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The Biology and feeding Ecology of Arctic charr in the Kerguelen Islands

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26 **Abstract**

27 Subsequent to their introduction in the 1950s, Arctic charr *Salvelinus alpinus* have been able to

28 establish a self-sustaining population that has adapted to the unique conditions of the Kerguelen

29 Islands in the sub-Antarctic. Here, 48 individuals (198-415 mm) were caught with gillnets and

30 their basic biology and feeding ecology were examined using stable isotope analysis. The Lac

31 des Fougères population split use of littoral and pelagic resources evenly, although larger fish

32 relied more heavily on littoral production and appear to follow the size-dependent life-history

33 habitat template seen in many Scandinavian lakes where smaller sized individuals occupy the

34 pelagic zone and larger individuals dominate the littoral habitat. In Kerguelen Arctic charr

35 mature at the same ages (5.6 years) as Arctic charr in both sub-Arctic and Arctic lakes. Whereas

36 mortality was average in comparison to comparator sub-Arctic lakes, it was high in comparison

37 to Arctic lakes. Maximal age (>7+) was at the lower end of the range typically seen in sub-

38 Arctic lakes. Although they inhabit a resource poor environment, Kerguelen Arctic charr

39 showed no evidence of cannibalism. Thus, while Arctic charr can survive and reproduce in the

40 relatively unproductive Kerguelen lake environments, survival and growth nevertheless appear to

41 be traded off against survival and longevity. The uniqueness of the population location and the

42 recency of its introduction suggest that further monitoring of the population has the potential to

43 yield valuable insights into both the adaptability of the species and its likely responses to

44 ongoing large-scale environmental change as represented by climate change.

45

46

48 **Introduction**

50 Originally devoid of freshwater fishes, the Kerguelen Islands archipelago in the Great Southern

51 Ocean (49°S, 70°E) witnessed the extensive introduction of salmonid fishes *(Salmo trutta, S.*

52 *salar, Oncorhynchus mykiss, O. tshawytscha, O. kisutch, Salvelinus namaycush, S. fontinalis* and

53 *S. alpinus*) between the years 1955 and 1993 when a total of approximately two million

54 individuals were introduced (Lecomte *et al.,* 2013). From the original introductions in 22

55 watersheds, 54 watersheds are now believed to be occupied by one or more species. Lack of

56 both native fishes and anthropogenic influences on the islands have facilitated studies of invasion

57 dynamics, improved understanding of the importance of adaptive processes and environmental

58 gradients in colonization success and provided a credible blueprint for the potential of salmonid

59 species invasions in other pristine environments (Labonne *et al.,* 2013). While several studies

60 have focused specifically on the post-introduction fate of *S. trutta* in the islands (e.g. Jarry *et al.,*

61 1998; Morat *et al.,* 2008; Hórreo *et al.,* 2011; Labonne *et al.,* 2013; Jaffal *et al.,* 2015; Aymes *et*

62 *al.,* 2016; Jarry *et al.,* 2018; Marandel *et al.,* 2018), none have focussed in detail on the fate of *S.*

63 *alpinus* despite its relative colonization success, i.e. one success in two trials (Lecomte *et al.,*

64 2013).

66 In comparison to other species introductions in the Kerguelen Islands, *S. alpinus* releases were

67 low, with only 2269 individuals having been released in two watersheds (Davaine & Beall,

68 1992). Introduced individuals originated from an Institut National de la Recherche Agronomique

69 hatchery facility used to stock Lake Geneva and are believed to have been genetically similar to

70 the source wild population (Lecomte *et al.,* 2013), although supplementation of the Lake Geneva

71 stock with Scandinavian fish occurred in the 1970s (Savary *et al.,* 2017). Introductions occurred

72 in 1991 at the Lac des Fougères outlet (2000 age 0+ individuals with no other coincidental

73 species releases) and in 1992 in the Lac d'Amor Basin (269 age-2+ individuals in a mixed

74 release with *S. trutta, S. salar, O. tshawytscha, O. kisutch and S. fontinalis*). When assessed in

75 2003, *S. alpinus* and *O. kisutch* were present at the Lac des Fougères outlet. In contrast, in 2009

76 *S. alpinus* were not reported in the Lac d'Amor Basin (Lecomte *et al.,* 2013), possibly as a result

3

77 of bacterial kidney disease noted to have been in the basin and known to pose a serious risk to

78 salmonid fishes (Jónsdóttir *et al.,* 1998).

79

80 Although the freshwater ecosystems of Kerguelen vary widely due to the presence of geothermal

81 activity (Renac *et al.,* 2020), they are generally considered to be low productivity, oligotrophic

82 systems (Stonehouse, 1982; Maire, 1985), with marine access having provided a necessary

83 buffer for resource poor freshwater environments (Davaine & Beall, 1992) and facilitated the

84 invasion success of introduced species such as brown trout (Jarry *et al.,* 2018). As a result

85 colonization success in Kerguelen appears to be linked to anadromous behaviour that may

86 explain the relative dominance of brown trout (Lecomte *et al.,* 2013) in comparison to *S.*

87 *fontinalis* and *O. mykiss*, both of which have shown colonization success in other environments

88 (e.g., western North America - Dunham *et al.,* 2002 and Chile - Arismendi *et al.,* 2014). In

89 Kerguelen *S. alpinus* are not known to have established anadromous populations, which suggests

90 their success in establishing resident populations will depend more critically on the attributes of

91 phenotypic plasticity and environmental tolerance known to have contributed to establishment

92 success of salmonids elsewhere (Arismendi *et al.,* 2014).

93

94 Climatically the Kerguelen Islands experience a cold sub-Antarctic climate characterized by a

95 mean annual temperature of 4.5°C ($\approx2°$C winter and $8°$C summer means), frequent winds

96 (66kmh^{-1} annual average), heavy cloud and rain, ranging from > 3200mm yr^{-1} in the west to

97 800mmyr^{-1} in the eastern side (Frenot *et al.,* 1997; Heirman *et al.,* 2012). Uniform wind stress

98 produces steady-state lake circulation patterns notable for the absence of stratification and

99 homothermic temperature profiles due to permanent mixing of lake waters (Marie, 1985;

100 Heirman *et al.,* 2012). The aquatic fauna, net of introduced fish, are limited to a few abundant

101 species of cladocerans, copepods and rotifers tending to dominate in the littoral as opposed to the

102 pelagic zone (De Smet, 2001), benthic Oligochaetes and free Nematodes, and a relatively

103 abundant chironomid (*Limnophyes pusillus*) present in all wetted areas (Davaine & Beall, 1997).

104 The relative scarcity of true planktonic species in Kerguelen parallels other studied sub-

105 Antarctic locations (e.g., Dartnall & Hollowday, 1985; Dartnall, 1995) and is likely influenced

106 by the degree of wind mixing evident in most Kerguelen lakes and ponds (De Smet, 2001).

107 While the environment is apparently harsh, dietary and habitat generalists tolerant of cold-water

4

108 environments (Power, 2002; Power *et al.,* 2008) such as *S. alpinus* should be adequately

109 equipped to succeed in the resource poor aquatic landscapes of the Keguelen Islands. Indeed, the

110 opportunistic, exploratory, and migratory behaviours of *S. alpinus* define their life history and

111 are traits that have been credited with their post-glacial colonization success of periglacial

112 habitats in the northern hemisphere (Power, 2002). Nevertheless, low prey diversity and reduced

113 resource abundance may structure Arctic charr populations, inducing size bi-modalities reflective

114 of cannibalism (Hammar, 2000) known to prevail among high latitude populations (e.g.,

115 Amundsen *et al.,* 1999; Power *et al.,* 2008).

116

117 In 2019 a test fishery of Lac des Fougères was undertaken to determine whether Arctic charr still

118 inhabited the basin where the largest introduction occurred. Here we describe the biological

119 attributes of individuals (e.g., length, weight, growth) obtained from that sampling and their

120 associated trophic ecology. Further, given the notably low productivity of Kerguelen lakes, the

121 limited diversity and abundance of aquatic insects (Maire, 1985), and the dominance of littoral

122 plankton in studied Kerguelen assemblages (De Smet, 2003), we tested the following hypotheses

123 that: [1] there would be evidence of cannibalism due to the resource poor conditions (e.g.,

124 Hammar 2000, 2014); and, [2] irrespective of cannibalism, when compared to pelagic-reliant

125 conspecifics there would be a fitness advantage for individuals with higher reliance on littoral

126 production reflected in larger sizes, faster growth and better condition. Finally, to contextualize

127 the Kerguelen population, we compare the traits estimated from the Kerguelen sample data (e.g.,

128 mean-age-at-maturity, mortality) to literature reported data for lacustrine populations and the

129 trophic ecology of Kerguelen *S. alpinus* to examples of similar single-species assemblages from

130 Arctic Canada and Scandinavia.

131

132 **Methods**

133

134 Sampling occurred using over-night gillnet sets (January 2-4, 2019) in Lac des Fougères (34.3ha,

135 49.42°S, 69.67°E, connect to marine coastal waters via a 1.25km stretch of river, Figure 1) with

136 a combination of sinking benthic nets (4 nets, 15.5-29.0mm mesh) and floating pelagic nets (2

137 nets, 28-45mm mesh). The care and use of field sampled animals complied with the Government

138 of France animal welfare laws, guidelines and policies (Comité d'Éthique) as approved by the

139 Terres Australes et Antarctiques Françaises administration under the auspices of permit number

140 (Référence du dossier) 2016122009113932-v2.

141

142 All captured Arctic charr were measured after removal from the net for total length (L_T, mm) and

143 weighed (mass in g). Sex, maturity stage and stomach fullness were determined in the field

144 immediately after killing, with sagittal otoliths removed and stored in envelopes for age

145 determination and a 1g piece of dorsal muscle tissue was excised from posterior to the dorsal fin

146 and above the lateral line (e.g., Guiguer *et al.,* 2001) and frozen for use in stable isotope analyses

147 (e.g., Fry, 2006). Age was estimated from sagittal annuli counts following Grainger (1953). Coincident

148 with fishing, sampling for benthic invertebrates and zooplankton was completed

149 opportunistically using standardized benthic invertebrate sampling methods (e.g., Eloranta *et al.,*

150 2017) and a 90 μm zooplankton net towed manually by wading and troughing or behind a small

151 inflated boat.

152

153 Differences between sexes were tested using one-way ANOVA, with sex included as a co-factor

154 in the subsequent analyses where significant ($P<0.05$) sex-related differences were found. The

155 weight-length relationship, after natural logarithmic transformation of the data, and growth were

156 estimated using linear regression (Diana, 2004), with differences between the sexes tested using

157 ANCOVA (Zar 2010). Average growth rate was determined as length-at-capture divided by

158 estimated age. Condition was estimated from a weight-length regression after testing for

159 allometry using relative condition which compensates for changes in form and condition as

160 length increases (Le Cren, 1951; Froese, 2006). Where multiple linear regression was used,

161 standardized (βeta) coefficients were computed following Zar (2010) as indicators of the relative

162 importance of each explanatory variable.

163

164 For the purposes of modelling the probability of maturity the sexes were pooled after testing for

165 differences in the proportion of mature individuals between the sexes using Fisher`s exact test

166 (one-tailed $P=0.3273$). The probability of maturity was modelled as a function of age and length

167 with logistic regression following methods described in Agresti (2002):

168   (1)   Maturity probability $= \dfrac{1}{1+\exp(\alpha + \beta X)}$

169   where X = age or length and α and β are estimated model parameters. Mean age-and length-at-

170   maturity were estimated from the models at the 0.5 probability point.

171

172   The instantaneous rate of mortality (M) was estimated based on the numbers of aged fish

173   captured, beginning with the first fully vulnerable age-class, using Chapman-Robson methods

174   (Chapman & Robson, 1960; Robson & Chapman, 1961) known to yield low errors and biases in

175   comparison to other methods (Dunn *et al.,* 2002). The validity of the assumed geometric model

176   used in the Chapman-Robson methods was verified using testing procedures described in Seber

177   (1982).

178

179   Dorsal muscle samples for stable isotope analyses (δ^{13}C, δ^{15}N) were dried in the laboratory at

180   50°C for 24 hours, ground to a fine, homogenate powder with a mortar and pestle and analysed

181   following methods described in Guiguer *et al.,* (2002) and Eloranta *et al.,* (2017) on a Delta Plus

182   Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany)

183   coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an

184   analytical accuracy of ± 0.2% (δ^{13}C) and ± 0.3% (δ^{15}N). Measurement accuracy was established

185   through the repeat analysis of internal laboratory standards calibrated against International

186   Atomic Energy Agency standards H6 for carbon and N1 and N2 for nitrogen, with all results

187   reported in delta notation (δ) relative to the international standard Vienna Peedee Belemnite,

188   VPBD, for δ^{13}C (Craig, 1957) and atmospheric nitrogen for δ^{15}N (Mariotti, 1983). As C:N ratios

189   in general did not exceed 4 (44 of 48), lipid extraction or correction using mathematical models

190   was not completed (Jardine *et al.,* 2013).

191

192   For all captured fish, obtained δ^{15}N values were used as an index of piscivory (cannibalism)

193   following Guiguer *et al.* (2002) and δ^{13}C values were used in the computation of percent littoral

194   reliance (PLR). A two-source mixing model was used to estimate PLR (Schwarcz, 1991; Vander

195   Zanden *et al.,* 2011) and corrected to account for trophic fraction between predator and prey

196   using the 0.4‰ value reported in Post (2002) for consumers analysed using muscle tissue.

197   Individuals with a PLR exceeding 50%, i.e. relying more heavily on littoral than pelagic

198   resources, were classified as reliant on littoral production and compared using ANOVA to

199   conspecifics relying more heavily on pelagic production (PLR<50%) to determine if there were

200   significant differences in average stomach fullness, average growth rate (mm/year) and

201   condition.

202   Percent littoral reliance was modelled as a function of key variables known to be associated with

203   differential habitat use including: length, δ^{15}N (trophic position), sex and depth as represented by

204   a binary variable (0, 1) for surface or bottom capture (e.g., Klemetsen *et al.,* 1989; Power *et al.,*

205   2012; Murdoch & Power 2013; Reist *et al.,* 2013) using a general linear model of the form:

206

207   (1) $\text{PLR (\%)} = a_0 + a_1 L + a_2 N + a_3 S + a_4 D + \varepsilon$

208

209   where L is fork-length (mm), N is the associated δ^{15}N measure obtained from the analysis of

210   dorsal muscle tissue, S is sex, D is the binary depth of capture variable, a_i is the ith estimated

211   model coefficient and ε is a normally distributed error term with mean zero and variance σ^2.

212   Models including all variables and combined subsets of variables were considered and the

213   modified information criterion (AIC_C) corrected for finite sample sizes was used for model

214   selection (Anderson, 2008). Akaike weights (w_i) which can be interpreted as the probability that

215   model *i* is the best approximating model for the data within the candidate set of models was also

216   computed (Anderson, 2008). Length as a function of age, sex and PLR were similarly estimated

217   using general linear models and AIC_C.

218

219   To contextualize the traits reported for Kerguelen *S. alpinus*, comparisons were made to other

220   literature studies of lacustrine Arctic charr populations from sub-Arctic and Arctic Canada,

221   Greenland, Iceland and Scandinavia. Consulted studies included: Sprules (1952), Skreslet

222   (1973), MacCallum & Regier (1984), Sparholt (1985), Naslund (1990), Vøllstand & L'Abée

223   Lund (1994), Jónsson & Skúlason (2000) Power *et al.* (2008), Berg *et al.* (2010) and Borgstrøm

224   *et al.* 2015). The division between Arctic and sub-Arctic environments was based on geography,

225   with Arctic lakes being those located on the Canadian Arctic Island Archipelago, Greenland,

226   Svalbard or Jan Mayen Island and sub-Arctic lakes being those located on Iceland, continental

227   North America or Scandinavia. Mean-age-at-maturity data estimates were taken directly from

228   each study. As most studies did not report values for males and females separately, where male

229   and female values were reported a weighted-average using sex-ratio information as weights was

230   computed. Maximum age was set equal to the maximal age reported in each study or rounded up

231   if the age plus (age+) aging system was used. Where available, the instantaneous rate of

232   mortality (M) was similarly taken directly from each study. In cases where an estimate was not

233   provided, but where catch-at-age data allowed, an estimation of M using Chapman-Robson

234   methods (see above) was made. Studies for which M was estimated included: Sprules (1952),

235   Skreslet (1973), MacCullum & Regier (1984), Sparholt (1985), Naslund (1990); Jónsson &

236   Skúlason (2000), Berg *et al.* (2010) and Borgstrøm *et al.* (2015). The Kerguelen trait estimates

237   were then tested for significant differences from the sub-Arctic and Arctic trait means using

238   Student's t-test (Zar, 2010).

239

240   To contextualize the trophic status of Kerguelen *S. alpinus*, comparisons were made to other

241   literature reported populations similarly sampled from single-species high Arctic or sub-Arctic

242   lakes in Canada or Scandinavia. Candidate lakes were included as comparators if they met the

243   following criteria: had a known sample size$\geq$ 25, provided mean and standard deviation or

244   standard error for both $\delta^{13}C$ and $\delta^{15}N$ and were obtained from a representative size range of the

245   population, i.e., did not selectively target only large or small fish. The division between high

246   Arctic and sub-Arctic lakes was as described above. Consulted studies included: Rognerud *et al.,*

247   2002; Karlsson & Byström 2005; Gantner *et al.,* 2010; van der Velden *et al.,* 2012; van der

248   Velden *et al.,* 2013; Eloranta *et al.,* 2017 and Power (unpublished data). Obtained data were

249   used to construct standard stable isotope cross-plots (mean$\pm$standard deviation along each

250   isotope axis) and estimate isotopic niche width (Jackson *et al.,* 2011). Distances among

251   population means were characterized using Euclidean distance and tested for significant

252   differences among groupings (high Arctic and sub-Arctic) where necessary using Welch's t-test

253   adjusted for significant differences among estimated group variances (Zar, 2010).

254

255   **Results**

256 Sampling yielded n=48 fish ranging in size from 198 to 415mm, with most (n=39) captured in

257 the bottom set sinking gillnets. The catch was equally split between the sexes, with females

258 being larger (one-way ANOVA, P=0.017) and heavier (P=0.029) than males but otherwise

259 equivalent (P>0.05, Table 1) in terms of all other biological characteristics (age, relative

260 condition, growth rate) and trophic indicators ($\delta^{13}C$, $\delta^{15}N$). Sex-dependent weight-length

261 regressions did not differ significantly (ANCOVA, P=0.802) and sexes were grouped to estimate

262 a combined weight-length regression (Table 2) for Lac des Fougères *S. alpinus,* the slope of

263 which (2.732) was significantly less than 3 (t-test=-3.199, P=0.002) and indicative of allometric

264 growth. Mean age-at-maturity was estimated at 5.59 years, or at 310mm in length terms. The

265 narrow range of ages (4-7) and the lack of younger samples precluded estimating a standard von

266 Bertalanffy growth model, but regression of length as a function of age, sex and PLR yielded a

267 significant model ($F_{2,44}$ = 44.148, r^2=0.667) with both age and PLR as significant explanatory

268 variables (Table 2). Age was approximately twice as important a determinant of length than PLR

269 (age β=0.646, sex β=0.341). Sex-specific survival rates over the age 5-7 interval did not differ

270 significantly, yielding over-lapping 95% confidence intervals (male: 0.479-0.831, female:0.434-

271 0.755) and data were aggregated to yield a single age 5-7 mortality rate estimate of 0.627 (95%

272 confidence interval=0.510-0.744). A test of the validity of the assumed geometric model

273 underlying the estimates found no evidence for departure from the critical assumption (P=0.617).

274

275 A maximal $\delta^{15}N$ of 9.07‰ and limited $\delta^{15}N$ range (2.03‰) provided no evidence of piscivory

276 or cannibalism and indicated a limited degree of trophic diversity among sampled individuals.

277 Examination of gut contents during the assessment of stomach fullness similarly yielded no

278 evidence of fish consumption immediately prior to capture. Percent littoral reliance estimated

279 using the mean plus one standard deviation of littoral captured Nematodes as the littoral end-

280 member and mean minus one standard deviation of zooplankton as the pelagic end member

281 indicated Lac des Fougères *S. alpinus* PLR ranged from 9 to 100%, mean±S.D.= 58.8±22.8%,

282 with peaks between 30 and 40% and 70 and 80% reliance (Figure 2). While PLR did not differ

283 significantly between the sexes ($F_{1,46}$=2.315, P=0.135), fish with higher PLR (>50%) differed

284 significantly in body size (length: $F_{1,46}$=13.408, P=0.001; weight: $F_{1,46}$=14.157, P<0.001),

285 growth rate ($F_{1,45}$=9.04216, P=0.004) and feeding ecology (stomach fullness: $F_{1,46}$=4.870,

286 P=0.032; $\delta^{15}N$: $F_{1,46}$=10.083, P=0.003), with fish more reliant on littoral production being larger,

287 faster growing, having fuller stomachs and feeding at a lower trophic level than their more

288 pelagic reliant conspecifics (Figure 3). Body condition, expressed as relative condition

289 ($F_{1,46}$=0.264, P=0.610) did not differ significantly between PLR groupings.

290

291 The "best" model (Akaike weight w_i = 0.511) for explaining variations in PLR among

292 individuals as determined by AIC_C included length ($F_{2,45}$= 49.466, P<0.001, positively related)

293 and $\delta^{15}N$ ($F_{2,45}$= 42.713, P<0.001, negatively related) as key explanatory variables and

294 explained 62.9% of the observed variation (Table 3). The "best" model was 2.21 times more

295 likely to be the best approximating model than the second model (Akaike weight w_i = 0.231)

296 which included length ($F_{3,44}$= 46.863, P<0.001), $\delta^{15}N$ ($F_{3,44}$= 43.213 P<0.001) and sex ($F_{3,44}$=

297 0.844, P=0.363). In the "best" model, standardized regression (βeta) coefficients indicated that

298 length (β=0.652) and $\delta^{15}N$ (β=-0.606) were approximately equivalent in relative importance as

299 explanatory variables.

300

301 A literature search yielded a total of n=41 sub-Arctic and n=13 Arctic lakes from Canada,

302 Greenland, Iceland and Scandinavia for at which estimates of two of the three traits describing

303 mean age-at-maturity, maximum age and the instantaneous rate of mortality could be obtained.

304 The Kerguelen mean age-at-maturity (5.59) did not differ significantly (t-test P=0.994) from the

305 sub-Arctic (mean±std. deviation:5.6±1.8, range:2-12) or the Arctic (t-test P=0.863; 5.7±2.5, 3-

306 11) lake values. Maximum age for sub-Arctic (12.4±3.3, 6-19) encompassed a range which

307 included Kerguelen (>7+), whereas the range for Arctic lakes (18.9±5.6, 10-28) did not. The

308 means for both groups differed significantly from the Kerguelen estimate (all t-test P<0.001).

309 Instantaneous rates of mortality for sub-Arctic lakes (0.594±0.209, 0.273-0.970) included a

310 wide-range of mortality estimates whose mean did not differ significantly (t-test P=0.367) from

311 the Kerguelen estimate (0.627), whereas the mean mortality of the Arctic lakes (0.346±0.106,

312 0.212-0.514) did differ significantly (t-test P<0.001). A bi-plot (Figure 4) of maximum age

313 versus M indicates thus indicated that estimated Kerguelen traits fell within the bounds of the

314 variation observed in sub-Arctic but not Arctic lakes, being included only in the ellipse

315 describing the mean±one standard deviation of the sub-Arctic lake data.

316

317   A total of 15 lakes from the high Arctic and sub-Arctic regions of Canada and Scandinavia

318   containing, or presumed to contain, monomorphic *S. alpinus* as the sole resident species with

319   suitable stable isotope data and required minimum sample size were identified in a search of the

320   published literature: Canadian Arctic Archipelago (n=9), Svalbard (n=1), Fenno-Scandinavian

321   Peninsula (n=3) and northern Labrador (n=2). Stable isotope cross-plots of the data indicated a

322   separation between high Arctic island and sub-Arctic mainland populations that differed

323   significantly in mean δ^{15}N ($F_{1,13}$ = 17.315, *P*=0.001), but not in mean δ^{13}C ($F_{1,13}$ = 0.305, *P*=

324   0.590) or ellipse area ($F_{1,13}$ = 3.290, *P*= 0.093). Plotted collectively in bivariate stable isotope

325   space, the Lac des Fougères *S. alpinus* sample data fall at the boundary between the two groups

326   (Figure 5) with an average Euclidean distance of 1.82 from the sub-Arctic mainland populations

327   and 3.37 from the high Arctic island populations, a difference that is statistically significant

328   (two-sample t-test *P*=0.046).

329

330   **Discussion**

331

332   The test fishery of Lac des Fougères yielded indications of an established *S. alpinus* population

333   that was both growing and reproducing, based on the span of ages captured (4+ to 7+) and the 29

334   years that have elapsed since the release of 0+ fish into the lake. Limited trophic diversity as

335   described by the range of δ^{15}N values, low maximal δ^{15}N values and lack of fish in stomach

336   contents provided no evidence of consistent cannibalism within the population, although as

337   temporally integrated indicators of diet, stable isotope data cannot preclude incidental

338   cannibalism. Life-history traits estimated for the population equated with those typically reported

339   in the literature for sub-Arctic, but not Arctic lakes, with the instantaneous mortality rate (M0

340   being higher and the maximal observed age lower than is characteristic of Arctic populations.

341   The sample as a whole was approximately evenly split between reliance on littoral (48.8%) and

342   pelagic (51.2%) production, a reliance that agreed well with literature-based prediction interval

343   estimates (37-84%) from Scandinavian lakes (e.g., Eloranta *et al.,* 2015). There were, however,

344   size-dependent strategies within the population, with smaller fish tending to rely more heavily on

345   pelagic production. As a consequence, heavy littoral reliance held clear fitness advantages, with

346   those relying more heavily on littoral sourced carbon growing faster and attaining larger sizes.

347   When compared to other sub-Arctic and Arctic allopatric populations of *S. alpinus*, the

348 Kerguelen population appears to have more in common with the sub-Arctic populations of

349 Labrador and northern Scandinavia than with high Arctic island populations.

350

351 As habitat generalists, lacustrine populations of Arctic charr will exploit all available habitat

352 types, with usage often being dependent on age, life-stage and co-occurring species in the lake

353 (Power *et al.,* 2008). Arctic charr appear pre-adapted to low aggression (Power, 2002) and in the

354 face of intra- or inter-specific competition niche shifts usually occur (Power *et al.,* 2008). Thus,

355 Arctic charr have been shown to interactively segregate from other co-occurring salmonids

356 (Nilsson, 1965; Fraser & Power, 1989; Klemetsen *et al.,* 2003) and in a competitive context may

357 exhibit faster growth rates with reduced survival and longevity (Fraser & Power, 1989) as

358 evidenced here. Stable isotope studies of Arctic charr feeding patterns completed elsewhere

359 suggest that resource use separation within populations has the effect of lowering resource

360 competition, but can impose developmental energetic constraints dictating limits on body size,

361 maturation rate and fecundity (Guiguer *et al.,* 2002; Power *et al.,* 2005). While reduced

362 survivorship was not apparent in the Kergueln charr when comparing to other sub-Arctic

363 lacustrine populations, Kerguelen Arctic charr did evidence reduce longevity with respect to the

364 mean for other sub-Arctic populations. Further when compared to Arctic populations, constraints

365 became evident in terms of both reduced mortality and longevity.

366

367 Detailed studies of life-history and ontogeny in northern Norway indicate similar size-based

368 differences in habitat use as noted in the Kerguelen sample, with larger individuals occupying

369 the littoral zone and smaller individuals occupying the pelagic zone (Klemetsen *et al.,* 1989).

370 While gear selectivity precluded profundal capture of smaller juveniles in Lac des Fougères, one

371 might presume use of either profundal habitats as has been noted in Norway, e.g. Takvatn

372 (Klemetsen *et al.,* 1989), or tributary streams as has been noted in Arctic Canada (Sinnatamby *et*

373 *al.,* 2012). In fish, differences in resource usage almost always occurs along a littoral-pelagic

374 gradient (Robinson & Wilson, 1994) and may be associated with the development of a

375 distinctive resource polymorphism marked by variable morphology (e.g., head shape, mouth

376 position and jaw size), with one form (morphotype) feeding in the pelagic zone on zooplankton

377 and another form feeding in the littoral zone on available macroinvertebrates (Skulason & Smith,

378 1995; Svanbëck & Eklöv, 2002, 2003). In Arctic charr, the development of resource

379 polymorphisms are common and in the absence of competition from other species may develop

380 into stable niches under conditions of intense intra-specific competition (Jonsson & Jonsson,

381 2001). Notably absent in the Kerguelen sample was any suggestion of morphological variation,

382 which has been described extensively from both North American (Guiguer *et al.,* 2002; Power *et*

383 *al.,* 2012) and European lakes (e.g., Hindar & Jonsson, 1982; Snorrason *et al.,* 1994; Pavlov

384 1997; Klemetsen *et al.,* 2003; Knudsen *et al.,* 2019). Time may explain the absence of

385 morphological and feeding correlates, although examples of the incipient divergence of traits

386 related to prey use in contemporary time frames exist (e.g., Michaud *et al.,* 2008). Thus, in

387 addition to providing a template for the detailed understanding of colonization dynamics, the

388 continued study of Kerguelen Arctic charr may provide insights into the mechanisms behind and

389 rates at which patterns of trait divergence can emerge in isolated populations of Arctic charr.

390

391 Although it occurs commonly in allopatric populations found at high latitudes in resource poor

392 environments with seasonally limited prey resources (Hammar, 1989, 2014; Svenning &

393 Borgstrøm, 2005), any suggestion of cannibalism was also notably absent from the Kerguelen

394 sample. Maximal $\delta^{15}N$ values varying between 8.8-9.0l and a small $\delta^{15}N$ range (2.0 l) indicative

395 of limited trophic diversity (Layman *et al.,* 2007) are inconsistent with cannibalism. In part, the

396 absence of cannibalism is related to fish sizes, which rarely exceeded 40cm in Kerguelen. In

397 Lake Hazen, Ellesmere Island, Guiguer *et al.,* (2002) noted cannibalism was size-limited and on

398 the basis of stable isotope data was practised by individuals >40 cm. Hobson & Welch (1995)

399 similarly gave 40 cm as the threshold for cannibalism on the basis of an isotopic analysis of

400 specimens from Char Lake, Cornwallis Island, as did Sparholt (1985) in a study of unexploited

401 Greenland lakes. Skreslet (1973) suggested 37 cm as the threshold above which Arctic charr

402 switched primarily to cannibalism in landlocked populations on Jan Mayen Island, whereas Riget

403 *et al.,* (1986) noted increasing cannibalism after 27cm, possibly facilitated by the presence of

404 three-spine sticklebacks (*Gasterosteus acculaeatus*). Cannibalism is most common in

405 carnivorous fishes whose diets include varying proportions of aquatic insects, crustaceans,

406 mollusks and fish and may rely on high conspecific densities and low prey diversity to develop

407 (Strictar Pereira *et al.,* 2017). Expressing catch biomass in catch per unit effort terms (per 100m^2

408 of net) yields a value 28g •m^{-2} considerable below 600-900g •m^{-2} range reported by Elornata *et*

409 *al.,* (2017) for Norwegian high alpine lakes suggests the low population densities when

14

410   combined with limited prey availability are unlikely to trigger the development of cannibalism in

411   Lac des Fougères. In addition, among Arctic charr, the phenomenon is more prevalent among

412   populations from the high Arctic (e.g. Canadian Arctic Archipelago, Svalbard, Jan Mayen)

413   decreasing in occurrence at more southerly latitudes, suggesting the prevalence of the trait may

414   be population-specific (Amundsen *et al.,* 1999).

415

416   Although aquatic productivity as measured by Chlorophyll-*a* in Kergulen lakes (mean=0.84

417   $\mu g \bullet L^{-1}$, Mairie 1985) is more similar to values observed in representative high Arctic island lakes

418   (mean=0.51 $\mu g \bullet L^{-1}$, Medeiros *et al.,* 2012; Dranga *et al.,* 2017) than values noted for

419   representative sub-Arctic lakes (mean =4.22 $\mu g \bullet L^{-1}$, Dranga *et al.,* 2017), the Lac des Fougères

420   population has closer isotopic affinity with the sub-Arctic populations than the High Arctic

421   Island populations. The similarity is likely results from the lack of cannibalism, which truncates

422   the range of possible $\delta^{15}N$ values in the fish. Variation in Arctic charr population size structure,

423   and by implication $\delta^{15}N$ or trophic structure (e.g., Bearhop *et al.,* 2004; Layman *et al.,* 2007) has

424   been linked with seasonality in food supply (Hammar, 2014), which has been noted to favour the

425   development of cannibalism (Griffiths, 1994). In Kerguelen, the limited seasonal range in

426   temperatures, i.e. mean summer-winter difference of approximately $6^{o}C$ (Frenot *et al.,* 1997;

427   Heirman *et al.,* 2012), and lack of ice cover reduce the likelihood of cannibalism developing by

428   removing the extended period of food shortages that have been linked with its occurrence

429   (Griffiths, 1994; Hammar, 2000). Thus low prey availability itself does not appear sufficient to

430   trigger the development of cannibalism, as has been suggest for high Arctic populations

431   (Hammar, 2000), unless coupled with strong seasonality in resource availability. Kerguelen

432   Arctic charr are able to subsist, grow and mature on the limited resources available without

433   having to resort to cannibalism as a survival strategy , possibly due to a low population density

434   and notable high growth efficiency in cold water (Larsson *et al.,* 2005; Forseth *et al.,* 2009).

435

Conclusion

Evidence from the test fishing of Lac des Fougères indicates that subsequent to their introduction, Arctic charr have been able to establish a self-sustaining population that has adapted to the unique conditions of the Kerguelen Islands. Like populations from similarly sized lakes in Scandinavia, the Lac des Fougères population relies heavily on littoral production and follows an apparent size-dependent life-history template also seen in many Scandinavian lakes where smaller sized individuals occupy the pelagic zone and larger individuals dominate the littoral habitat. Mortality is equivalent with that typically observed in other sub-Arctic lake populations, but is high in comparison to Arctic lake populations. While maximum age is within the range observed for other sub-Arctic populations, it is low. Thus, while Arctic charr can survive and reproduce in the relatively unproductive Kerguelen lake environment, survival and growth nevertheless appear to be traded-off against survival to limit maximal age. Although expected, cannibalism does not appear to be occurring in the Kerguelen population, likely as a result of the lack of a seasonal pulse and the absence of prey resources that dominate in northern environments where cannibalism has been noted to increase with latitude as the seasonal pulse effect intensifies. The Kerguelen climate also appears to allow the Lac des Fougères population to trophically function more like northern hemisphere sub-Arctic than high Arctic island populations. The uniqueness of the population location and the recency of its introduction suggest that further monitoring of the population has the potential to yield valuable insights into both the adaptability of the species and its likely responses to ongoing large-scale environmental change as represented by climate change.

References

Amundsen, P.-A., Svenning, M.-A., & Siikavuopio, S. I. (1999). An experimental comparison of cannibalistic response in different Arctic charr *(Salvelinus alpinus* (L.)) stocks. *Ecology of Freshwater Fish*, 8, 43-48.

Agresti, A. (2002).*Categorical data analysis* (2nd ed., p.710), New York, NY: John Wiley and Sons.

Anderson, D. R. (2008). *Model based inference in the life sciences: A primer on evidence* (p. 184). New York, NY: Springer-Verlag.

Arismendi, I., Penaluna, B. E., Dunham, J. B., Garcıa de Leaniz, C., Soto, D., Fleming, I. A., Gomez-Uchida, D., Gajardo, G., Vargas, P. V., & Leon-Munoz, L. (2014). Differential invasion success of salmonids in southern Chile: Patterns and hypotheses. *Reviews in Fish Biology and Fisheries*, 24, 919–941.

Aymes. J. C., Vignon, M., Beall, E., Guéraud, F., & Gaudin, P. (2016). Age validation of the Kerguelen Islands brown trout, *Salmo trutta* L., and selection of the otolith optimal zone for investigating chronological data series. *Fisheries Research*, 176, 22-29.

Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., & Macleod, H. (2004). Determining trophic niche width: a novel approach using stable isotopes. *Journal of Animal Ecology*, 73, 1007-1012.

Berg, O. K., Finstad, A. G., Olsen. P. H., Arnekleiv, J. A., & Nilsseen, K. (2010), Dwarfs and cannibals in the Arctic: production of Arctic char (*Salvelinus alpinus* (L.)) at two trophic levels. *Hydrobiologia*, 652, 337-347.

Borgstrøm, R., Isdahl, T., & Svenning, M.-A. (2015). Population structure, biomass, and diet of landlocked Arctic charr (*Salvelinus alpinus*) in a small, shallow High Arctic lake. *Polar Biology*, 38, 309-317.

Chapman D. G., & Robson D. S. 1960. The analysis of a catch curve. *Biometrics*, 16, 354–368.

Craig, H. (1957). Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. *Geochimica et Cosmochimica Acta*, 12, 133–149.

Dartnall, H. J. G., & Hollowday, E. D. (1985). Antarctic rotifers. *British Antarctic Survey Scientific Reports*, 100: 46 pp.

Dartnall, H. (1995). The rotifers of Heard Island: preliminary survey, with notes on other freshwater groups. *Papers and Proceedings of the Royal Society of Tasmania*, 129, 7–15.

Davaine, P. & Beall, E. (1992). Relationships between temperature, population density, and growth in a sea trout population (*S. trutta* L.) of the Kerguelen Islands. *ICES Journal of Marine Science*, 49, 445–451.

De Smet, W. H. (2001). Freshwater Rotifera from plankton of the Kerguelen Islands (Subantarctica). *Hydrobiologia*, 446/447, 261-272.

De Smet, W. H. (2003). *Pourriotia carcharodonta*, a new genus and species of monogonont rotifer from subantarctic Îles Kerguelen (Terres Australes et Antarctiques Françaises). *Annales de Limnologie - International Journal* of *Limnology*, 39, 273-280

Dianna, J. S. (2004). *Biology and Ecology of Fishes* (2nd ed. p. 498). Traverse City, MI: Cooper Publishing Group, LLC.

Dranga, A. S, Hayles, S., & Gajewski, K. (2017). Synthesis of limnological data from lakes and ponds across Arctic and Boreal Canada. *Arctic Science*, 4, 167–185.

Dunham, J. B., Adams, S. B., Schroeter, R. E., & Novinger, D. C. (2002). Alien invasions in aquatic ecosystems: Toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. *Reviews in Fish Biology and Fisheries*, 12, 373–391.

Dunn, A., Francis R. I. C. C., & Doonan, I. J. (2002). Comparison of the Chapman-Robson and regression estimators of Z from catch-curve data when non-sampling stochastic error is present. *Fisheries Research*, 59, 149-159.

Eloranta, A. P., Kahilainen, K. K., Amundsen, P.-A., Knudsen, R., Harrod, C., & Jones, R. I. (2015). Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. *Ecology and Evolution*, 5, 1664-1675.

Eloranta, A. P., Sánchez-Hernández, J., Amundsen, P.A., Skoglun, S., Brush, J. M., Henriksen, E. H., & Power, M. (2017). Water level regulation affects niche use of a lake top predator, Arctic charr (*Salvelinus alpinus*). *Ecohydrology*, 10, 1-9.

Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Näslund, I., & Berglund, I. (2009). Thermal growth performance of juvenile brown trout *Salmo trutta*: no support for thermal adaptation hypotheses. *Journal of Fish Biology,* 74, 133–149.

Fraser, N. C., & Power, G. (1989). Influences of lake trout on lake-resident Arctic char in Northern Quebec, Canada, *Transactions of the American Fisheries Society*, 118, 36-45.

Frenot, Y., Gloaguen, J. C., & Trehen, P. (1997). Climate change in Iles Kerguelens and colonization of recently deglaciated areas by *Poa kerguelensis* and *P. annua*. In B. Battaglia, J. Valencia, & D. W. H. Walton (eds.) *Antarctic communities: species, structure and survival* (pp.358-366). Cambridge: Cambridge University Press.

560   Froese, R. (2006) Cube law, condition factor and weight-length relationships: history, meta-
561   analysis and recommendations. *Journal of Applied Ichthyology*, 22, 241-253.
562
563   Fry, B. (2006) *Stable Isotope Ecology* (p. 308). New York, NY: Springer Science+Business
564   Media.
565
566   Gantner, N., Power, M. Iqaluk, D., Meili, M., Borg, H., Sundbom, M., Solomon, K. R., Lawson,
567   G., & Muir, D. C. G. (2010). Mercury Concentrations in Landlocked Arctic char (*Salvelinus*
568   *alpinus*) from the Canadian High Arctic: Part I - insights from trophic relationships in 18 lakes.
569   *Environmental Toxicology & Chemistry*, 29, 621-632.
570
571   Grainger, E. H. (1953). On the Age, Growth, Migration, Reproductive Potential and Feeding
572   Habits of the Arctic Char (*Salvelinus alpinus*) of Frobisher Bay, Baffin Island. *Journal of the*
573   *Fisheries Research Board of Canada*, 10, 326-370,
574
575   Griffiths, D. (1994). The size structure of lacustrine Arctic charr (Pisces: Salmonidae)
576   populations. *Biological Journal of the Linnean Society*, 51, 337-357.
577
578   Guiguer, K. R. R. A. Reist, J. D. Power, M. & Babaluk, J. A. (2002). Using stable isotopes to
579   confirm the trophic ecology of Arctic charr morphotypes from Lake Hazen, Nunavut, Canada.
580   *Journal of Fish Biology*, 60, 348-362.
581
582   Hammar, J. (1989). Freshwater ecosystems of polar regions: vulnerable resources. *Ambio*, 18, 6–
583   22.
584
585   Hammar, J. (2000). Cannibals and parasites: conflicting regulators of bimodality in high latitude
586   Arctic char, *Salvelinus alpinus*. *Oikos*, 88, 33–47.
587
588   Hammar, J. (2014). Natural resilience in Arctic charr *Salvelinus alpinus*: life history, spatial and
589   dietary alterations along gradients of interspecific interactions. *Journal of Fish Biology*, 85, 81-
590   118.
591
592   Heirman, K., de Batist, M., Arnaud, F., & de Beaulieu, J.-L. (2012). Seismic stratigraphy of the
593   late Quaternary sedimentary infill of Lac d'Armor Kerguelen archipelago): a record of glacier
594   retreat, sedimentary mass wasting and southern Westerly intensification. *Antarctic Science*, 24,
595   608-618.
596
597   Hindar, K., & Jonsson, B. (1982). Habitat and food segregation of dwarf and normal Arctic charr
598   (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. *Canadian Journal of Fisheries*
599   *and Aquatic Sciences*, 39, 1030-1045.

600   Hobson, K. A., & Welch, H. E. (1995). Cannibalism and trophic structure in a high Arctic lake:
601   insights from stable-isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 52,
602   1195-1201.
603

Hórreo, J. L., Ayllón, F., Perez, J., Beall, E., & Garcia-Vazquez, E. (2011). Interspecific hybridization, a matter of pioneering? Insights from Atlantic Salmon and Brown Trout. *Journal of Heredity*, 102, 237-242.

Jackson, A. L., Inger, R., Parnell, A. & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80, 595–602.

Jaffal, A., Betoulle, S., Biagianti-Risbourg, S., Terreau, A., Sanchez, W., & Paris-Palacios, S. (2015). Heavy metal contamination and hepatic toxicological responses in brown trout (*Salmo trutta*) from the Kerguelen Islands. *Polar Research*, 34, 22784.

Jardine T. D., Hunt, R. J., Faggotter, S. J., Valdez, D., Burford, M. A., & Bunn, S. E. (2013). Carbon from periphyton supports fish biomass in waterholes of a wet-dry tropical river. *River Research and Applications*, 29, 560-573.

Jarry, M., Davaine, P., & Beall, E. (1998). A matrix model to study the colonization by brown trout of a virgin ecosystem in the Kerguelen Islands. *Acta Biotheortica*, 46, 253–272.

Jarry, M., Beall, E., Davaine, P., Gouraud, F., Gaudin, P., Aymes, J.-C., Labonne, J., & Vignon, M. (2018). Sea trout (*Salmo trutta*) growth patterns during early steps of invasion in the Kerguelen Islands. *Polar Biology*, 41, 925-934.

Jónsdóttir, H., Malmquist, H. J., Snorrason, S. S., Gudbergsson, G., & Gudmundsdóttir, S. (1998). Epidemiology of *Renibacterium salmoninarum* in wild Arctic charr and brown trout in Iceland. *Journal of fish Biology*, 53, 322-339.

Jonsson, B., & Jonsson N. (2001). Polymorphism and speciation in Arctic charr. *Journal of Fish Biology*, 58, 605-638.

Jónsson, B. & Skúlason, S. (2000). Polymorphic segregation in Arctic charr *Salvelinus alpinus* (L.) from Vatnshlídarvatn, a shallow Icelandic lake. *Biological Journal of the Linnean Society*, 69, 55–74.

Karlsson, J., & Byström, P. (2002). Littoral energy mobilization dominates energy for top consumers in subarctic lakes. *Limnology and Oceanography*, 50, 538-543.

Klemetsen, A., Amundsen, P.-A., Muladal, H., Rubach, S., & Solbakken, J. I. (1989). Habitat shifts in a dense, resident Arctic charr *Salvelinus alpinus* population. Physiology and Ecology Japan Special Volume 1, 187–200.

Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12, 1–59.

Knudsen, R., Eloranta, A. P., Siwertsson, A., Paterson, R. A., Power, M., & Sandlund, O. T. (2019). Introduction of *Mysis relicta* (Mysida) reduces niche segregation between deep-water Arctic charr morphs. *Hydrobiologia*, 840, 245-260.

Labonne, J., Vignon, M., Prevost, E., Lecomte, F., Dodson, J. J., Kaeuffer, R., Aymes, J. C., Jarry, M., Gaudin, P., Davaine, P., & Beall, E., (2013). Invasion dynamics of a fish-free landscape by brown trout (*Salmo trutta*). *PLoS One*, 8, e71052.

Larsson, S., Forseth, T., Berglund, I., Jensen, A. J., Näslund, I., Elliott, J. M., & Jonsson, B. (2005). Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology*, 50, 353–368.

Layman, C. G., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide from community-wide measures of trophic structure. *Ecology*, 88, 42-48.

Lecomte, F., Beall, E., Chat, J., Davaine, P., & Gaudin, P. (2013). The complete history of salmonid introductions in the Kerguelen Islands, Southern Ocean. *Polar Biology*, 36, 457–475.
Le Cren, E. D. (1951). The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology*, 20, 201–219.

Loewen, T. N., Gillis, D., & Tallman, R. F. (2010). Maturation, growth and fecundity of Arctic charr, *Salvelinus alpinus* (L.), life-history variants co-existing in lake systems of Southern Baffin Island, Nunavut, Canada. *Hydrobiology*, 650, 193–202.

MacCullum, W. R. & Regier, H. A. (1984). The biology and bioenergetics of Arctic charr in Char Lake, N.W.T., Canada. In Johnson, L. & Burns, B. L. (eds.) *Biology of the Arctic Charr. Proceedings of the International Symposium on Arctic charr, Winnipeg, Manitoba, May 1981*. (pp. 329-340). Winnipeg: University of Manitoba Press.

Maire P. (1985). Contribution à l'étude hydrobiologique du Lac Studer, écologie du phytoplancton et production primaire. Îles Kerguelen, Terres Australes et Antarctiques Françaises. Thèse. Université de Metz , 126 p.

Marandel. L., Gaudin, P., Guéraud, F., Glise, S., Herman, A., Plagnes-Juan, E., Véron, V., Panserat, S., & Labonne, J. (2018). A reassessment of the carnivorous status of salmonids: Hepatic glucokinase is expressed in wild fish in Kerguelen Islands. *Science of the Total Environment*, 612, 276-285.

Mariotti, A. (1983). Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. *Nature,* 303, 685–687.

Medeiros, A. S., Biastoch, R. G., Luszczek, C. E., Wang, W. A., Muir, D. C. G., & Quinlan, R. (2012). Patterns in the limnology of lakes and ponds across multiple local and regional environmental gradients in the eastern Canadian Arctic. *Inland Waters*, 2, 59-76.

694   Michaud, W., Power, M., & Kinnison, M. (2008). Trophically mediated divergence of Arctic
695   charr (*Salvelinus alpinus* L.) populations in contemporary time. *Evolutionary Ecology Research*,
696   10, 1051-1066.
697
698   Morat, F., Betoulle, S., Robert, M, Thailly, A. F., Biagianti-Risbourg, S., & Lecomte-Finiger, R.
699   2008. What can otolith examination tell us about the level of perturbations of Salmonid fish from
700   the Kerguelen Islands? *Ecology of Freshwater Fish*, 17, 617–627.
701
702   Murdoch, A., & Power, M. 2013. The effect of lake morphometry on thermal habitat use and
703   growth in Arctic charr populations: implications for understanding climate-change impacts.
704   *Ecology of Freshwater Fish*, 22, 453-466.
705
706   Naslund, I. (1990). The development of regular seasonal habitat shifts in a landlocked Arctic
707   charr, *Salvelinus alpinus* L., population. *Journal of Fish Biology*, 36, 401-414.
708
709   Nilsson, N. A. (1965). Food segregation between salmonoid species in north Sweden. *Institute of*
710   *Freshwater Research Drottningholm Report*, 46, 58-78.
711
712   Pavlov, S. D. (1997). Sympatric forms of charrs (gen. *Salvelinus*) from Ayan Lake (Taimyr
713   Peninsula). *Journal of Ichthyology*, 37, 485-494.
714   Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and
715   assumptions. *Ecology*, 83, 703-718.
716   Power, G. (2002). Charrs, glaciations and seasonal ice. *Environmental Biology of Fishes*, 64, 17-
717   35.
718   Power, M., Dempson, J. B. Reist, J. D, Schwarz C. J., & Power, G. (2005). Latitudinal variation
719   in fecundity among Arctic char populations in eastern North America. *Journal of Fish Biology*,
720   67, 255-273.
721   Power, M., Reist, J. D., & Dempson, J. B. (2008). Fish in high latitude Arctic lakes. In W. F.
722   Vincent & J. Laybourn-Parry (eds.), *Polar Lakes and Rivers: Limnology of Arctic and Antarctic*
723   *Aquatic Ecosystems* (pp. 249-268). Oxford: Oxford University Press.
724
725   Power, M., O'Connell, M. F., & Dempson, J. B. (2012). Determining the consistency of thermal
726   habitat segregation within and among Arctic charr morphotypes in Gander Lake, Newfoundland.
727   *Ecology of Freshwater Fish*, 21, 245-254.
728
729   Reist, J. D., Power, M., & Demspon, J. B. (2013). Arctic charr *(Salvelinus alpinus)*: a case study
730   of the importance of understanding biodiversity and taxonomic issues in northern fishes.
731   *Biodiversity,* 14, 45-56.
732
733   Renac, C., Moine, B., Goudour, J.-P., LeRomancer. M., & Perrache, C. (2020). Stable isotope
734   study of rainfall, river drainage and hot springs of the Kerguelen Archipelago, SW Indian Ocean.
735   *Geothermics*, 83, 101725.
736

737   Riget, F. F., Nygaard, K. H., & Christensen, B. (1986). Population structure, ecological
738   segregation, and reproduction in a population of Arctic char (*Salvelinus alpinus*) from Lake
739   Tasersuaq, Greenland. *Canadian Journal of Fisheries and Aquatic Sciences*, 43, 985-992.

740

741   Robson, D. S., ^& Chapman, D. G. (1961). Catch curves and mortality rates. *Transactions of the*
742   *American Fisheries Society*, 90, 181–189.

743

744   Robinson, B. W., & Wilson, D. S. (1994). Character release and displacement in fishes a
745   neglected literature. *American Naturalist*, 144, 596-627.

746

747   Rognerud, S., Grimalt, J. O., Rosseland, B. O., Fernandez, P., Hofer, R., Lackner, R., Lauritzen,
748   B., Lien, L., Massabuau, J. C., & Ribes, A. (2002). Mercury and organochlorine contamination
749   in brown trout (*salmo trutta*) and Arctic charr (*salvelinus Alpinus*) from high mountain lakes in
750   Europe and the Svalbard archipelago. *Water, Air, and Soil Pollution: Focus*, 2, 209–232.

751

752   Savary. R., Dufresnes, C., Champigneulee, A., Caudron, A., Dubey, S., Perrin, N., Fumagalli, &
753   L. (2017). Stocking activities for the Arctic charr in Lake Geneva: Genetic effects in space and
754   time. *Ecology and Evolution*, 7, 5201–5211.

755

756   Schwarcz, H. P. (1991). Some theoretical aspects of isotope paleodiet studies. *Journal of*
757   *Archaeological Science*, 18, 261-275.

758

759   Seber, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters* (2nd ed., P
760   654). London, Edward Arnold.

761

762   Sinnatamby, R. N., Babaluk, J. A., Power, G., Reist, J. D., & Power, M. (2012). Summer habitat
763   use and feeding of juvenile Arctic charr, *Salvelinus alpinus*, in the Canadian High Arctic.
764   *Ecology of Freshwater Fish*, 21, 309-322.

765

766   Skreslet, S. (1973). The Ecosystem of the Arctic Lake Nordlaguna, Jan Mayen Island. III.
767   Ecology of Arctic Char, *Salvelinus alpinus* (L.). *Astarte*, 6, 43-54.

768

769   Skulason, S., & Smith, T. B. (1995). Resource polymorphism in vertebrates. *Trends in Ecology*
770   *and Evolution*, 10, 366-370.

771

772   Snorrason, S. S., Skulason, S., Jonsson, B., Sandlund, O. T., Malmquist, H. J., & Jonasson, P. M.
773   (1994). Trophic specialisation in Arctic charr *Salvelinus alpinus* (Pisces: Salmonidae):
774   morphological divergence and ontogenetic niche shifts. *Biological Journal of the Linnean*
775   *Society*, 52, 1-18.

776   Sparholt, H. (1985). The population, survival, growth, reproduction and food of Arctic charr,
777   *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland. *Journal of Fish Biology*, 26, 313-
778   330.

779

780   Sprules, W. M. (1952). The Arctic charr of the west coast of Hudson Bay. *Journal of the*
781   *Fisheries Research Board Canada*, 9, 1-15.

782

783 Stonehouse B. (1982). La zonation écologique sous les hautes latitudes australes. *Comité*
784 *National Français des Recherches Arctiques et Antarctiques*, 51 , 531-537.
785

786 Strictar Pereira, L., Agostinho, A. A., & Winemiller, K. O. (2017). Revisiting cannibalism in
787 fishes. *Reviews in Fish Biology and Fisheries*, 27, 449-513.
788

789 Svanbäck, R., & Eklöv, P. (2002). Effects of habitat and food resources on morphology and
790 ontogenetic trajectories in perch. *Oecologia*, 131, 61-70.
791

792 Svanbäck, R., & Eklöv, P. (2003). Morphology dependent foraging efficiency in perch: a trade-
793 off for ecological specialization? *Oikos*, 102, 273-284.
794

795 Svenning, M.-A., & Borgstrøm, R. (2005). Cannibalism in Arctic charr: do all individuals have
796 the same propensity to be cannibals? *Journal of Fish Biology*, 66, 957-965.

797 van der Velden, S., Reist, J. D., Babaluk, J. A., & Power, M. (2012). Biological and life-history
798 factors affecting total mercury concentrations in Arctic charr from Heintzelman Lake, Ellesmere
799 Island, Nunavut. *Science of the Total Environment*, 433, 309-317
800

801 van der Velden, S., Evans, M. S., Dempson, J. B., Muir, D. C. G., & Power, M. (2013).
802 Comparative analysis of total mercury concentrations in anadromous and non-anadromous Arctic
803 charr (*Salvelinus alpinus*) from eastern Canada. *Science of the Total Environment*, 447, 438-449.
804

805 Vander Zanden, M. J., Vadeboncoeur, Y., & Chandra, S. (2011). Fish reliance on littoral–benthic
806 resources and the distribution of primary production in lakes. *Ecosystems*, 14, 894–903.
807

808 Vøllstand, L. A., & L'Abée Lund, J. H. (1994). Evolution of the life history of Arctic charr *Salevlinus*
809 *alpinus*. *Evolutionary Ecology*, 8, 315-327.
810

811 Zar, J. H. (2010). *Bisostatistical analysis* (5th ed., P. 944). Upper Saddle River, NJ: Prentice
812 Hall.
813

Table 1

1 Table 1: Summary biological information (mean∀standard deviation) by sex for *S. alpinus*
2 captured in Lac des Fougères. Variables that are significantly different at the 0.05 level are
3 underlined.
4
5
6

Biological Variable	Males	Females
Sample size	24	24
<u>Length (mm)</u>	28.6±4.6	31.8±4.4
<u>Weight (g)</u>	287.5±132.8	378.2±146.2
Age	5.8±0.9	6.1±0.9
Relative condition	1.0±0.1	1.0±0.1
Growth rate (mm/year)	5.0±0.6	5.3±0.5
% Littoral Reliance	49.8±19.0	58.6±21.2
$*^{13}C$	-23.2±1.3	-22.7±1.4
$*^{15}N$	8.1±0.4	8.0±0.5

7
8

Table 2

1   Table 2: Model coefficients, associated standard error and *P*-values for regression estimated
2   weight-length, age- and length-at-maturity and length-at-age models for *S. alpinus* captured in
3   Lac des Fougères. Also given are the regression F and proportion of explained variation
4   statistics.
5

Model	Coefficient	Std. error	*P*
Weight-Length ($F_{1,48}$ =1066.100, r^2 =0.959)			
Intercept	-1.547	0.124	< 0.001
Slope	2.732	0.084	< 0.001
Age-at-Maturity ($F_{2,46}$ =33.838, r^2 =0.601)			
$\forall$	7.686	2.905	0.011
$\exists$	-1.374	0.539	0.014
Length-at-Maturity ($F_{2,46}$ =31.967 r^2 =0.582)			
$\forall$	-7.143	2.879	0.017
$\exists$	0.230	0.095	0.020
Length-at-age ($F_{2,44}$ =44.148, r^2 =0.667)			
Intercept	5.016	2.857	0.086
Age	3.518	0.497	< 0.001
Percent littoral reliance	7.990	2.138	0.001

6

Table 3

1   Table 3: Summary of information-theoretic model selection statistics for models explaining the
2   littoral feeding reliance of Lac des Fougères *S. alpinus* as a function of length (cm), $\delta^{15}N$ (l), age,
3   and capture depth (surface, bottom. K defines the number of estimated model parameters. RSS
4   is the regression residual sum of squares. AIC_C is the small sample bias adjusted Akaike
5   information criterion. Δ_i is the difference between the model-specific AIC_C and the AIC_C of the
6   best fitting model and w_i is the model-specific Akaike information weight.
7
8

Model	K	RSS	AIC_C	Δ_i	w_i
Length, $*^{15}N$	4	0.7229	-192.460	0.000	0.511
Length, $*^{15}N$, Sex	5	0.7093	-190.874	1.586	0.231
Length, $*^{15}N$, Depth	5	0.7164	-190.400	2.060	0.182
Length, $*^{15}N$, Sex Depth	6	0.7034	-188.656	3.802	0.076

9

Table 4

1
2   Table 4: Estimated regression coefficients, standardized regression coefficients (β_i), F-test and
3   associated *P*-value and observed power for the best approximating model for explaining the
4   percent littoral reliance of Lac des Fougères Arctic charr as judged using the AIC_C criterion.
5
6

Variable	Coefficient	β_i	F	*P*	Power
Intercept	1.861		32.066	< 0.001	0.999
Length	0.028	0.652	49.466	< 0.001	1.000
$*^{15}N$	- 0.268	- 0.606	42.713	< 0.001	1.000

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1 **TABLE and FIGURE Captions**

2

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20 associated *P*-value and observed power for the best approximating model for explaining the

21 percent littoral reliance of Lac des Fougères Arctic charr as judged using the AIC_C criterion.

22

23 Figure 1: Map of Kerguelen Island and position relative southern hemisphere land masses (left

24 panel), sampling loca~~lisa~~tion for Kerguelen Island Arctic charr (middle panel) and bathymetry of

25 Lac des Fougères (right panel)

26

27 Figure 2: Bi-variate stable isotope plot of Lac des Fougères *S. alpinus.* Black circles indicate the

28 predominantly littoral feeding individuals, while open circles indicate predominantly pelagic

29 feeding individuals. Ellipses correspond to approximately one standard deviation. Crosses denote

30 the mean ∀ one standard deviation of pelagic zooplankton and littoral captured nematodes used

31 to define a two compartment mixing model end members required to determine percent littoral

32 reliance. The inset histogram plots percent littoral reliance of all Lac des Fougères *S. alpinus*

33 computed using the mixing model.

34

35 Figure 3: Means ± S.E. (filled bars) and mean~~s~~±95% confidence interval~~s~~ (whiskers) of length

36 and average growth rate (top panel) and stomach fullness index and trophic level index, $*^{15}N$,

37 (bottom panel) for Lac des Fougères *S. alpinus* having high (> 50%) and low (< 50%) littoral

38 reliance as computed using a standard two compartment mixing model. In the top panel length is

39 plotted with black bars and whiskers~~white and grey~~ and growth rate with white bars and

40 whiskers~~black and hashed lines~~. In the bottom panel stomach fullness index is similarly plotted

41 with black bars and whiskers ~~and white~~ and $*^{15}N$ with white~~black and hashed lines~~ bars and

42 whiskers.

43 Figure 4: Plot of literature estimates of mortality versus observed maximum age for n=41 sub-

44 Arctic and n=13 Arctic lakes populated by Arctic charr. The black dot plots the estimates derived

45 for Kerguelen. The white and grey dots, respectively, plot the literature obtained estimates for

46 sub-Arctic and Arctic lakes. The solid lined and dashed ellipse, respectively, encompass the

47 mean∀one standard deviation of the data for sub-Arctic and Arctic lakes. The inset ~~inset~~ box-

48 and-whisker plot gives mean age-at-maturity data for the same set of lakes. The boxes plot the

49 means ± S.E. and the whiskers plot the means±95% confidence intervals. The single open
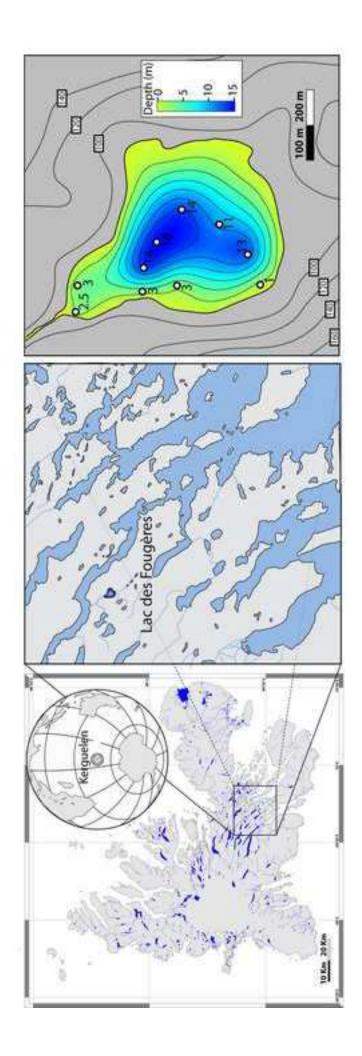
50 square plots the data for Kerguelen.

51

52 Figure 4~~5~~: Bi-variate staple isotope plot of in Lac des Fougères Arctic charr plotted as a black

53 circle (□) and allopatric populations from the sub-Arctic plotted as grey squares (–□–) and high

54 Arctic island populations plotted as open square (ᴳ). A: Arresjøen, Svalbard (Rognerud *et al.,*

55 2002), B: Resolute Lake, Cornwallis Island (Gantner *et al.,* 2010), C: 12 Mile Lake Cornwallis

56 Island (Gantner *et al.,* 2010), D: 9 Mile Lake, Cornwallis Island (Gantner *et al.,* 2010), E: Crazy

57 Lake, Baffin Island, (van der Velden *et al.,* 2013), F: Heintzelman Lake, Ellesmere Island (van

58 der Velden *et al.,* 2012), G: Unnamed Lake, Pangnirtung Fjord, Baffin Island (van der Velden *et*

59 *al.,* 2012), H: Lake C, Ellesmere Island (Power unpublished data), I: Small Lake, Cornwallis

60 Island (Gantner *et al.,* 2010), J : Lake G, Ellesmere Island (Power unpublished data), K:

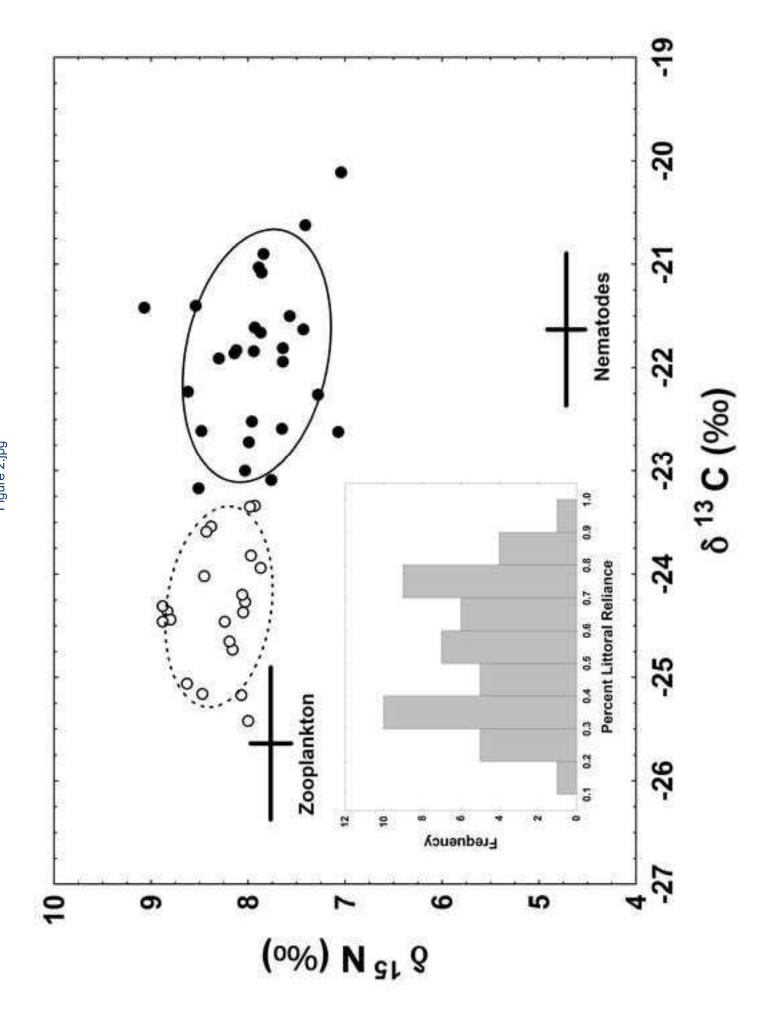61 Rauozutjaure, Sweden (Karlsson & Bystr`m 2005), L: Esker Lake, Labrador (van der Velden *et*

62   *al.,., 2012),* M: Unnamed Lake, Hebron Fjord Labrador (Power unpublished data), N:Cazajarvi,

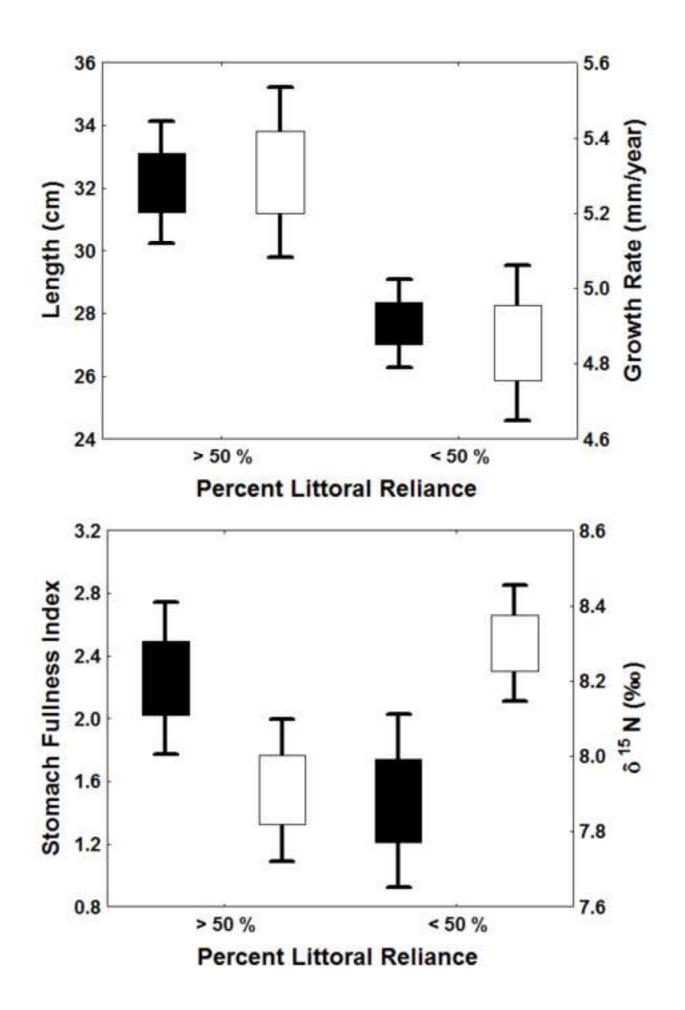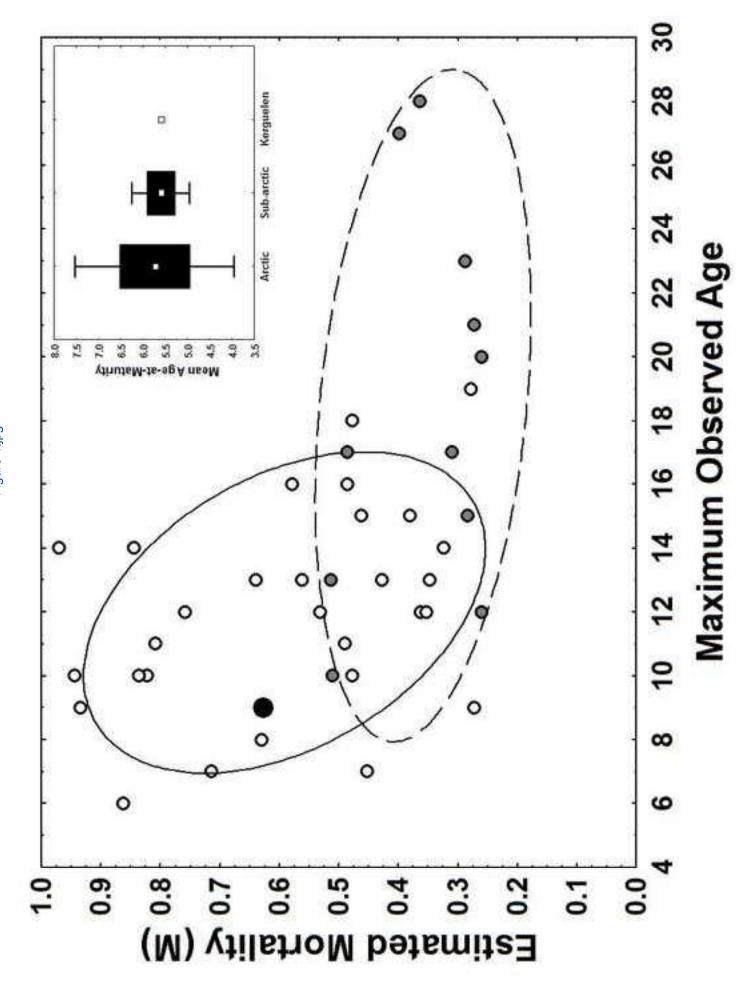63   Norway (Eloranta *et al.,* 2017), O: Govdajarvi, Norway (Eloranta *et al.,* 2017).

Figure 1

Figure 2

Figure 3   Click here to access/download;Figure;Figure 3 revised.tif ±

Figure 4

Figure 5