Predation by brown trout (*Salmo trutta*) along a diversifying prey community gradient

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37   **Abstract:** Predation has a fundamental role in aquatic ecosystems, but the relative

38   importance of factors governing prey selection by predators remains controversial. In

39   this study, we contrast five lakes of a subarctic watercourse to explore how prey

40   community characteristics affect prey selection and growth rate of the common top

41   predator brown trout (*Salmo trutta*). The lakes constitute a distinct gradient of

42   different coregonid prey fish, ranging from monomorphic whitefish (*Coregonus*

43   *lavaretus*) to polymorphic whitefish co-occurring with vendace (*Coregonus albula*).

44   The brown trout was a morph/species- and size-specific pelagic predator, selecting the

45   small-sized, pelagic whitefish morph or vendace over the benthic whitefish morphs. In

46   all lakes, the average prey size increased with predator size, but small-sized prey were

47   also included in the diet of large predators. The selection of small-sized, pelagic prey

48   fish appeared to be a favourable foraging strategy for the brown trout, yielding higher

49   growth rates and an earlier ontogenetic shift to piscivory. The findings emphasize that

50   piscivory appear to be shaped by the diversity, size-structure and abundance of

51   available prey in a given community.

52   Keywords: Feeding ecology, piscivory, coregonids, prey selection, predator-prey size

53   relationship.

54   **Introduction**

55   Predator-prey interactions are essential for the population dynamics of both

56   predator and prey (e.g. Sinclair et al. 2003; Myers et al. 2007; Persson et al. 2007).

57   Most predators are selective feeders, having a diet that constitutes only a subset of the

58   available prey (reviewed by Stephens and Krebs 1986). The feeding selectivity of the

59   predator is influenced by the relative species composition of the prey community, and

60   predators are anticipated to select prey that provide an optimum energy gain relative

61   to the time spent on foraging (Stephens and Krebs 1986; Sih and Christensen 2001).

62   The diet selection depends on characteristics of both the predator (e.g. morphological

63   adaptations) and the prey (e.g. energetic value, predation susceptibility), and predators

64   may furthermore exhibit functional responses where their consumption rate is

65   influenced by the prey abundance (Abrams and Ginzburg 2000). Hence, several

66   factors may contribute to the feeding patterns of a predator, and potential outcomes

67   may range from predators feeding randomly to predators that feed highly selectively

68   on specific prey (Eggers 1977; Sih and Moore 1990). Although these basic

69   mechanisms of predator-prey interactions are of major interest in aquatic ecology

70   (reviewed in Werner and Gilliam 1984; Sih and Christensen 2001), they are often

71   difficult to study comprehensively in natural communities (Roughgarden 1986;

72   Kramer et al. 1997).

73   In lakes, predation by piscivorous fish may affect the prey fish communities

74   directly, i.e. by reducing prey fish density or altering size-structure (Persson et al.

75   1996), or indirectly by determining prey fish behaviour with respect to foraging,

76   habitat use, shoaling, diurnal activity patterns or growth (Turner and Mittelbach 1990;

77   Lima 1998). Habitat utilization is an important factor in predator-prey interactions

78   (Persson and Greenberg 1990; Byström et al. 2003) and, in contrast to the open-water

79   pelagic habitat, the littoral and profundal zones of lakes may provide refuges for prey

80   fish in terms of structural complexity and darkness, respectively. Predator-prey

81   relationships are also highly size dependent (Juanes 1994; Persson et al. 1996; Scharf

82   et al. 2000). Due to gape-size limitations, predatory fish usually experience an

83   ontogenetic diet shift from invertebrates to fish at a certain size depending on

84   availability, size and species-specific characteristics of the prey (Werner and Gilliam

85   1984; Mittelbach and Persson 1998). Some prey fish may on the other hand be able to

86   grow out of the "predation window", i.e. the size range where they are vulnerable to

87   predation (Claessen et al. 2002). Different prey species may furthermore have

88   different growth trajectories, leading to different time frames of predation

89   susceptibility. However, studies combining field data on prey diversity, size structure

90   and abundance with prey utilization of top predators are scarce.

91   Subarctic lakes in northern Europe usually represent relatively pristine, low

92   diversity ecosystems often dominated by salmonid fish. Brown trout (*Salmo trutta* L.)

93   is a common top-predator in many of these lakes, particularly in systems dominated

94   by two closely related coregonid fish (whitefish *Coregonus lavaretus* (L.) and/or

95   vendace *Coregonus albula* (L.)) where the brown trout may reach a large body size

96   through piscivory (Næsje et al. 1998; Vehanen et al. 1998). The coregonids in these

97   northern lakes exhibit extensive polymorphism and highly variable life-histories

98   (Kahilainen et al. 2003; Kahilainen et al. 2005; Amundsen et al. 2004a), and likely

99 constitute heterogeneous prey assemblages for the piscivorous brown trout,

100 potentially resulting in contrasting predator-prey interactions.

101   This study compares the predator-prey relationships of brown trout and

102 coregonids between five lakes of the subarctic Paatsjoki-Pasvik watercourse in

103 northern Europe. Three whitefish morphs have been identified in this watercourse

104 (Amundsen et al. 2004b; Kahilainen and Østbye 2006, Østbye et al. 2006), and

105 vendace is also present as an introduced, non-native species in the lower reaches

106 (Amundsen et al. 1999). The five lakes therefore comprise a gradient of different

107 coregonid prey communities for the brown trout, including one lake with a single

108 whitefish morph present, two lakes inhabited by three sympatric morphs, and two

109 lakes where the whitefish morphs co-occur with vendace. These study lakes in the

110 same watercourse thus enable comparisons of predator-prey interactions along a

111 gradient of increasing diversity of coregonid prey in otherwise similar lakes. The

112 following hypotheses were tested: (1) the predator (i.e. brown trout) prey selectively

113 on coregonids and prefers the habitat with the most profitable prey community; (2) the

114 predator switches to piscivory at smaller sizes if the prey community includes

115 abundant small-sized prey; (3) prey size selection is a positive function of predator

116 size, and (4) predator growth rate is positively correlated with the density of potential

117 prey in the environment.

Materials and methods

Study sites and fish communities

120   The headwaters of the Paatsjoki-Pasvik watercourse (68–69°N, 26–30°E)

121 discharge into Lake Inari (surface area 1102 km^2) in northern Finland, run throughout

122 Russia for 30 km and finally form the border between Norway and Russia for a

123 distance of approximately 120 km before entering the Arctic Ocean (Fig. 1). The total

124   catchment area of the watercourse is 18 403 km^2. The five lakes in the present study

125   are Lake Vuontisjärvi (referred to as Lake 1), Lake Muddusjärvi (Lake 2) and Lake

126   Paadar (Lake 3) on the Finnish side and Lake Skrukkebukta (Lake 4) and Lake

127   Vaggatem (Lake 5) on the Norwegian side. The surface area of the lakes varies from 7

128   to 48 km^2 with maximum and mean depths of 30–73 m and 6.5–14 m, respectively

129   (Table 1). All the lakes are oligotrophic (totP 6–9 µg·L^{-1}, totN 145–170 µg·L^{-1}),

130   neutral (pH of 6.8–7.2), and with some humic impacts (Secchi-depths between 3–8

131   m). The ice-free season in the lakes lasts from May/June to October/November.

132   All study lakes have a coregonid dominated fish fauna. Beside coregonids and

133   brown trout, the most common fish species include perch (*Perca fluviatilis* L.), pike

134   (*Esox lucius* L.), burbot (*Lota lota* (L.)), grayling (*Thymallus thymallus* (L.)), nine-

135   spined stickleback (*Pungitius pungitius* (L.)), and minnow (*Phoxinus phoxinus* (L.))

136   (Table 1). Brown trout is the most abundant salmonid predator in all lakes, consisting

137   of both stocked (>60% of the catches in all lakes) and native fish (Kahilainen and

138   Lehtonen 2002; Jensen et al. 2004). Stocked and native fish are approximately equal

139   sized (±20 cm) at start of the first growing season in lake at early summer (Kahilainen

140   & Lehtonen 2001). In the present study, the native and stocked brown trout have been

141   pooled in the analyses as they have similar diet preferences and growth patterns

142   (Kahilainen and Lehtonen 2001; Jensen et al. 2004).

143   The whitefish occur as three morphologically and ecologically distinct morphs.

144   Adaptive radiation and incipient ecological speciation is a likely explanation for the

145   adaptive evolution of these whitefish morphs (Østbye et al. 2006), and in this study

146   the morphs are considered as different biological species. In allopatry, the large

147   sparsely rakered (LSR) whitefish has a wide niche utilizating all principal habitat

148   types and prey (Amundsen et al. 2004a; Kahilainen et al. 2007). In sympatry, each

149   whitefish morph is specialized to one principal niche including a profundal dwelling

150   benthivore, the small sparsely rakered whitefish (SSR whitefish), a littoral dwelling

151   benthivore, LSR whitefish, and a pelagic planktivore, the densely rakered whitefish

152   morph (DR whitefish) (Amundsen et al. 1999, 2004a; Kahilainen et al. 2004). Lake 1

153   is inhabited by a single LSR morph, whereas all three whitefish morphs (SSR, LSR

154   and DR) occur in sympatry in lakes 2 and 3 (Kahilainen et al. 2004). In lakes 4 and 5,

155   the sympatric whitefish morphs co-occur with an introduced non-native coregonid

156   species, the vendace, which has become a highly abundant pelagic species after

157   invading these lakes in the early 1990's (Amundsen et al. 1999; Bøhn and Amundsen

158   2001, Bøhn et al. 2004). The somatic growth rates differ between the whitefish

159   morphs, being highest in LSR whitefish, intermediate to low in the DR whitefish and

160   lowest in the SSR whitefish (Kahilainen and Lehtonen 2003; Bøhn and Amundsen

161   2004). The vendace in Lake 4 and 5 have very slow growth rates, attaining maximum

162   sizes well below 15 cm (Bøhn et al. 2004).

163   **Field sampling**

164   A total of 2430 brown trout were sampled throughout June to October in 1998–

165   2004 by gillnets and fishing rod equipment (sampling details in Kahilainen and

166   Lehtonen 2003; Jensen et al. 2004, 2006). The total lengths and weights of the fish

167   were measured to an accuracy of 1 mm and 1 g, respectively, and stomachs were

168   removed and frozen (–20 ºC) for further analysis. In addition, scales and otoliths were

169   taken for age determination.

170   Prey fish samples were collected from the study lakes during September in

171   1998–2004. For prey fish sampling in lakes 1–3, gillnet series with mesh-sizes (knot

172   to knot) of 12, 15, 20, 25, 30, 35, 45 and 60 mm were used in the littoral and

173   profundal habitats, and a small pair-trawl (5 m high, 8 m wide and cod-end mesh size

174   3 mm) was used in the pelagic (details in Kahilainen et al. 2004). In lakes 4–5, prey

175   fish were caught in the littoral and profundal habitats using bottom gillnets series with

176   mesh-sizes of 10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm, and in the pelagic using

177   floating gillnet series with mesh sizes of 8, 10, 12.5, 15, 18.5, 22, 26 and 35 mm.

178   Prey fish were identified to species and whitefish to morph according to head

179   and gillraker morphology (Amundsen et al. 2004a; Kahilainen and Østbye 2006). The

180   total lengths and weights of the prey fish were determined to an accuracy of 1 mm and

181   1 g, respectively. Habitat use of coregonids was evaluated using catch per unit effort

182   (CPUE based on number of caught fish) of different morphs/species in the littoral,

183   profundal and pelagic (details in Kahilainen et al. 2004; Amundsen et al. 2004a).

184   Coregonids were the dominant fish species in all the study lakes (proportion in

185   catches > 80% in every lake) and the subsequent analyses was concentrated only on

186   this prey resource.

187   To assess the density of pelagic coregonids, areas deeper than 6 m were sampled

188   using a SIMRAD EY-500 echosounder equipped with downfacing split-beam

189   transducers operating at 120 kHz frequency (ES120-7F in lakes 1–3 and ES120-4×10

190   in lakes 4 and 5). Transects were placed equidistantly in lakes 1–3 (Kahilainen et al.

191   2004), whereas a combination of zigzag and parallel transects was applied in lakes 4

192   and 5. Details of equipment and settings are described in Kahilainen et al. (2004).

193   **Laboratory and data analyses**

194   The prey items in brown trout stomachs were identified as far as possible. Prey

195   fishes were identified to species by the remaining external features, and whitefish to

196   morph by gillraker examination (Kahilainen and Lehtonen 2002; Amundsen et al.

197   2004b). Fish prey other than coregonids (e.g. nine-spined sticklebacks, perch, arctic

198   charr and burbot) were pooled as other fish, whereas aquatic insects (including

199   Ephemeroptera, Trichoptera, Plecoptera, Odonata, Chironomidae and Coleoptera)

200   were pooled as invertebrates. Prey abundance (A_i, volume %), i.e. the proportion of

201   each diet category in the stomachs (sum of all categories = 100%), was calculated as

202   follows:

203                $A_i = 100 \times \Sigma S_i / \Sigma S_{tot}$

204   where S_i is fullness for diet category i and S_{tot} is the total stomach fullness (Amundsen

205   et al. 1996).

206   The similarity in coregonid composition between the brown trout stomach

207   contents and the proportional coregonid CPUEs from different habitats (littoral,

208   profundal, pelagic) was calculated using Schoener's (1970) index:

209    $$\alpha = 1 - 0.5\left(\sum_{i=1}^{n}\left|P_{xi} - P_{yi}\right|\right)$$

210   where P_{xi} is the proportion of coregonid species/morph i consumed by brown trout

211   population x, P_{yi} the proportion of coregonid species/morph i dwelling in habitat y,

212   and n the number of coregonid taxa in the lake. The index was also used to compare

213   the similarity in brown trout diets between the lakes. The index gives α-values from 0

214   to 1, where 0.00 and 1.00 indicates no overlap and complete overlap, respectively. An

215   index value $\geq$ 0.60 is considered to represent a biologically significant similarity

216   (Wallace 1981).

217   The total length of undigested prey fish in the brown trout stomachs were

218   measured to an accuracy of 1 mm, and the length of partially or entirely digested

219   coregonid preys were estimated from the otolith length (Kahilainen and Lehtonen

220   2001). The average coregonid prey length (log-transformed) in brown trout stomachs

221   was compared statistically between the lakes using ANCOVA with predator length as

222   covariate. Pairwise comparisons were made with Tukey's HSD test.   The relationship

223   between coregonid prey and brown trout length was furthermore estimated using

224   linear regression analysis for each lake separately. In order to get a general model of

225   the predator-prey length relationship between brown trout and coregonids in the

226   studied lakes, data were pooled from all lakes and performed a quantile regression

227   analysis estimated the median, upper (99th quantile) and lower (1th quantile) bounds

228   of the relationship (Cade et al. 1999).

229   Brown trout age was determined from both scales and otoliths in lakes 1–3 and

230   from otoliths in lakes 4–5. The somatic growth rate of brown trout was measured by

231   the annual specific growth rate (G, year $^{-1}$):

232    $$G = 100 \, (\ln W_2 - \ln W_1) \, (t_2 - t_1)^{-1}$$

233   where W_2 and W_1 are average body weights in age classes t_2 and t_1, respectively. G

234   was estimated between different age classes for wild fish, and between years after

235   stocking for stocked fish. The specific growth rates of the same age class in different

236   lakes were compared with ANOVA, and pair-wise comparisons between age classes

237   were made with Tukey's HSD test.

238   Hydroacoustic data were analyzed using EP500 (lakes 1–3) and Sonar5 (lakes 4

239   and 5) post-processing software. The analysis was started at a depth of 3 m and

240   stopped 0.5 m above the bottom. Integration threshold was –60 dB for all lakes, and

241   all targets were assumed to be coregonids with the exception of very small fish

242   targets, which were likely nine- or three-spined sticklebacks. These were excluded

243   from the coregonid density estimates by setting the target strength (TS) thresholds

244   between –54 and –59 dB based on TS-distributions. The coregonid density of each

245   transect was computed using observed TS-distributions (for details see Kahilainen et

246   al. 2004). The mean density of each lake and the variance of the means were

247   computed by taking variable transects length into account (Shotton and Bazigos

248 1984), and 95% confidence limits were estimated assuming a Poisson distribution

249 (Jolly and Hampton 1990).

Results

251 **Predator diet selection**

252 The brown trout were mainly piscivorous in all lakes. In lakes 1 and 2, an

253 ontogenetic diet shift from invertebrates to fish was observed with increasing brown

254 trout length, but in lakes 3–5 all examined length groups were almost exclusively

255 piscivorous (Fig. 2). In all lakes, coregonids were the dominant fish prey for the

256 brown trout and other fish (nine-spined stickleback, perch, burbot and Arctic charr)

257 were only occasionally eaten. In Lake 1, brown trout fed on the only available

258 whitefish morph (LSR), whereas the diet shifted to the pelagic DR whitefish in lakes 2

259 and 3 with the three sympatric morphs present. In Lake 4, brown trout preyed on DR

260 whitefish and vendace, whereas the predation shifted almost exclusively to vendace in

261 Lake 5 (Fig. 2). The profundal SSR whitefish was not found in any of the brown trout

262 stomachs.

263 According to Schoener's index (α), the similarity between the coregonid

264 proportions in the predator diet and the fish catches differed between habitats (except

265 in Lake 1 where LSR whitefish was the only coregonid present). In lakes 2–5, the

266 highest similarity (α = 0.80–0.96) was consistently found for the pelagic habitat

267 (Table 2). The similarity was somewhat lower for the profundal in lakes 2–4 (α =

268 0.51–0.76), and was generally the lowest for the littoral habitat of the lakes (α = 0.20

269 – 0.60). The brown trout diet similarity between lakes was biologically significant in

270 two cases; between lakes 2 and 3 and between lakes 4 and 5, where α was 0.99 and

271 0.69, respectively (Table 2, Fig. 3). In the other comparisons, the brown trout diets

272 were less similar (α < 0.60).

273 **Predator diet versus prey diversity, size distribution and abundance**

274   The average coregonid prey length in the brown trout stomachs was

275 significantly different between the lakes and showed a decreasing trend from Lake 1

276 towards Lake 5 (Fig. 3a), irrespective of the predator length (ANCOVA, $F_{4,1793} =$

277 129.4, $P < 0.0001$). The prey length further differed significantly in all pair-wise

278 comparisons between the lakes (Tukey's HSD tests, $P < 0.001$), except between Lake

279 1 and 2 ($P > 0.05$). In Lake 1, the brown trout stomachs included prey fish larger than

280 those observed in the pelagic habitat, suggesting that feeding to a large extent

281 occurred in the benthic habitats. Accordingly, the pelagic fish density in Lake 1 was

282 the lowest of all the study lakes. In lakes 2–5, the brown trout tended to select similar

283 sized (lakes 2-3) or slightly (lakes 4-5) smaller coregonid prey than those observed in

284 the catches (fig. 3). This difference in prey size is likely due to selectivity differences

285 between gillnet and pelagic trawl.

286   There was furthermore a high similarity between the brown trout diet and the

287 available coregonid prey in the pelagic in all the lakes (Fig. 3b, Table 2), and the diets

288 generally reflected the differences in prey communities between lakes. In Lake 1, only

289 LSR whitefish was available, in lakes 2 and 3 DR whitefish dominated strongly and in

290 lakes 4 and 5 DR whitefish co-occurred with vendace. Accordingly, the lakes divided

291 into three distinct groups in terms of the brown trout diet: 1) allopatric LSR was the

292 single prey species in Lake 1, 2) DR whitefish dominated the diet in lakes 2–3 and 3)

293 vendace and DR whitefish were the most important prey in lakes 4–5. The mean

294 density of pelagic coregonid prey increased from group 1 (10 individuals ha^{-1}) to

295 group 2 (640–1180 individuals ha^{-1}) and peaked in group 3 (2640–2690 individuals

296 ha^{-1}) (Fig. 3c). Differences between the three groups were statistically significant

297 according to the confidence limits of the density estimates.

298 **Predator–prey size relationship**

299   Within all lakes, the length of coregonid fish prey increased significantly with

300 predator size, but the slope of the regression was subject to large between-lake

301 variations (Fig. 4, Table 3). Prey length increased most rapidly with predator length in

302 Lake 1, where the abundance and diversity of coregonid prey was the lowest (Figs. 3

303 and 4). With the exception of Lake 4, the slopes generally decreased with increasing

304 abundance of small pelagic coregonid prey, and the lowest slope was observed in

305 Lake 5 (Figs 3 and 4, Table 3).

306   In the quantile regressions of the predator-prey length relationship, the median,

307 lower and upper bound slopes all increased significantly with increasing size of the

308 predator (Fig. 4b, Table 4). The range of prey sizes consumed expanded with

309 increasing predator size as the upper bound exhibited a steeper slope than the lower

310 one. The maximum, median and minimum prey sizes of a 40 cm predator were

311 estimated to be approximately 16 cm, 10 cm and 5 cm, i.e. 40%, 25% and 12%,

312 respectively, of the predator size. For all three parameters the relative prey length

313 decreased with increasing predator size. The slope of the lower bound (i.e. the 1%

314 quantile) was very low suggesting a continuum of small-sized coregonid prey in the

315 diet even when the predator attained considerably large sizes.

316 **Predator growth rate**

317   The annual specific growth rate (G) of brown trout during the first lake-year

318 (age class 1) differed significantly between the lakes (ANOVA, $F_{4,528} = 9.7$, $P <$

319 0.0001), and was significantly lower in Lake 1 ($G = 48.9$ g/year) compared to the

320 other lakes (range 80.9–93.9 g/year; Tukey's HSD tests, $P < 0.0001$) (Fig. 5).

321 Furthermore, there were no significant differences in growth rates between the three

322 age classes of brown trout in Lake 1 (ANOVA, $F_{2,59} = 1.3$, $P = 0.274$), whereas there

13

323   was a significant decrease in the specific growth rates of age class 2 and 3 compared

324   to age class 1 in Lake 2–5 (Tukey's HSD tests, $P < 0.0001$). When comparing the

325   growth rates of age classes 2 and 3, no significant differences were found between the

326   lakes (ANOVA, $F_{4,216} = 2.1$, $P = 0.088$ and $F_{4,112} = 0.3$, $P = 0.902$).

Discussion

328   Individuals of a variety of predator taxa are known to shift habitat and diet in

329   order to increase foraging gain, and these shifts may be a result of different

330   availability of prey resources and ontogenetic changes in resource use (Werner and

331   Gilliam 1984; Stephens and Krebs 1986). The present study examined different size

332   groups of a predator feeding in five different prey communities. Brown trout larger

333   than 20 cm was highly piscivorous in all the lakes, feeding almost exclusively on

334   coregonid prey fish. A minor exception was represented by the inclusion of

335   invertebrates in the smallest length groups in Lake 1 and 2. The switch to piscivory in

336   gape-limited predators depends on the availability of small-sized prey fish (e.g. Juanes

337   1994; Mittelbach and Persson 1998), and the delayed switch to complete piscivory

338   observed in Lake 1 and 2 was most likely related to a low abundance of small-sized

339   pelagic prey, particularly in Lake 1. In contrast, the brown trout switched earlier to

340   piscivory in lakes 3–5 with high abundances of pelagic prey available. Our findings

341   are equivalent to the general observations of an ontogenetic niche shift to piscivory at

342   lengths of 20-30 cm in salmonids (Keeley and Grant 2001), and furthermore support

343   the interpretation of pelagic fish as highly preferred prey for piscivorous brown trout.

344   In general the foraging patterns were changing from the consumption of a

345   monomorphic and mainly benthic dwelling coregonid, LSR whitefish, in Lake 1,

346   towards the pelagic specialist vendace dominating the diet in Lake 5. This reflects the

347   selective predation by the brown trout. We used Schoener's similarity index to

348   explore the main feeding habitat of the brown trout, and as the highest similarity

349   between the coregonid composition in the environment and in the pooled brown trout

350   diets were found for the pelagic habitat, our data support the conclusion that the

351   brown trout predominantly feeds in the open waters of the lakes. This is also

352   supported by the fact that nine-spined sticklebacks and minnows, which are common

353   prey for benthic predators like perch, pike and burbot in the watercourse (Amundsen

354   et al. 2003), rarely were observed in the brown trout stomachs. Furthermore, despite

355   the presence of LSR whitefish in all lakes, the piscivorous brown trout in Lake 2–5

356   were feeding almost exclusively on DR whitefish and vendace, i.e. the species that

357   predominantly occupied the pelagic habitat of these lakes. In Lake 1 in contrast, the

358   brown trout utilized prey fish larger than those observed in the pelagic habitat,

359   suggesting that the predator chose to forage on larger prey in the benthic habitat when

360   the abundance of small, pelagic whitefish was low. Foraging of piscivorous brown

361   trout has been reported elsewhere to occur in both littoral (e.g. Næsje et al. 1998) and

362   pelagic habitats (e.g. Hyvärinen and Huusko 2006). Our results suggest that the brown

363   trout is a piscivore that may utilize different coregonid prey species in different

364   habitats, but selectively switches to feed on relatively small-sized pelagic DR

365   whitefish or vendace when these are abundant.

366   For potential prey species, habitat selection is a trade-off between optimal

367   foraging and predator avoidance behavior (Lima and Dill 1990). In many systems, the

368   most profitable habitat for feeding is also considered to have the highest risk of

369   predation (Werner and Gilliam 1984; Byström et al. 2003). This is obviously the case

370   for DR whitefish and vendace feeding on zooplankton in the pelagic (Bøhn and

371   Amundsen 2001; Kahilainen et al. 2007), which is also the prime feeding habitat for

372   the piscivorous brown trout (Kahilainen and Lehtonen 2002). The profundal is

373   apparently the least profitable foraging habitat in these lakes, and is mainly inhabited

374   by the slow-growing SSR whitefish morph. The low light levels in this habitat provide

375   a good prey refuge from brown trout, and SSR whitefish was never found in the

376   brown trout stomachs. This is in accordance with the general description of brown

377   trout as a visual predator, relying upon good light conditions for efficient predation

378   (Langeland et al. 1991; Schulz and Berg 1992).

379   A positive relationship between body size of predator and prey has been

380   recognized in a large number of animal taxa (Werner and Gilliam 1984; Wootton

381   1998; Sinclair et al. 2003). Whereas piscivorous fish are able to ingest prey fish up to

382   approximately 50% of their own length (Juanes 1994), the prey-predator size-ratio of

383   20–30% found in the present study was close to the average ratios found in other

384   studies of piscivores (Hoyle and Keast 1987; Hambright et al. 1991; Mittelbach and

385   Persson 1998). Our results show a positive relationship between predator size and

386   prey size in all lakes, but the strength of the correlation was dependent on species

387   composition, size structure and abundance of the prey. The steepest incline in prey

388   size with increasing predator size was seen in Lake 1 (slope = 0.23) where allopatric

389   LSR whitefish was the only coregonid prey fish present, whereas the slope decreased

390   to almost zero in Lake 5 which was dominated by a small-sized, high-abundant

391   vendace population (slope = 0.03). Lake 4 represented an exception in this general

392   trend of predator-prey length slopes, obviously related to a more pronounced

393   availability of larger-sized (>13 cm) pelagic prey than in Lake 3 and 5.

394   In Lake 1, the growth rate of brown trout during the first year in the lake

395   appeared to be limited by the low availability of small-sized prey as compared to the

396   other lakes. The growth rates of larger age classes of the predator seemed in contrast

397   not to be limited by the prey size distribution in any of the lakes, as the growth rates

398   of these age classes were similar between all lakes. Thus, although prey size increased

399   with increasing predator size, large predators were not growth limited by the absence

400   of large prey. First year growth and the ontogenetic switch to piscivory were on the

401   other hand clearly enhanced by high abundance of small-sized prey fish.

402   Energetically, a positive correlation between predator and prey size is expected to

403   occur since larger prey contain more energy than smaller prey, but this may be

404   counteracted by increased energetic costs of searching, pursuing and handling, and

405   lower capture rates of larger-sized prey (Townsend and Winfield 1985; Crawley and

406   Krebs 1992; Sih and Christensen 2001). When combining all lakes, the quantile

407   regression showed a moderate, positive correlation between brown trout and

408   coregonid prey size. Although this shows that larger predators include larger prey in

409   their diet, the emerging pattern is that the size range of utilized prey broadens with

410   predator size, and that relatively small prey is continuously included in the diet.

411   Furthermore, the size of the coregonid prey was generally < 15 cm, suggesting that

412   coregonids up to this size are most vulnerable to predation and thus are inside the

413   predation window of brown trout (Bøhn et al. 2002; Kahilainen and Lehtonen 2003),

414   which apparently is quite narrow.

415   To maximize foraging efficiency and growth, a predator should select the most

416   abundant and available prey resources (i.e. Elliott and Hurley 2000). The prey fish

417   density in the pelagic habitat was lowest in the single-morph whitefish lake (Lake 1)

418   and increased markedly towards the vendace-dominated lake (Lake 5). In Lake 2 and

419   3, DR whitefish dominated the pelagic habitat at medium densities (see also

420   Kahilainen et al. 2004, 2005), whereas the highest pelagic prey densities were

421   observed in the vendace-invaded lakes 4 and 5. Our study showed that the ontogenetic

422   shift to piscivory and the growth rate of brown trout during the first year in the lake

423 was positively related to the abundance of pelagic prey fish and also demonstrated the

424 energetic profitability of pelagic foraging of the piscivorous trout. The apparent

425 profitability of selecting small-sized fish prey further suggests that the impact of such

426 a piscivore feeding strategy may be greater than earlier assumed (Miller et al. 1988),

427 and could have significant effects on prey morphology (Brönmark and Miner 1992)

428 and community structure (Hambright et al. 1991; Tonn et al. 1992; Byström et al.

429 2003). Thus, high densities of small-sized prey, in particular vendace and DR

430 whitefish, resulted in early shifts to piscivory, whereas low densities and higher

431 growth rates of the available prey fish apparently delayed the ontogenetic shift to

432 piscivory and reduced the predator growth.

433   In conclusion, our study demonstrates that brown trout is a habitat, species and

434 size-specific piscivore. The small sized pelagic prey, DR whitefish and vendace, were

435 consistently selected over the larger, benthic coregonid morph. A weak positive

436 correlation was observed between predator and prey length, but the continuous

437 inclusion of small prey suggests that this may represent favourable prey even for large

438 predators. Brown trout furthermore switched to piscivory earlier and had a higher

439 growth rate in lakes with small sized pelagic prey present. In the absence of small-

440 sized pelagic prey species like DR whitefish and vendace, the brown trout in contrast

441 shifted to larger fish prey and apparently also to feeding in the littoral habitat. Hence,

442 the brown trout is apparently also a flexible fish predator, being able to change

443 feeding habitat and prey selection in accordance with the availability of suitable prey.

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638 **Tables**

639 **Table 1.** Abiotic and biotic background data from the five study lakes. Whitefish

640 morphs and other fish species present in the study lakes in addition to brown trout are

641 indicated with abbreviations.

	Lake 1	Lake 2	Lake 3	Lake 4	Lake 5
Latitude (°N)	69°01'	69°00'	68°51'	69°33'	69°13'
Longitude (°W)	27°05'	27°00'	26°35'	30°70'	29°14'
Country	Finland	Finland	Finland	Norway	Norway
Surface area (km^2)	11	48	21	7	15
Altitude (m.a.s.l.)	151	146	144	21	52
Max depth (m)	31	73	56	38	30
Mean depth (m)	6.5	8.5*	11.7	14	4
Secchi depth (m)	8	3	6*	4–5.5	3–4.5
Color (mg Pt/l)	8*	15*	15*	16	17
pH	7.2*	7.2*	7.1*	6.9	6.8
Tot P (μ/l)	7*	5*	6*	7	9
Tot N (μ/l)	170*	160*	160*	156	145
Coregonid species & morphs	LSR	LSR,SSR, DR	LSR,SSR, DR	LSR,DR, VEN	LSR,DR, VEN
Other fish species	b,c,d,e,f, g,h	a,b,c,d,e,f, g,h,	b,c,d,e,f, g,h	b,c,e,f,g,h	b,c,e,f,g,h

642 **Note:** *, Data from Lapland Regional Environment Centre; LSR, large sparsely

643 rakered whitefish; SSR, small sparsely rakered whitefish, DR, densely rakered

644 whitefish; VEN, vendace; a, arctic charr; b, grayling; c, minnow, d, three-spined

645 stickleback; e, nine-spined stickleback; f, perch; g, pike; h, burbot.

646 **Table 2.** Similarity (Schoener's α) between pooled brown trout stomach contents and

647 proportional coregonid CPUE in different habitats of the study lakes. Values ≥ 0.60

648 are considered to represent biologically significant similarities and are given in bold

649 (except lake 1 with only one prey type present).

Habitat	Lake 1	Lake 2	Lake 3	Lake 4	Lake 5
Littoral	1	**0.60**	0.53	0.30	0.20
Profundal	1	**0.76**	**0.75**	**0.62**	0.51
Pelagic	1	**0.95**	**0.96**	**0.80**	**0.93**

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651 **Table 3.** Estimated parameters from linear regressions of the predator-prey total

652 length relationships in the studied lakes. Slope and intercept are indicated with ± 95%

653 CL.

Lake	n	Slope (± 95% CL)	Intercept (± 95% CL)	r^2	*P*
1	119	0.23 ± 0.11	2.52 ± 4.55	0.12	< 0.001
2	677	0.13 ± 0.02	6.38 ± 1.02	0.14	< 0.001
3	202	0.06 ± 0.03	5.68 ± 1.28	0.06	< 0.001
4	364	0.13 ± 0.05	4.11 ± 1.94	0.07	< 0.001
5	437	0.03 ± 0.02	8.66 ± 0.96	0.02	< 0.01
1–5	1799	0.11 ± 0.02	5.84 ± 0.72	0.08	< 0.001

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Figure captions

Fig. 1. (a) Map of Northern Europe showing the location of the Paatsjoki-Pasvik watercourse. (b) Map of the Paatsjoki-Pasvik watercourse indicating the location of study lakes 1–5. For details of the lakes see Table 1.

Fig. 2. Diet composition of different total length groups of brown trout from the studied lakes (a) – (e) = lakes 1–5. The number of examined stomachs containing prey items is indicated above the bars.

Fig. 3. (a) Coregonid length distribution in the pelagic catches and in brown trout diet in study lakes. Number of samples (n) and the average total length (TL) are also indicated. (b) Proportion of different coregonids in pelagic CPUE (upper circle) and brown trout diet (lower circle) for each lake. (c) Coregonid density with 95 % confidence limits (upper and lower bound values indicated) in pelagic areas (depth > 6 m) estimated with echosounding.

Fig. 4. (a) Predator-prey total length relationships in lakes 1–5 (a-1 to a-5) estimated with linear regression analysis. Solid line indicates regression line and hatched lines 95% confidence limits. See Table 3 for estimated parameters. (b) Quantile regression of the pooled predator-prey size relationships with median (solid line) and 1 and 99% quantiles (hatched lines). The estimated slopes from the quantile regression were 0.12 (median), 0.17 (upper bound, 99% quantile), and 0.07 (lower bound, 1% quantile), respectively ($P < 0.001$).
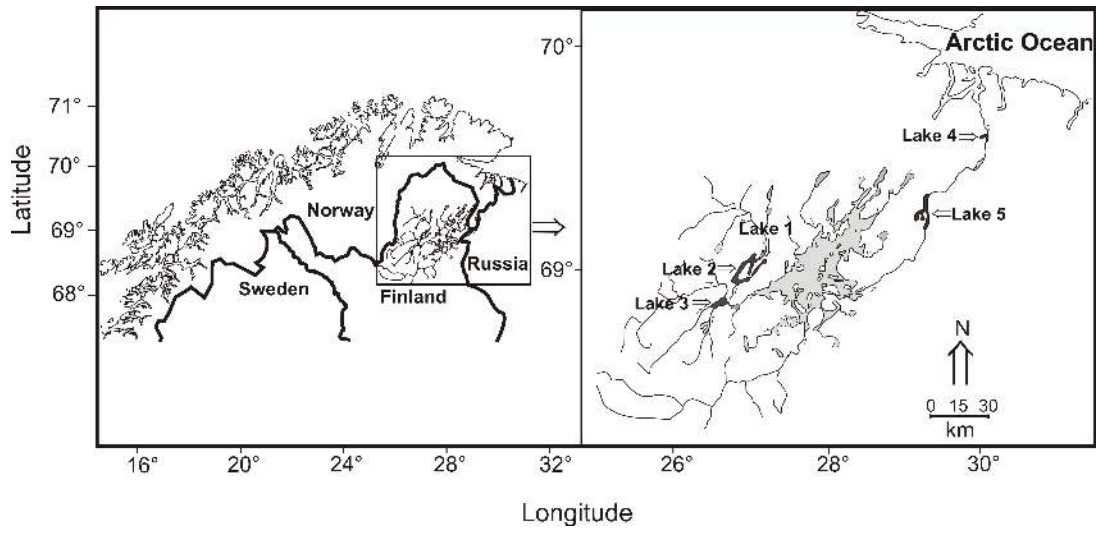
Fig. 5. Annual specific growth rate (G, year $^{-1}$) of brown trout with 95% confidence limits in lakes 1–5.

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685   Fig. 1.

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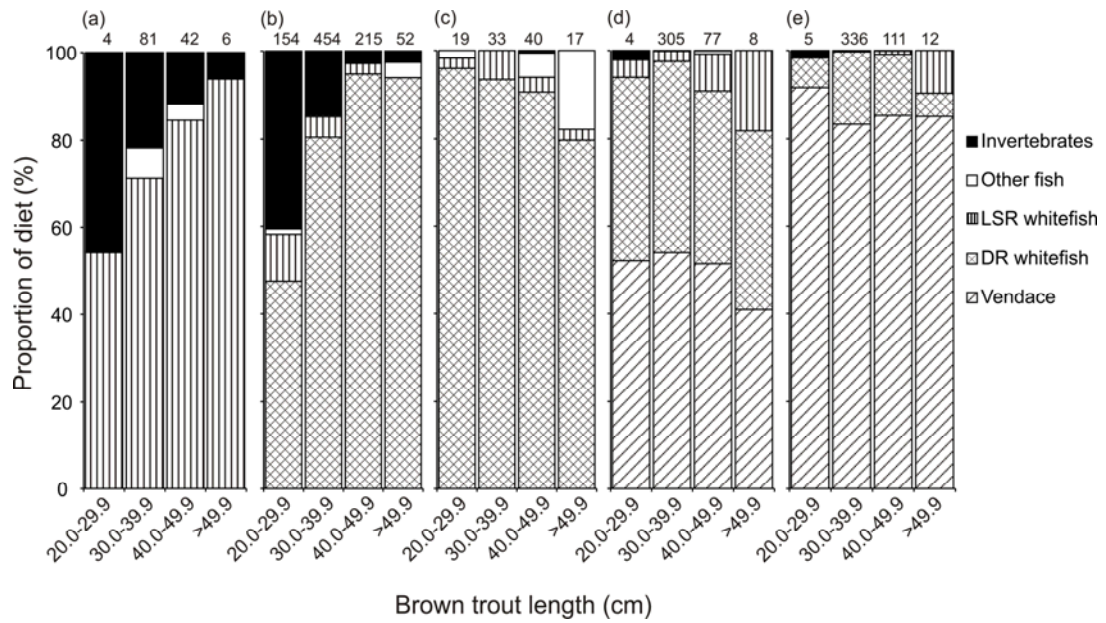694

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703   Fig. 2.

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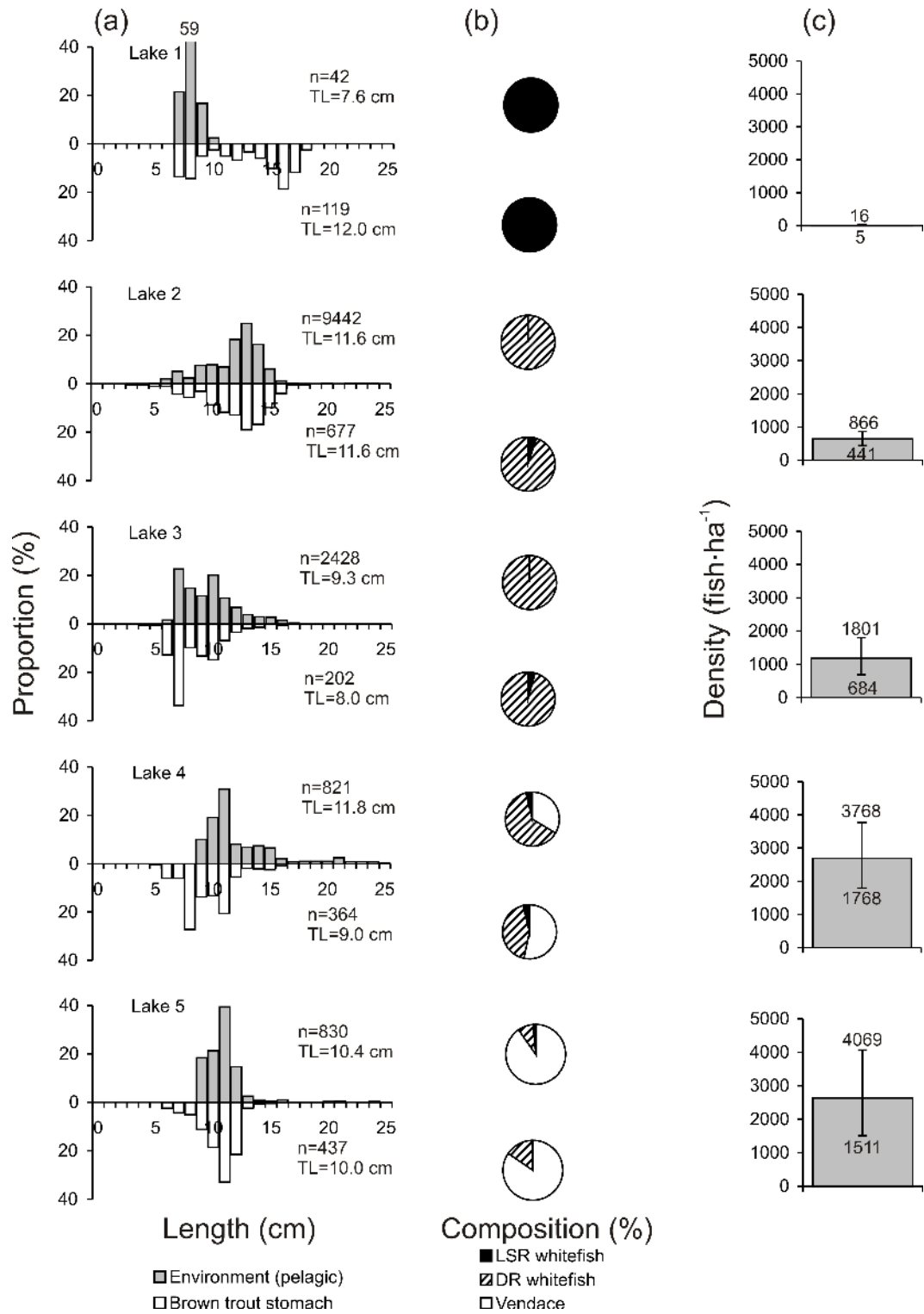709

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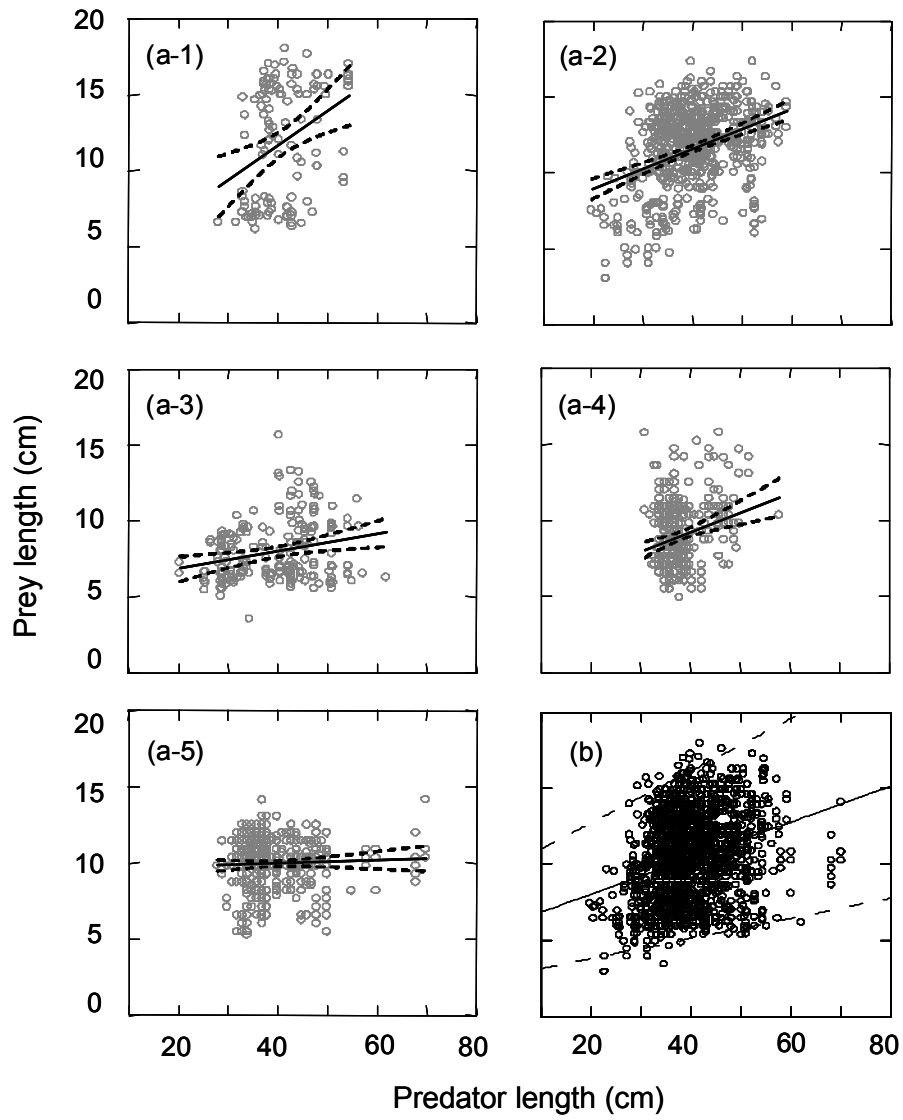715

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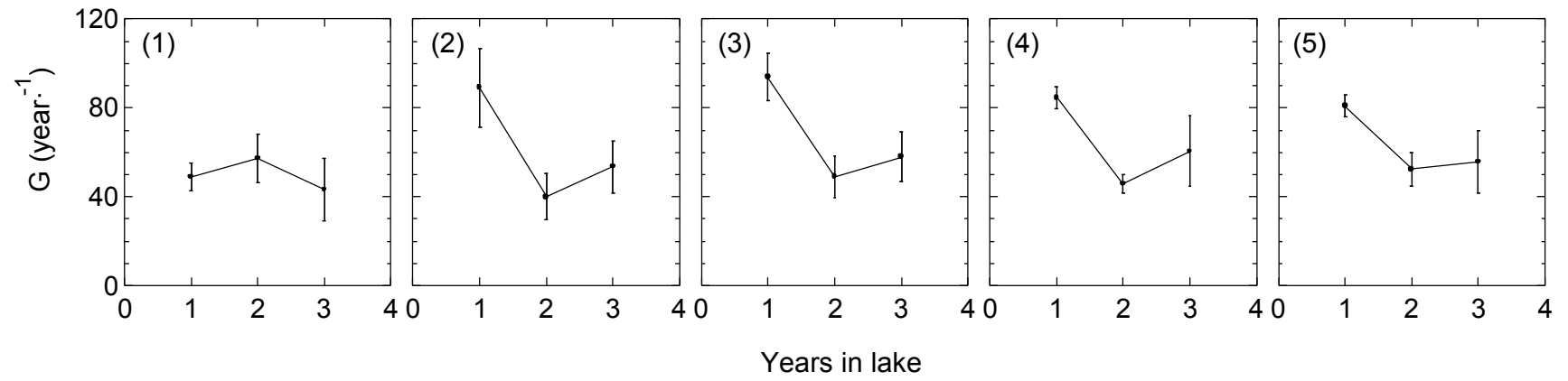718

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720   Fig. 3.

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724   Fig. 4.

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734 Fig. 5.

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