freshwater, post marine migration, during August and September 2012 from the three watercourses in south-western Greenland. From these, n = 169 were subsampled for stable Isotope analyses (Figure 1 and Table 1). At all three localities, Arctic charr were sampled in rivers using electrofishing and fishing rods. At Kapisillit and Quinqua, lakes were sampled with gill nets and fishing rods with lure and spinners, while at Equalit sampling in the lake was conducted with fishing rods only. Electrofishing was conducted using a Terik Technology AS backpack electroshocker (www.terik.no) powered by 12 volts DC (VDC) (10–13.5 VDC) provided by a battery, output 170–1500 V, max. 12 A, frequency 35–70 Hz. Gill net fishing was conducted using Nordic multi-mesh benthic gillnets made up of 12 panels of different mesh sizes (5–55 mm, *e.g.*, Appelberg *et al.*, 1995). The gill nets were set in the littoral zone of the lakes perpendicular to the shoreline. At Kapisillit, four nets were used in the two lowermost lakes for one night each, while at Quinqua three nets were set for one night in the part of the lake furthest from the outlet to the fjord.

All Arctic charr were measured for total length (L_T) from the tip of the snout to the tip of the longest lobe of the caudal fin without compressing the lobes along the midline, and weighted, mass (g). For a subsample, sex and maturity stage (n = 169) and stomach fullness (n = 102; see below) were determined in the field immediately after killing.

TABLE 1 Number of Arctic charr *S. alpinus* (*n*) sampled for stomach contents and stable isotopes, total body length (L_T, mm), mass (g), age, proportion of empty stomachs and number of freshwater- and marine-dependent feeding individuals from three study sampling localities in south-western Greenland

Location	n	Mean length (s.d.)	Range	Mean mass (s.d.)	Range	Mean age (s.d.)	Range	Proportion of empty stomachs (%)	Number (percentage) of freshwater feeding individuals	Number (percentage) of marine feeding individuals
Kapisillit	50	301 (120)	84–522	394 (358)	3–1380	5.1 (2.1)	1–10	78	11 (22.0)	39 (78.0)
Equalit	36	291 (98)	130–435	313 (275)	20–770	4.7 (1.6)	2–9	58	23 (63.9)	13 (36.1)
Quinqua	83	312 (145)	91–652	500 (627)	4–2660	5.0 (2.1)	1–11	49	17 (20.5)	66 (79.5)

Degree of maturation was determined by visual inspection of the gonads following Loewen *et al.* (2010). Sagittal *otoliths* were removed and stored dry in envelopes for age determination while stomach contents were preserved in 96% ethanol for further examination.

2.3 | Analyses of stomach content and determination of age

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 percentage 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 (Hyslop, 1980). Schoener's index was used as a proxy for diet overlap between watercourses and is usually considered as biologically significant when the value of the index exceeds 60% (Wallace, 1981). Age was estimated from sagittal annuli counts.

2.4 | Stable isotope analyses of Arctic charr muscles and potential prey

To correlate Arctic charr δ^{13}C and δ^{15}N signatures to the signatures of their potential marine diet, marine prey stable isotope values for polar cod (*Boreogadus saida* (Lepechin)), Atlantic cod (*Gadus morhua* (L.)), American plaice (*Hippoglossoides platessoides* (Fabricius)), capelin (*Mallotus villosus* (Cuvier)), krill (*Thysanoessa raschii* (SARS)), copepod (*Calanus finmarchius* (Gunnerus)) and shrimp (*Pandalus borealis* (Krøyer))) were obtained from Hansen *et al.* (2012), while data on amphipods (*Thermisto* spp.), armhook squid (*Gonatus fabricii* (Lichtenstein)) and sandlance (*Ammodytes* spp.) were obtained from Dixon *et al.* (2019) and Power (unpublished data). In western Greenland, δ^{13}C and δ^{15}N signatures change with latitude (Hansen *et al.*, 2012), so samples of potential marine prey from the Nuuk area (Dixon et al. 2019; Hansen *et al.*, 2012; Power unpublished data) were related to Arctic charr from the Kapisillit watercourse, while samples from the Qaqortoq area (Hansen *et al.*, 2012; Power,

unpublished data) were related to Arctic charr from the Equalit and Quinqua watercourses.

For stable isotope analyses (δ^{13}C, δ^{15}N, δ^{34}S) a sample of dorsal muscle tissue (*e.g.*, Pinnegar & Polunin, 1999) was dissected from the same subsample of Arctic charr used for stomach contents analyses and stored in alcohol until analysed. Muscle tissue is commonly used to determine long-term diet, and in temperate and northern fish typically reflects the summer period of somatic growth, with the tissue turnover of muscle depending on growth rate (Trueman *et al.*, 2005). For rapidly growing salmonid fishes, the isotopic value of muscle will equilibrate to diet within the order of a few months (Perga & Gerdeaux, 2005; Phillips & Eldridge, 2006; Trueman *et al.*, 2005). As a consequence, muscle tissue is considered a useful surrogate for the study of temporally integrated feeding in anadromous salmonid fishes (Doucett *et al.*, 1999b; Etheridge *et al.*, 2008; van der Velden *et al.*, 2012), with the stable isotope ratios of a consumer reflecting the isotopic values of the prey consumed during the time period that the tissue was synthesised (Fry, 2006). Further, the stable value ratio of δ^{34}S reflects whether individuals have previously been to sea (Doucett *et al.*, 1999a).

The dorsal muscle tissues from the Arctic charr were dried at 50°C for 24 h at the University of Waterloo and the dried tissue was ground to a fine powder with a mortar and pestle. Previous storage in ethanol precluded the need to further consider lipid removal given the lipid loss that occurs due to dissolution during ethanol storage (Correa, 2012). Stable isotope analyses (δ^{13}C, δ^{15}N, δ^{34}S) were completed using the methods described in Guiguer *et al.* (2002), Power *et al.* (2009) and van der Velden *et al.* (2012). Analyses for δ^{13}C and δ^{15}N were performed using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy). Analyses of tissue samples for δ^{34}S were completed using an Isochrom Continuous Flow Stable Isotope Ratio Mass Spectrometer (GV Instruments, Micromass, Manchester, UK) connected to a Costech Elemental Analyzer (CNSO 4010, Costech Analytical Technologies Inc., Valencia, USA). All analytical results were expressed in standard per mil (‰) notation expressed against the relevant international standard.

Working internal laboratory standards were calibrated against the International Atomic Energy Agency standards CH6 for carbon, N1 and N2 for nitrogen, and SO-5, S1 and S2 for sulphur and were run as

controls throughout the analysis to ensure the continued accuracy of all measurements (±0.2‰ for carbon, ±0.3‰ for nitrogen and ± 0.5‰ for sulphur in an organic material). Analytical precision was assessed by mean differences of one in ten duplicate samples, where the mean ± s.d. was 0.14 ± 0.2‰ for δ^{13}C, 0.18 ± 0.2‰ for δ^{15}N and 0.18 ± 0.2‰ for δ^{34}S.

2.5 | Data analyses

Possible differences in age or L_T between the captured fish from the three watercourses were tested using ANOVA. Two-compartment mixing model analysis was completed (Kline *et al.*, 1998; Phillips, 2012; Schawarcz, 1991) to estimate the proportion of marine-sourced sulphur in the diets of sampled Arctic charr given characterization of the marine and freshwater sulphur values as end-members in model computations (*e.g.*, Schawarcz, 1991). Ocean water sulphate has a mean δ^{34}S value of +20.99‰ that is constant with both location and depth (Rees *et al.*, 1978), implying that fully marine δ^{34}S values for biota will not exceed that upper limit. The δ^{34}S of organic sulphur in living organisms incorporated by assimilatory processes is generally depleted by 0–5‰ relative to ocean water (Sharp, 2007), suggesting a basal value for marine organisms of 16‰. Marine fish along the West Greenland coast have an estimated mean trophic position of 4.5 (Linnebjerg *et al.*, 2016), meaning that organic sulphur passed along the food chain would be expected to have fractionated 4.5 times relative to basal organisms. Using the mean fractionation value for fish (0.775‰) computed from data reported in McCutchan *et al.* (2003) suggests fully marine fish will have δ^{34}S values approximating 19.5‰ and this value was used here as the marine end-member in mixing model computations. Nonmarine end-member values for each study system were derived specifically for the system and based on the δ^{34}S analysis of common lower trophic level organisms sampled at each site, including Simuliidae, Chironomidae and Trichoptera. Benthic invertebrates were sampled by use of a kick net, while flying insects were collected with a malaise trap. Use of system-specific end-members in mixing model analysis corrects for baseline differences, thereby facilitating direct comparison among systems (Swanson *et al.*, 2011).

The rate of increase in marine feeding dependency was nonlinearly modelled for all individuals with a marine feeding dependency proportion of >0.20, with 0.20 taken to be the threshold below which individuals could be considered to be essentially dependent on freshwater prey resources. Considered models included those widely used by biologists to model processes such as enzyme kinetics, nutrient uptake and ingestion rates (Berges *et al.*, 1994), including the rectangular hyperbola, Freundlich and polynomial models (*e.g.*, Ratkowsky, 1983). Model coefficient estimates were obtained using nonlinear regression methods (Ratkowsky, 1983). Final model selection was based on the use of the Akaike information criterion adjusted for small sample bias (AIC$_C$) and Akaike weights (w_i), where the w_i term can be interpreted as the probability that model i is the best approximating model for the data within the considered candidate set of models considered (Anderson, 2008).

The probability of full anadromy was modelled as a function of total body length (mm; L_T) with logistic regression (Agresti, 2002). Individuals were classified as fully anadromous when the proportion of marine feeding >0.80, with 0.80 taken to be the threshold above which individuals could be considered to be essentially dependent on marine prey resources.

Prey δ^{15}N and δ^{13}C values were corrected for trophic enrichment (Δ) using, respectively, mean fractionation factors of 3.8 (Linnebjerg *et al.*, 2016) and 0.7 (Søreide *et al.*, 2006), and are presented as post-fractionation equivalents (plotted prey δ values = prey isotope values + Δ) when compared or plotted with Arctic charr stable isotope values (Jensen *et al.*, 2012). The SIBER package Stable Isotope Bayesian Ellipses in R (version 2.0.3, Jackson & Parnell, 2016) was used to estimate isotopic niche widths. The simmr Package (version 0.4.1, Parnell, 2019) was used to create iso-space plots.

To analyse if either δ^{13}C or δ^{15}N were dependent on L_T of the fish, a general linear model (GLM) with a Gaussian error distribution and identity link function were used. Collection site was included as a grouping variable to compare the strength of ontogenetic shifts among populations. All statistical analyses were conducted using R Program version 3.5.1 (http://www.r-project.org) built in to the Rstudio version 1.3.83 (www.rstudio.com).

The probability of maturity was modelled using logistic regression with age as the independent variable following methods described in Agresti (2002) with mean age at maturity estimated from the model at
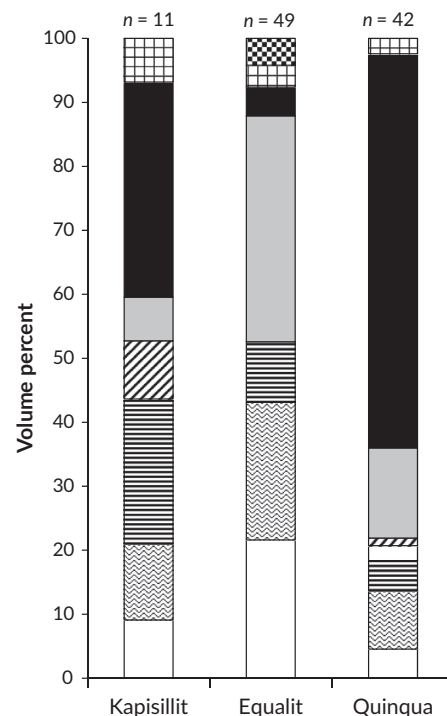

FIGURE 2 Stomach contents from Arctic charr *S. alpinus* sampled in Kapisillit, Quinqua and Equalit watercourses in south-western Greenland: vegetation; trichoptera; terrestrial insects; simuliidae; lymnaeidae; gammaridae; fish; chironomidae; other invertebrates

probability point 0.5. Differences between watercourses were tested using an analysis of residual sum of squares following Chen *et al.* (1992) and Haddon (2001).

3 | RESULTS

Arctic charr from the three watercourses (Figure 1) were all caught in river or lake habitats. There were no differences in total body length (L_T, ANOVA $P > 0.05$) or age (ANOVA $P > 0.05$) among the three watercourses (Table 1).

3.1 | Stomach contents

The stomach content data of Arctic charr (Figure 2) showed relatively high diet similarity (Schoener's index) between Kapisillit and Quinqua (62%) as a result of feeding on terrestrial insects, some *Chironomidae*/chironomids and fish prey. Arctic charr from both these watercourses had medium diet similarity with Equalit (39–45%), mainly because of the high reliance on benthic Simulidae larvae in the latter population. All identified stomach contents contained prey that originated from limnic or terrestrial habitats, including the 40% of the marine dependent feeders which had stomach contents.
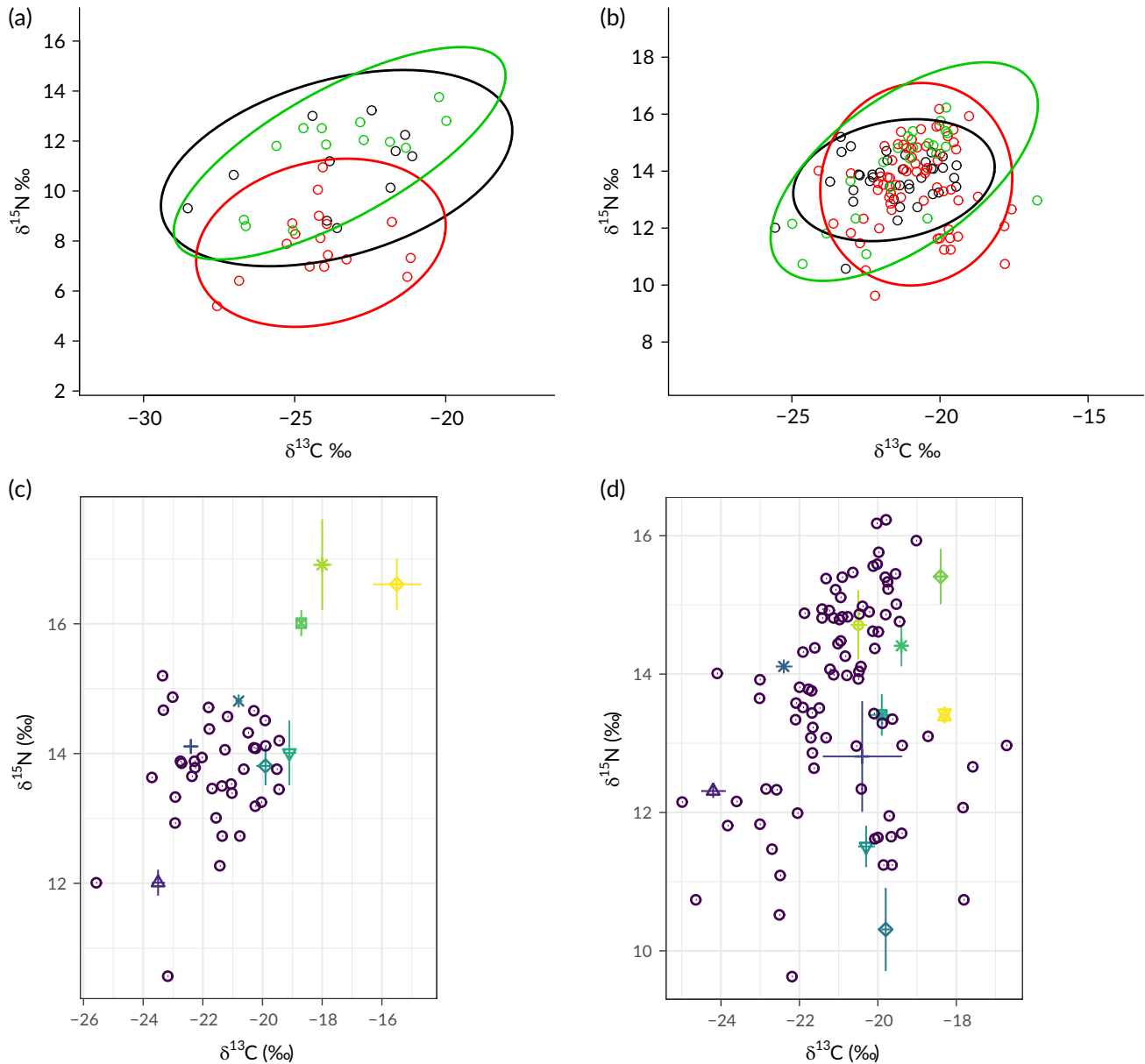

FIGURE 3 (a) & (b): Standard ellipse area (SEAc) based on raw isotope data for Arctic charr *S. alpinus* from three different localities in southwestern Greenland: Kapisillit (black), Quinqua (red), Equalit (green). (a) Freshwater-dependent feeding fish. (b) Marine-dependent feeding fish. (c) & (d) Stable isotope values of Arctic charr and their potential marine prey from (c) Kapisillit: ◢, amphipod; +, sandlance; ✳, armhooksquid; ◆, copepod; ✦, krill; ▪, capelin; ✳, Atlantic cod; ◆, American plaice; and (d) Equalit and Quinqua watercourses: ◢, amphipod; +, sandlance; ✳, armhooksquid; ◆, copepod; ✦, krill; ▪, capelin; ✳, Atlantic cod; ◆, American plaice; ◆, polar cod; ★, shrimp. Potential prey: amphipods (Amphipoda); armhook squid (Gonatidae); shrimp; copepod (Copepoda); krill (Euphausiacea); sand lance (Ammodytidae); capelin (*Mallotus villosus*); Atlantic cod (*Gadus morhua*); American plaice (*Hippoglossoides platessoides*); polar cod (*Boreogadus saida*). Note that prey isotope values have been corrected for fractionation and are plotted as post-fractionation values (*i.e.*, measured isotope value + fractionation factor)
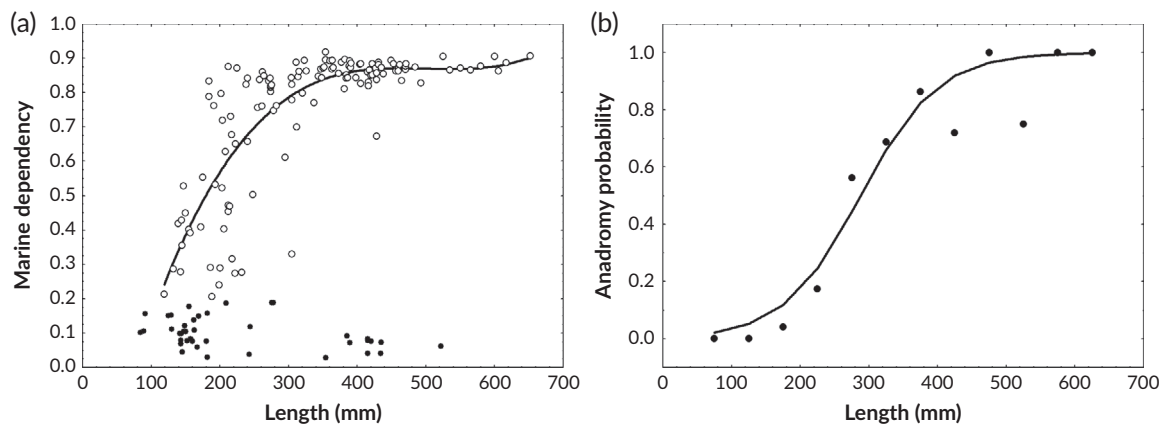
FIGURE 4 (a) Marine feeding dependency of analysed Arctic charr *S. alpinus* from three watercourses in south-western Greenland computed using a single compartment mixing model and system-specific sulphur baselines. Individuals plotted as black dots had marine feeding dependencies of <0.20 and were treated as essentially freshwater residents. Non- or partially freshwater residents, plotted as open circles, increased marine feeding dependence as a function of length. (b) Logistic model describing the probability of full anadromy (>0.80 marine feeding dependency) as a function of length

TABLE 2 Summary of information-theoretic model selection statistics for models explaining changes in marine feeding dependency as a function of length in Arctic charr from three watercourses in south-western Greenland

Model	K	AIC$_C$	Δ_i	w_i
Second-order polynomial	3	−598.51	5.15	0.07
Third-order polynomial	4	−603.66	0.00	0.93
Rectangulat hyperbola	2	−391.58	212.08	0.00
Freundlich	2	−384.45	219.21	0.00
Modified Freunlich	3	−390.92	212.73	0.00

Note: K defines the number of estimated model parameters. AIC$_C$ is the small sample bias adjusted Akaike information criterion. Δ_i is the difference between the model-specific AIC$_C$ and the AIC$_C$ of the best fitting model and w_i. defines the model-specific Akaike information weights.

3.2 | Stable isotope values

Among the three watercourses there was a large similarity in the esti-mated SIBER ellipses for freshwater- (Figure 3a) and marine-dependent feeders (Figure 3b). The $\delta^{13}C$ or $\delta^{15}N$ values from the marine-dependent feeders and their potential prey (Figure 3c,d) indi-cated that they had a mixed diet while in the marine environment, feeding mainly on pelagic fishes (capelin, polar cod), some benthic fishes (sandlance) and marine crustaceans (amphipods, krill).

There was an increase in the $\delta^{13}C$ value (GLM, $n = 169$, $F = 36.515$, $P < 0.001$), $\delta^{15}N$ value ($n = 169$, $F = 130.678$, $P < 0.001$) and $\delta^{34}S$ value ($n = 169$, $F = 97.264$, $P < 0.001$) with increasing L_T. The strength of the correlation between L_T and $\delta^{13}C$ value ($n = 3$, $F = 1.266$, $P = 0.28$) and L_T and $\delta^{34}S$ value ($n = 3$, $F = 0.401$, $P = 0.67$) did not differ between collection sites. However, for L_T and $\delta^{15}N$ value ($n = 3$, $F = 5.514$, $P = 0.005$) the strength of the correlation differed between the three locations (Kapisillit: $n = 50$, $F = 27.590$, $P < 0.001$; Equalit: $n = 36$, $F = 9.344$, $P = 0.004$; Quinqua: $n = 83$, $F = 97.000$, $P < 0.001$).
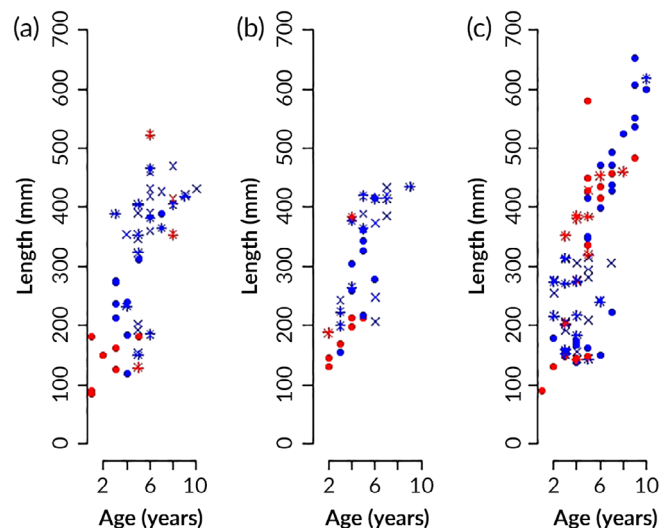

FIGURE 5 Length at maturity for Arctic charr *S. alpinus* from the (a) Kapisillit, (b) Equalit and (c) Quinqua watercourses in south-western Greenland. The fish were divided into sex and stage of maturity (symbols) and feeding strategy (colours). Closed circles, immature fish; crosses, mature females; stars, mature males. Red, freshwater dependent feeders; blue, marine dependent feeders

3.3 | Life history strategies

Analysed $\delta^{34}S$ values for Arctic charr ranged from 1.28 to 18.26‰, with differences evident among the study systems ($F_{2166} = 991.229$, $P < 0.001$) mean ± s.d.: Kapisillit ($n = 50$, $12.58 ± 6.27$‰), Quinqua ($n = 83$, $13.57 ± 4.74$‰), Equalit ($n = 36$, $13.00 ± 3.87$‰). Differences depended on baseline differences between the systems ($F_{2,19} = 14.495$, $P < 0.001$), with baseline organism $\delta^{34}S$ values (simulidae, three-spine sticklebacks, terrestrial insects) lowest at Kapisillit (mean 2.99‰) and highest at Equalit (9.78‰).

Arctic charr with marine feeding dependencies of <0.20 (*i.e.*, less than 20% of their prey were marine) showed no tendency to increase

TABLE 3 Number (percentage) of immature and mature Arctic charr from three watercourses in south-western Greenland

Locality	Length (mm)	<210	210–259	260–299	300–359	360–400	>400
Kapisillit (n = 70)	Immature (n = 24)	15 (44)	4 (80)	3 (100)	1 (14)	1 (13)	0
	Mature males (n = 23)	9 (27)	1 (20)	0	4 (57)	4 (50)	5 (39)
	Mature females (n = 23)	10 (29)	0	0	2 (29)	3 (38)	8 (62)
Equalit (n = 82)	Immature (n = 53)	45 (94)	2 (18)	1 (20)	0	1 (14)	4 (57)
	Mature males (n = 20)	3 (6)	8 (73)	3 (60)	2 (50)	1 (14)	3 (43)
	Mature females (n = 9)	0	1 (9)	1 (20)	2 (50)	5 (71)	0
Quinqua (n = 85)	Immature (n = 46)	20 (71)	5 (71)	9 (90)	8 (73)	1 (25)	3 (12)
	Mature males (n = 23)	7 (25)	2 (29)	1 (10)	3 (27)	3 (75)	7 (28)
	Mature females (n = 16)	1 (4)	0	0	0	0	15 (60)

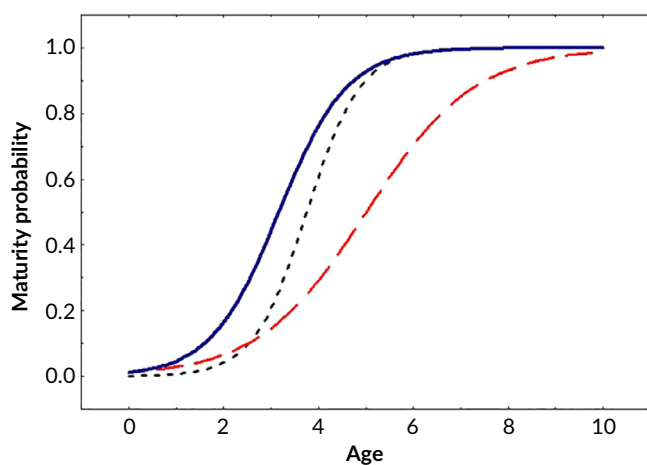*Note:* The fish are divided into length groups.

FIGURE 6 Mature probability at age for Arctic charr *S. alpinus* at three different watercourses in south-western Greenland: ------, Kapisillit; - - - -, Quinqua; ——, Eqaluit

marine feeding dependency as a function of length, whereas those with marine feeding dependencies >0.20 (n = 128) showed a persistent increase in the use of marine prey resources with size (Figure 4a). A third-order polynomial best described the pattern of change (Table 2), having the lowest the AIC_C from among the considered model forms. On average over the size range 125–400 mm, Arctic charr increased reliance on marine prey at the rate of 2.15% per 10 mm increment in length.

Logistic regression indicated a strong relationship between the probability of full anadromy, defined as a marine feeding dependency of >0.80, and length (r^2 = 0.929, model P < 0.001) that implied an average size at full anadromy of 288 mm (Figure 4b).

Small freshwater resident charr were 3–7 years old with mature females having an average body length of 150 mm. Within the anadromous individuals, mature females had an average body length of 410 mm (Kapisillit) and 480 mm (Quinqua). Most of the largest individuals in the 4–9 years age range were marine dependent feeders (Figure 5, Table 3), with some freshwater exceptions that had δ^{15}N values consistent with piscivory (*i.e.*, >13‰). Mature females had an

average body length of 340 mm (Table 3). The maturity probability at age differed between the three watercourses ($F_{8, 220}$ = 4.795 P < 0.001), with the lowest age at maturity at Equalit and the highest in Quinqua (Figure 6).

4 | DISCUSSION

We demonstrated that life histories within studied watercourses were variable, with both resident and anadromous life history strategies being used and life history having consequent implications for differences in measured trophic niches. There was a strong link between dependency on marine feeding, with consistently high δ^{13}S values for larger Arctic charr indicating consistent and persistent use of the marine environment prior to their capture in freshwater. While there were differences among life history strategies in terms of their isotopic niches, among watercourses there were similarities for a given life history. In addition, there was common late season use of freshwater prey by both anadromous and freshwater resident fishes. Overall, the differences and similarities among life histories and watercourses indicate complex resources and habitat use patterns in West Greenland Arctic charr.

The stomach contents of Arctic charr from the three different watercourses were dominated by prey of freshwater or terrestrial origin, irrespective of whether stable isotope values indicated heavy or low reliance on marine feeding. Prey typical for freshwater residency (*i.e.*, freshwater and terrestrial insects) have been noted previously in Norwegian late August–early September post marine-migrating Arctic charr and brown trout, with the diets of both previously marine feeding and freshwater resident fish appearing to be similar during the early autumn period (Rikardsen *et al.*, 2003). Among marine migrants (*i.e.*, with high δ^{34}S values) such feeding may be opportunistic, although the maximal observed marine dependency values of 92% indicated that post marine-migration feeding in freshwater can make important contributions to the diet of Arctic charr and may play an essential role in meeting ongoing basal metabolic costs (Cunjak *et al.*, 1987) and determining eventual prespawning or prewinter condition. For example, manipulative experiments with late summer nutrient additions to Alaskan streams have shown increased growth rates of

stream-resident salmonids linked to improved growth, survival and reproduction (Wipfli et al., 2003).

The freshwater diet found in the stomach contents did not reflect the large variability in the interindividual stable isotopic values of carbon and nitrogen within each locality. This contrasts with the commonly seen trophic specialization within salmonid species in freshwater systems (Knudsen et al., 2016; Power et al., 2009), but also among subgroups within the marine environment in subArctic areas (Knudsen et al., 2011a). Stable isotope analyses indicated consistent differences in resource utilization patterns across the studied watercourses. In each watercourse there were individuals with low δ^{34}S typical of freshwater feeding (Doucett et al., 1999a). There were also a substantial number of individuals in each watercourse with high δ^{34}S values indicative of marine feeding. Individuals with high δ^{34}S values were also usually among the largest individuals and had high δ^{13}C values also generally associated with use of marine prey items (pelagic fish and crustaceans). The different trophic subgroups could represent a combination of trophically separated ecotypes such as freshwater resident and anadromous lifestyles within a single genetic population (i.e., a partially migratory subpopulation; Swanson et al., 2010) or the existence of genetically separated morphotypes of Arctic charr with divergent trophic niches (e.g., sympatric morphs; Simonsen et al., 2017).

The anadromous individuals from the three watercourses appear to grow well, reaching sizes of >400 mm by age 6 years as seen in other northern populations (Dempson & Green, 1985; Johnson, 1980; Klemetsen et al., 2003; Rikardsen et al., 2003; Rubin, 1993). Arctic charr are able to sustain positive growth even at very low water temperatures (Knudsen et al., 2015), which is clearly supported by the growth pattern of anadromous individuals from the Greenland watercourses studied here. Further, the anadromous individuals (i.e., high δ^{34}S values) seem to mature at a larger size, which is typically seen elsewhere (Dempson & Green, 1985; Rikardsen et al., 2003). The combination of growth trajectories, age and size at maturity and variable δ^{13}C and δ^{15}N values suggests several freshwater resident life history patterns in each system, that is, the often reported presence of normal and dwarf morphotypes (e.g., Hindar & Jonsson, 1993; Johnson, 1980; Svedäng, 1990). Such patterns can occur if reproductively separated morphotypes with distinctly different trophic niches exists in sympatry, such as small-sized benthivorous or zooplanktivorous or large-growing piscivorous populations (e.g., Moccetti et al., 2019; Power et al., 2009). Several earlier Greenland studies have documented multiple sympatric populations of Arctic charr in landlocked lakes (Riget et al., 2000b; Sparholt, 1985). To our knowledge, this is the first observation from Greenland of potentially polymorphic freshwater populations existing alongside anadromous Arctic charr (but see Doenz et al., 2019). Such multiple life history types among sympatric morphs have been documented from other systems outside Greenland with anadromous populations of Arctic charr (Jonsson & Jonsson, 2001; Santaquiteria et al., 2016; Simonsen et al., 2017; Smalås et al., 2013). Thus, our findings indicate that the south-western Greenland sea-run Arctic charr populations may have high similarity and parallels with the trophic behaviour and partially migratory patterns observed in Arctic charr populations elsewhere.

The high similarity across watercourses in realized trophic niche (i.e., stable isotope values) and the life history strategies of anadromous Arctic charr suggests constancy of trophic opportunity in the marine environment over distances of hundreds of kilometres along the Greenland coast, with the trophic niches of marine-feeding Arctic charr including relatively few, but essential, marine prey groups. Marine crustacean and pelagic fishes appear to be important prey groups for fjord-migrating salmonids in south-western Greenland as in many other northern areas (Elliott, 1997; Grønvik & Klemetsen, 1987; Knudsen et al., 2011b; Knutsen et al., 2001; Rikardsen et al., 2007). The relatively narrow trophic niche of south-western Greenland anadromous Arctic charr could make these populations more vulnerable to ecosystem shifts precipitated by human disturbances and/or climate change if the populations of keystone prey resources in the marine environment are negatively affected (i.e., decline in abundance). A similar observation was made by Davidsen et al. (2017) in regard to the strong trophic niche similarities of anadromous brown trout in the marine waters along a 400 km costal area of Norway. SubArctic and Arctic populations of Arctic charr, including anadromous populations, appear to have relatively fixed cold-water adaptations (Siikavuopio et al., 2014), which may make them more susceptible to the negative effects of shifting prey resources and temperatures in the fjord environment. While the anadromous lifestyle depends on access to a more energy-rich marine environment in comparison to that available in freshwater habitats (Gross et al., 1988), the acquired energetic gain must balance out the costs associated with migration, including altered competition, predation and parasitism (Chapman et al., 2012). Based on the linkage between marine dependency and growth observed for Arctic charr in south-west Greenland the gains from migration more than offset the costs, with the isotopic values of anadromous fish converging to closely resemble the values of the marine prey groups soon after their first feeding migration. The convergence suggests that marine productivity begins to drive growth as soon as the fish migrate. Thus, alterations to the abiotic environment (e.g., temperature) and/or climate-induced changes in potential prey resources have the potential to alter the balance of migratory gains and costs, and change the consequences of migration (e.g., Finstad & Hein, 2012), for example growth or the incidence of migratory behaviour.

AUTHOR CONTRIBUTIONS

JGD, MP, RK, ADS, GK, LR and JVA contributed to ideas, data generation, data analysis and manuscript preparation. JGD, MP, RK and JVA contributed to funding.

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