1 **Introduced European smelt (*Osmerus eperlanus*) affects food web and**

2 **fish community in a large Norwegian lake**

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Abstract

Invasive and introduced fishes can affect recipient ecosystems and native species via altered competitive and predatory interactions, potentially leading to top-down and bottom-up cascading impacts. Here, we describe a case from a large lake in southern Norway, Storsjøen, where the illegal introduction of a small, predominantly planktivorous fish species, European smelt (*Osmerus eperlanus*), has led to changes in the native fish community and lake food web. Survey fishing data collected before (2007) and after (2016) the introduction indicates that smelt has become the numerically dominant fish species both in benthic and pelagic habitats, with concurrent reductions in the relative abundance of native European whitefish (*Coregonus lavaretus*) and Arctic charr (*Salvelinus alpinus*) populations. Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) data indicate minor changes in the trophic niches of native whitefish and Arctic charr despite partly overlapping niches with the introduced smelt. In contrast, brown trout (*Salmo trutta*) showed an earlier shift to piscivory, a more pelagic niche and increased growth rate, likely because of the smelt induced increase in pelagic prey fish abundance. The main trophic pathway supporting top predators (i.e., large brown trout) in Storsjøen has, therefore, shifted from a littoral to a more pelagic base. Our study demonstrates that small-sized introduced fishes can alter lake food-web dynamics, with contrasting impacts on native fishes. This knowledge is vital for future evaluation and mitigation of potential impacts of smelt introductions on lake ecosystems.

Introduction

51 Invasive and introduced species are major global threats to biodiversity and ecosystem

52 services (Rahel 2002; Pejchar and Mooney, 2009; Early et al. 2016). Besides potential

53 negative impacts on the relative abundances of species in native communities, non-

54 native species can trigger major changes in the structure and function of recipient

55 ecosystems e.g. via altered food-web dynamics (e.g. Vander Zanden et al. 1999). In

56 lakes, fish species that occupy intermediate trophic levels can have particularly

57 important structuring roles due to their potential impacts on prey at lower trophic levels,

58 competitors at the same trophic level and predators at the highest trophic levels

59 (Amundsen et al. 2008; Wootton 2017). Hence, invasive planktivorous and/or

60 benthivorous fish species are of major concern for lake management authorities,

61 particularly if they develop high population densities and cause local extinctions of

62 native species.

63 European smelt (*Osmerus eperlanus*; hereafter smelt) is a relatively small-sized,

64 omnivorous fish species found in the lakes and coastal areas of western Europe. Smelt

65 feed mainly on zooplankton, but also include zoobenthos and small conspecifics in their

66 diet (Hammar et al. 2018). Smelt is typically the main food resource for large, pelagic

67 predatory fishes, such as pikeperch (*Sander lucioperca*) and brown trout (*Salmo trutta*)

68 and thus play a key role in the pelagic food-web compartment of many temperate lakes

69 (e.g. Nyberg et al. 2001; Sandlund et al. 2005; Keskinen et al. 2012; Hammar et al.

70 2018). Compared to other examples of non-native pelagic fishes, such as vendace

71 (*Coregonus albula*) in Europe (e.g. Bøhn et al. 2008; Bhat et al. 2014) and rainbow

72 smelt (*Osmerus mordax*) in North America (e.g. Mercado-Silva et al. 2006; Gaeta et al.

73 2015), the potential impacts of introduced smelt on native fish communities and

74   recipient lake ecosystems remains unexplored. Recent research from large

75   Scandinavian lakes indicates that smelt can show variable life history strategies and

76   large fluctuations in population size (Sandlund et al. 2017; Hammar et al. 2018). Such

77   population fluctuations (cf. Strayer et al. 2017 for "boom-bust dynamics") have the

78   potential to affect the niche use of generalist predatory fishes, although the expectation

79   remains to be explored in ecosystems recently occupied by smelt.

80   Here, we studied the impacts of introduced smelt on the native fish community

81   and lake food web of a large lake in southern Norway, Lake Storsjøen (hereafter

82   Storsjøen). Based on genetic analyses, smelt was translocated to Storsjøen from a large,

83   nearby lake Mjøsa, and first discovered by local fishermen in 2008 (Hagenlund et al.

84   2015). Since then, the smelt population has shown high reproductive success and

85   population growth (Hagenlund et al. 2015), but their impacts on native fish species and

86   the lake food web are not known. To study these potential impacts, we used comparable

87   survey fishing and stable isotope data collected before (2007) and after (2016) the smelt

88   introduction to Storsjøen. Stable isotope analysis (SIA) provides a powerful method to

89   study temporally integrated variation in fish diets and the structure (e.g. food-chain

90   length) and function (e.g. littoral *versus* pelagic energy flow pathways) of lake food

91   webs (Post 2002; Boecklen et al. 2011; Layman et al. 2012). SIA has been widely used

92   to study the impacts of invasive fishes on recipient ecosystems and native communities

93   (e.g. Cucherousset et al. 2012 and references therein). Following the smelt introduction

94   in Storsjøen, we expected that (1) the native planktivorous fish species, i.e. European

95   whitefish (*Coregonus lavaretus*; hereafter whitefish) and Arctic charr (*Salvelinus*

96   *alpinus*), would show decreased abundance but little change in their trophic niches,

97   whereas the predominantly littoral benthivorous grayling (*Thymallus thymallus*) would

98   remain unaffected. In contrast, we expected that (2) predatory brown trout would shift

99   to a more pelagic trophic niche, with an earlier onset of piscivory and increased growth

100 rate due to the greater availability of small pelagic prey fish. Study results are further

101 discussed in respect to potential long-term ecosystem impacts of the smelt introduction.

102

103 **Materials and methods**

104 *Study lake*

105 Lake Storsjøen is a large, deep, oligotrophic lake situated in Hedmark county, south-

106 eastern Norway (Table 1). The lake is regulated for hydropower purposes at the lake

107 outlet with a dam and it drains through the River Rena to Norway's largest river system,

108 Glomma. Besides whitefish, Arctic charr, grayling and brown trout, the introduced

109 smelt coexist with six other native fish species: pike (*Esox lucius*), perch (*Perca*

110 *fluviatilis*), burbot (*Lota lota*), minnow (*Phoxinus phoxinus*), roach (*Rutilus rutilus*) and

111 alpine bullhead (*Cottus poecilopus*).

112

113 *Sample collection and preparation*

114 The collection and preparation of fish samples were conducted according to permitting

115 requirements of the Hedmark County Council and at the request of the hydropower

116 company (Glommens og Laagens Brukseierforening) operating at Storsjøen. Fish were

117 collected with survey gillnets in early summer and autumn in 2007 and 2016 (Online

118 Resource 1). In each sampling period, the gillnets were set overnight (12–15-hr fishing

119 time) in the littoral (0–10 m), profundal (>15 m) and pelagic (0–21 m below the surface)

120 habitats. Both Jensen series consisting of single-mesh (knot-to-knot mesh sizes 6–52

121 mm) nets (Jensen 1977) and Nordic multi-mesh survey gillnets (12 panels of 2.5 m x

122 1.5 m with mesh sizes 5–55 mm; see Appelberg et al. 1995) were used in both seasons

123   and years. In 2007, the benthic single-mesh gillnet series consisted of 12 nets (25 x 1.5

124   m) with mesh sizes of 6, 8, 10, 12.5, 16, 21, 26, 29, 35, 39, 45 and 52 mm, whereas only

125   the nine largest mesh sizes (12.5–52 mm) were used in 2016. The floating pelagic

126   gillnets were set at 0–6 and 15–21 m depth below the surface. The single-mesh floating

127   gillnets were 25 x 6 m and they consisted of the same mesh sizes as the benthic gillnets

128   (12 nets in 2007, nine nets in 2016). In 2016, pelagic sampling was extended with

129   floating 27.5 x 6 m multi-mesh Nordic survey gillnets (11 mesh sizes of 6.25–55 mm)

130   that were set at the same two depths as the single-mesh pelagic gillnets (see Online

131   Resource 1 for more details of the survey fishing). The survey fishing data were used

132   to evaluate between-year differences in habitat use and abundance of dominant fish

133   species, based on catch per unit effort (CPUE) estimates calculated as number of fish

134   caught per 100 m^2 of gillnet per night. To standardize the data between years, only

135   catches in Nordic survey gillnets set in June 2007 and 2016 were included in CPUE

136   calculations in the littoral and profundal habitats (see Fig.1 and Online Resource 1).

137   Since no pelagic Nordic nets were set in 2007, the pelagic CPUE calculations were

138   based on catches in the standard floating nets with 12–55 mm mesh set in June and

139   August/September 2007 and 2016 (Fig.1 and Online Resource 1).

140   Each fish was identified, measured (standard length: ± 1 mm) and weighed (wet

141   mass: ± 1.0 g). Scales were collected from each brown trout for subsequent growth

142   analyses, conducted by back-calculation of the length at different ages prior to capture

143   (Shearer 1992). From random subsamples of fish, the stomach and a small piece of

144   dorsal muscle tissue were dissected, stored frozen at -20°C and later prepared for

145   stomach contents (SCA) and stable isotope (SIA) analyses, respectively. Additional

146   scale (n = 26 in 2007; n = 48 in 2016) and muscle tissue (n = 4 in 2007; n = 26 in 2016)

147   samples of large brown trout (length = 260–800 mm) were collected from fish caught

148   during an annual trolling contest, "Storsjødreggen", arranged in June 2007 and June

149   2016.

150   For SCA, the prey taxa were identified to genus, family or order level, and their

151   relative volumetric contributions to the stomach contents were estimated visually. The

152   prey taxa were later grouped as: (1) zooplankton (mainly *Daphnia* sp. and *Bosmina* sp.,

153   some *Holopedium* sp., *Cyclops* sp., *Heterocope* sp. and *Diaptomus* sp.), (2)

154   *Bythotrephes* sp. predatory cladocera, (3) zoobenthos (e.g. larvae of Chironomidae,

155   Trichoptera, Ephemeroptera and Plecoptera, Gastropoda, Dytiscidae), (4) surface

156   insects (adult stages of aquatic and terrestrial insects), (5) fish (mainly smelt but also

157   whitefish, minnow, alpine bullhead and perch), (6) fish eggs (mainly smelt eggs), and

158   (7) other unidentified prey. These prey groups were subsequently used to test for dietary

159   differences between the introduced smelt and the native whitefish, Arctic charr,

160   grayling and brown trout populations, as well as to compare the diets of whitefish,

161   grayling and brown trout between the two study years to evaluate potential smelt

162   impacts on resource use of native fishes.

163

164   ***Stable isotope analyses***

165   Littoral and pelagic basal resources and invertebrates were sampled on 1 August 2007

166   and 23 August 2016 for SIA to study the overall food-web structure in Storsjøen and to

167   provide baselines for isotopic mixing models reflecting the trophic niches of brown

168   trout, whitefish and grayling. Insufficient SIA data (n $\leq$ 2 in one of the years) were

169   obtained from other native fishes, including Arctic charr, to conduct reliable between-

170   year comparisons of trophic niche changes following the smelt introduction. In 2007,

171   zooplankton and littoral benthic invertebrate samples were collected using a 60-µm

172   plankton net and a 500-µm mesh kick net, respectively. In 2016, benthic

173   macroinvertebrates were collected using a 500-µm mesh kick net and hand-picking in

174   the shallow littoral areas (0–1 m depth) and a 243-µm mesh benthic sledge in the deep

175   littoral (2–8 m) and profundal (20–34 m) areas. The macroinvertebrate samples were

176   subsequently sieved through a 500-µm mesh. Pelagic zooplankton taxa were collected

177   by taking several vertical hauls with an 80-µm plankton net throughout the uppermost

178   30 m of the water column. All benthic and pelagic invertebrates were sorted, cleaned

179   of detritus and other unwanted material, identified to genus or family level and stored

180   frozen at –20°C prior to final preparation for SIA. Only soft body tissue was dissected

181   from mollusks and trichopterans with cases. Because only a few zooplankton (n = 2)

182   and littoral benthic invertebrate (n = 5) samples were collected in 2007, the invertebrate

183   SIA data from the two years were finally pooled to obtain more representative littoral

184   and pelagic baselines and to account for spatial and temporal isotopic variation at low

185   trophic levels (cf. Syväranta et al. 2006). Pooling of the invertebrate SIA data was

186   supported by the absence of significant between-year differences in $\delta^{13}C$ values of

187   *Lymnaea* sp. snails (W = 36, n = 18, P = 0.123), implying long-term stability of the

188   littoral isotopic end-member.

189   All frozen fish and invertebrate SIA samples were later dried (for 48 h in an

190   oven at 60°C in 2007 and in a freeze-drier in 2016) and homogenized using a mortar or

191   a metallic pestle. The final SIA were performed at the Institute for Energy Technology

192   (IFE; Kjeller, Norway) in 2007 and at the Environmental Isotope Laboratory

193   (University of Waterloo, Canada) in 2016. Analytical precision was <0.3‰ for both

194     $\delta^{13}C$ and $\delta^{15}N$, based on repeat analysis of an internal laboratory standard (2007) or

195   duplicates (2016). See Sandlund et al. (2013) and Eloranta et al. (2016) for more details

196   about the analytical procedures in Kjeller and Waterloo, respectively.

197   The relative trophic position (TP) of brown trout, whitefish and grayling in the

198   food web of Storsjøen was estimated using the two-source isotopic mixing model

199   described in Post (2002). The SIAR package (Stable Isotope Analysis in R; version 4.2;

200   Parnell et al. 2010; Parnell and Jackson 2013) was used to estimate the reliance of

201   whitefish, grayling, brown trout, Arctic charr and smelt populations on littoral *versus*

202   pelagic carbon sources. To study ontogenetic dietary shifts of brown trout, the relative

203   reliance of individuals on littoral carbon sources (LR) was estimated using the carbon

204   isotope two-source mixing model described in Post (2002). The input data in TP, LR

205   and SIAR computations included individual $\delta^{13}C$ and $\delta^{15}N$ values from fish muscle

206   tissue and mean ± SD $\delta^{13}C$ and $\delta^{15}N$ values of littoral and pelagic invertebrates. In

207   addition, the commonly used trophic fractionation corrections of 0.4 ± 1.3‰ for $\delta^{13}C$

208   and 3.4 ± 1.0‰ for $\delta^{15}N$ (Post 2002) were incorporated in SIAR computations.

209   We ran sensitivity analyses (see Online Resource 2) to see if our results from

210   SIA data were influenced by the chosen trophic fractionation corrections or by lipid-

211   normalization of the $\delta^{13}C$ values for fish with presumably high lipid content (i.e., C:N

212   ratio >4). We found virtually no effect of different trophic fractionation corrections for

213   the SIAR results. The main patterns in linear regression analyses of brown trout

214   ontogenetic dietary shifts also remained the same after lipid-normalization, although

215   the lipid-normalization did elevate and reduce individual variation in $\delta^{13}C$ values of

216   large, piscivorous brown trout caught in 2016. As elaborated more in the Online

217   Resource 2, we are confident that our main results based on SIA data are robust.

218

219   ***Statistical analyses***

220   One-way non-parametric multivariate analyses of variance (NPMANOVA; see

221   Anderson 2001) were performed in PAST program (Hammer et al. 2001) to test for

222 dietary differences between smelt, whitefish, Arctic charr, grayling and brown trout

223 (samples pooled from both years). NPMANOVA was also used to test for between-year

224 differences in diets of whitefish, grayling and brown trout, whereas no between-year

225 comparisons were done for other fish species due to insufficient sample sizes. When

226 significant ($P < 0.05$) dietary differences were observed in NPMANOVA, similarity

227 percentage analysis (SIMPER) was used to determine which prey taxa contributed most

228 to the dietary difference between species or years.

229   All other statistical analyses were performed in R v. 3.4.1 (R Core Team 2017)

230 and key results are summarized in Table 2. Depending on the data normality and

231 homoscedasticity, we used either parametric t-tests or non-parametric Mann-Whitney-

232 Wilcoxon tests to test for between-year differences (2007 $versus$ 2016) in standard

233 length, Fulton's condition factor, $\delta^{13}C$ and TP of brown trout, whitefish and grayling

234 caught with survey gillnets. For the same fish, we used Levene's test for the equality of

235 variances to test for between-year differences in individual variation in $\delta^{13}C$ and TP.

236 Taken together, analyses were expected to reflect the effects of smelt introduction on

237 the size, nutrition, diet and trophic niche width (cf. Bearhop et al. 2004) of native fish

238 species. Unfortunately, the available CPUE data did not allow any statistical

239 comparisons because only the sampling location and period was reported and thus it

240 was impossible to distinguish from which specific Nordic net each fish was removed.

241 Moreover, due to limited resources available for the field work, only a few Nordic nets

242 (n = 2–5) were set to each habitat in each period. Nevertheless, we believe that the

243 available data of habitat use and relative abundance of different fish species provide

244 important insights to the potential impacts of introduced smelt on the native fish

245 community in Storsjøen.

246   In addition to between-species comparisons including all SIA data collected in

247   both years, we compared the SIAR estimates of whitefish, grayling and brown trout

248   sampled in 2007 and 2016 to test for potential trophic niche shifts following the smelt

249   introduction. The *siarmcmcdirichletv4* function in the SIAR package (Parnell and

250   Jackson 2013) was run with default settings (i.e., iterations = 200000, burnin = 50000,

251   howmany = 10000, thinby = 15). The differences in the resulting SIAR estimates were

252   considered statistically significant when the 95% Bayesian credibility intervals showed

253   no overlap between the groups (i.e., species or years).

254   We used linear regression analysis to assess between-year differences in

255   ontogenetic dietary shifts of brown trout. Specifically, we explored the effects of year

256   (included as a factor) and individual length on brown trout trophic position (TP) and

257   littoral reliance (LR). For both TP and LR, we fitted three linear regression models, all

258   including log-transformed length as a covariate and year as either an additive effect,

259   varying with length (interaction effect), or non-existing. The models were subsequently

260   compared based on AICc values from the MuMIn package v.1.40.4 (Bartoń 2018). The

261   most supported model (i.e., the lowest AICc score and ΔAICc > 2 compared to the

262   second-best model) was chosen as the prediction model. We also checked for possible

263   violations of the assumptions for the linear regression analysis. Two small individuals

264   (<200 mm) with unexpectedly high TP were identified as outliers in the 2016 data and

265   removed from the modelling dataset.

266   Finally, we used linear regression analysis to test for between-year differences

267   in brown trout growth patterns. Here, brown trout length at the year of capture (y) was

268   used as the response variable, while sampling year (included as a factor) as well as

269   back-calculated length and age for the previous year (y–1) and their interaction were

270   used as explanatory variables. A few exceptionally old individuals (>10 years, n = 5)

271   were excluded from the analyses to balance age structure between the years.

272

273   **Results**

274   The survey fishing data demonstrated changes in the Storsjøen fish community

275   following the smelt introduction. Smelt became the numerically dominant fish species

276   in the shallow littoral and deep profundal habitats, and equally abundant as whitefish in

277   the pelagic habitat (Fig. 1a–c). The littoral catches of whitefish and Arctic charr seemed

278   to decline, whereas brown trout apparently became more abundant and grayling

279   remained unaffected in the littoral zone. The profundal catches showed somewhat

280   contrasting patterns, since both whitefish and particularly burbot seemed to become

281   more abundant in the catch following the smelt introduction. In contrast, the catches of

282   previously relatively abundant Arctic charr apparently declined in both the profundal

283   and pelagic habitats.

284   The SIA data (Fig. 2) indicate clear isotopic separation of the littoral and pelagic

285   food-web compartments (δ^{13}C) as well as consumers at different trophic levels (δ^{15}N).

286   The isotope biplots (Fig. 2) and the SIAR littoral reliance estimates (Fig. 3a) indicate

287   that grayling and minnow are littoral benthivores whereas smelt and Arctic charr are

288   heavily reliant on pelagic and/or profundal food resources. Whitefish and brown trout

289   seem to have more generalist trophic niches and utilize both littoral and pelagic food

290   resources. Piscivorous brown trout and burbot occupy the highest trophic position, but

291   they also show the highest variation in δ^{13}C and δ^{15}N, suggesting that some individuals

292   are generalists while some others have specialized littoral or pelagic invertebrate or fish

293   diets (Fig. 2).

294   Whitefish and grayling showed no significant between-year differences (Table

295   2, Fig. 3b) in condition, trophic niche, and individual variation of δ^{13}C ($P > 0.150$).

296   Grayling were larger (Table 2) and showed higher individual variation of TP in 2016

297   than in 2007 ($F_{1,28} = 15.33$, $P < 0.001$), but the latter might be partly due to larger sample

298   size in 2016 (Table 2). The limited SIA data from Arctic charr indicated no shift in δ^{13}C

299   and δ^{15}N values and a high niche overlap with the introduced smelt (Fig. 2 and 3).

300   The results from SIA were supported by SCA data indicating significant dietary

301   segregation between smelt, whitefish, Arctic charr, grayling and brown trout

302   (NPMANOVA: *pseudo* $F_{4,280} = 38.1$, $P < 0.001$; all pairwise comparisons: $P < 0.001$).

303   Based on SIMPER results, the dietary segregation was mainly due to the

304   zooplanktivorous diet of smelt, generalist diet of whitefish, dominance of *Bythotrephes*

305   sp. in Arctic charr diet in 2007, and specialized benthivorous diet of grayling (Fig. 4),

306   with the average between-species dissimilarities of main prey groups ranging from 26

307   to 48%. Brown trout and burbot were generalist piscivores that also fed on

308   invertebrates, (Fig. 4). While prey fishes were not identified in 2007, the data from 2016

309   indicate that smelt of standard length 90–110 mm were the dominant prey fish for both

310   brown trout and burbot. There were significant between-year differences in the diets of

311   whitefish (*pseudo* $F_{1,89} = 3.7$, $P = 0.021$) and brown trout (*pseudo* $F_{1,75} = 3.5$, $P = 0.025$),

312   but not of benthivorous grayling (*pseudo* $F_{1,22} = 1.0$, $P = 0.422$). According to SIMPER,

313   the between-year differences resulted from decreased zooplanktivory and increased

314   benthivory and egg-predation by whitefish, and from decreased consumption of surface

315   insects and increased benthivory and piscivory by brown trout in 2016 following the

316   smelt introduction (Fig. 4). While *Bythotrephes* sp. was the main dietary item for Arctic

317   charr, and relatively common prey for whitefish and small brown trout in 2007, it was

318   completely absent in fish stomachs analysed in 2016.

319   As hypothesized, brown trout shifted from littoral towards a more pelagic

320   trophic niche following the smelt introduction, as indicated both by the SIAR estimates

321   (Fig. 3b) and significantly lower $\delta^{13}C$ values in 2016 (Table 2). There were no

322   corresponding between-year differences in brown trout size, condition and TP (Table

323   2), nor in individual variation of brown trout $\delta^{13}C$ and TP ($P > 0.100$). There were,

324   however, clear between-year differences in ontogenetic (size-related) changes in brown

325   trout trophic position (TP) and reliance on littoral carbon sources (LR). According to

326   the most supported model for TP (Tables 3 and 4, Fig. 5a), brown trout underwent an

327   ontogenetic shift to a higher trophic position (i.e., piscivory) at a smaller size in 2016

328   following the smelt introduction. The between-year difference in TP was particularly

329   evident for brown trout larger than 300 mm. However, it should be noted that two small

330   individuals (<150 mm) with exceptionally high TP were excluded from regression

331   analysis, but they indicate that even very young and small brown trout had the potential

332   to attain high TP in 2016 following the smelt introduction. For LR, two models were

333   equally supported based on AIC (ΔAICc ~ 1.8), but we selected the most supported and

334   parsimonious (additive) model as the added interaction term in the second-best model

335   seemed to be non-significant and give little extra information. Hence, the most

336   supported model for LR included an additive effect of year (Tables 3 and 4, Fig. 5b),

337   and predicted a generally lower reliance of brown trout on littoral food (i.e. carbon)

338   resources in 2016 as compared to 2007, as well as a negative effect of length, indicating

339   an ontogenetic shift from littoral towards a pelagic diet with increasing size. Finally,

340   the linear regression model based on back-calculated length data indicated increased

341   growth rate of brown trout following the smelt introduction, being particularly evident

342   for large (>300 mm) and old (>5 years) individuals (Fig. 6, Table 5).

343

Discussion

The potential impacts of introduced European smelt on native fishes and recipient lake food webs have remained unexplored. Here, we have demonstrated that the predominantly planktivorous smelt can achieve high abundance and have contrasting impacts on native fishes soon after the introduction. Following the smelt introduction in Storsjøen, the relative abundance of predominantly pelagic Arctic charr and whitefish seems to have reduced, but their trophic niches have remained largely unaffected. No major changes in abundance or niche use were observed for littoral benthivorous grayling. In contrast, brown trout apparently became more abundant in the littoral zone and shifted earlier (i.e., at smaller size) to a pelagic, piscivorous trophic niche and grew better, likely due to the increased abundance of pelagic prey fish. Our study provides further evidence that introduced fishes occupying intermediate trophic levels can have high but contrasting impacts on native species and alter the energy mobilization pathways supporting top predators in lake ecosystems.

Our survey fishing data suggests that smelt has become the numerically dominant fish species in all major habitats in Storsjøen, as has the smelt source population in Lake Mjøsa (Sandlund et al. 1985a; Hagenlund et al. 2015). Whitefish and Arctic charr are among the most common fish species found in the pelagic and profundal habitats of large and deep lakes in northern Europe (e.g. Eloranta et al. 2015; Sandlund et al. 2010, 2016). These two salmonids are highly valued among commercial and recreational fishermen, but subjected to various anthropogenic disturbances such as warming, eutrophication, overfishing and invasion of competitive and predatory fishes, particularly in their southernmost distribution areas (e.g. Graham and Harrod 2009; Jeppesen et al. 2012). Although smelt in some cases might act as an important

368   pelagic prey species for Arctic charr (Hammar et al. 2018), the putative negative

369   impacts of smelt on coexisting fishes in Storsjøen likely result from strong competitive

370   and predatory interactions, as observed for invasive rainbow smelt in North American

371   lakes (e.g. Hrabik et al. 1998; Mercado-Silva et al. 2007). By being an efficient predator

372   of large-bodied cladocerans, smelt can reduce food availability and thereby reduce the

373   recruitment success of native pelagic fishes (e.g. Johnson and Goettl 1999; Beisner et

374   al. 2003; Mercado-Silva et al. 2007). In addition to resource competition, smelt may

375   have indirect negative impacts on whitefish and Arctic charr by facilitating faster

376   growth and earlier piscivory of brown trout, thereby increasing the number of predators

377   large enough to prey upon whitefish and Arctic charr. Large smelt can also have direct

378   predatory effects on small fish (Sandlund et al. 2005; Sletter et al. 2007) and affect lake

379   fish communities and food webs via intraguild predation and cannibalism, potentially

380   inducing smelt population fluctuations (cf. He and Labar 1994; Stetter et al. 2007;

381   Hammar et al. 2018). However, it should be noted that survey gillnet fishing (CPUE)

382   data are inherently sensitive to temporal and spatial fluctuations, inducing variation in

383   age distribution, year class strength and growth rate of different fish species. Hence,

384   future monitoring is needed to confirm whether the native whitefish and Arctic charr

385   populations in Storsjøen are truly declining due to the smelt introduction.

386   As compared to native pelagic fishes, smelt had minor or contrasting impacts

387   on native benthic fishes. Grayling are littoral benthivores (Eloranta et al. 2011) and

388   showed minor niche overlap with the more pelagic, planktivorous smelt. Besides niche

389   stability, the invariable grayling SIA values suggest minor between-year differences in

390   the littoral isotopic baseline. Due to missing SIA data from 2007, the potential impacts

391   of smelt introduction on the trophic niche of other benthic fishes remains unclear.

392   However, our limited CPUE and SCA data from burbot suggest increased utilization of

393   the deep profundal habitat and predation on smelt. Previous studies in nearby Lake

394   Mjøsa demonstrated that smelt can constitute 84–90% of fish prey in burbot stomachs

395   (Sandlund et al. 1985b). In our study, the observed intermediate and highly variable

396   isotopic values suggest that burbot are generalist predators that utilize both shallow-

397   and deep-water prey resources and hence integrate these spatially distinct lake habitats

398   and food-web compartments in Storsjøen (cf. Harrison et al. 2017). Increased burbot

399   abundance and predation may also contribute to the putative population decline of

400   Arctic charr, which commonly utilize the profundal zone as a refuge for intense

401   resource competition and predation (Eloranta et al. 2011, 2013; Sandlund et al. 2010,

402   2016).

403   Our findings provide further evidence that invasion of intermediate consumers

404   can alter lake food webs via altered competitive and predatory interactions (e.g. Vander

405   Zanden et al. 1999; Beisner et al. 2003; Rush et al. 2012). As indicated by the SIA data,

406   the main top predator in Storsjøen, brown trout, have shifted towards a more pelagic

407   trophic niche and become piscivorous at a smaller size than before smelt introduction.

408   As observed for predatory lake trout (*Salvelinus namaycush*) in North American lakes,

409   such alterations in littoral *versus* pelagic resource use can have marked consequences

410   ranging from individual (e.g. maximum and maturation size) to ecosystem (e.g.

411   coupling of habitats and food-web compartments) responses (McMeans et al. 2016).

412   Although we lack data for invertebrate communities and annual population fluctuations,

413   smelt may have affected community and food-web stability in Storsjøen via increased

414   competitive and predatory impacts as well as increased littoral–pelagic coupling by

415   predatory brown trout (cf. Schindler and Scheuerell 2002; Vander Zanden and

416   Vadeboncoeur 2002). Our data also demonstrates that the increased availability of

417   profitable pelagic prey fish (i.e., smelt) has led to an increase in annual growth of

418   predatory brown trout. These results concur with previous studies from North American

419   lakes where the growth of native predatory walleye (*Sander vitreus*) increased

420   substantially following invasion of pelagic rainbow smelt (Jones et al. 1994; Johnson

421   and Goettl 1999). Although recreational fishermen seem content with the improved

422   brown trout growth in Storsjøen, it remains to be seen whether the initial positive trends

423   are followed by population declines of both smelt and brown trout, as observed in some

424   North American lakes hosting rainbow smelt and predatory walleye (Johnson and

425   Goettl 1999). The presumed seasonal and long-term fluctuations in abundance and

426   niche use of smelt and predatory fishes (see e.g. Gaeta et al. 2015 and Hammar et al.

427   2018) calls for monitoring studies to examine the potential for cascading impacts on

428   lower trophic levels, such as zooplankton abundance and community composition (e.g.

429   Johnson and Goettl 1999).

430   To the best of our knowledge, this is the first stable isotope study demonstrating

431   the impacts of introduced European smelt on native fishes and the recipient lake food

432   web, although some recent studies have included limited examinations of linkages

433   between introduced smelt and the native predatory and planktivorous fishes (Korlyakov

434   and Mukhachev 2009; Sterligova and Ilmast 2017). The findings are highly relevant for

435   the future evaluation, management and mitigation of environmental consequences

436   associated with smelt introduction to Storsjøen as well as to other European lakes.

437   However, our study lacks information about potential impacts on lower trophic levels,

438   particularly on the abundance and composition of pelagic zooplankton but also littoral

439   and profundal benthos. The available SCA data suggests that the large-sized

440   *Bythotrephes* sp. cladoceran has disappeared or decreased in numbers, being one of the

441   main prey for pelagic fishes in 2007, but completely absent from fish stomachs in 2016

442   following the smelt introduction. Disappearance of this zooplankton prey might have

443 contributed to the putative population declines of native planktivorous fishes,

444 particularly of Arctic charr whose stomach contents were dominated by *Bythotrephes*

445 sp. in 2007. Hence, annual monitoring of the invertebrate and fish communities would

446 provide a more holistic view of the potential whole ecosystem-level impacts and status

447 of native fish populations, particularly if combined with monitoring of water quality

448 and of a reference lake lacking smelt. Monitoring of the smelt population would also

449 enable detection of possible boom-and-bust cycles (cf. Strayer et al. 2017), as seen in

450 invasive rainbow smelt (Gorman 2007). Moreover, more comprehensive, including

451 seasonal, studies of diets and parasites of smelt and the coexisting native fishes would

452 provide valuable insights to the prevailing food-web dynamics in Storsjøen. Overall,

453 more research on the role of European smelt in lake ecosystems is urgently needed,

454 given the extent and complexity of impacts (e.g. top-down and bottom-up trophic

455 cascades, contaminant bioaccumulation) induced by its invasive sibling in North

456 American lakes, the rainbow smelt (e.g. Vander Zanden and Rasmussen 1996; Rooney

457 and Paterson 2009).

458 　　　To conclude, our findings support previous studies demonstrating complex and

459 often unwanted impacts of introduced smelt on native fishes and lake ecosystems (see

460 e.g. Rooney and Paterson 2009 and references therein). Although smelt species are

461 profitable prey for predatory fish, they may induce major trophic cascades and reduce

462 recruitment success of some highly valued native fishes. To conserve the populations

463 of native pelagic salmonids (e.g. whitefish and Arctic charr) at their southern

464 distribution limits, it is essential to prevent new introductions and secondary spreading

465 of smelt. This is particularly true in temperate lakes which are also subjected to other

466 anthropogenic disturbances such as eutrophication, acidification and water level

467 regulation for hydropower (Dudgeon et al. 2006; Hirsch et al. 2017). Overall, improved

468   management and monitoring of lakes invaded by European smelt is a necessity for

469   successful mitigation of the potential negative impacts. Yet, total removal of the

470   European smelt would likely prove impossible as realized with its invasive sibling in

471   North American lakes (Gaeta et al. 2015).

472

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636 **Tables**

637

638 **Table 1** Characteristics of the study lake, Storsjøen, southeastern Norway. [*]Analysed

639 from a surface water sample (collected on 23 August 2016) at Analysesenteret,

640 Trondheim, Norway

Parameter	Value
Surface area (km^2)	47
Mean depth (m)	138
Maximum depth (m)	309
Altitude (m a.s.l.)	251
Maximum regulation amplitude (m)	3.6
pH[*]	7.27
Turbidity (NTU)[*]	0.27
Total nitrogen ($\mu g\ l^{-1}$)[*]	180
Total phosphorus ($\mu g\ l^{-1}$)[*]	4.1
Total organic carbon ($mg\ l^{-1}$)[*]	2.9
Colour[*]	20

641

642 **Table 2** Summary of the mean ± SD values, ranges (min–max) and between-year statistical comparisons (*t*-tests) of standard length, condition,

643 δ^{13}C and trophic position (TP) of brown trout, whitefish and grayling caught with survey gillnets before (2007) and after (2016) the smelt

644 introduction to Storsjøen. Statistically significant differences (*P* < 0.05) for *t*- and Mann-Whitney-Wilcoxon-tests (marked with [*]) are

645 highlighted in bold

Species	Parameter	2007			2016			Statistics	
		n	Mean ± SD	Range	n	Mean ± SD	Range	*t* / *W*[*]	*P*
Brown trout	Length (mm)	72	258 ± 85	135 – 560	54	243 ± 79	140 – 518	2146[*]	0.322
	Condition	12	0.92 ± 0.08	0.79 – 1.19	15	0.92 ± 0.10	0.71 – 1.13	0.14	0.888
	δ^{13}C (‰)	12	-24.3 ± 2.2	-27.6 – -19.7	15	-26.9 ± 2.2	-30.1 – 22.5	3.01	**0.006**
	TP	12	2.36 ± 0.70	1.39 – 3.51	15	2.17 ± 0.43	1.15 – 2.97	0.84	0.412
Whitefish	Length (mm)	364	284 ± 101	100 – 414	100	315 ± 70	115 – 438	16162[*]	0.086
	Condition	364	0.82 ± 0.10	0.60 – 1.14	100	0.81 ± 0.11	0.45 – 1.06	18346[*]	0.547
	δ^{13}C (‰)	15	-28.5 ± 1.1	-30.1 – 26.5	40	-28.2 ± 2.1	-30.4 – -22.6	322[*]	0.685
	TP	15	2.46 ± 0.14	2.22 – 2.82	40	2.34 ± 0.32	0.98 – 2.87	369[*]	0.199
Grayling	Length (mm)	47	270 ± 88	112 – 440	21	318 ± 67	178 – 457	-2.81	**0.006**
	Condition	9	0.81 ± 0.11	0.60 – 0.99	21	0.80 ± 0.10	0.59 – 1.17	1028[*]	0.236
	δ^{13}C (‰)	9	-20.5 ± 2.5	-25.6 – -18.7	21	-22.1 ± 1.6	-27.7 – 20.1	1.81	0.098
	TP	9	2.02 ± 0.09	1.93 – 2.22	21	1.94 ± 0.29	1.58 – 2.42	107[*]	0.602

646

647 **Table 3** Model selection table based on AICc values for three candidate linear

648 regression models exploring trophic position (TP) and littoral reliance (LR) of brown

649 trout in Storsjøen. The most supported models (i.e. the most parsimonious models with

650 ΔAIC <2) are highlighted in bold. See Table 4 for summaries of the most supported

651 models and Fig. 5 for graphical visualization of the model outputs, illustrating brown

652 trout ontogenetic niche shifts before (2007) and after (2016) the smelt introduction

Model	df	AICc	ΔAIC
TP ~ log (Length) + Year + log (Length) x Year	**5**	**37.2**	**0**
TP ~ log (Length) + Year	4	41.6	4.4
TP ~ log (Length)	3	54	16.8
LR ~ log (Length) + Year	**4**	**-39.5**	**0**
LR ~ log (Length) + Year + log (Length) x Year	5	-37.7	1.8
LR ~ log (Length)	3	3.1	42.6

653

654   **Table 4** Summary of the most supported models (see Table 3) predicting brown trout

655   trophic position ($F_{3,51} = 84.2$, $R^2_{adj} = 0.82$, $P < 0.001$) and littoral reliance ($F_{2,54} = 61.4$,

656    $R^2_{adj} = 0.68$, $P <0.001$) as a function of year (included as a factor) and log-transformed

657   length (mm). Statistically significant parameters ($P <0.05$) are highlighted in bold. See

658   Fig. 5a,b for graphical visualization of the model results, demonstrating ontogenetic

659   dietary shifts of brown trout before (2007) and after (2016) the smelt introduction
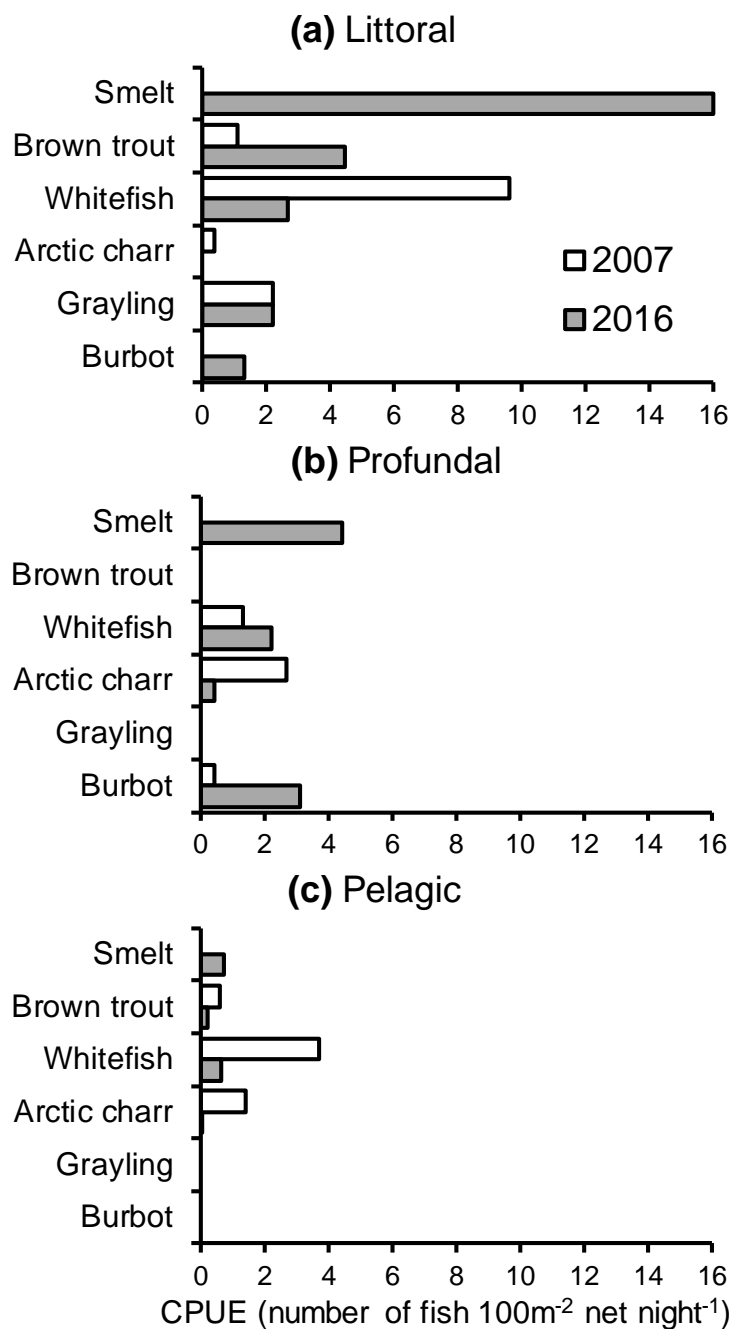
Response	Parameter	Estimate	SE	*t*	*P*
Trophic position	Intercept	–6.58	1.20	–5.47	**<0.001**
	Year	–3.68	1.57	–2.34	**0.020**
	(log) Length	1.55	0.20	7.67	**<0.001**
	(log) Length x Year	0.68	0.26	2.60	**0.010**
Littoral reliance	Intercept	3.56	0.35	10.10	**<0.001**
	Year	–0.39	0.05	–8.04	**<0.001**
	(log) Length	–0.46	0.06	–7.89	**<0.001**

660

661 **Table 5** Summary of the linear model ($F_{4,172} = 368.3$, $R^2_{adj} = 0.89$, $P < 0.001$), predicting

662 brown trout length in the year of capture (y) as a function of year (a factor with two

663 levels, 2007 and 2016), back-calculated length (Length $_{y-1}$) and age (Age $_{y-1}$) in the

664 previous year ($y-1$), and the interaction between the two latter explanatory variables

665 (Length $_{y-1}$ x Age $_{y-1}$). Statistically significant parameters ($P < 0.05$) are highlighted in

666 bold. See Fig. 6 for graphical visualization of brown trout growth patterns before (2007)

667 and after (2016) the smelt introduction

Parameter	Estimate	SE	t	P
Intercept	29.02	16.87	1.72	0.087
Year	37.87	6.02	6.29	**<0.001**
Length $_{y-1}$	1.17	0.09	12.72	**<0.001**
Age $_{y-1}$	4.60	4.27	1.08	0.280
Length $_{y-1}$ x Age $_{y-1}$	–0.03	0.01	–2.13	**0.034**

668

Figures

(a) Littoral

(b) Profundal

(c) Pelagic

CPUE (number of fish 100m^{-2} net night^{-1})

670

671 **Fig. 1** Abundance of dominant fish species in Storsjøen before (2007) and after (2016)

672 smelt introduction, based on catch per unit of effort (CPUE; number of fish 100m^{-2} net

673 night^{-1}) estimates from survey fishing in (A) littoral, (B) profundal and (C) pelagic

674 habitats. The CPUE estimates in (A) and (B) are based on benthic Nordic gillnet catches

675   in June, whereas CPUE in (C) are based on catches in pelagic standard gillnets with

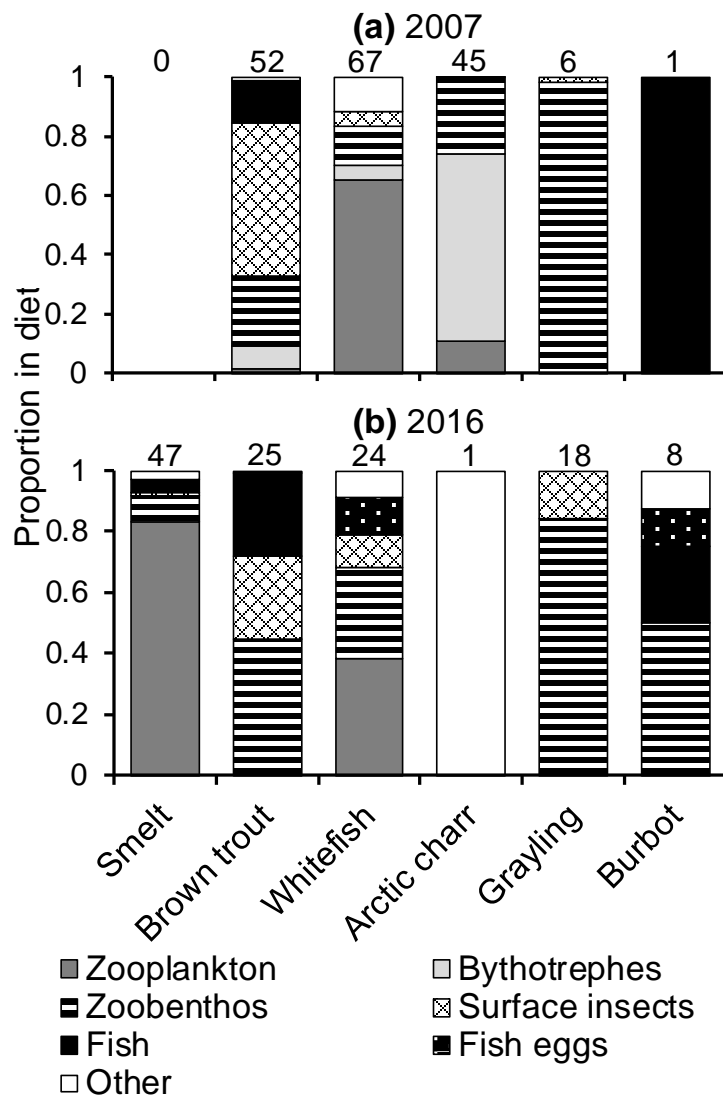676   12–55 mm mesh set in June and August/September 2007 and 2016.

677
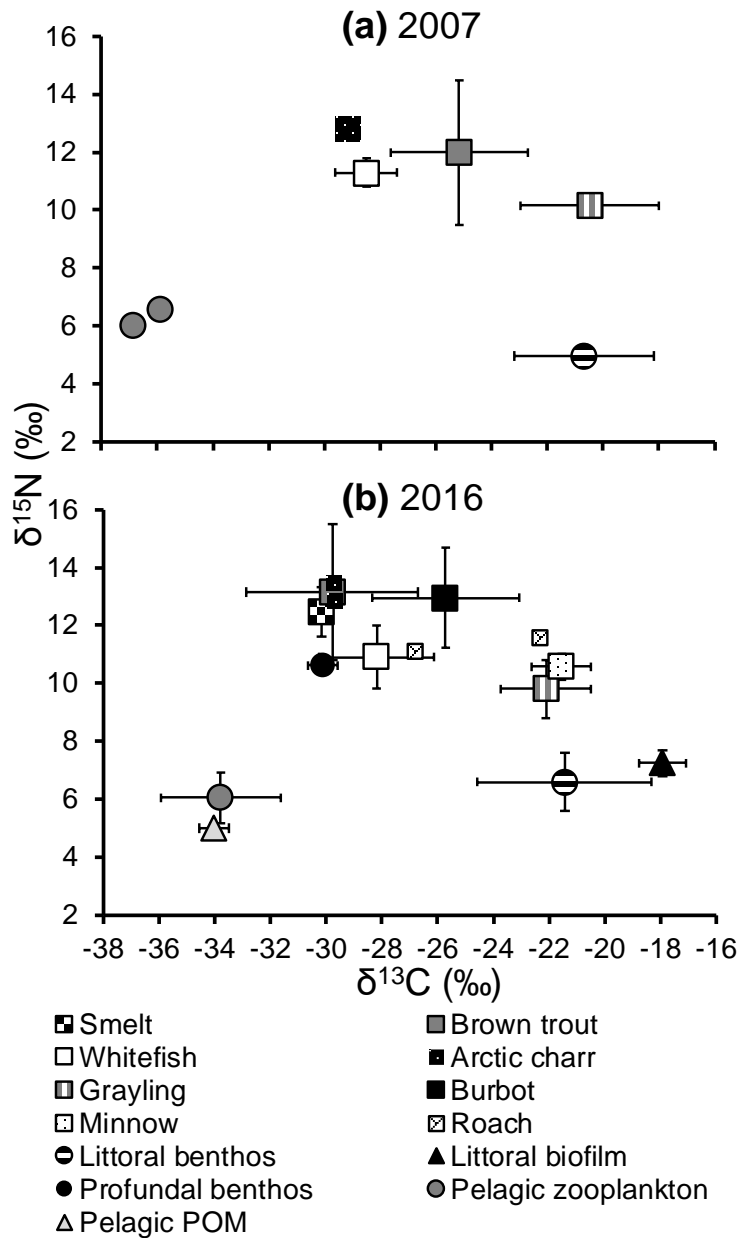
Fig. 2 Stable isotope biplot showing the mean ± SD δ¹³C and δ¹⁵N values of littoral and

pelagic basal resources, invertebrates and different fish species collected from Storsjøen

(A) before and (B) after smelt introduction. Individual values are shown for the two

zooplankton samples analysed in 2007 and for the two Arctic charr and roach analysed

in 2016.
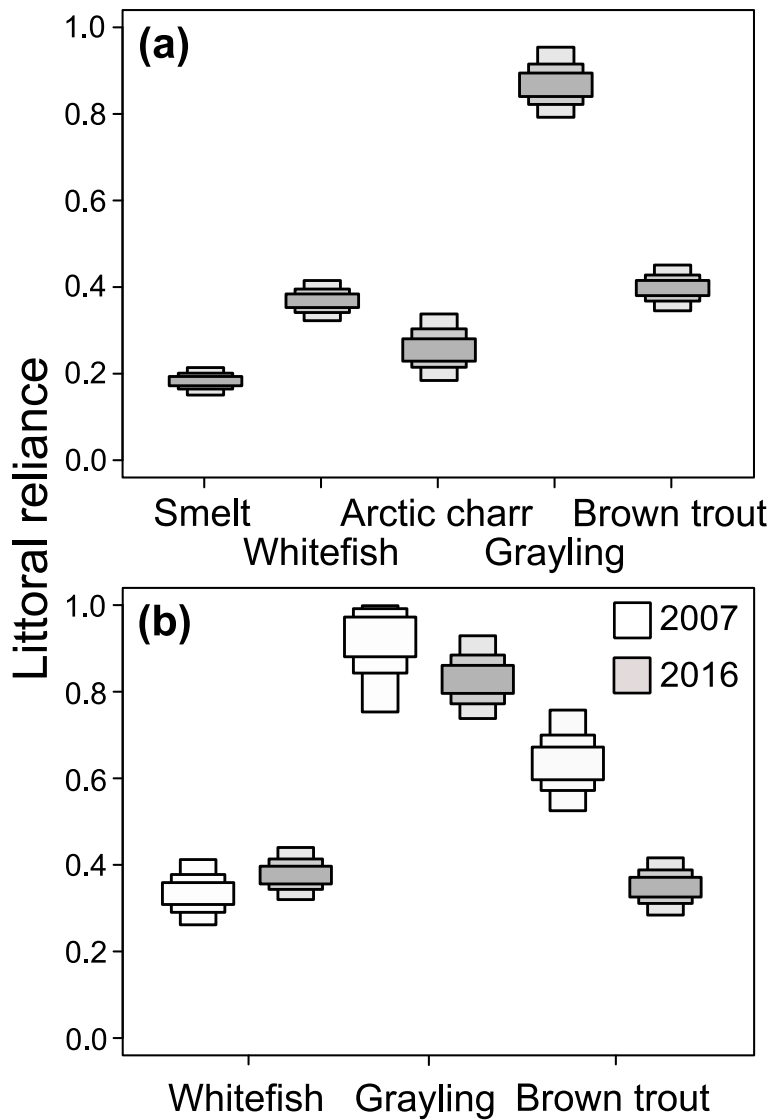
Fig. 3 (a) Between-species and (b) between-year comparisons of littoral reliance of different fish species in Storsjøen, based on results from SIAR two-source isotopic mixing model. The boxes indicate the 95, 75 and 50% Bayesian credibility intervals for the source proportion estimates

(a) 2007

(b) 2016

Smelt   Brown trout   Whitefish   Arctic charr   Grayling   Burbot

■ Zooplankton   ☐ Bythotrephes
⊟ Zoobenthos   ⊠ Surface insects
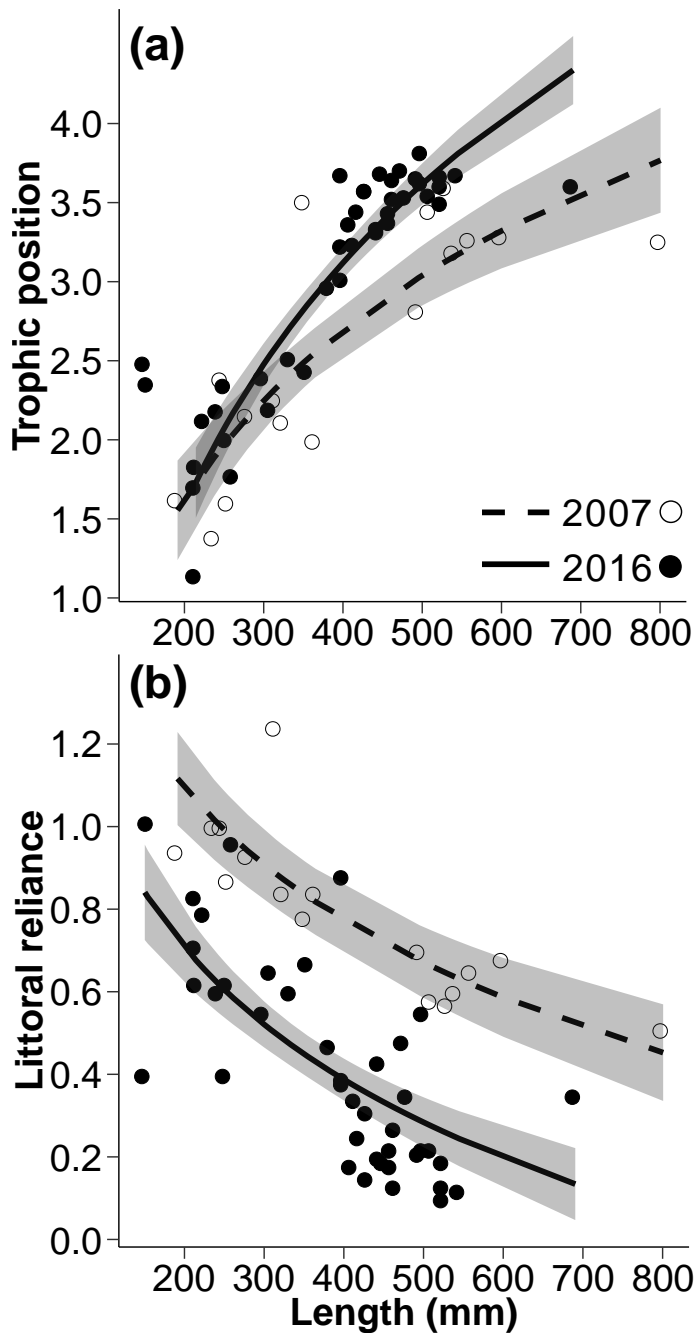■ Fish   ▨ Fish eggs
☐ Other

689

690   **Fig. 4** Proportion of different prey taxa in the stomach contents of dominant fish species

691   collected (a) before and (b) after the smelt introduction in Storsjøen. The numbers of

692   analysed fish are shown above the bars

693

Fig. 5 Ontogenetic shifts in (A) trophic position and (B) littoral reliance of brown trout

caught from Storsjøen before (2007) and after (2016) smelt introduction. The lines

present predicted values from the most supported models for the 2007 (dashed line,

open circles) and 2016 (solid line, closed circles) data, based on linear models with year

(included as a factor) and log-transformed length (mm) as explanatory variables (see

699   Tables 3 and 4). The grey shadings depict the 95% confidence intervals for the predicted

700   TP and LR estimates

701
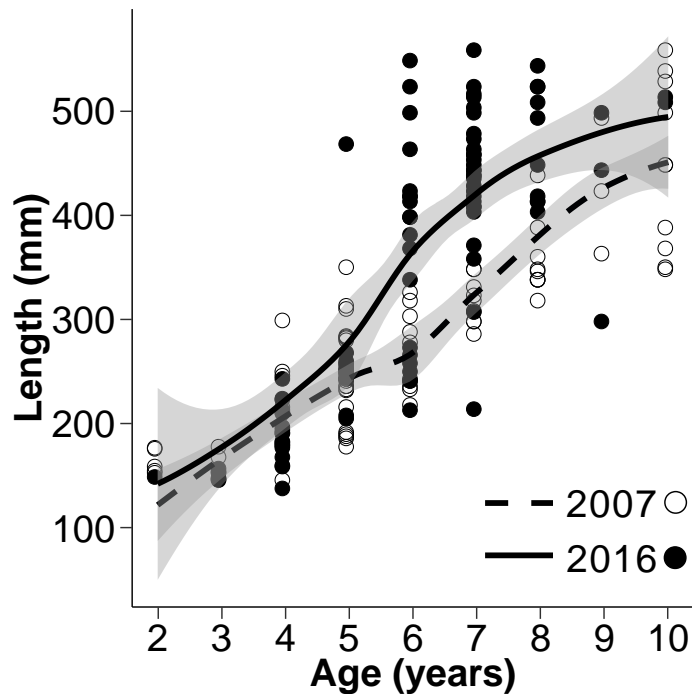
Fig. 6 Growth patterns of brown trout before (2007) and after (2016) the smelt

introduction to Storsjøen. The lines show predicted lengths for the 2007 (dashed line,

open circles) and 2016 (solid line, closed circles) data, based on a linear model with

year as well as back-calculated length and age in the previous year and their interaction

as explanatory variables (see Table 5). The grey shadings depict the 95% confidence

intervals for the predicted lengths