

## Interactive Effects of Lake Morphometry and Sticklebacks on the Trophic Position of Arctic charr, *Salvelinus alpinus* (L.), across Lakes in Western Greenland

Ignasi ARRANZ<sup>1,2\*</sup> , Thomas A. DAVIDSON<sup>3,4</sup> , Lluís BENEJAM<sup>1</sup> , Sandra BRUCET<sup>1,5</sup> , Javier SÁNCHEZ-HERNÁNDEZ<sup>6</sup> , Frank LANDKILDEHUS<sup>3</sup> , Torben L. LAURIDSEN<sup>3,4,7</sup> , Nestor MAZZEO<sup>8</sup> , Nicolas VIDAL<sup>8,9</sup> , Korhan ÖZKAN<sup>10</sup> , Irene GALLEGO<sup>11</sup> , Juliane WISCHNEWSKI<sup>3,4</sup> , Rosemberg F. MENEZES<sup>12</sup> , Shurkhuu TSERENPIL<sup>13</sup> , Erik JEPPESEN<sup>3,4,7,14\*</sup> 

<sup>1</sup> Aquatic Ecology Group, University of Vic – Central University of Catalonia, Vic, Catalonia, Spain

<sup>2</sup> Laboratoire Evolution et Diversité Biologique, UMR5174, Université Toulouse 3 Paul Sabatier, CNRS, IRD, Toulouse, France

<sup>3</sup> Department of Bioscience, Aarhus University, Silkeborg, Denmark

<sup>4</sup> Arctic Research Centre, Aarhus University, Silkeborg, Denmark

<sup>5</sup> ICREA, Catalan Institution for Research and Advanced Studies, Barcelona, Catalonia, Spain

<sup>6</sup> Departamento de Biología, Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Madrid, Spain

<sup>7</sup> University of Chinese Academy of Sciences, Sino-Danish Centre for Education and Research

<sup>8</sup> Departamento de Ecología y Gestión Ambiental, Centro Universitario Regional del Este (CURE), Universidad de la República

<sup>9</sup> Departamento de Ecología y Evolución, Facultad de Ciencias Universidad de la República, Montevideo, Uruguay

<sup>10</sup> Institute of Marine Sciences, Middle East Technical University, Mersin, Turkey

<sup>11</sup> Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

<sup>12</sup> Universidade Federal da Paraíba, Centro de Ciências Agrárias, Departamento de Fitotecnia e Ciências Ambientais, Areia, Paraíba, Brazil

<sup>13</sup> Nuclear Research Center, National University of Mongolia, Ulaanbaatar, Mongolia

<sup>14</sup> Limnology Laboratory, Department of Biological Sciences and Centre for Ecosystem Research and Implementation, Middle East Technical University, Ankara, Turkey

### ABSTRACT

The structure and functioning of Arctic ecosystems have been drastically modified by global warming, with fish species potentially performing habitat shifts such as the northern expansion of generalist and warm-adapted species. The freshwater fish species Arctic charr (*Salvelinus alpinus*, hereafter charr) plays a key role in Arctic lake food webs, but sticklebacks (*Gasterosteus aculeatus*) may impact the trophic position (TP) of charr by affecting their habitat choice and food resources. In the present study, we used multiple regression analyses to examine the role of lake morphology (i.e., depth and area) and the influence of sticklebacks on the TP of charr (estimated from  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) sampled in nine Arctic lakes in Western Greenland between 2011 and 2013. Results showed that charr populations exhibited larger TP values when co-occurring with sticklebacks. Specifically, for larger and deeper lakes, a significant positive effect on TP values was observed for medium-sized (25 to 35 cm) charr. Moreover, the TP of sticklebacks had a null effect on the TP values of the largest charr (> 40 cm), suggesting that the largest-sized charr individuals did not prey on sticklebacks. We conclude that charr undergoes flexible ontogenetic trophic trajectories depending on the species composition of the Arctic fish community structure (here presence or absence of sticklebacks) and abiotic lake features.

**Keywords:** Ecosystem size, food webs, polar regions, predator-prey interactions, salmonids

### How to Cite

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#### \* CORRESPONDING AUTHOR

ignasiarranz@gmail.com

ej@bios.au.dk

Phone : +06 131 828 82

## Introduction

Arctic biomes have been profoundly modified by global warming as the increased air temperature and ice cover retreat have altered the structure and functioning of food webs (Quinlan et al. 2005; Kortsch et al. 2015; Coumou et al. 2018). Arctic charr (*Salvelinus alpinus*, hereafter charr) plays a key role in structuring Arctic food webs by interacting across multiple trophic levels, coupling benthic–pelagic compartments and maintaining community stability (Eloranta et al. 2013; Jeppesen et al. 2017). So far, however, the combined impact of lake morphology and ecological interactions with other sympatric fish species is a little studied subject, although it may determine the charr population structure in species-poor oligotrophic high-latitude lakes (Eloranta et al. 2015; Knudsen et al. 2016).

Arctic food webs are relevant model systems for evaluating ecological interactions because of their relatively low species diversity and simple structure (Jeppesen et al. 2017; Rolls et al. 2017). In Greenland lakes, charr is commonly the sole fish species, but it often lives in sympatry with three-spined stickleback (*Gasterosteus aculeatus*, hereafter stickleback) at lower latitudes in Greenland (Wootton 1985; Laske et al. 2019). However, the strength of the charr and stickleback interactions is body-size dependent because charr undergoes ontogenetic trophic shifts following a positive trophic-level–body-size relationship (i.e., trophic level increasing with body size), as demonstrated by many animal taxa but particularly by salmonids (McCann et al. 2005; Romanuk et al. 2011). Typically, adult charr is the top predator in Arctic food webs, feeding on small-sized fish species such as sticklebacks (Jeppesen et al. 2017), but cannibalism among charr also occurs (Amundsen 2016). Given that young and small-sized charr may share similar food resources with sticklebacks in the littoral zone, small-sized charr and sticklebacks are usually segregated by microhabitat feeding site selection, with sticklebacks feeding on small benthic microcrustaceans and small charr usually on chironomids or zooplankton (Jørgensen and Klemetsen 1995). Given the fact that sticklebacks affect the ontogenetic niche shifts of other salmonids such as brown trout *Salmo trutta* (Sánchez-Hernández et al. 2017), stickleback presence might influence the trophic position (TP) of charr populations in Arctic lakes.

A key environmental factor controlling the ecological interactions among species is habitat morphology – defined as the ecosystem size or the space where a species performs its ecological activities (Connell 1961). Controlling for environmental conditions is important to understand ecological interactions, as e.g. interspecific

competition strength may change due to the lake morphology (Post et al. 2000; Eloranta et al. 2015). Lake morphology has been observed as a key driver of charr TP, in which charr populations display high foraging plasticity and occupy different niches at large ecosystem size (Adams and Huntingford 2002; Eloranta et al. 2015; Doenz et al. 2019). Moreover, lake morphology modifies the cross-habitat linkages between littoral and pelagic food web compartments and the charr food resources (Murdoch and Power 2013; Eloranta et al. 2015). However, conflicting effects of lake morphology on the food chain length have been observed because of the complexity of food webs (Eloranta et al. 2010; Murdoch and Power 2013) and also due to the lack of studies using the same compositional communities. Therefore, it is a priority to develop approaches that are universal enough to include the differences in environmental conditions among lakes in order to identify general mechanisms driving changes in the trophic ecology in fish.

In the present study, we investigated the role of lake morphology and ecological interactions with sticklebacks on charr TP in Arctic lakes and, with this, the food web structure and food chain length. The studied Arctic lakes are excellent model systems for assessing trophic interactions under both allopatric (only charr populations) and sympatric (charr populations co-occurring with sticklebacks) community compositions. We used a Bayesian Stable Isotope Mixing Model (*i*) to estimate the TP (from  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of the two fish species in nine Greenland lakes and (*ii*) to assess the effects of lake morphology and stickleback presence on the TP of the model organism. We hypothesized that lake morphology (defined here as the living space where a species performs their ecological activities; Connell 1961) would be positively related to the food chain length, resulting in enhanced TP of the top predator; i.e., the ecosystem-size hypothesis (Post et al. 2000; Eloranta et al. 2015). We also tested the hypothesis that the ecological role of charr would be influenced by lake morphology through biotic interactions triggering ontogenetic shifts (hereafter the trophic-ontogenetic hypothesis; Sánchez-Hernández et al. 2017; Kahilainen et al. 2019; Klobucar and Budy 2020). To support this hypothesis, we predicted that the TP and population density of sticklebacks would trigger a switch to charr trophic level during their ontogeny/development, leading to a higher TP.

## Materials and Methods

### Study Site

Nine lakes were studied along the coast of western Greenland (latitudinal and longitudinal gradients 64°–76°N and 51°–54°E, respectively;

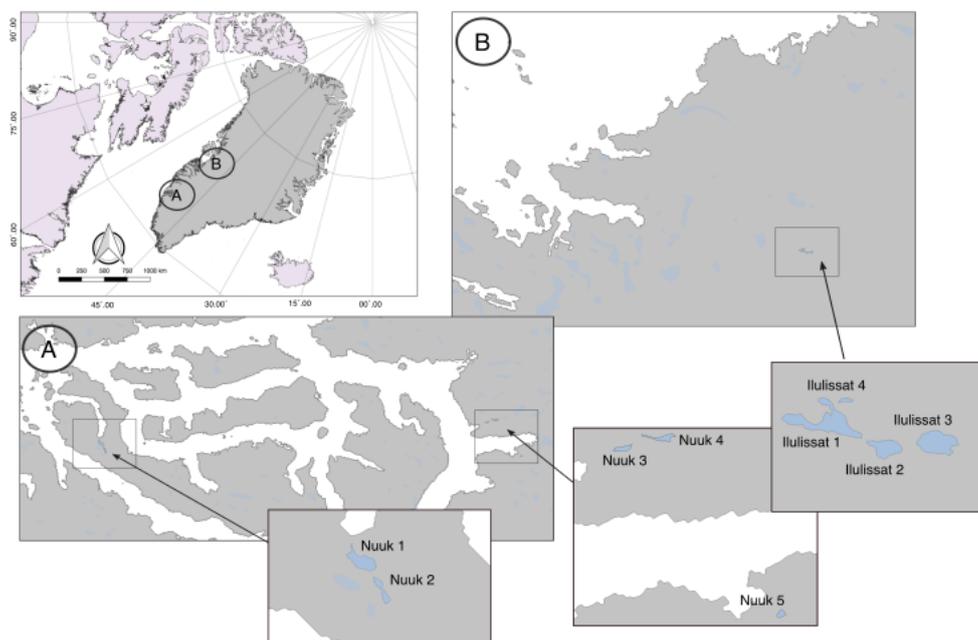
Figure 1). Sampling was carried out once in each lake in summer (on 7 or 27 August) during the period 2011-2013. The studied lakes cover two regions (4 lakes at Ilulissat in the north and 5 lakes at Nuuk in the south; Figure 1). The lakes in the region of Ilulissat hold only allopatric charr, whereas charr and sticklebacks co-occur in the Nuuk region. The range distribution of sticklebacks is limited along both the eastern and western coast up to about 70°N (Wootton 1985; Laske et al. 2019), but in the

Holocene Thermal Optimum, ca. 8,000 years ago, sticklebacks occurred up to 80°N (Fredskild 1985). Sticklebacks usually occupy the littoral zone that, in most oligotrophic high-latitude lakes, is dominated by benthic production (Eloranta et al. 2015). Lake area was determined based on satellite images, and maximum depth was measured in situ for each lake. A summary of the parameters characterising the morphometry of each lake is found in Table 1.

**Table 1.** Background data on the study lakes

Lake code	Lake area (ha)	Lake depth (m)	Charr			Sticklebacks			
			Number individuals	Average TP ( $\delta^{15}\text{N}$ )	Abundance (CPUE)	Average size (cm)	Number individuals	Average TP ( $\delta^{15}\text{N}$ )	Abundance (CPUE)
Nuuk 1	80	35	77	4.50	8.56	18.69	11	3.23	1.23
Nuuk 2	32	13	258	4.72	28.67	18.86	30	4.59	3.34
Nuuk 3	15.6	9.5	96	3.63	16.00	23.40	58	3.60	9.67
Nuuk 4	17.3	12.0	37	4.17	12.33	23.29	25	3.92	8.34
Nuuk 5	10.0	10.5	14	4.25	4.66	38.88	14	3.26	4.67
Ilulissat 1	39.8	29.4	46	4.32	7.67	20.48	-	-	-
Ilulissat 2	14.0	20.4	123	4.06	20.50	26.76	-	-	-
Ilulissat 3	24.3	49.7	43	3.41	21.50	9.49	-	-	-
Ilulissat 4	1.3	5.3	28	4.37	14.00	19.50	-	-	-

Charr and stickleback abundances are expressed as a measure of CPUE (catch per unit effort)



**Figure 1.** Map of Greenland (top left) showing the geographical location of the studied lakes at Nuuk (A) and Ilulissat (B)

### Lake Sampling

Fish were captured using sinking Lundgren multimesh gill nets (1.5 m high). For each lake, the nets were randomly placed at the bottom in open water near the shore (in the middle of the water column, at half the max depth). Depending on lake size, the number of nets varied from one to eight and the nets were set during the afternoon and left overnight (~8 hours fishing time) to

maximize fish catchability (Prchalová et al. 2009). Each charr individual was counted, measured (fork length in mm and weight in g) and examined for the occurrence of parasites in the visceral cavity and flesh, the tapeworm *Diphyllobothrium* sp. being the most common species found (Henriksen et al. 2016). Interspecific density-dependent effects were estimated as the total number of sticklebacks captured divided by the number of nets and hours

(catch per unit effort, stickleback CPUE, ind. nets<sup>-1</sup> hours<sup>-1</sup>). A clean piece of a white muscle tissue (without parasites) was removed from a subset of 392 charr and 138 sticklebacks and frozen at -20°C for SIA.

Benthic and pelagic invertebrates were sampled to determine the overall food-web structure in the study lakes. Benthic invertebrates were collected using a 500 µm mesh kick net within the submerged vegetation or in the shallow littoral zone (0–1 m depth) and an Ockelmann benthic sledge in deeper areas (> 2m). Only soft body tissue of the benthic invertebrates was selected for Stable Isotope Analysis (shells, cases of mollusks and trichopterans were discarded). Pelagic zooplankton taxa were collected by undertaking several vertical hauls with a 140 µm plankton net, and phytoplankton was collected by pumping water through a 11 µm net. However, it was difficult to obtain enough material for measurements due to the high fish predation on zooplankton and low productivity of plankton biomass (Jeppesen et al. 2017).

### Lake Morphology

The studied lakes vary markedly in lake morphology (lake depth and area, Table 1). We performed a Principal Component Analysis (PCA) to determine the variation in lake morphology and reduce information to one dependent variable, which was then modelled as a function of charr TP. Thus, we estimated lake morphology as a synthetic variable of the lake area and depth extracted from the first PCA axis (91% variance explained). Positive values of the first PCA axis indicate larger and deeper lakes.

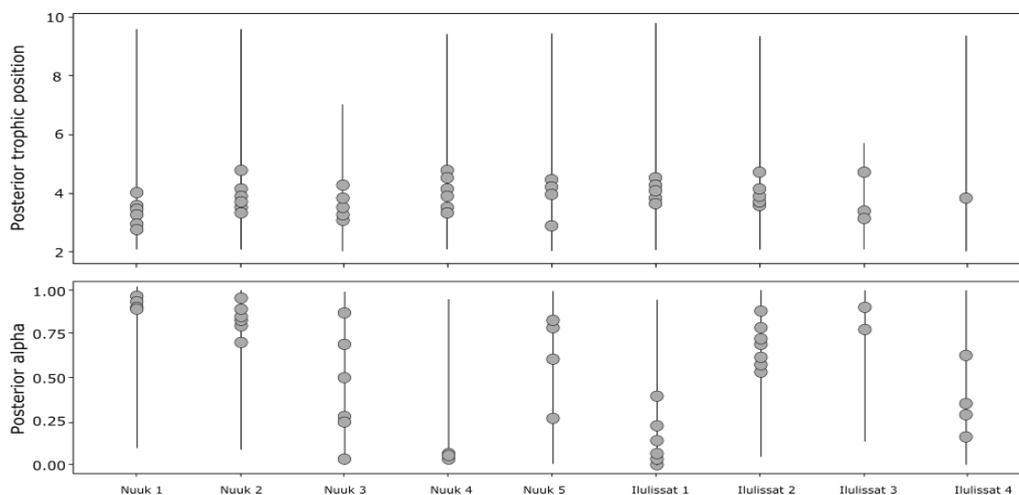
### Trophic Position (TP) of Charr and Sticklebacks

In the laboratory, muscle samples were oven-dried at 60°C for 24 h, homogenised by grinding into

a fine powder, weighed (0.5 – 1.5 mg animal tissue) and packed into tin capsules for stable isotopes analysis at the UC Davis Stable Isotope Facility, U.S.A. The analyses were performed on a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). We expressed stable isotope data in parts per thousand (per mil, ‰) deviations from international standards (Vienna Pee Dee Belemnite and atmospheric N<sub>2</sub> for δ<sup>13</sup>C and δ<sup>15</sup>N, respectively) using the following equation:

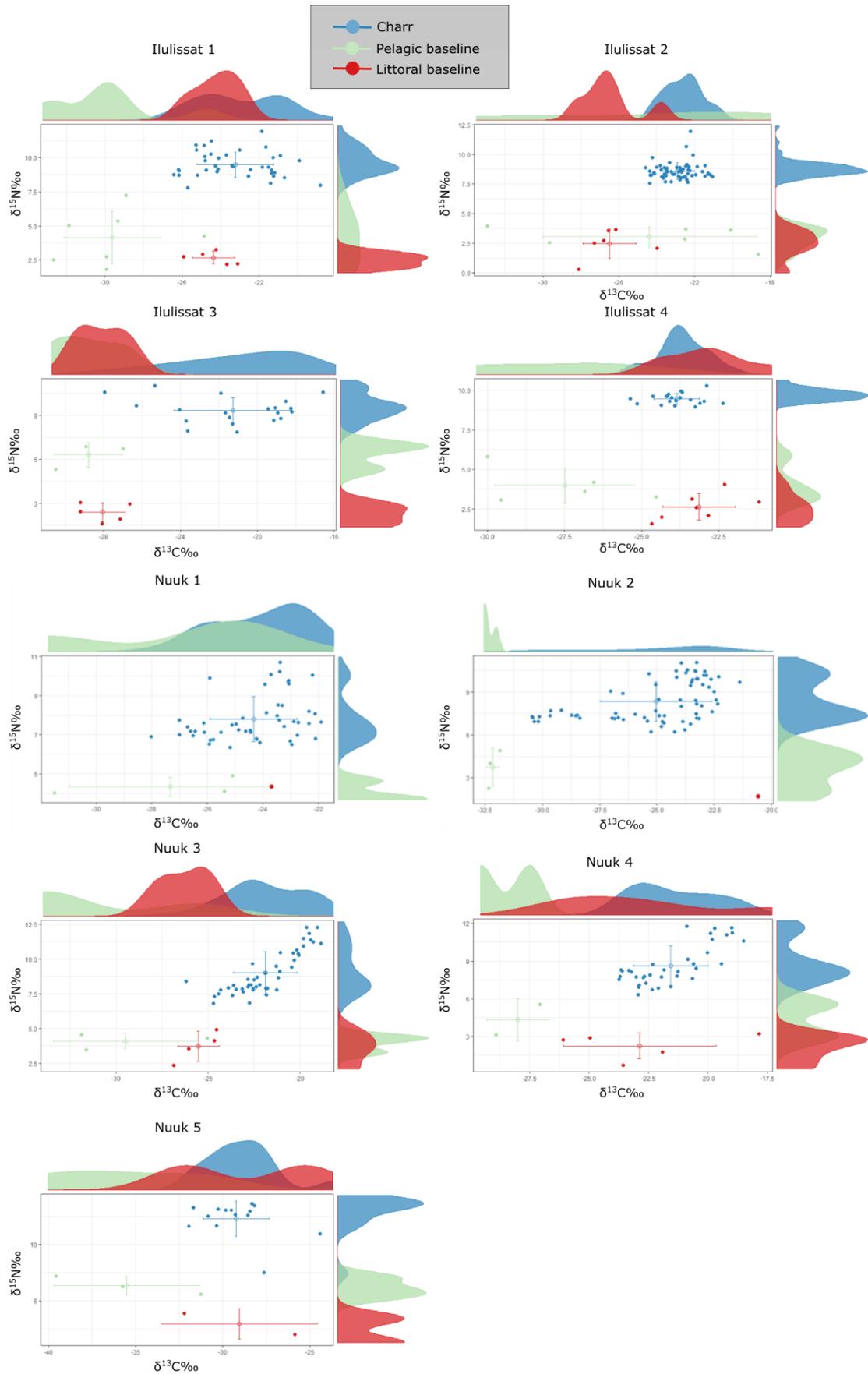
$$\text{Equation 1: } \delta X = \frac{R_{\text{sample}}}{R_{\text{standard}} - 1} \times 1000$$

where X = δ<sup>13</sup>C or δ<sup>15</sup>N and R = ratio of heavy/light isotope content (<sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N). Internal precision was <0.2‰. We extracted δ<sup>13</sup>C and δ<sup>15</sup>N isotope values for the fish data using trophic discrimination factor (TDF) by Post (2002). Because δ<sup>13</sup>C and δ<sup>15</sup>N cannot be used for cross-site comparison as they depend on the level in primary consumers, we determined charr and stickleback TP with 20,000 iterations and five chains by using a Bayesian Stable Isotope Mixing Model “twoBaselinesFull” of the R package “tRophicPosition” (Quezada-Romegialli et al. 2018). This approach includes isotopic variation in the baseline indicator (all primary consumers, divided into littoral and pelagic/benthic parts) and in the fish muscle tissue to provide reliable estimates of charr and sticklebacks TP (Figures 2 and 3). We first classified the charr individuals into 5 cm size intervals (0–4 cm; 5–9 cm; 10–14 cm; 15–19 cm and so on) to illustrate differences in TP along ontogeny within and among the fish populations. Stickleback TP was estimated without size partitioning.



**Figure 2.** Variation in charr TP and  $\alpha$  (i.e., relative use of pelagic + profundal – derived from δ<sup>15</sup>N) across the lakes

The upper panel shows posterior TP estimations and the lower panel estimated  $\alpha$  at each location.



**Figure 3.**  $\delta^{15}\text{N}$  —  $\delta^{13}\text{C}$  biplot and results of the Bayesian Stable Isotope Mixing Model for the different lakes Charr (blue and left-hand plots), baseline resources (green and red) and sticklebacks (blue and right-hand plots)

### Statistical Analyses

Simple linear regressions were performed for each lake to test positive TP–body-size relationships with:

$$\text{Equation 2: } Y_i = \beta_0 + \beta_1 X_i + \varepsilon_i$$

where  $Y$  = median charr TP in lake  $i$ ;  $X$ , body size class;  $\beta_1$ ,  $\beta_0$ , linear parameters and  $\varepsilon_i$ , error term.

We assessed if the  $\beta_1$  of the linear regression in Equation 2 showed positive (i.e., expected TP–body-size relationship), null, or negative (i.e., breakdown of the TP–body-size relationship) effects on each lake and each lake group (presence/absence of sticklebacks).

We computed Generalized Linear Models (GLM) to quantify the effects of environmental gradients on the TP of charr populations per size class. The response variable was charr TP and the predictors were lake morphology (first PCA axis), stickleback TP and CPUE. Because the stickleback TP and CPUE were strongly correlated, we separated these variables into two GLM models. Continuous variables were standardized (mean = 0 and standard deviation = 1) to obtain the same units prior to fitting the GLM models. Thus, the effect sizes of the variables can be contrasted by their respective  $t$ -values. The variables were  $\log_{10}$  transformed if they violated the assumptions of normality (Shapiro-Wilk test,  $p$ -value < 0.05). The probability ( $p$ -value) of rejecting the null hypothesis of the GLM models was set to 95% (level of significance 0.05). Variance inflation factors (VIF) were calculated to identify multicollinearity among predictors. For all predictors, VIF values were less than two, indicating a low degree of multicollinearity (Belsley et al. 1980). All analyses were performed with the software R 4.1.0 (R Development Core Team 2021).

## Results

### TP–Body-Size Relationships

We found clear changes in charr TP with body size, particularly in the lakes Nuuk 3, Nuuk 4 and Ilulissat 2 (Figure 4), indicating that TP increases with increasing body size. By grouping lake systems (at catchment scale) into stickleback density, there was also a significant positive TP–body-size relationship in Nuuk 3 and 4 with high stickleback density, as expected, suggesting an increase of charr TP with ontogeny (Figure 5).

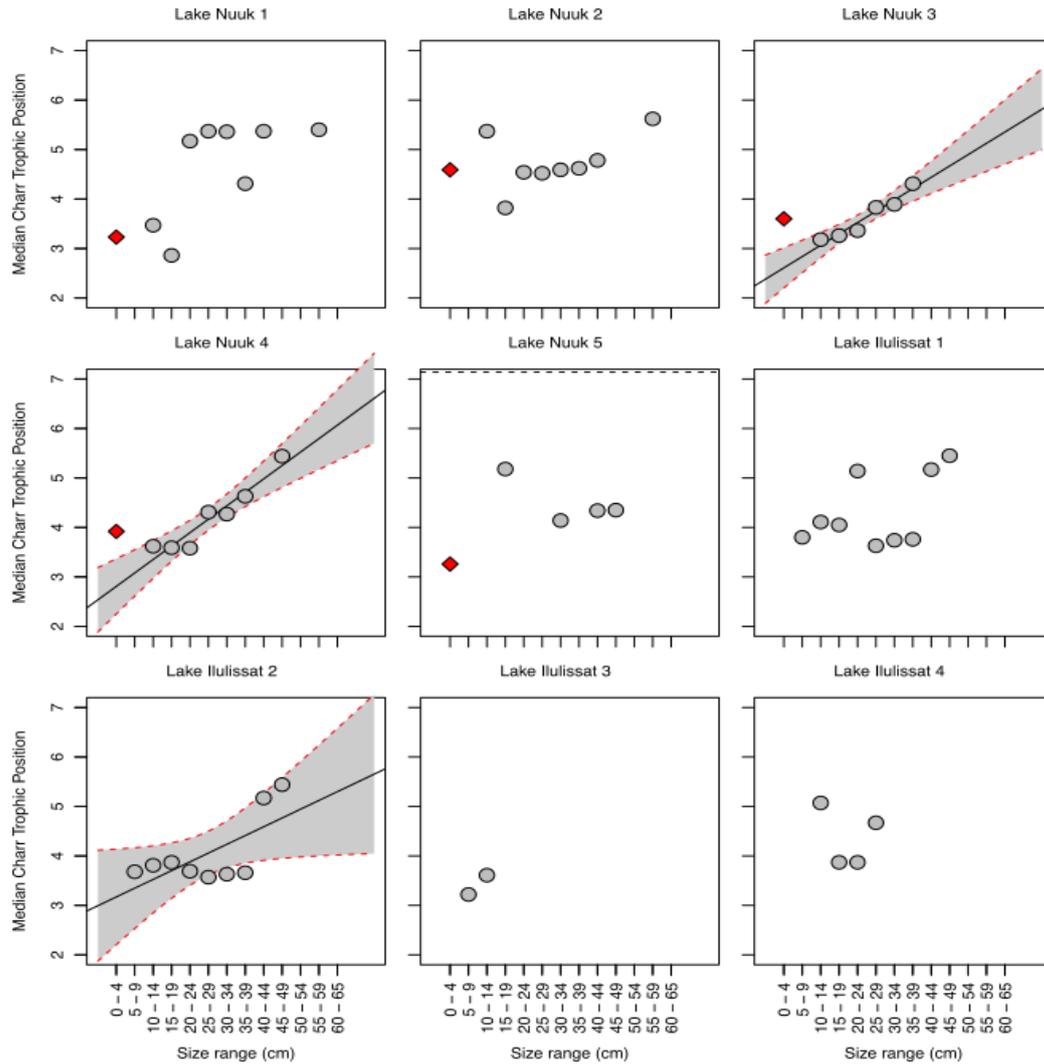
However, charr TP showed non-significant TP–body-size relationship with absence or low density of sticklebacks, where charr populations only exhibited a steep increase of TP in the largest sizes classes and non-linear relationships, respectively (Figure 5).

### Determinants of the Trophic Position of Charr

GLM revealed differences in the response of charr TP to the lake morphology across body size classes (Figure 6). In the first model (using stickleback TP values as a predictor of stickleback effects), larger and deeper lakes predominantly showed a positive effect on TP values of medium-sized charr populations (from 25 to 35 cm), indicating that increasing lake morphology leads to enhanced TP of charr populations (Figures 6 and 7). Moreover, the presence of sticklebacks gradually increased the TP of charr, with the most significant changes occurring in 35–39 cm charr individuals (Figures 6 and 7). In contrast, the TP values of sticklebacks showed a null effect on the TP values of the largest charr (> 40 cm), suggesting that the largest charr individuals did not interact with sticklebacks. Moreover, a significant positive interaction was found in charr individuals of 25–29 cm; at locations without sticklebacks, the TP values of charr decreased with increasing lake morphology, whereas in lakes with sticklebacks the TP values of charr increased (Figure 7).

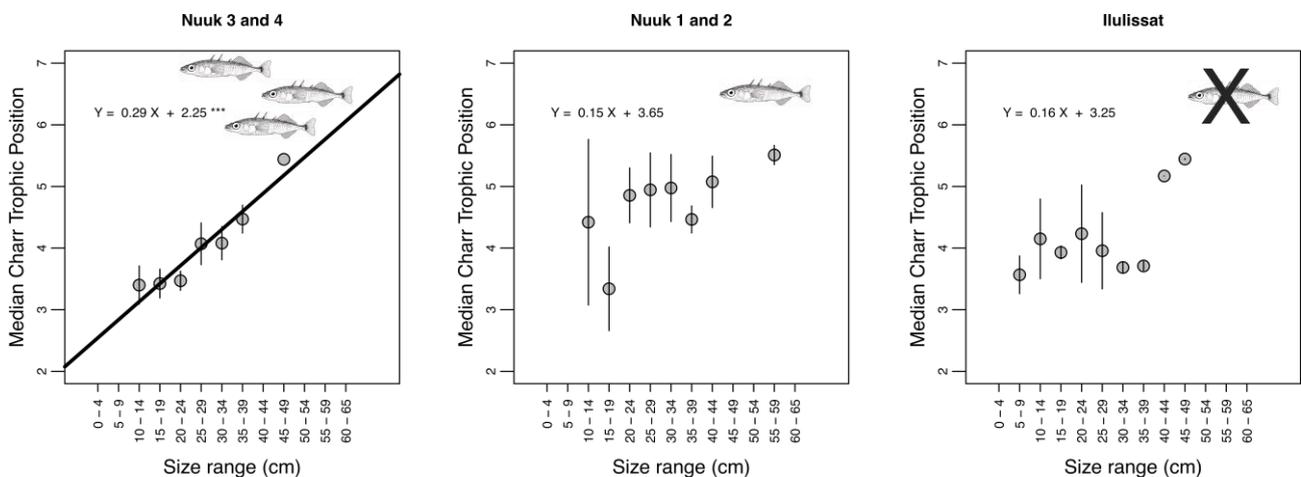
The second model (with stickleback density, CPUE, as a predictor of stickleback effects) showed results similar to those of the first model: *i*) lake morphology had a significant positive effect on the medium-sized charr (from 30 to 34 cm), *ii*) a gradual increase of TP values of charr appeared with increasing stickleback abundance simultaneously with an abrupt decline in the TP of the largest charr individuals, *iii*) the effects of the interaction between stickleback abundance and lake morphology were most pronounced for medium-sized charr (Figures 6 and 7).

Although anadromy was not examined in our study, which might bias charr TP, we further evaluated the effects of the distance of the lake to the sea on charr TP in the subset of Nuuk lakes at different levels of connectivity to the sea (Figure 8). In our results, we did not detect an independent influence of lake distance to the sea on charr TP (Figure 8).

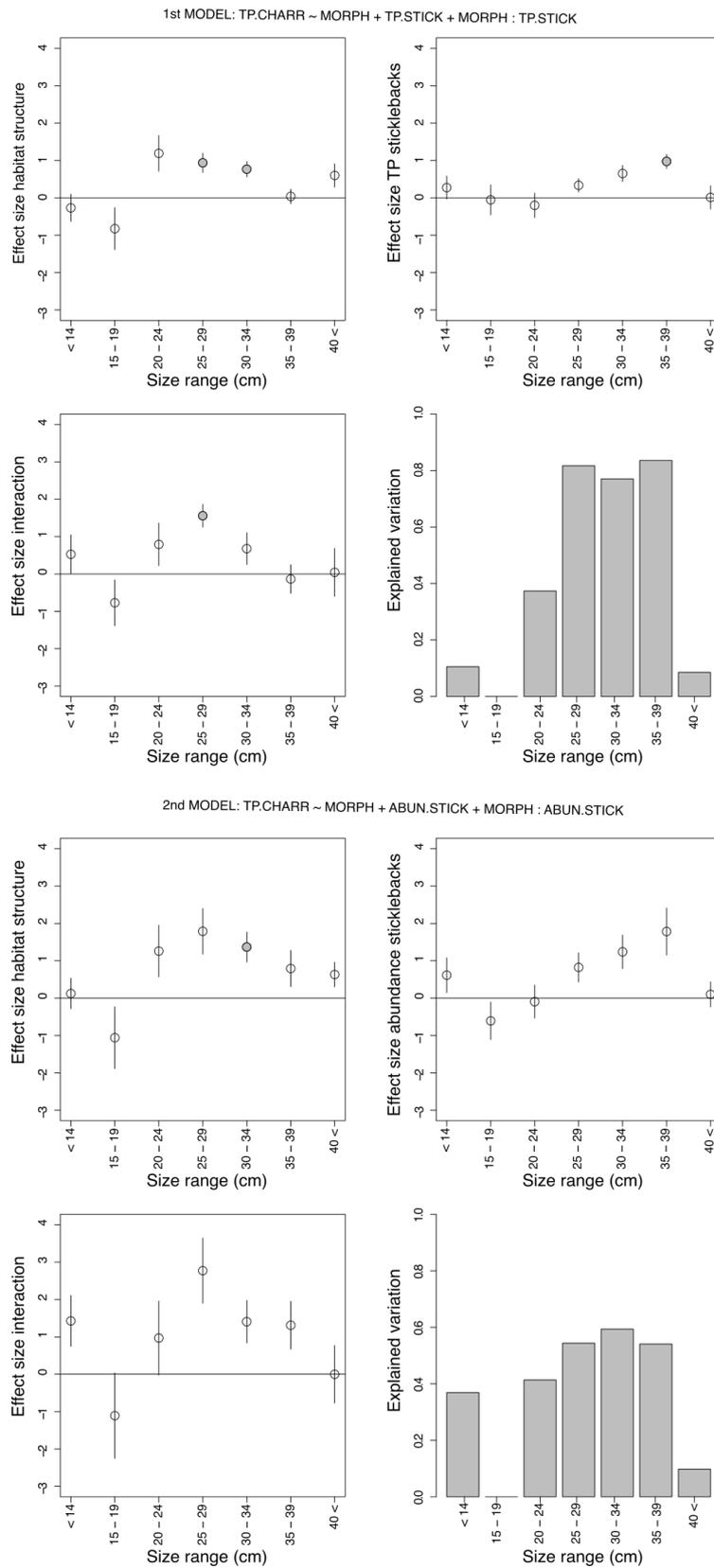


**Figure 4.** The relationships between size range (in 5 cm; X-axis) and charr trophic position (Y-axis) at each location

Grey dots represent the charr trophic position in each body size class [i.e., length in cm: first size class = [0 – 4), second size class = [5 – 9), and so on]. Red rhombuses represent TP stickleback medians. Only significant regressions ( $p$ -value < 0.05) between body size class and charr trophic position with 95 % confidence intervals are shown.

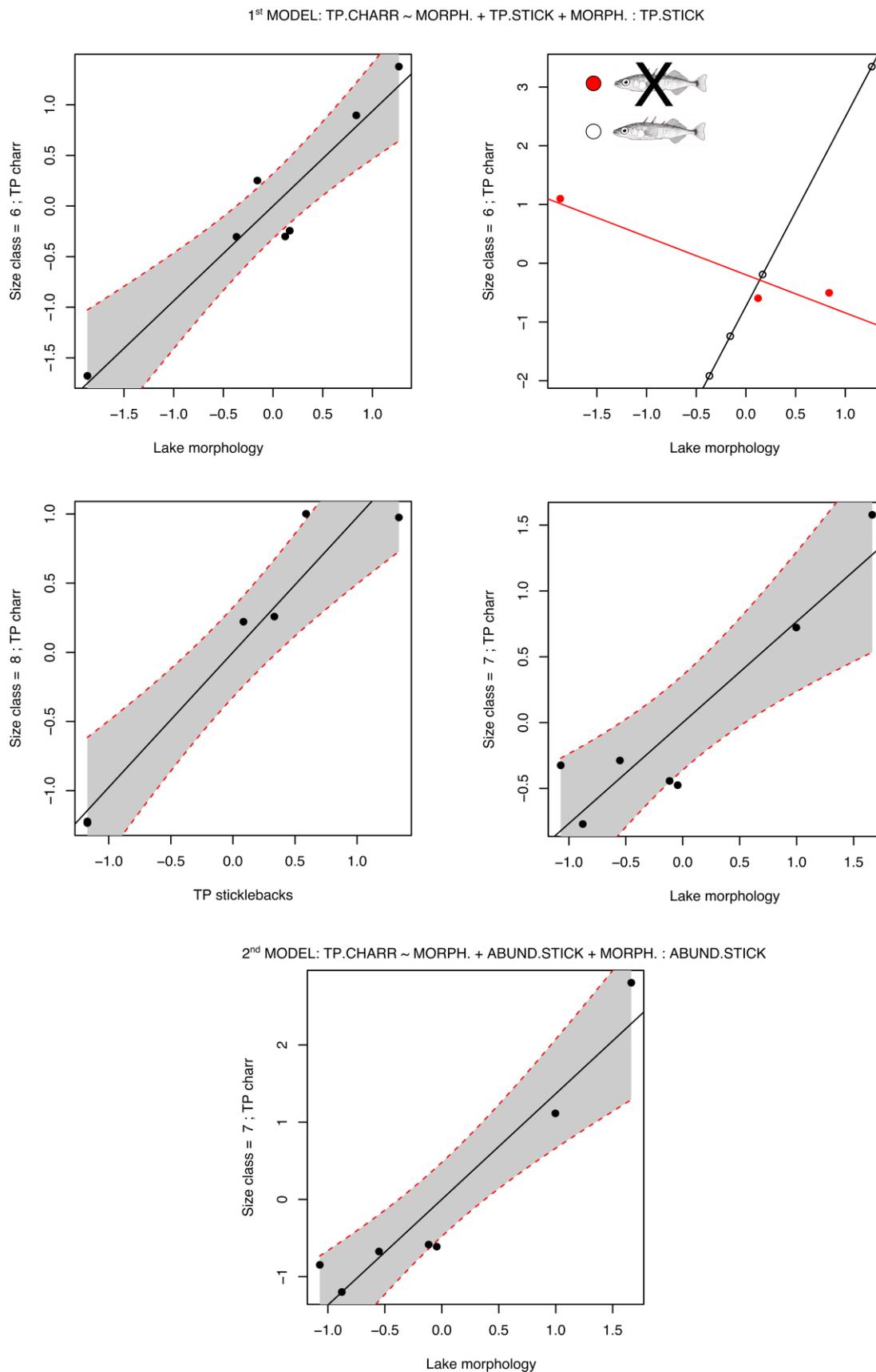


**Figure 5.** Effects of stickleback density on the trophic position of charr at catchment scale (lakes Nuuk 3 and 4; high stickleback density; lakes Nuuk 1 and 2: low stickleback density; lakes in Ilulissat: no sticklebacks) The points represent the average and standard error of the trophic position (TP) for each body size class of charr. Regression coefficients are shown at the top of each plot.



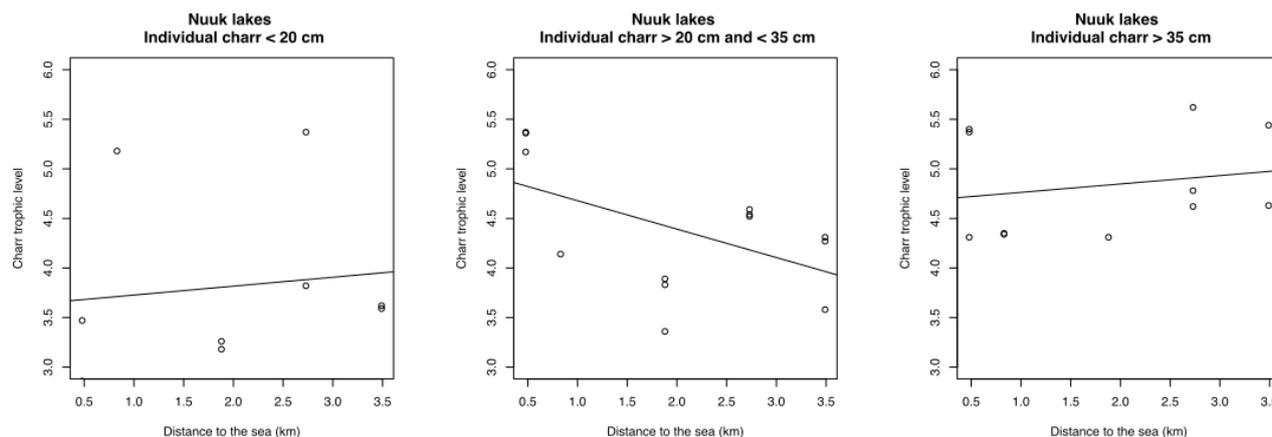
**Figure 6.** The effects of lake morphology (lake size/depth), stickleback trophic position and abundance, and their interactions, on the trophic position (TP) of charr for each body -size class

Y-axes indicate the effect size (estimate and standard error) of the driver and x-axes the body size classes. Grey points display significant results ( $p$ -value  $< 0.05$ ).



**Figure 7.** Significant effects of lake morphology (lake size/depth) and sticklebacks (both TP, first model, and abundance, second model)

Grey shadow at 95% shows confidence intervals. X-axes indicate the predictors and Y-axes the residuals for each model and charr body size class. For the interaction effect, the red line indicates lakes without sticklebacks and the black line lakes with sticklebacks. For more information, see Figure 6.



**Figure 8.** Effects of lake distance to the sea on charr TP

To avoid confounding effects of the presence and absence of sticklebacks and to gather a proper number of observations, only Nuuk lakes were considered. Solid lines indicate the trend of the relationship, but no fish size group showed a significant ( $p$ -value < 0.05) trend, suggesting weak effects of lake distance to the sea on charr TP. The points represent charr TP in each size category and lake. Size group category: 1–4, <20 cm; 5–7, >20 cm and <35 cm; >8, >35 cm. Size groups were based on the first quartile (first group), first quartile – third quartile (second group), and third quartile (3<sup>rd</sup> group). Sea distance was estimated using visual analysis of lakes on Google Earth.

## Discussion

Compared to more complex food webs in territories other than Scandinavia, the West Nordic islands and northern Canada (Eloranta et al. 2010; Murdoch and Power 2013), as well as studies of Greenland charr populations focusing on population size structure (Sparholt 1985; Riget et al. 2000; Jeppesen et al. 2017) and marine feeding (Davidsen et al. 2020), the present study is the first to focus on specific-size charr TP in species-poor oligotrophic high-latitude lakes with the same fish community composition. While in several lakes, such as Nuuk 3 and 4, charr TP increased with increasing body size following the typical pattern of a positive TP–body-size relationship as many other animal taxa (McCann et al. 2005; Romanuk et al. 2011), in other lakes, e.g. Lake Nuuk 1 and Ilulissat 1, charr displayed no clear trophic shifts, which is similar to the findings of previous studies of other model fish (Layman et al. 2005; Schriever and Williams 2013). Moreover, our findings highlight the importance of the simple fish community composition for understanding the TP of salmonids. Thus, charr had a greater TP in lakes with than without sticklebacks, as observed also in other studies of other salmonid species (Sánchez-Hernández et al. 2017 and references therein). This suggests that ecological interactions are pivotal factors in structuring food webs and food web lengths (Simberloff 1982; Vander Zanden et al. 1999).

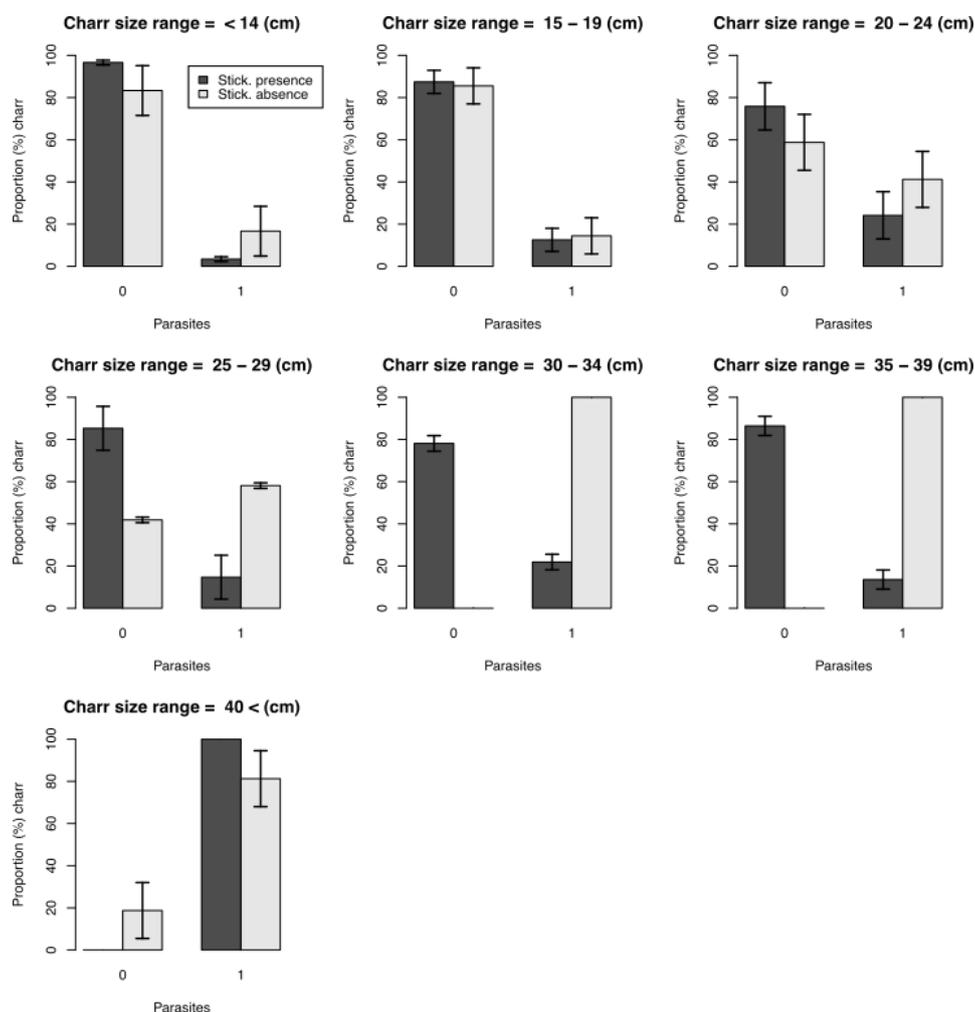
Our results demonstrate the occurrence of contrasting trophic positions and habitat uses of charr across all body size classes in Greenland lakes, confirming that charr is a highly adaptive species (Knudsen et al. 2016). Only the TP of medium-sized

charr responded positively to an increase in lake size/depth. This matches the ecosystem-size hypothesis that the larger ecosystems hold greater home range areas, thereby providing more niche space for larger organisms (Reiss 1988) and a longer food web length (Post et al. 2000). Interestingly, medium-sized charr display different responses to lake size/depth depending on the presence of sticklebacks (as interactive effects; Figures 6 and 7); thus, the TP of charr between 25 and 29 cm exhibited a positive response to increasing size/depth in lakes with sticklebacks (Figure 7), while a negative influence was observed in lakes without sticklebacks (Figure 7). Given that sticklebacks mainly inhabit littoral parts (Eloranta et al. 2015), increased lake morphology would increase the niche differentiation among species and also within body size classes, suggesting low intra- and inter-specific competition (Eloranta et al. 2013). This also indicates that the presence of stickleback is a more important factor than lake morphology in shaping the TP of charr and thus the food chain length of lacustrine systems of Greenland.

General fish ecology theory suggests that young individuals of species with large adult sizes such as charr might utilise resources similar to those used by older individuals of a smaller species such as stickleback (Persson and Greenberg 1990). In our study, the TP of the smallest and largest charr individuals seemed not to be determined by the lake morphology but solely by the ecological interactions of sticklebacks, suggesting idiosyncrasies to the type of driver and body size class. The ecological interactions between the young (small-sized) charr

individuals and sticklebacks may cause a reduction in charr TP, but when the charr grow, their TP appears to increase as a function of the density and TP of sticklebacks. However, the TP of the largest charr (> 40 cm) seemed to be invariant to the abundance and TP of sticklebacks. A possible explanation is that the largest charr migrate to the pelagic zone likely to feed on zooplankton, thus alleviating the competition for littoral resources, or that they specialise in feeding on small-bodied zooplankton (Eloranta et al. 2013), leading to a decrease in TP. However, in the Ilulissat lakes, the 40-cm charr showed an abrupt enrichment

of  $\delta^{15}\text{N}$ , suggesting a probable trophic shift with ontogeny from feeding on invertebrates to their conspecifics (Knudsen et al. 1996). Eloranta et al. (2010) also reported that most of the charr >50 cm in a sub-Arctic lake with a fish community consisting of charr and brown trout underwent an ontogenetic dietary shift to cannibalism. In line with the previous findings, the presence of parasites may determine the cannibalistic role of charr (Hammar 2000), which in our analysis was confirmed by high rates of parasite infestation of charr > 45 cm in the Ilulissat lakes (Figure 9).



**Figure 9.** Proportion of charr with parasites in each size category.

Dark bars are charr caught in the Nuuk region, and light bars are charr caught in the Ilulissat region.

Instead of strict cannibalism, some of the largest charr individuals in our study lakes with sticklebacks (e.g., Nuuk 3 and 4) probably have a diet partly consisting of invertebrates, as suggested by the high individual variation in  $\delta^{15}\text{N}$  signatures. McCarthy et al. (2004) proposed that in a sub-Arctic lake with a multispecies fish community (sticklebacks, minnows *Phoxinus* sp., brown trout), the wide variation in  $\delta^{15}\text{N}$  values for large piscivorous charr may result from individual differences in isotopic fractionation (some

individuals prey only on fish, while others switch between fish and invertebrates). Fraser et al. (1998) highlighted that in a deep lake, with low abundance of sticklebacks, piscivorous charr fed mainly on other charr to alleviate the resource competition of small-sized charr. Accordingly, charr may undergo flexible ontogenetic dietary trajectories (switching between fish and invertebrates) depending on the fish community composition, with concomitant consequences for the variability of TP.

The contrasting trophic responses of charr may also be attributed to the strong interspecific competition in the Arctic lake systems that are characterised by food resource scarcity (Bolnick et al. 2010; Brodersen et al. 2012), as has been reported for other salmonids, e.g. sockeye salmon *Oncorhynchus nerka* and brown trout (Brodersen et al. 2012). In Faroese lakes, Brodersen et al. (2012) found that when sticklebacks lived in sympatry with brown trout, the salmonid shifted its niche preferences. Jørgensen and Klemetsen (1995) observed that small charr and sticklebacks were segregated at microhabitat level for feeding in the littoral zone of Lake Takvatn (northern Norway). In an enclosure experiment, O'Neill (1986) showed that sticklebacks competed with young individuals of sockeye salmon by reducing the abundance of food resources. In our study, the interspecific competition between sticklebacks and charr caused a reduction of the trophic level of charr by potentially reducing the amount of resources and habitat space.

Our results may potentially be affected by migration of the fish. Migration to the sea, if it occurs, often takes place in early summer, and charr specimens (typically in the size range 15 – 70 cm; Gulseth and Nilssen 2001) remain in estuarine or coastal water until at the end of the summer for feeding before returning to freshwater (Radtke et al. 1996). These anadromous specimens exhibit elevated  $\delta^{15}\text{N}$  values compared with resident populations (Murdoch et al. 2015), and migration may also enhance the basic level of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Gregory-Eaves et al. 2007). Enhanced basic levels in the lakes will not affect the TP of fish, while higher  $\delta^{15}\text{N}$  obtained when feeding in the sea will. However, we found no relationship between the TP of the different size groups (first size group = <20 cm; second = >20 cm and <35 cm; third = >35 cm) in the Nuuk lakes with different distances to the sea (Figure 8). Therefore, we assume that our results are not violated by sea-based higher  $\delta^{15}\text{N}$ .

A promising area for future research is to explore the effects of poleward expansion of generalist species and environmental shifts driven by global change on cold-water species such as charr. Eutrophication in high-latitude lakes induced by climate change could lead to reduced littoral primary production and changes in charr TP. Moreover, the increasing snowmelt caused by glacier retreat may lead to connection between lakes and the sea due to higher runoff in Arctic streams. Consequently, some fish-free lakes will probably be colonised by charr and also by northward-moving sticklebacks (Bennike et al. 2008). Anadromous migration by sticklebacks may extend their range of distribution towards the north where they were once present up to Thule

(80°N) in the Holocene Thermal Optimum (ca. 8,000 years ago, Fredskild 1985). (Re)-spreading of the species to new areas in Arctic food webs may alter ecological interactions, so further development of SIA may be valuable to unravel mechanisms driving changes in trophic ecology by key fish species such as charr in Arctic food webs.

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