

1 **Introduced European smelt (*Osmerus eperlanus*) affects food web and**
2 **fish community in a large Norwegian lake**

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19

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27 **Abstract**

28 Invasive and introduced fishes can affect recipient ecosystems and native species via
29 altered competitive and predatory interactions, potentially leading to top-down and
30 bottom-up cascading impacts. Here, we describe a case from a large lake in southern
31 Norway, Storsjøen, where the illegal introduction of a small, predominantly
32 planktivorous fish species, European smelt (*Osmerus eperlanus*), has led to changes in
33 the native fish community and lake food web. Survey fishing data collected before
34 (2007) and after (2016) the introduction indicates that smelt has become the numerically
35 dominant fish species both in benthic and pelagic habitats, with concurrent reductions
36 in the relative abundance of native European whitefish (*Coregonus lavaretus*) and
37 Arctic charr (*Salvelinus alpinus*) populations. Stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) data
38 indicate minor changes in the trophic niches of native whitefish and Arctic charr despite
39 partly overlapping niches with the introduced smelt. In contrast, brown trout (*Salmo*
40 *trutta*) showed an earlier shift to piscivory, a more pelagic niche and increased growth
41 rate, likely because of the smelt induced increase in pelagic prey fish abundance. The
42 main trophic pathway supporting top predators (i.e., large brown trout) in Storsjøen has,
43 therefore, shifted from a littoral to a more pelagic base. Our study demonstrates that
44 small-sized introduced fishes can alter lake food-web dynamics, with contrasting
45 impacts on native fishes. This knowledge is vital for future evaluation and mitigation
46 of potential impacts of smelt introductions on lake ecosystems.

47

48 **Keywords:** alien species, energy flow pathways, lake food web, predatory fish,
49 resource competition, stable isotope analysis

50 **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

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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 m² 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: \pm 1 mm) and weighed (wet
141 mass: \pm 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

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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
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173 macroinvertebrates were collected using a 500- μ m mesh kick net and hand-picking in
174 the shallow littoral areas (0–1 m depth) and a 243- μ m 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- μ m mesh. Pelagic zooplankton taxa were collected
177 by taking several vertical hauls with an 80- μ m 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 $\delta^{13}\text{C}$ 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 $<0.3\text{‰}$ for both
194 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from fish muscle
206 tissue and mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of littoral and pelagic invertebrates. In
207 addition, the commonly used trophic fractionation corrections of $0.4 \pm 1.3\text{‰}$ for $\delta^{13}\text{C}$
208 and $3.4 \pm 1.0\text{‰}$ for $\delta^{15}\text{N}$ (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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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
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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, $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\Delta AICc > 2$ 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 ($\delta^{13}\text{C}$) as well as consumers at different trophic levels ($\delta^{15}\text{N}$).
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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, 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 $\delta^{13}\text{C}$ ($P > 0.150$).
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 $\delta^{13}\text{C}$
299 and $\delta^{15}\text{N}$ 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.

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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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 ($\Delta\text{AICc} \sim 1.8$), 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

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344 **Discussion**

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

358 Our survey fishing data suggests that smelt has become the numerically
359 dominant fish species in all major habitats in Storsjøen, as has the smelt source
360 population in Lake Mjøsa (Sandlund et al. 1985a; Hagenlund et al. 2015). Whitefish
361 and Arctic charr are among the most common fish species found in the pelagic and
362 profundal habitats of large and deep lakes in northern Europe (e.g. Eloranta et al. 2015;
363 Sandlund et al. 2010, 2016). These two salmonids are highly valued among commercial
364 and recreational fishermen, but subjected to various anthropogenic disturbances such
365 as warming, eutrophication, overfishing and invasion of competitive and predatory
366 fishes, particularly in their southernmost distribution areas (e.g. Graham and Harrod
367 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
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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

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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

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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

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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 (µg l ⁻¹)*	180
Total phosphorus (µg l ⁻¹)*	4.1
Total organic carbon (mg l ⁻¹)*	2.9
Colour*	20

641

642 **Table 2** Summary of the mean \pm SD values, ranges (min–max) and between-year statistical comparisons (*t*-tests) of standard length, condition,
 643 $\delta^{13}\text{C}$ 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 \pm SD	Range	n	Mean \pm SD	Range	<i>t</i> / <i>W</i> *	<i>P</i>
Brown trout	Length (mm)	72	258 \pm 85	135 – 560	54	243 \pm 79	140 – 518	2146*	0.322
	Condition	12	0.92 \pm 0.08	0.79 – 1.19	15	0.92 \pm 0.10	0.71 – 1.13	0.14	0.888
	$\delta^{13}\text{C}$ (‰)	12	-24.3 \pm 2.2	-27.6 – -19.7	15	-26.9 \pm 2.2	-30.1 – -22.5	3.01	0.006
	TP	12	2.36 \pm 0.70	1.39 – 3.51	15	2.17 \pm 0.43	1.15 – 2.97	0.84	0.412
Whitefish	Length (mm)	364	284 \pm 101	100 – 414	100	315 \pm 70	115 – 438	16162*	0.086
	Condition	364	0.82 \pm 0.10	0.60 – 1.14	100	0.81 \pm 0.11	0.45 – 1.06	18346*	0.547
	$\delta^{13}\text{C}$ (‰)	15	-28.5 \pm 1.1	-30.1 – -26.5	40	-28.2 \pm 2.1	-30.4 – -22.6	322*	0.685
	TP	15	2.46 \pm 0.14	2.22 – 2.82	40	2.34 \pm 0.32	0.98 – 2.87	369*	0.199
Grayling	Length (mm)	47	270 \pm 88	112 – 440	21	318 \pm 67	178 – 457	-2.81	0.006
	Condition	9	0.81 \pm 0.11	0.60 – 0.99	21	0.80 \pm 0.10	0.59 – 1.17	1028*	0.236
	$\delta^{13}\text{C}$ (‰)	9	-20.5 \pm 2.5	-25.6 – -18.7	21	-22.1 \pm 1.6	-27.7 – -20.1	1.81	0.098
	TP	9	2.02 \pm 0.09	1.93 – 2.22	21	1.94 \pm 0.29	1.58 – 2.42	107*	0.602

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 $\Delta\text{AIC} < 2$) 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

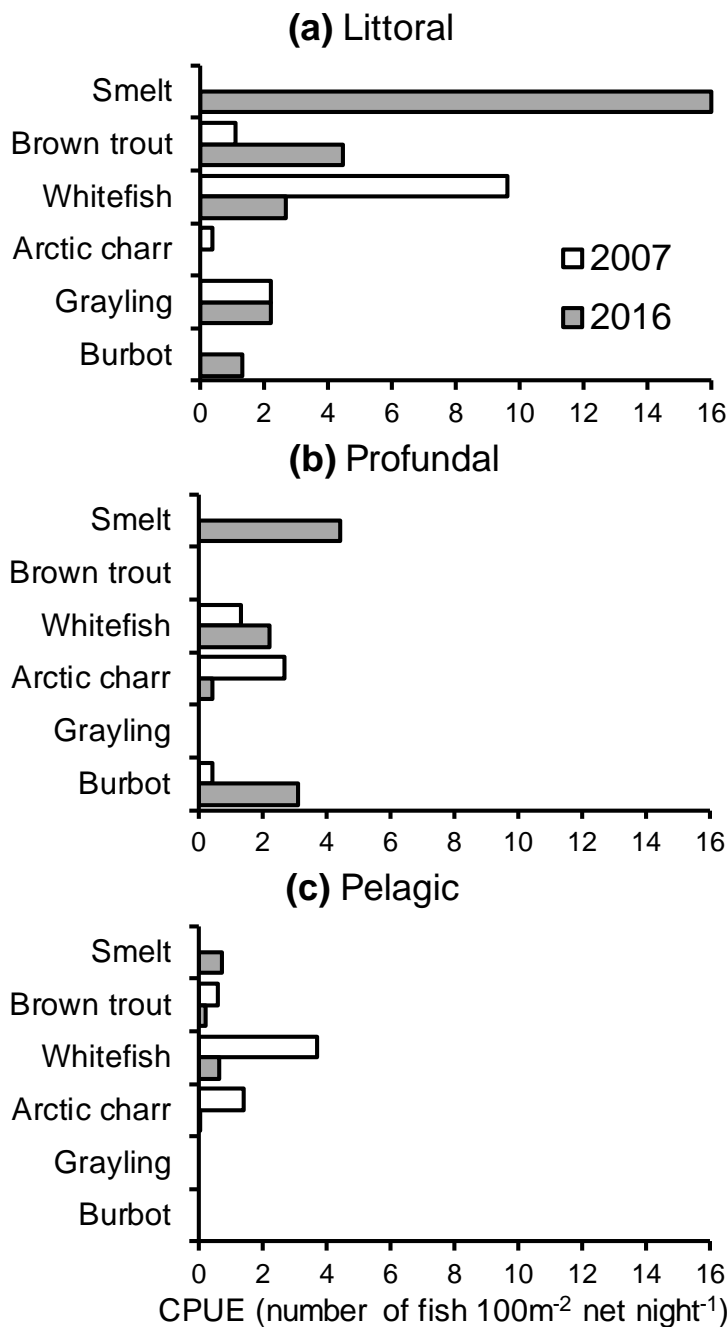
Response	Parameter	Estimate	SE	<i>t</i>	<i>P</i>
Trophic position	Intercept	-6.58	1.20	-5.47	<0.001
	Year	-3.68	1.57	-2.34	0.020
	(log) Length	1.55	0.20	7.67	<0.001
	(log) Length x Year	0.68	0.26	2.60	0.010
Littoral reliance	Intercept	3.56	0.35	10.10	<0.001
	Year	-0.39	0.05	-8.04	<0.001
	(log) Length	-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 ($\text{Length}_{y-1} \times \text{Age}_{y-1}$). 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

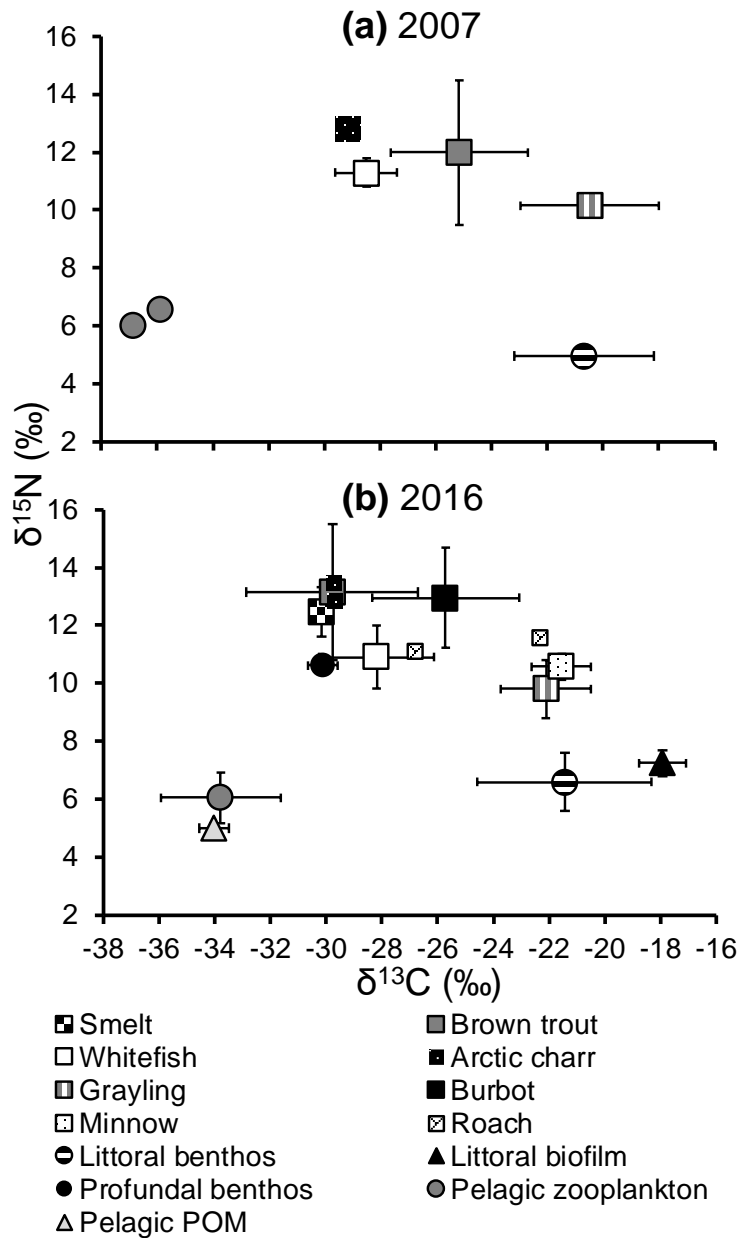


670

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 net673 night⁻¹) estimates from survey fishing in (A) littoral, (B) profundal and (C) pelagic

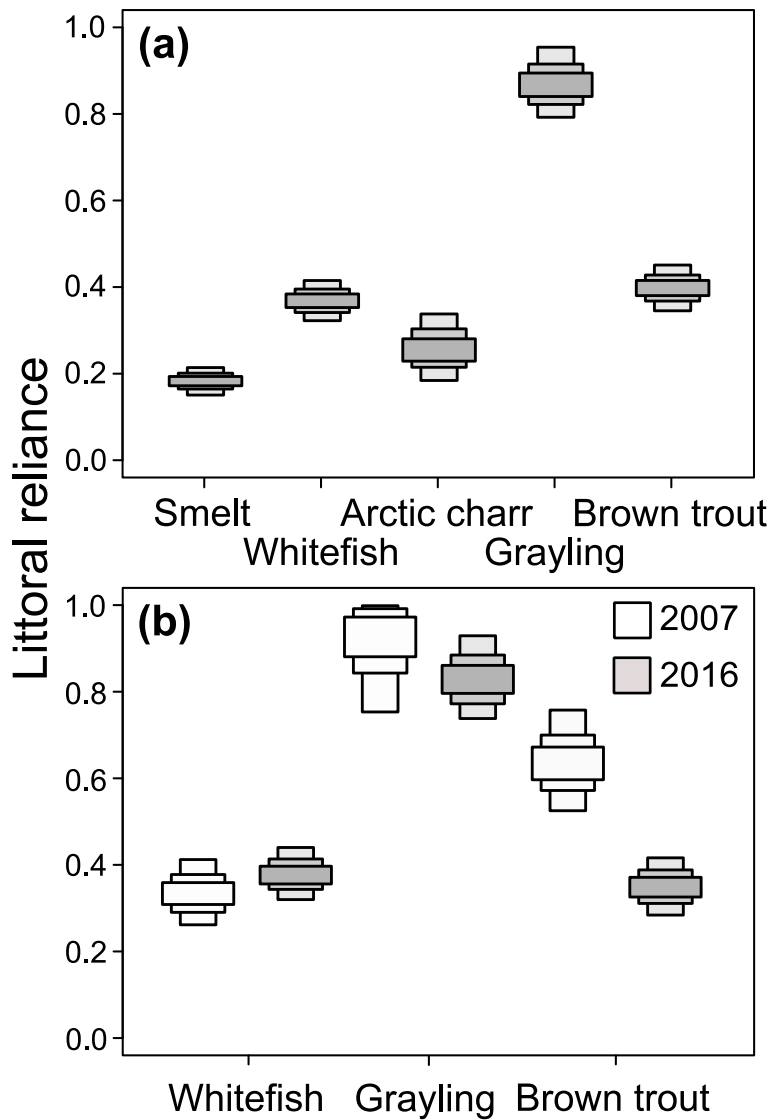
674 habitats. The CPUE estimates in (A) and (B) are based on benthic Nordic gillnet catches

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

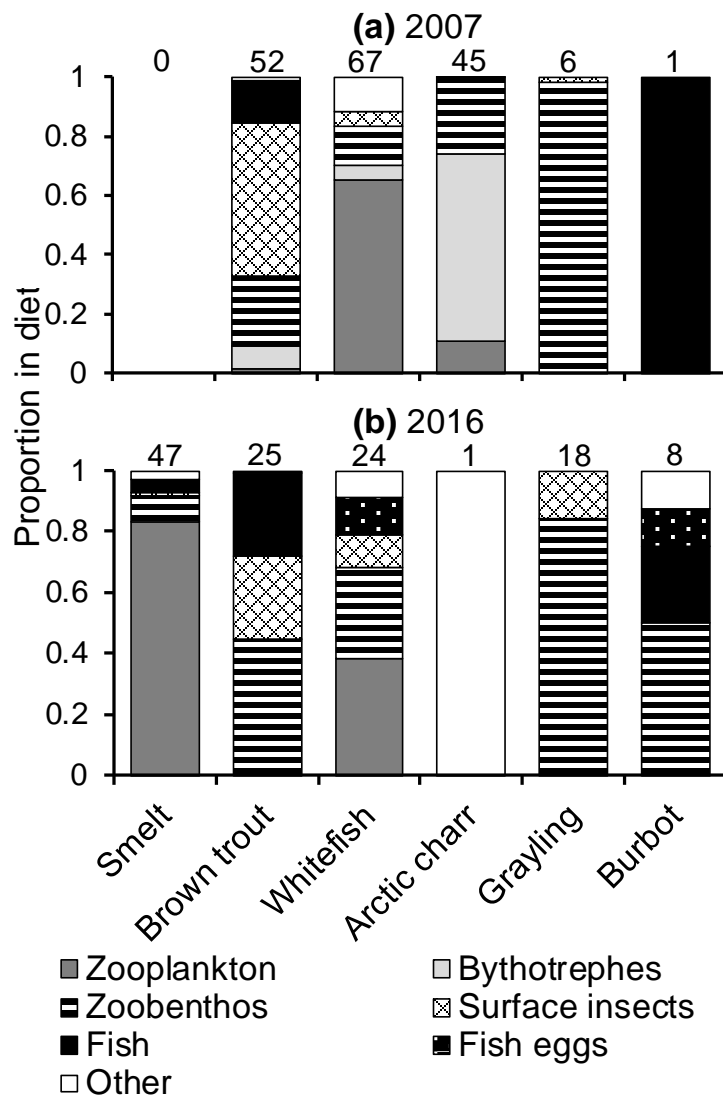
678 **Fig. 2** Stable isotope biplot showing the mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of littoral and
 679 pelagic basal resources, invertebrates and different fish species collected from Storsjøen
 680 (A) before and (B) after smelt introduction. Individual values are shown for the two
 681 zooplankton samples analysed in 2007 and for the two Arctic charr and roach analysed
 682 in 2016.



683

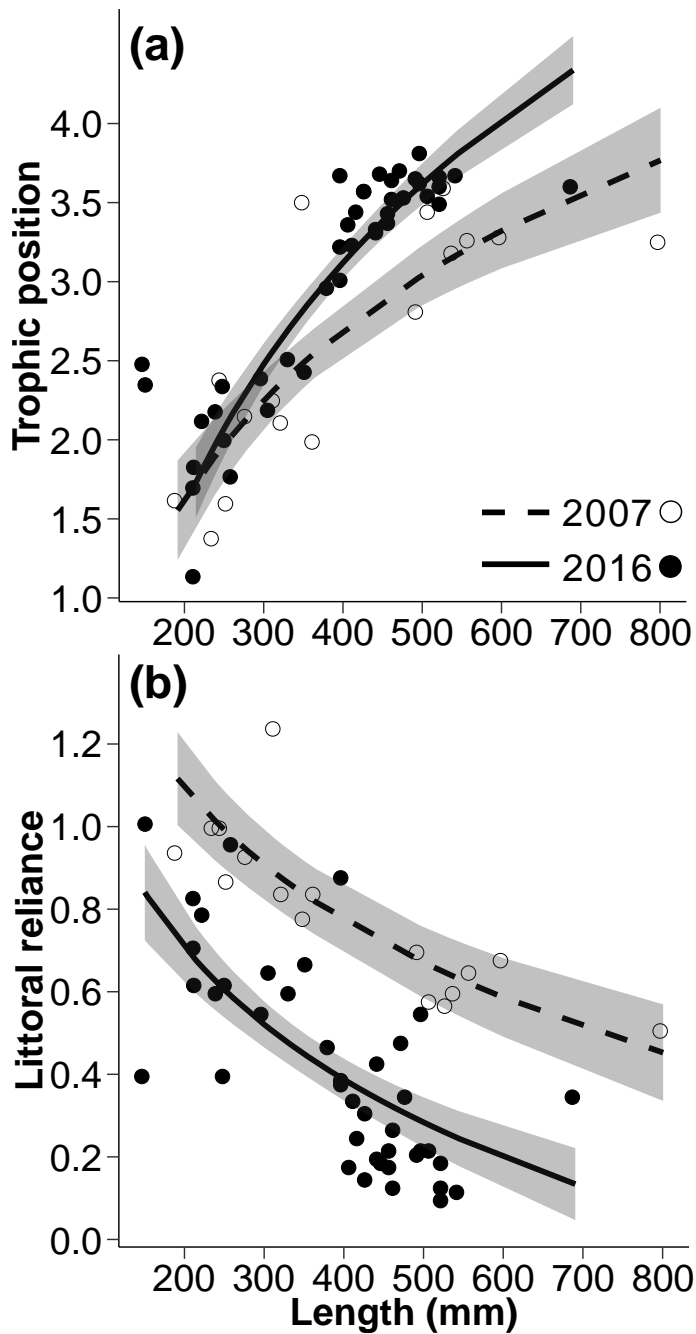
684 **Fig. 3** (a) Between-species and (b) between-year comparisons of littoral reliance of
 685 different fish species in Storsjøen, based on results from SIAR two-source isotopic
 686 mixing model. The boxes indicate the 95, 75 and 50% Bayesian credibility intervals for
 687 the source proportion estimates

688



689

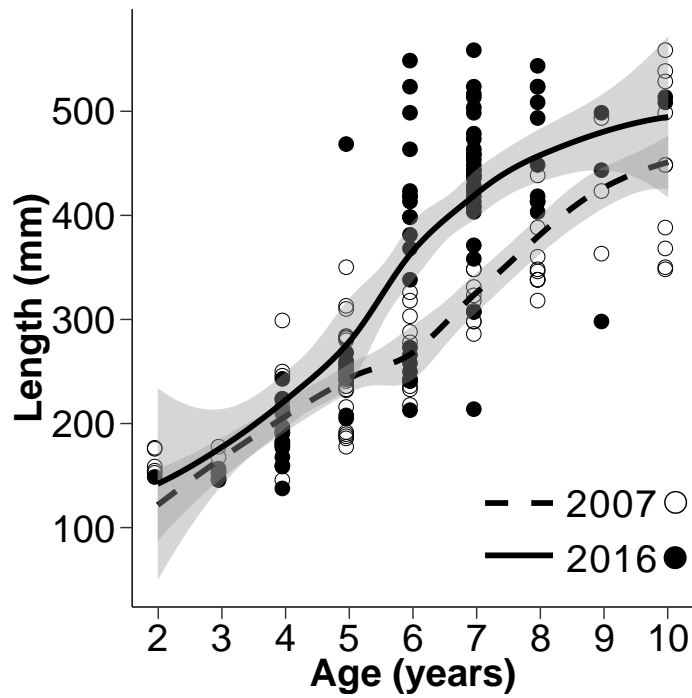
690 **Fig. 4** Proportion of different prey taxa in the stomach contents of dominant fish species
 691 collected (a) before and (b) after the smelt introduction in Storsjøen. The numbers of
 692 analysed fish are shown above the bars



693

694 **Fig. 5** Ontogenetic shifts in (A) trophic position and (B) littoral reliance of brown trout
 695 caught from Storsjøen before (2007) and after (2016) smelt introduction. The lines
 696 present predicted values from the most supported models for the 2007 (dashed line,
 697 open circles) and 2016 (solid line, closed circles) data, based on linear models with year
 698 (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

702 **Fig. 6** Growth patterns of brown trout before (2007) and after (2016) the smelt
 703 introduction to Storsjøen. The lines show predicted lengths for the 2007 (dashed line,
 704 open circles) and 2016 (solid line, closed circles) data, based on a linear model with
 705 year as well as back-calculated length and age in the previous year and their interaction
 706 as explanatory variables (see Table 5). The grey shadings depict the 95% confidence
 707 intervals for the predicted lengths