

1 **The association between parasite infection and growth rates**
2 **in Arctic charr – do fast growing fish have more parasites?**

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21 **Abstract**

22 Trophically transmitted parasites are known to impair fish growth in experimental studies, but
23 this is not well documented in natural populations. For Arctic charr (*Salvelinus alpinus* (L.)),
24 individual growth is positively correlated with food consumption. However, increased food
25 consumption will increase the exposure to trophically transmitted parasites. Using a correlative
26 approach, we explore the association between parasite abundance and the individual growth of
27 Arctic charr from five lakes within the same watercourse. The studied parasite species differ in
28 their life cycles and cost to the host. We predicted a positive association between parasite
29 abundance and fish growth for parasites of low pathogenicity reflecting high consumption rates,
30 and a negative association at higher parasite abundances for more costly parasites. We found
31 no direct negative associations between parasite abundance and fish growth. The relationship
32 between parasite abundance and growth was linearly positive for the low costly *Crepidostomum*
33 sp. and concave for the more costly *Eubothrium salvelini*. In natural fish populations the
34 negative effects of parasites on fish growth might be outweighed by the energy assimilated from
35 feeding on the intermediate host. However, experimental studies with varying food
36 consumption regimes are needed to determine the mechanisms underlying our observations.

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44 **Introduction**

45 Parasites occur in all animal populations and, by definition, have negative effects on their hosts
46 (Poulin & Morand, 2000; Dobson et al., 2008). For fishes, parasite infections can result in
47 reduced growth rates as seen for juvenile rainbow smelt (*Osmerus mordax*, Mitchill, 1814)
48 infected with *Proteocephalus* sp. (Sirois & Dodson, 2000), 3-spined sticklebacks (*Gasterosteus*
49 *aculeatus*, L.) infected with *Schistocephalus solidus* (Müller, 1776) (Pennycuick, 1971) and
50 sockeye salmon (*Onchorynchus nerka*, Walbaum, 1792) infected with *Eubothrium salvelini*
51 (Schrank, 1790) (Boyce, 1979). It might therefore seem paradoxical that parasite infection
52 typically increases with fish length (Poulin, 2000). This can be attributed to the accumulation
53 of parasites with host age, as age is closely related to body size in fish (Pacala & Dobson, 1988;
54 Zelmer & Arai, 1998; Poulin, 2000). However, within a fish age class there is often substantial
55 variation in size because of differences in individual growth rates (Wootton, 1998). Whether
56 parasites contribute to the variation in fish growth rates is not well studied. Here, we investigate
57 the association between parasitism and growth rates of Arctic charr (*Salvelinus alpinus* (L.)).

58

59 Many helminth parasites infect their hosts via the ingestion of parasitized prey. Such trophically
60 transmitted parasites display aggregated distributions in host populations (Shaw & Dobson,
61 1995; Poulin, 2013). Trophic niche specialization can be an important determinant of parasite
62 burden for many fishes (Bell & Burt, 1991; Williams et al., 1992), including Arctic charr
63 (Knudsen et al., 2004, 2014). Because parasites are harmful to their hosts, it would seem
64 obvious that predators should avoid parasitized prey. However, there might be no selection
65 pressure to avoid parasitized prey if the cost of becoming infected is low (Lafferty, 1992).

66

67 For Arctic charr, individual growth rates are positively correlated with food consumption
68 (Larsson & Berglund, 2005; Amundsen et al., 2007). Elevated consumption rates should
69 increase the exposure to trophically transmitted parasites, and heavy infections of such parasites
70 are observed in large-sized Arctic charr (Hammar, 2000; Gallagher & Dick, 2010; Henriksen
71 et al., 2016). Des Clers (1991) modelled the functional relationship between sealworm
72 (*Pseudoterranova decipiens*, Krabbe, 1878) burden, food consumption and size of Atlantic cod
73 (*Gadus morhua* L.) under the assumption that the parasite did not affect fish growth. The study
74 found a linear increase in parasite burden with food consumption, and an exponential increase
75 with the length of fish (des Clers, 1991). Fish that ate more grew faster and had more parasites.
76 For 3-spined sticklebacks infected with the large-sized cestode *S. solidus*, individual fish are
77 able to sustain high growth rates if access to food is not limiting (Barber et al., 2008). However,
78 the relationship between growth rates and parasite infection and food consumption depend on
79 the energetic value of the intermediate host that is consumed and the cost of the parasite
80 (Lafferty, 1992). For low-cost parasites, a positive linear assumption might be expected. In
81 contrast, for parasites that are costly, e.g. through causing mechanical damage, or evoking
82 energetically costly immune responses, one might expect a density-dependent response where
83 higher infections result in reduced host growth rates due to energy allocation to the immune
84 system rather than growth. This might influence investment in gonad development since there
85 is a trade-off between immunity and reproductive effort (Nordling et al., 1998; Lochmiller &
86 Deerenberg, 2000). For instance, high infections of *Diphyllbothrium* spp. may inhibit gonadal
87 development in Arctic charr (Curtis, 1984).

88

89 In the present study, we investigate infections of five trophically transmitted parasites within
90 three Arctic charr age classes from five lakes in the same watercourse. Of the five parasites,
91 three species (*Eubothrium salvelini*, *Diphyllbothrium* spp. and *Proteocephalus* sp.) use

92 copepods as intermediate hosts, while the remaining two (*Cyathocephalus truncatus* (Pallas,
93 1781) and *Crepidostomum* sp.) are transmitted via benthic invertebrates, mainly amphipods or
94 insect larvae (*Crepidostomum* sp. only). In addition, at least two of the parasites, *E. salvelini*
95 and *Diphyllobothrium* spp., can infect charr via paratenic fish hosts. Because the parasites vary
96 in their cost and which intermediate hosts they parasitize we expect them to associate differently
97 with individual growth rates. Three of the studied parasites have been described as costly to
98 Arctic charr development or growth: *E. salvelini* (Bristow & Berland, 1991; Saksvik et al.,
99 2001), *Diphyllobothrium* sp. (Bylund, 1972; Curtis, 1984; Halvorsen & Andersen, 1984) and
100 *C. truncatus* (Vik, 1958). *Proteocephalus* sp. and *Crepidostomum* sp. are intestinal parasites
101 where there are no clear evidence of high costs for infected fish. Our main research questions
102 are:

- 103 1. Is there a correlation between parasite infection and Arctic charr growth rates, and does
104 the direction or shape of the association differ between parasite species?
- 105 2. Does parasite infection relate to the probability that Arctic charr are sexually mature?

106

107 We hypothesize that

- 108 1. For low-cost parasites, like *Crepidostomum* sp. and *Proteocephalus* sp., there is a linear
109 positive relationship between fish growth and parasite intensity reflecting higher
110 consumption rates. For more costly parasites like *C. truncatus*, *Diphyllobothrium* spp.
111 and *E. salvelini* the association is non-linear with highly infected individuals having a
112 reduced size compared to moderately infected fish.
- 113 2. High infections of costly parasites will reduce the probability that an individual will
114 sexually mature.

115

116 **Materials and methods**

117 **Study lakes**

118 The five study lakes are all located in the Målselv river system in Troms county, northern
119 Norway (Table 1). All lakes are dimictic and oligotrophic. Three lakes, Fjellfrøsvatn, Lille
120 Rostavatn and Takvatn, are larger in size ($> 6 \text{ km}^2$ surface area) and situated between 100 and
121 215 meters above sea level. Moskanjavri and Vuomajavri, are smaller ($< 2 \text{ km}^2$ surface area)
122 shallower lakes located above the tree line (at 595 and 709 m.a.s.l. respectively). These two
123 lakes are remote ($> 10 \text{ km}$ from nearest road) and Vuomajavri is located within Dividalen
124 national park, and therefore under strong regulation regarding access with motorized
125 transportation (e.g. snowmobile or helicopter) as well as fishing equipment. The number of
126 sympatric fish species differ between the lakes (1-6 species; Table 1), but Arctic charr is the
127 most abundant fish species in all five lakes.

128

129 **Fish sampling and processing**

130 Fjellfrøsvatn, Lille Rostavatn and Takvatn were sampled in August 2010 using multi-meshed
131 gill nets with panels from 10 mm to 45 mm. Moskanjavri was sampled using the same method
132 in August 2016. Vuomajavri was sampled during the ice-covered period in April and May in
133 2016 and 2017 using traditional ice-fishing methods with baited hooks as required by
134 legislation. All fish were measured (fork length, mm), weighed (g), and assigned to sex and
135 maturation status (male vs. female and immature vs. mature). Sagittal otoliths were collected
136 and age was determined by surface readings of otoliths submerged in glycerol. Stomachs were
137 opened and fullness determined on a scale from 0 to 100 %. Prey groups were identified and
138 the contribution of each prey category to the total stomach fullness was calculated as a
139 percentage for each fish individual (Amundsen et al., 1996).

140

141 **Parasite sampling**

142 The number of *Diphyllobothrium* spp. cysts on the stomach wall was counted. There are two
143 species of *Diphyllobothrium* present in charr from these systems, *D. dendriticum* and *D.*
144 *ditremum*, and cyst counts provide an estimate of their combined total number (Kuhn et al.,
145 2017). Both *Diphyllobothrium* parasites are trophically transmitted to charr via ingestion of
146 infected copepods or small fish that are paratenic hosts (Halvorsen, 1970; Henriksen et al.,
147 2016). They mature in piscivorous birds (Halvorsen, 1970). All intestines were frozen and later
148 screened for parasites as described by Kuhn et al., (2016). A total of four taxa of metazoan
149 parasites were identified from the intestines; *Proteocephalus* sp., *Eubothrium salvelini*,
150 *Cyathocephalus truncatus* and *Crepidostomum* sp. All intestinal parasites use charr as their final
151 hosts. *Proteocephalus* sp. and *E. salvelini* are trophically transmitted from copepods, whereas
152 *C. truncatus* infects charr via the amphipod *Gammarus lacustris*. *Crepidostomum* sp. infects
153 charr via *G. lacustris* or insect larvae (Soldánová et al., 2017).

154

155 **Statistical analysis**

156 **Parasite infracommunities across lakes and diets.**

157 Because of the strong association between charr diet and parasite infection (Knudsen et al.,
158 2004, 2008) we investigated if parasite infracommunities (the community of parasites within a
159 single host individual (Bush et al., 1997)), could be predicted by individual diets and lake. This
160 relationship was modelled using canonical correspondence analysis (CCA) in the R package
161 ‘Vegan’ (Oksanen et al., 2013).

162

163 **Associations between parasite infection, growth and maturation**

164 The association between parasite infection and growth was examined using multiple regressions
165 with fish length as the response variable. As predictors we included the abundance of the
166 individual parasite species, and age and lake to control for differences in growth rates between
167 populations and cohorts. Fish sex was also included to test if there were differences between
168 males and females. We hypothesized that some associations between growth and parasitism
169 might be non-linear. To test for this we included a quadratic term (i.e. second order polynomial)
170 for all parasite species. Potential associations between parasite infection and probability of
171 maturation were examined using logistic regression with immature and mature fish as the
172 binomial response variable, controlling for age, lake, length and sex. For all models we included
173 interaction terms between parasites to see if co-infections could have a multiplicative rather
174 than additive effect. The models were then stepwise simplified using AIC values to end up with
175 the most parsimonious model. All statistical analyses were run in the software R (R Core Team,
176 2018).

177

178 **Results**

179 **Parasite infracommunity was predicted by lake and diet**

180 Infracommunities of parasites differed between lake populations (Fig. 1). *Crepidostomum* sp.,
181 *Diphyllobothrium* spp. and *E. salvelini* were most common (Table 2). *Proteocephalus* sp. and
182 *C. truncatus* were only prevalent in lakes Lille Rosta and Vuoma respectively, where they had
183 a high mean abundance (Table 2). In the CCA, Arctic charr were separated based on their
184 parasite infracommunities (Fig. 1). Arctic charr from Fjellfrøsvatn, Moskanjavri and Takvatn
185 clustered together and were mostly infected with *E. salvelini* and *Crepidostomum* sp (Fig. 1).
186 Arctic charr from Vuoma were mainly infected with the benthic transmitted *C. truncatus* and

187 *Crepidostomum* sp. strongly associated to a benthic diet (especially *G. lacustris*) (Fig. 1). In
188 contrast, Lille Rosta Arctic charr showed a clear separation from the other populations with
189 infracommunities dominated by copepod-transmitted *Proteocephalus* sp. and
190 *Diphyllobothrium* species and a diet dominated by zooplankton (Fig. 1). Diet and lake
191 accounted for 61.3 % of the total inertia in parasite infracommunity composition.

192

193 **Faster growing Arctic charr had higher infections of *Crepidostomum* sp. and *E. salvelini***

194 There was substantial variation in growth within age classes (Fig. 2). Model diagnostic plots
195 identified four clear outliers that were removed from multiple regression analysis. Interestingly,
196 these were all large (>350 mm) Arctic charr from lake Vuoma with very low parasite infections.
197 Lake, age, *Crepidostomum* sp. and *E. salvelini*. predicted variation in growth (Table 3, stepwise
198 multiple regression, $F_{8, 178} = 44.9, p < 0.001$, adjusted $r^2 = 0.65$). For *E. salvelini* a second-order
199 polynomial term significantly improved model fit (Fig. 3), whereas the association between
200 *Crepidostomum* sp. and fish size was linear (Fig. 3). The two parasites were not correlated
201 (Spearman rank correlation = 0.06, $P = 0.44$) and differed in their abundance range (*E. salvelini*
202 range 0 – 54, *Crepidostomum* sp. range 0 – 496). On average, when keeping all other predictors
203 constant, an increase of 10 *Crepidostomum* was associated with a 1.2 mm increase in length.
204 The association between length and *E. salvelini* abundance was concave, and positive until
205 around ~ 30 parasites, thereafter decreasing (Fig. 3).

206

207 **No associations were found between parasite infection and maturation probability**

208 Logistic regression indicated no association between the abundance of any parasite species
209 and Arctic charr maturation probability (Wald test, all $P > 0.19$). Following stepwise model

210 selection the final model included only age (Wald $\chi^2 = 13.3$, $df = 1$, $P < 0.001$), lake (Wald χ^2
211 $= 17.8$, $df = 4$, $P = 0.001$) and sex (Wald $\chi^2 = 9.4$, $df = 1$, $P = 0.002$).

212

213 **Discussion**

214 We found no evidence of any negative associations between parasite abundance and Arctic
215 charr growth rates. In contrast, there was a linear positive association between parasite intensity
216 and growth rate for the trematode *Crepidostomum* sp.. For *E. salvelini* the association was
217 concave and heavily infected fish were shorter than Arctic charr with moderate (~30 parasites)
218 infections. However, these heavily infected individuals were still larger than average sized fish.
219 Both *Crepidostomum* sp. and *E. salvelini* survive ~ 1 year in the fish (Thomas, 1958; Hernandez
220 & Muzzall, 1998), and are therefore indicative of feeding over the last year. In experimental
221 studies, *Eubothrium salvelini* can adversely affect the growth of salmonids (Boyce, 1979;
222 Saksvik et al., 2001) including Arctic charr (Gerdeaux et al., 1995). This tapeworm can infect
223 Arctic charr via both benthic and pelagic copepods as well as fish (Boyce, 1974; Poulin et al.,
224 1992; Hernandez & Muzzall, 1998), and is therefore difficult to use as a trophic tracer (Knudsen
225 et al., 2008, 2014). This was evident from our canonical correspondent analysis (CCA) where
226 *E. salvelini* was associated with surface insects in the stomachs, which are not hosts for the
227 parasite. The observed concave relationship could suggest that the presence of the parasite
228 might be harmful at elevated intensities, e.g. through infected Arctic charr individuals having
229 to allocate more energy to maintenance than growth.

230

231 We expected a positive relationship between *Crepidostomum* sp. and Arctic charr growth rates
232 because *Crepidostomum* spp. are small parasites (usually < 1 cm) with low pathogenicity to the
233 fish (Awachie, 1968). The intermediate hosts for *Crepidostomum* are large benthic prey items,

234 insect larvae and *G. lacustris* (Soldánová et al., 2017). Arctic charr feeding on *G. lacustris* have
235 high somatic growth rates (Hooker et al., 2017), and the positive association between
236 *Crepidostomum* sp. and Arctic charr growth could indicate elevated consumption rates on these
237 intermediate hosts. The linearity of the association suggests that the cost of high intensities of
238 *Crepidostomum* sp. is negligible. However, the assumption that parasite intensity exactly
239 represents transmission rates and thereby consumption rates of fish may be too simplistic.
240 Fishes elicit both adaptive and innate immune responses towards helminths, but the success of
241 these responses in preventing parasite establishment or expelling current infections is poorly
242 understood (Alvarez-Pellitero, 2008; Dezfuli et al., 2016). Lysne et al. (2006) suggested that
243 Atlantic cod (*Gadus morhua* L.) infected with the directly transmitted gill parasite *Lernaecoera*
244 *branchialis* (L.) grew faster than uninfected cod because the latter group spent energy to avoid
245 parasite establishment. A trade-off between immune function and growth have been observed
246 in other animals (Van Der Most et al., 2011), including 3-spined sticklebacks (Barber et al.,
247 2001). If such a trade-off exists for Arctic charr, the positive association between parasite
248 infection and growth rates observed for *Crepidostomum* sp. and *E. salvelini* could be a result of
249 slow-growing individuals allocating energy to immune functions rather than growth despite
250 having high consumption rates.

251

252 *Diphyllbothrium* spp. can live for several years in the fish and are considered harmful (Vik,
253 1957; Bylund, 1972). Because of its longevity, we expected this parasite to associate negatively
254 with growth, since high parasite loads would be indicative of long-term exposure to the parasite.
255 However, no evidence of negative association was found. Previous studies have suggested
256 elevated mortality of charr infected with *Diphyllbothrium*, particularly for *D. dendriticum*
257 (Henricson, 1978; Halvorsen & Andersen, 1984). We cannot address mortality rates in our data,
258 but the reduced growth rates observed in Arctic charr experimentally infected with *D.*

259 *dendriticum* (Blanar et al., 2005) were not observed in the present study of charr from natural
260 systems. However, because the majority of *Diphyllobothrium* spp. in Arctic charr in this
261 watercourse probably are *D. ditremum* (Henriksen et al., 2016; R. Knudsen, unpublished data),
262 we cannot rule out detrimental effects of *Diphyllobothrium* on Arctic charr from systems where
263 the relative abundance of *D. dendriticum* is higher.

264

265 *Cyathocephalus truncatus* and *Proteocephalus* sp. were the least prevalent parasite species
266 across all lakes. Thus, the sample size of infected fish was much reduced, and a larger sample
267 may have been required to detect any significant associations. *Proteocephalus* sp. was only
268 abundant in lake Lille Rosta, where the Arctic charr population feed mainly in the pelagic
269 (Knudsen et al., 2010, present study). The parasite resides in the intestine of Arctic charr, and
270 probably lives for up to 1 year in the fish (Scholz, 1999). Although not described as having
271 deleterious effects on rainbow trout (Ingham & Arme, 1973), results from other fish species
272 suggests that the pathogenicity of *Proteocephalus* species might vary between fish species and
273 stages (Ingham & Arme, 1973; Joy & Madan, 1989; Sirois & Dodson, 2000).

274

275 *Cyathocephalus truncatus*, was only abundant in lake Vuoma, where the fish fed heavily on
276 benthic prey items, mostly *G. lacustris*. Although previously described as highly pathogenic
277 (Vik, 1958), we did not observe a negative association with Arctic charr growth.
278 *Cyathocephalus truncatus* only lives for 2 months in the fish (Vik, 1958; Amundsen et al.,
279 2003) and the correlative approach used in the present study is problematic because the
280 infection history of each Arctic charr individual is unknown. It is worth noting that we caught
281 four large (34 – 37 cm) 6-year old individuals in lake Vuoma that, despite having fed heavily
282 on the intermediate host *Gammarus lacustris*, had very low *C. truncatus* infections. Considering

283 the high prevalence and abundance of *C. truncatus* in the lake, this could potentially suggest
284 that Arctic charr exposed to high parasite intensities can develop an immune response to prevent
285 future establishment of *C. truncatus*. For instance, reduced parasite establishment rates were
286 seen for rainbow trout repeatedly infected with *Diplostomum spathaceum* (Rudolphi, 1819)
287 (Stables & Chappell, 1986; Höglund & Thuvander, 1990). An important factor to consider is
288 that diet and parasite infections vary seasonally in Arctic charr (Amundsen et al., 2003;
289 Knudsen et al., 2008). Lake Vuoma was sampled in April and May by ice-fishing, whereas the
290 four other lakes were sampled in August using gill-nets. It is possible that the different sampling
291 periods (month and year) and methods could have influenced our results.

292

293 We expected that heavy parasite loads would delay maturity because there is a trade-off
294 between investments in immune responses and reproductive effort (Nordling et al., 1998;
295 Lochmiller & Deerenberg, 2000). It has previously been shown that *Diphyllbothrium* spp. can
296 inhibit gonadal development at elevated infection intensities (Curtis, 1984). However, if
297 individuals invest in reproduction at the cost of immune defense one would expect that mature
298 individuals suffer higher parasite infections. For instance, the cost of reproduction is associated
299 with immune suppression in male Arctic charr (Skarstein et al., 2001). Despite this, we could
300 not detect any negative or positive effects of parasite intensity on maturation probability. It
301 could be that the scale we used was too coarse-grained, and that potential effects manifest in
302 egg numbers or egg size, rather than the timing of maturation.

303

304 The results of the present study substantiate the complex nature of the host-parasite relationship
305 where the effects of parasites on hosts from wild populations are difficult to predict, particularly
306 for parasites that are trophically transmitted. More long-term studies are needed to investigate

307 effects of parasites on Arctic charr at the population level. Some of the parasites in the present
308 study (e.g. *E. salvelini* and *C. truncatus*) are known to manipulate the intermediate host to
309 facilitate predation from the final fish host (Poulin et al., 1992; Knudsen et al., 2001). Lafferty
310 (1992) suggested that if the strength of the manipulation is strong enough and the cost of the
311 parasite is relatively benign, such parasites may induce a net positive effect on their host. The
312 Arctic charr, with its highly plastic growth rates (Klemetsen, 2013), might be an ideal system
313 for testing this in controlled feeding experiments in future studies.

314

315 **Conclusion**

316 Whereas directly transmitted parasites have a negative effect on their fish host (e.g. Johnsen &
317 Jensen, 1991; Krkosek et al., 2013), the association is not straightforward for trophically
318 transmitted parasites. Although laboratory studies using experimental infections will show
319 negative effects of parasites on fish growth, the situation in natural systems may be quite
320 different. This is because high consumption rates, the behavior associated with acquiring
321 parasite infections, is beneficial to the fish. Therefore, potential negative effects on fish growth
322 could be mitigated by a positive effect of higher feeding rates that translates into elevated
323 infections with trophically transmitted parasites. Parasite infections observed in the present
324 study have been assimilated over a period between some months up to a few years. Growth,
325 however, has varied over the lifespan of the host (up to 6 years in the present study). It is
326 therefore problematic to draw lines between cause and effect. An experimental approach where
327 the relationship between food consumption, parasite infection, immunity and other
328 physiological parameters is tested properly clearly deserves attention in future work.

329

330

331

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515

516 **Tables**

517 **Table 1.** Characteristics of the five study lakes from the Målselv river system.

Lake name	Location (Lat, Lon)	Altitude (m)	Surface Area	Max. depth	Fish community
Fjellfrøsvatn	69°05'N, 19°20'E	125	6.5 km ²	80 m	AC, BT
Lille Rostavatn	69°00'N, 19°35'E	102	12.9 km ²	92 m	AC, BT, B, G, AS, CM
Moskanjavri	68°92'N, 20°19'E	595	1.8 km ²	< 15 m	AC, BT, B
Takvatn	69°07'N, 19°05'E	214	15.0 km ²	80 m	AC, BT, TS
Vuomajavri	68°67'N, 19°51'E	709	1.3 km ²	< 15 m	AC

518 AC = Arctic charr (*Salvelinus alpinus*), BT = brown trout (*Salmo trutta*), B = burbot (*Lota lota*), AS = Atlantic
519 salmon (*Salmo salar*), CM = common minnow (*Phoxinus phoxinus*), G = grayling (*Thymallus thymallus*), TS =
520 three-spined stickleback (*Gasterosteus aculeatus*).

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524 **Table 2.** Prevalence (P) and mean abundance (MA, standard error in parentheses) of the five
525 different parasite species in Arctic charr from the five study lakes (n = number of Arctic charr
526 examined). Lake abbreviations: FF = Fjellfrøsvatn, LR = Lille Rostavatn, MO = Moskanjavri,
527 TA = Takvatn, VU = Vuoma. *Diphyllbothrium* spp. abbreviated to *Diph.* spp.

Lake	n	Prevalence					Mean abundance (SE)				
		<i>Crep</i>	<i>Cyat</i>	<i>Diph</i>	<i>Eub</i>	<i>Prot</i>	<i>Crep</i>	<i>Cyat</i>	<i>Diph</i>	<i>Eub</i>	<i>Prot</i>
FF	54	68.5	3.7	68.5	96.3	9.3	24.6 (9.9)	0.1 (0.1)	4.6 (0.9)	11.5 (1.5)	0.1 (0.1)
LR	33	36.4	3.0	97.0	69.7	93.9	9.9 (8.5)	0.1 (0.1)	84.3 (14.0)	1.7 (0.4)	124.5 (20.3)
MO	18	100	5.6	33.3	88.9	0.0	44.1 (11.1)	0.1 (0.1)	0.9 (0.6)	12.9 (2.8)	-
TA	48	62.5	4.2	53.2	95.8	6.3	12.3 (2.6)	<0.1 (<0.1)	2.0 (0.4)	10.7 (1.0)	<0.1 (0.1)
VU	40	90.0	97.5	20.0	0.0	0.0	58.5 (14.4)	29.5 (4.7)	0.3 (0.1)	-	-

529 **Table 3.** Summary statistics from multiple regression model predicting Arctic charr fork length.
 530 Full model summary: Residual standard error = 24.35 on 178 degrees of freedom, adjusted $r^2 =$
 531 0.65, $F_{8,178} = 24.35$, $P < 0.001$.

Predictor variable	Coefficient (SE)	<i>t</i> value	<i>P</i> value
<i>E. salvelini</i>	3.20 (0.60)	5.35	< 0.001
<i>E. salvelini</i> ^2	-0.05 (0.01)	-3.44	< 0.001
<i>Crepidostomum</i> sp.	0.12 (0.03)	4.16	< 0.001
Age	15.50 (2.64)	5.86	< 0.001
Lake Lille Rosta	44.86 (6.31)	7.11	< 0.001
Lake Moskanjavri	51.79 (6.80)	7.61	< 0.001
Lake Takvatn	-16.79 (5.23)	-3.21	0.002
Lake Vuoma	-15.93 (6.67)	-2.39	0.018

532

533

534 **Figure legends**

535 **Figure 1.** Canonical correspondence analysis of parasite abundances (*Crepidostomum* sp,
 536 *Cyathocephalus truncatus*, *Diphyllbothrium* spp., *Eubothrium salvelini* and *Proteocephalus*
 537 sp.) as a function of lake and charr diet: benthos, insects (surface) or plankton. Individual Arctic
 538 charr are given as circle, the mean for each lake is given as large triangle. The two primary axes
 539 accounted for 95.9 % of the total inertia (61.3 %) explained by the model. Lake abbreviations:
 540 FF = Fjellfrøsvatn (gray), LR = Lille Rostavatn (blue), MO = Moskanjavri (green), TA =
 541 Takvatn (red), VU = Vuoma (yellow).

542

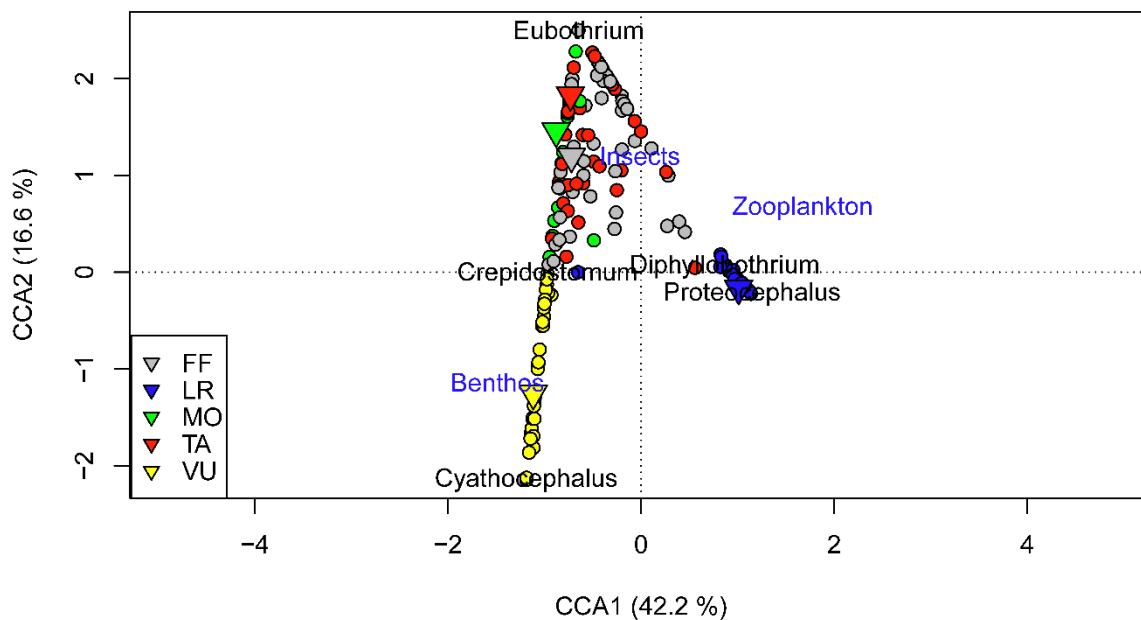
543 **Figure 2.** Variation in size distributions of the three age classes of Arctic charr examined. All
544 five study lakes are pooled together. Boxplots show median (bold line), upper and lower
545 quartiles (boxes) and 95 % confidence levels (whiskers).

546

547 **Figure 3.** Predicted relationship between Arctic charr length and the abundance of (a)
548 *Eubothrium salvelini* and (b) *Crepidostomum* sp. from the multiple regression analysis. Mean
549 values for age and lake were set to Fjellfrøsvatn. Stipled lines indicate the standard error of the
550 mean. The average size of Fjellfrøsvatn Arctic charr is given by the dotted line.

551

552 **Figure 1**

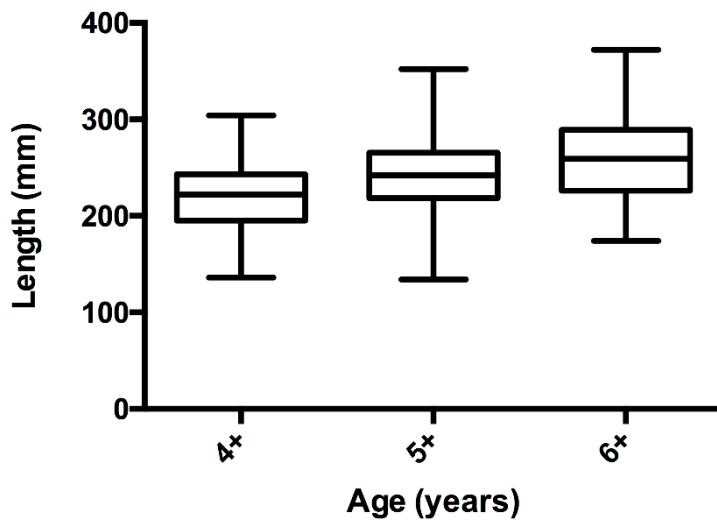


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556 **Figure 2**

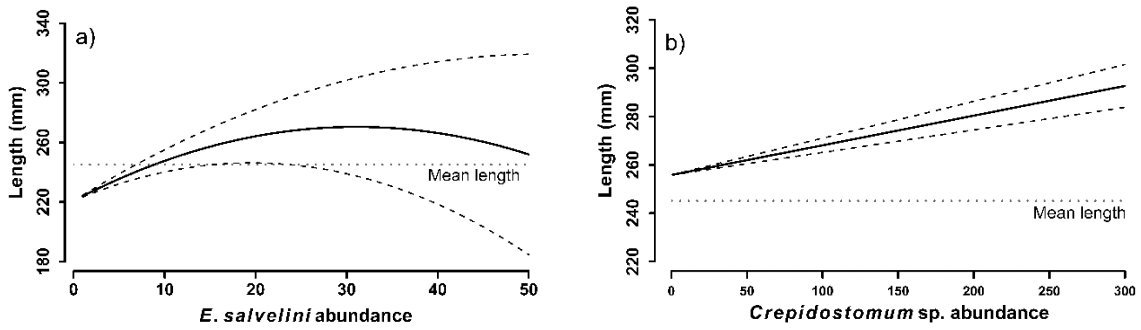


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559 **Figure 3**

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