Predicting the contributions of novel marine prey resources from angling and anadromy to the diet of a freshwater apex predator

1   **Predicting the contributions of novel marine prey resources from angling and**

2   **anadromy to the diet of a freshwater apex predator**

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Abstract

1. Anadromous fishes can be important prey resources for piscivorous fauna in lowland rivers. Freshwater anglers exploiting large-bodied cypriniform fishes use high quantities of pelletized marine fishmeal baits that can contribute substantially to fish diets. This marine-derived energy pathway also potentially provides a marine prey resource for freshwater piscivores. However, large-bodied cypriniform fishes are often in a size refuge against predation due to their large sizes.

2. Stable isotope (δ^{15}N and δ^{13}C) analysis assessed how novel marine prey resources influenced the diet of a freshwater apex predator, Northern pike *Esox lucius*, in an impounded river basin (lower River Severn, Western England). Up to three groups of prey resources were present: anadromous European shad (*Alosa* spp.), cypriniform fishes with dietary specialisms based on marine fishmeal baits, and freshwater prey. The availability of these prey resources to *E. lucius* varied according to river connectivity and levels of angling exploitation in different river reaches.

3. Where the three prey groups were present, *E. lucius* were more enriched in δ^{13}C values (range: -24.74 to -16.34 ‰) compared to river reaches where aspects of the marine prey groups were absent. (range: -28.30 to -21.47) In all reaches, δ^{13}C increased as *E. lucius* length increased. In the reach where all prey groups were present, the isotopic niches of three *E. lucius* size categories

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41 were strongly partitioned; this was not apparent in reaches where the marine

42 pathways were unavailable.

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44 4. Stable isotope mixing models suggested that freshwater prey were the most

45 important prey item, contributing between 42 and 96 % to the diet of

46 individual *E. lucius*. However, where present, anadromous fishes and

47 cypriniform fishes specialising on marine fishmeal baits were also important

48 prey items, contributing substantially to the diet of larger *E. lucius* (length >

49 650 mm). The total dietary contributions of the marine resources varied

50 considerably among the individual larger fish (22 to 58 % of total diet).

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52 **5.** The presence of two marine resource pathways in a lowland river thus

53 strongly influenced the diet of an apex predator, but with contributions being a

54 function of their spatial availability, *E. lucius* body size and individual trophic

55 specialisations. These results emphasise how the anthropogenic activities of

56 river engineering and human subsidies can affect the trophic dynamics of apex

57 predators.

58   **Introduction**

59

60   Allochthonous resource subsidies can substantially alter food web and community

61   dynamics of the receiving systems through, for example, increased primary and

62   secondary productivity (Polis, Anderson & Holt, 1997; Marcarelli et al., 2011).

63   Although the response of food-webs to allochthonous subsidies can vary (Marczak,

64   Thompson & Richardson, 2007), these subsidies are increasingly recognised as

65   important drivers of the behaviour and abundance of many consumer species

66   (Newsome et al., 2014, 2015).

67

68   In freshwater ecosystems, the transfer of nutrients from allochthonous resource

69   subsidies can play a primary role in food-web structuring (Takimoto, Iwata &

70   Murakami, 2002; Samways, Soto & Cunjak, 2018). The benefits to freshwater

71   nutrient budgets via marine derived nutrient (MDN) transfer from anadromous

72   salmonid fishes (via excretion, gamete release and carcass decomposition) have been

73   well established (e.g. Wipfli et al., 2003; Zhang et al., 2003; Schindler et al., 2005;

74   Richardson et al., 2016). However, anadromous fishes can also play an important role

75   in the transfer of MDN to freshwaters via their direct consumption by freshwater apex

76   predators (MacAvoy et al., 2000; Guillerault et al., 2017). Where the upstream

77   migration of anadromous fishes is impeded by blockages such as weirs and dams

78   (Ovidio & Philippart, 2002; Clavero, Blanco-Garrido & Prenda, 2004), their

79   downstream aggregations potentially provide important foraging opportunities for

80   piscivorous fauna (Sorel et al., 2016).

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82   Fishery management activities often enhance freshwater angling experiences by

83   diversifying the species available through the release of large-bodied invasive species,

84   such as carp *Cyprinus carpio* and European barbel *Barbus barbus* (Hickley & Chare,

85   2004). To target these fishes, catch-and-release anglers can release large amounts of

86   'groundbait' to attract fish (Jackson et al., 2013), with the quantities used often

87   exceeding 1 kg of bait per day (Niesar et al., 2004). These baits are increasingly based

88   on marine fishmeal, with the intensive use of pelletised marine fishmeal now common

89   in freshwater angling in Western Europe (Arlinghaus & Mehner, 2003; Bašić et al.,

90   2015; Gutmann Roberts et al., 2017). This MDN subsidy can alter the trophic

91   interactions between consumers (Bašić et al., 2015), assist invasions (Jackson et al.,

92   2013), and are increasingly recognised as an important dietary resource to

93   benthivorous and omnivorous fishes (Gutmann Roberts et al., 2017; Mehner et al.,

94   2018). Where high concentrations of marine fishmeal have been released into

95   freshwaters, it can be traced through food webs using stable isotope analyses (SIA),

96   with $\delta^{13}C$ differentiating between freshwater (depleted $\delta^{13}C$) and marine energy

97   sources (enriched $\delta^{13}C$) (Grey, Waldron & Hutchinson, 2004; Jardine et al., 2005;

98   Rasmussen, Trudeau & Morinville, 2009).

99

100   The presence of both anadromous fishes and freshwater fishes with diets comprising

101   mainly of marine fishmeal thus potentially provide apex predators in lowland rivers

102   with additional prey resources to freshwater prey. However, the ability of these

103   predators to exploit these marine derived resources will at least partially depend on

104   their ability to consume large bodied prey. This is because anadromous fishes entering

105   freshwater to spawn tend to be relatively large, with even the smallest *Alosa* spp.

106   migrants to European rivers generally being above 300 mm body length (Aprahamian,

107   1988). Cypriniform fishes that have diets specialising on pelletised fishmeal also tend

108   to be relatively large (> 380 mm) (Amat Trigo, Gutmann Roberts & Britton, 2017;

109   Gutmann Roberts et al. 2017). Given that freshwater apex fish predators, such as

110   Northern pike *Esox lucius*, are gape-limited in their prey selection (Craig, 2008;

111   Nilsson & Brönmark, 2000) then these marine derived resources might only be

112   available to the larger individuals in their populations. This influence of predator body

113   size on their prey sizes is important, as apex predator populations often couple

114   multiple energetic pathways in aquatic food webs through their exploitation of a wide

115   range of prey resources (e.g. Rooney, McCann, & Moore, 2008). Thus, traits that

116   influence prey size in apex predators will influence their ability to couple these energy

117   pathways (Nilsson & Brönmark, 2000; Rooney et al., 2008).

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119   Correspondingly, the aim here was to quantify how spatial variation in the availability

120   of marine prey resources (large bodied anadromous fish and cypriniform fishes

121   consuming MDN angler baits) influenced the diet of a gape-limited apex predator in a

122   lowland river. Where present, the exploitation of marine energy pathways by a

123   freshwater apex predator should lead to enriched $\delta^{13}C$ values and distinct population

124   dietary niches versus those fish that forage where the marine energy pathways are

125   absent (MacAvoy et al., 2000; Samways et al., 2018). The apex predator was *E.*

126   *lucius*, with their populations studied in the River Severn basin, Western England

127   (Fig. 1), where individuals grow to relatively large sizes (body lengths > 1 m; mass >

128   12 kg). In this basin, there is considerable spatial variation in the availability of

129   marine prey resources. Impoundments affect the upstream access of migrating

130   anadromous fishes (mainly *Alosa* spp.; Aprahamian, 1988); inputs of MDN based

131   angling bait are affected by spatial differences in fish community structure and

132   varying levels of angling activity (Gutmann Roberts et al., 2017). Using SIA to test

133   the influence of the presence/ absence of these MDN subsidies on *E. lucius* diet, the

134   objectives were to (1) assess the spatial variability in stable isotope data of the marine

135   and non-marine prey resources; (2) quantify the relationships between *E. lucius* body

136   length (as a proxy of gape size) and their stable isotope data; (3) determine the

137   influence of the marine prey resources on *E. lucius* trophic niche sizes (as isotopic

138   niches); and (4) assess how the diet composition of *E. lucius* at individual and

139   population levels are influenced by differences in the spatial availability of the marine

140   prey resources.

141

142   **Methods**

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144   *Study area*

145   The presence of impoundments (weirs, sluices) in the area of study in the lower River

146   Severn basin enabled its split into three study reaches based on longitudinal

147   connectivity (Fig. 1c). These included two contiguous reaches of the River Severn

148   (one immediately upstream of the other but separated by a weir), and a reach of the

149   Warwickshire Avon. The lower River Severn reach (hereafter referred to as the

150   downstream Severn reach) was located between Diglis Weir (upstream limit) and

151   Upper Lode Weir (downstream limit) (52.1819°, -2.2241° to 51.9943°, -2.1735°; Fig.

152   1(c)). Although a relatively long river reach (> 20 km), most of the *E. lucius* were

153   sampled within the initial 1 km downstream of Diglis Weir where river widths were

154   to 40 m and depths to at least 5 m. The upstream River Severn reach was located on

155   the River Severn above Diglis Weir, Worcester (52.1819°, 2.2241° to 52.3728°, -

156   2.3086°; Fig. 1c). In this reach, river widths were to 30 m and depths to 4 m. The

157 lower reach of the Warwickshire Avon ('Warwickshire Avon'; 51.9955°, -2.1579° to

158 52.1152°, -2.0702°; Fig. 1c) was up to 20 m wide, with depths to 4 m and is separated

159 from the Severn by the presence of flow regulation structures (two separate weirs).

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161

162 *Sampling of Esox lucius*

163 The habitat characteristics of the study reaches resulted in fish sampling by traditional

164 methods (electric fishing, seine netting, fyke netting) being inefficient or unfeasible,

165 other than within limited off-channel areas provided by boat marinas. Consequently,

166 sample collection of *E. lucius* was primarily via catch and release angling. This was

167 facilitated by the Environment Agency, the inland fishery regulatory body of England,

168 who established an *E. lucius* angling network within the Severn catchment. Within

169 this network, participating anglers recorded their catches and were trained in

170 collecting scale samples. Whilst the primary purpose of scale collection was for fish

171 age determination for management purposes, they concomitantly provided material

172 suitable for stable isotope analysis in this study (Hutchinson & Trueman, 2006; Bašić

173 & Britton, 2015). Scales tend to have a longer stable isotope half-life than muscle and

174 fin tissue (Busst & Britton, 2017). Consequently, between August 2014 and July

175 2017, anglers collected scales from captured *E. lucius* and recorded the location and

176 date of capture and fish fork length (Supplementary material, Table S1). Note, angling

177 effort for *E. lucius* was variable between reaches, being highest in the downstream

178 Severn reach and lowest in the upstream Severn reach, resulting in spatial variation in

179 *E. lucius* sample sizes. Due to this method of sample collection, there was no

180 opportunity for the collection of complementary data, such as stomach contents via

181 stomach flushing or gape size measurements. Angling for *E. lucius* is also not

182   permitted on the river between mid-March and mid-June, a period covering the

183   majority of the *Alosa* spawning season.

184

185   *Spatial and temporal variation in the availability of putative prey of Esox lucius*

186   Upper Lode weir is passable by anadromous *Alosa* spp. that enter the river each year

187   to spawn between April and June, generally at lengths between 300 and 450 mm

188   (Aprahamian, 1988). Diglis weir and the weirs leading into the River Warwickshire

189   Avon are, however, considered impassable to *Alosa* spp. Therefore, the downstream

190   Severn reach was considered as the only reach within the study where this

191   anadromous energy pathway was present for *E. lucius.* Although anadromous Atlantic

192   salmon *Salmo salar* adults also enter the River Severn to spawn they are not resident

193   in the study reaches or available as a prey resource as they can ascend all weirs on the

194   main river during their upstream migration to spawning grounds located in the upper

195   catchment. The Warwickshire Avon is inaccessible to migrating *S. salar* due to

196   impassable engineering structures in the lower river (Tewkesbury weir).

197   Quantification of the levels of use of pelletized marine fishmeal baits by anglers

198   within each reach could not be assessed directly (e.g. by creel census). However,

199   large-bodied cypriniform fishes (mainly *B. barbus*, but also chub *Squalius cephalus*)

200   in the downstream Severn reach have already been identified as specialising on

201   pelletised fishmeal (Gutmann Roberts et al., 2017). Correspondingly, all reaches

202   could potentially contain prey resources that include cypriniform fish specialising on

203   marine fishmeal baits, but with the downstream Severn reach the only reach where

204   both marine prey resource groups could be present (i.e. *Alosa* spp. and cypriniform

205   fishes specialising on fishmeal baits). Note that throughout the catchment, whilst *B.*

206   *barbus* populations were present and targeted by anglers, they were invasive, having

207   been introduced in 1956 (Wheeler & Jordan, 1990; Antognazza et al., 2016).

208

209   *Sampling for putative prey species of Esox lucius*

210   Samples for stable isotope analysis of the putative prey species of *E. lucius* were

211   collected throughout the study period from the downstream Severn and Warwickshire

212   Avon reaches only, as logistical constraints prevented the collection of comparative

213   putative prey species from the upstream Severn reach. The putative prey samples

214   from the downstream Severn and Warwickshire Avon reaches were small cypriniform

215   fishes (< 400 mm; *R. rutilus*, *S. cephalus*, *B. barbus*), and macro-invertebrates

216   (Gammaridae, Chironomidae and Asellidae), as macro-invertebrates can be important

217   prey resources for *E. lucius*, especially where individuals are less than 600 mm

218   (Chapman, Mackay & Wilkinson, 1989; Venturelli & Tonn, 2005; Pedreschi et al.,

219   2015). Fish were sampled by angling in the main river channels and by seine netting

220   in boat marinas, while macroinvertebrates were sampled by sweep netting in littoral

221   areas. Samples of larger (> 400 mm) *B. barbus* and *S. cephalus* were collected via

222   angling (Gutmann Roberts et al., 2017), ensuring that the putative prey resources of *E.*

223   *lucius* included larger cypriniform fish that can specialise on pelletised fishmeal

224   (Gutmann Roberts et al., 2017). In addition, scale samples of *Alosa* spp. in the

225   downstream Severn reach were collected opportunistically and non-invasively during

226   their spawning periods (April to June), such as by collecting scales from carcasses

227   from otter *Lutra lutra* predation. For all putative prey fish, identification was to

228   species, with measurement (fork length, nearest mm) and the collection of 3 to 5

229   scales from the body area between the dorsal fin and lateral line. For macro-

230   invertebrates, identification was to family.

231

Stable isotope analysis

233 For SIA, all captured *E. lucius* from the upstream Severn reach were analysed (n = 8;

234 lengths 420 to 901 mm). At the Warwickshire Avon reach, higher numbers of angler-

235 captured fish enabled analysis of 19 *E. lucius* across their length range (455 to 1020

236 mm). At the downstream Severn reach, 30 *E. lucius* were analysed (508 to 1060 mm).

237 Scale decalcification was not performed prior to their SIA. Whilst comparisons of

238 acidified versus non-acidified scales have revealed significant differences in their

239 isotopic data, the actual changes tend to be minor with, for example, Ventura &

240 Jeppesen (2010) showing that the process produced mean changes in $\delta^{13}C$ ($\pm$ SD) of

241 0.18 ± 0.12 and in $\delta^{15}N$ of -0.21 ± 0.24; conclusions were that these changes were not

242 biologically relevant. Scale preparation for SIA thus focused on cleaning scales

243 (distilled water) prior to the removal of the outer portion of the scale only. This

244 process ensured the analysed tissue was only from the most recent growth of each fish

245 (generally, the last full year of growth; Hutchinson & Trueman, 2006; Bašić &

246 Britton, 2015). For the majority of fish analysed, only one scale was used per

247 individual, as this provided enough material for analysis. For smaller prey fishes (<

248 120 mm), up to three scales had to be used. For macro-invertebrates, three replicate

249 samples were used per family, where a sample comprised of between one and three

250 individuals (dependent on their body sizes). All samples were then dried to constant

251 mass at 60 °C prior to their analysis at the Cornell Isotope Laboratory, New York,

252 U.S.A. Stable isotope analytical details were as per (Busst & Britton, 2017), with lipid

253 correction not necessary as C:N ratios indicated very low lipid content (< 3.5; Post et

254 al., 2007).

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Data analyses

256

257 As samples were collected across years, data were first subject to analysis of variance

258 (ANOVA) to test for differences in *E. lucius* δ^{15}N and δ^{13}C values among years at

259 each reach. As these results did not show consistent significant differences within

260 reach (Supplementary material, Table S2), the stable isotope data were combined

261 across all years without correction. The relationship between *E. lucius* body length

262 and δ^{15}N and δ^{13}C were determined for each reach using linear regression. Analysis of

263 covariance (ANCOVA) was then used to test for independent and interactive effects

264 of both reach and fish length on δ^{15}N and δ^{13}C. Both models included reach as a

265 factor (fixed, 3 levels: Warwickshire Avon, upstream Severn, downstream Severn)

266 and fish length as a covariate, together with their interaction. Thus, a significant (α =

267 0.05) interaction term would indicate that the relationship between the respective

268 isotope value and body length varied according to reach. Where there was a

269 significant main effect of reach, Tukey's post-hoc tests were used for pairwise

270 comparisons between factor levels. In addition, differences in the SI data of all

271 putative prey were tested between the downstream Severn and Warwickshire Avon

272 reaches using t-tests. Prior to analyses, normality and homoscedasticity of data were

273 assessed by visual inspection of the residual plots

274

275 The *E. lucius* stable isotope data were then analysed in two ways. First, the isotopic

276 niche of *E. lucius* was estimated using metrics based on standard ellipses obtained by

277 applying the data within a Bayesian framework, completed within the package 'Stable

278 Isotope Bayesian Ellipses in R' (SIBER; Jackson et al., 2011). Niche metrics were

279 first assessed for all *E. lucius* at each reach and then, for the downstream Severn and

280 Warwickshire Avon reaches where sample sizes were highest by three distinct size

281   categories: $\geq 400 < 650$ mm; $\geq 650 < 850$ mm; and ≥ 850 mm. SIBER metrics were

282   only calculated for sample sizes greater than or equal to five (Table 2). Isotopic niche

283   sizes were calculated as standard ellipse areas (SEA), with these representing the core

284   40 % of the isotopic data (Jackson et al., 2011). This bivariate measure of the

285   distribution of individuals in isotopic space thus is a representation of a population's

286   typical resource use (Jackson et al., 2011; Jackson et al., 2012). Additional

287   calculations were the total area of the convex hull encompassing the data points (TA),

288   the correction applied to SEA to account for small sample sizes (SEA_C), and the

289   Bayesian standard ellipse areas (SEA_B) and their 95% credible intervals. For SEA_B,

290   significant differences in the size of isotopic niches were identified when $\geq 95\%$ of

291   posterior draws for one area were smaller than the other. The area of niche overlap

292   between two or more ellipses was also calculated where appropriate.

293

294   Then, for *E. lucius* at the downstream Severn and Warwickshire Avon reaches, their

295   SI data were applied to Bayesian mixing models to predict the relative proportions (as

296   posterior probability distributions) of the putative prey resources that contributed to

297   their diet. This was not completed for the upstream Severn due to the low *E. lucius*

298   sample size (n < 5) and lack of SI data on their putative prey. The mixing models

299   were completed in the package 'Mixing Models for Stable Isotope Analysis in R'

300   (MixSIAR; Stock et al., 2018). MixSIAR was used to assess the proportional prey

301   contributions to *E. lucius* diet in the two reaches according to the three size categories

302   outlined above for the niche metrics (to assess group level contributions), and then

303   individually, by including individual as a covariate to explain variability in mixture

304   proportions. This enabled assessment of differences in individual level contributions

305   versus group level contributions. All models were run using 'normal' run length

306 (chain length: 100,000 iterations with burn-in of 50,000, with posterior thinning (thin:

307 50) and 3 chains). Model diagnostics were based on Gelman-Rubin and Geweke, with

308 sufficient convergence to accept the results (Stock & Semmens, 2016). The isotopic

309 fractionation values between the prey resources and *E. lucius* (δ^{15}N 3.35 ± 0.25 ‰;

310 δ^{13}C 3.49 ± 0.25‰) were based on values obtained for other piscivorous fish through

311 controlled feeding experiments (Barnes et al., 2007), with correction for scales from

312 dorsal muscle (Heady & Moore, 2013; Busst, Bašić & Britton, 2015; Busst & Britton,

313 2016). Mixing model outputs were reported as means of all feasible solutions with

314 standard deviation and the 5th to 95th credible intervals of the distribution ranges.

315

316 Before the mixing models were run, there was consideration of how the putative prey

317 data were entered. For the larger bodied (> 380 mm) cypriniform prey (*B. barbus* and

318 *S. cephalus*), there was considerable range in their δ^{13}C isotope values (-28.4 to -19.4

319 ‰), with individuals with enriched δ^{13}C the result of their dietary specialisation on

320 pelletised fishmeal released by anglers (Gutmann Roberts et al., 2017). Due to this

321 considerable δ^{13}C range, this 'Cypriniform' prey resource was split into two groups

322 ('marine' and 'freshwater'). This grouping was based on the Bayesian stable isotope

323 mixing model results of Gutmann Roberts et al. (2017), where cypriniform prey

324 resources with δ^{13}C of -22.90 to -19.40 ‰ had relatively high predicted proportions of

325 MDN to their diet (predicted mean ± SE MDN contribution to diet: 0.50 ± 0.17;

326 Supplementary material, Table S3). These fish were thus grouped as 'Cypriniform-

327 marine' in the mixing models. Cypriniform prey resources with δ^{13}C of -28.04 to -

328 23.04 ‰ had relatively low proportions of MDN in their diet (mean ± SE MDN

329 contribution to diet: = 0.24 ± 0.11; Table S3). These fish were then grouped as

330 'Cypriniform-freshwater' in the mixing models. The differences in MDN dietary

331   contributions between the two groups were significant (t-test; $t = -5.66$, $P < 0.001$;

332   Supplementary material, Table S3). Smaller bodied (< 380 mm) cypriniform fishes

333   (*R. rutilus*, *B. barbus* and *S. cephalus*) were then all assigned to the appropriate group

334   based on their isotope value and thus were incorporated within the 'Cypriniform-

335   freshwater' group. This was due to the high similarity of their SI data with the larger

336   non-MDN cypriniforms. Importantly, this also reduced the overall number of prey

337   resources used in the mixing models, enhancing model performance and reducing

338   prediction uncertainty (Phillips & Gregg, 2003; Phillips, Newsome & Gregg, 2005).

339

340   The putative prey resources that could be entered into each mixing model were thus

341   macro-invertebrates (combined data for Gammaridae, Chironomidae and Asellidae,

342   due to similarity of SI data; *cf.* Results), *Alosa* spp., 'Cypriniform-freshwater' fish and

343   'Cypriniform-marine' fish, with the prey resources analysed separately for each reach.

344   However, the use of all of these resources in the models for each *E. lucius* size

345   category was not appropriate. This was because of the *E. lucius* size-specific gape

346   limitations, where smaller individuals are limited in their ability to consume larger-

347   bodied prey items (Nilsson & Brönmark, 2000). The use of angler-captured fish

348   meant the gape sizes of *E. lucius* could not be measured directly. Therefore, for each

349   individual *E. lucius* analysed, their maximum ingestible prey size (MP) was estimated

350   as a function of their fork length (FL) (MP = (0.13FL)+0.40; Nilsson & Brönmark,

351   2000). To incorporate these maximum prey lengths into the analysis, mixing models

352   were run for three size categories of *E. lucius* outlined earlier. The mean MP was

353   determined for each reach and size category, and only prey resources under the mean

354   MP were entered into their mixing model (Table 1). Although this meant that the

355   mixing models differed between the size categories, it ensured the final models were

356   parsimonious and ecologically realistic.

357

358   All statistical analysis and graphical outputs were performed using R (Version 3.5.2;

359   R Development Core Team 2018). Where error is expressed around the mean, it

360   represents ± 95% confidence limits unless otherwise stated.

361

362   **Results**

363

364   *Stable isotope relationships with length* in *Esox lucius*

365   There was a significant increase in $\delta^{13}C$ with increasing length for *E. lucius* within

366   reaches (Fig. 2; Table 2; Warwickshire Avon: $R^2 = 0.34$, $F_{1,17} = 10.08$; $P < 0.01$,

367   upstream Severn: $R^2 = 0.71$, $F_{1,6} = 17.76$, $P < 0.01$; downstream Severn: $R^2 = 0.47$,

368    $F_{1,28} = 24.75$, $P < 0.001$). This increase was also independent of reach (ANCOVA:

369    $F_{1,51} = 75.21$, $P < 0.001$). The $\delta^{13}C$ values also differed significantly between reaches

370   (ANCOVA: $F_{2,51} = 33.24$, $P < 0.001$), where *E. lucius* from the Warwickshire Avon

371   had depleted $\delta^{13}C$ versus both the downstream Severn (-3.49 ‰, $t = -7.87$, $P < 0.001$)

372   and upstream Severn (-1.80 ‰, $t = -2.91$, $P = 0.01$). Fish from the downstream Severn

373   reach also had significantly enriched $\delta^{13}C$ values versus the upstream Severn reach

374   (+1.70 ‰, $t = 2.84$, $P = 0.02$). The interaction between length and reach was not

375   significant (ANCOVA: $F_{2,51} = 2.86$, $P = 0.06$).

376

377   The relationship between $\delta^{15}N$ and fish length was not significant in the Warwickshire

378   Avon ($R^2 = 0.04$, $F_{1,17} = 0.29$; $P = 0.60$) and downstream Severn ($R^2 = 0.01$, $F_{1,28} =$

379   1.29, $P = 0.28$) (Fig. 2; Table 2). There was, however, a significant increase in $\delta^{15}N$

380   with fish length at upstream Severn (Fig. 2; Table 2; $R^2 = 0.51$, $F_{1,6} = 6.12$, $P = 0.04$).

381   The relationship between $\delta^{15}N$ and fish length was not significant independent of

382   reach (ANCOVA: $F_{1,51} = 1.78$, $P = 0.19$), but $\delta^{15}N$ did differ significantly between

383   reaches (ANCOVA: $F_{2,51} = 63.38$, $P < 0.001$). Fish in the Warwickshire Avon had

384   significantly higher $\delta^{15}N$ than at the other reaches (downstream Severn +2.81 ‰, $t =$

385   10.27, $P < 0.01$; upstream Severn +3.06 ‰, $t = 8.04$, $P < 0.01$).

386

387   *Isotopic niche of Esox lucius*

388   The isotopic niche size (as SEA_B) of *E. lucius* was largest for the Warwickshire Avon,

389   followed by downstream Severn and was smallest at upstream Severn (Table 3). The

390   position, size and location of the ellipses varied in niche space, where *E. lucius*

391   isotopic niche from the Warwickshire Avon occupied more space on the $\delta^{15}N$ axis

392   and less space on the $\delta^{13}C$ axis compared with the downstream Severn reach that

393   showed the opposite pattern (Fig. 3).

394

395   Isotopic niche sizes (as SEA_B) by the three size categories of *E. lucius* revealed that in

396   the Warwickshire Avon, the largest niche was in fish of 651 to 850 mm and the

397   smallest niche for fish > 850 mm (Table 3; Fig. 4). These niches also showed a high

398   degree of overlap across all size categories with, for example, the niche of the largest

399   size category (> 850 mm) sitting entirely within the niche for fish of 651 to 850 mm

400   (Fig. 4). By contrast, the isotopic niches by size category in the downstream Severn

401   reach had greater separation along the $\delta^{13}C$ axis (Table 3; Fig. 4). The niche size for

402   fish of 400 to 650 mm was relatively small compared to the two larger size categories

403   and did not overlap (Table 3; Fig. 4). The isotopic niche for fish of > 850 mm was the

404   largest within the downstream Severn reach and was considerably $\delta^{13}C$ enriched,

405 resulting in it sharing only 40 % of its niche space with that for fish of 651 to 850 mm

406 (Table 2; Fig. 4).

407

408 *Spatial and temporal variation in $\delta^{13}C$ and $\delta^{15}N$ of putative prey resources*

409 The $\delta^{13}C$ values of macro-invertebrates did not differ between reaches (Warwickshire

410 Avon: -30.23 ± 0.46 ‰; downstream Severn: -29.67 ± 0.39 ‰; *t-test*: *t* = -0.92 , *d.f.* =

411 17, *P* = 0.37; Table 1; Fig. 4). There was, however, significant $\delta^{13}C$ enrichment in the

412 putative prey resources between the reaches (*t-test*: *t* = 7.82, *d.f.* = 168.67, *P* < 0.001;

413 Table 1; Fig 4). This significant $\delta^{13}C$ enrichment was thus due to significant

414 differences in the fish prey resources (Warwickshire Avon: -26.48 ± 0.31;

415 downstream Severn: -22.78 ± 0.34; *t-test*: *t* = -8.01, *d.f.* = 145.62, *P* < 0.001; Table 1;

416 Fig. 4).

417

418 The putative prey resources were significantly enriched in $\delta^{15}N$ in the Warwickshire

419 Avon (16.02 ± 0.24 ‰) versus the Severn (12.28 ± 0.13 ‰) reaches (*t-test*: *t* = -7.81,

420 *d.f.* = 168.67, *P* < 0.001; Table 1; Fig. 4). Differences were in both

421 macroinvertebrates and fish prey resources (macroinvertebrates: *t-test*: *t* = 12.64, *d.f.*

422 = 15.10, *P* < 0.001; prey fish: *t-test*: *t* = - 8.0, *d.f.* = 145.62, *P* < 0.001; Table 1; Fig.

423 4).

424

425 *Stable isotope mixing model predictions of Esox lucius diet composition*

426 At both the Warwickshire Avon and downstream Severn reaches, *E. lucius* isotopic

427 niches across all size categories were positioned between the putative prey resources

428 (Fig. 4). At the Warwickshire Avon, whilst the cypriniform fishes specialising on

429 marine fishmeal baits were present, the gape limitations in the size range of the

430   analysed *E. lucius* meant none were considered as available prey in mixing models.

431   Thus, all dietary contributions in this reach were of freshwater origin (Table 1), with

432   predictions that macro-invertebrate prey resources were contributing substantially to

433   the diet of *E. lucius* < 650 mm (Table 4). Freshwater fishes and macroinvertebrates

434   were then important prey items at sizes > 650 mm (Table 4).

435

436   In the downstream Severn reach, whilst freshwater fish were predicted as the most

437   important prey resource in all size categories, the two marine prey resources were

438   increasingly important prey items as *E. lucius* body length increased. Overall, the

439   proportions dietary contributions of *Alosa* spp. increased from 0.05 ± 0.04 in fish <

440   650 mm to 0.13 ± 0.06 in fish of length > 850 mm (Table 4). Whilst gape limitations

441   precluded cypriniform fishes specialising on marine fishmeal bait from diet

442   predictions for *E. lucius* < 650 mm, in the larger size categories, the predicted

443   contributions were 0.24 ± 0.13 for 650 to 850 mm and 0.20 ± 0.14 for fish > 850 mm

444   (Table 4).

445

446   When predicted at the individual level, there was less dietary variability in *E. lucius* in

447   the Warwickshire Avon than in the downstream Severn reach (Table 4; Fig. 5). At the

448   downstream Severn reach, individual variability in diet increased with increasing gape

449   size, with the highest individual variability apparent for fish > 850 mm (Table 4). For

450   these fish, the 'Cypriniform-freshwater' prey had an estimated range of between 0.37

451   and 0.71 contribution to individual diet, *Alosa* spp. between 0.06 and 0.25 and

452   cypriniform fishes specialising on marine fishmeal bait between 0.18 and 0.33 (Table

453   4; Fig. 5b). The highest mean proportional contribution of marine resources to the diet

454   of an individual fish was 58 % (Fig. 5b).

455

Discussion

457

458   Stable isotope analysis revealed the presence of marine subsidies within an

459   impounded lowland river resulted in their substantial contribution to the assimilated

460   diet of large-bodied *E. lucius*. Results showed considerable dietary niche partitioning

461   between *E. lucius* size categories when anadromous *Alosa* spp. and cypriniform fish

462   specialising on marine fishmeal bait were available as prey. Where these resources

463   were not available, this niche partitioning was not evident. Stable isotope mixing

464   models revealed that in the downstream Severn reach, up to 33 % of *E. lucius*

465   population diet could be attributed to the marine subsidies at the population level,

466   with the greatest proportion of this marine resource contributed by cypriniform fishes

467   (20 % of total population diet). There was, however, considerable variation among

468   individuals, with between 22 and 58 % of individual diets consisting of the two

469   marine resources.

470

471   These results are consistent with studies on individual specialisation that suggest long

472   term differences in the diet of consumers can result in considerable variation of $\delta^{13}C$

473   within populations (Matthews & Mazumder, 2004). Other apex predators have also

474   been reported to couple distinct energetic pathways within complex food webs. For

475   example, Matich, Heithaus & Layman (2011) revealed that two pelagic shark species

476   coupled distinct food webs through dietary variations resulting from one species being

477   dietary specialists and the other being generalists. Individual specialisation in *E.*

478   *lucius* has also been previously documented (Beaudoin et al., 1999; Kobler et al.,

479   2009). It has been hypothesised as a potentially important mechanism in reducing

480   intraspecific competition, with Kobler et al., (2009) showing substantial behavioural

481   diversification in individual *E. lucius* that helped to reduce intra-specific competitive

482   interactions. Here, the diet diversification in the larger *E. lucius* was through their

483   specialisation on the marine prey subsidies that were all lengths >280 mm. Although

484   it could not be tested whether the fish specialising on these subsidies had different

485   behavioural traits to those that primarily consumed freshwater prey, they did require

486   functional traits that enabled the capture and handling of large prey. Whilst it could

487   also not be tested whether the consumption of these larger prey was a response to

488   intra-specific competition, the exploitation of marine subsidies by these individuals

489   resulted in higher intrapopulation variation and individual specialisation, as has been

490   shown elsewhere (e.g. Beaudoin et al., 1999; Bolnick et al., 2002; Araújo, Bolnick &

491   Layman, 2011). In doing so, the two marine energy pathways present in the

492   downstream Severn reach were coupled with those from non-marine sources at the

493   apex of this riverine food web.

494

495   The δ^{13}C of *E. lucius* differed significantly between the reaches, but with the effect of

496   the interaction of reach and fish length on δ^{13}C not being significant. There was,

497   however, high variability in δ^{13}C of larger *E. lucius* in the downstream Severn reach

498   that could potentially have strongly influenced this non-significant result. There was

499   also considerable variability in the contribution of marine resources to the diet of the

500   larger fish in the downstream Severn reach. Nevertheless, within this reach, the

501   dietary contributions of the two marine subsidies did increase with *E. lucius* body

502   length, explained by their prey selection being dependent on gape size, with this a

503   function of their body length. This finding is important, as in the dietary analyses of

504   *E. lucius*, individual diets tend to primarily consist of smaller prey (e.g. < 200 mm

505 length), irrespective of whether that fish can consume larger prey (Craig, 2008;

506 Sandlund, Museth & Øistad, 2016). This results from both a limited availability of

507 larger prey and larger prey having higher handling times that incurs an increased risk

508 of kleptoparasitism (Nilsson & Brönmark, 2000; Craig, 2008). Here, the stable

509 isotope data suggested that individual *E. lucius* over 650 mm could consume

510 relatively large fishes, with, for example, the approximate sizes of *Alosa* spp. in the

511 River Severn during their spawning period being > 300 mm (Aprahamian, 1988).

512 Moreover, the MDN prey resource from angling bait comprised of fishes of only

513 above 380 mm length. The presence of anadromous *Alosa* spp. in diet was also

514 interesting given they are only available for a relatively short period each year,

515 generally April to June, a period coincident with the post-spawning period of *E. lucius*

516 (Craig, 2008). Utilisation of these gape dependent resources resulted in isotopic niche

517 differences between populations with and without MDN pathways. This finding is

518 also consistent with Samways et al. (2018), who found that whilst the total ecological

519 niche space did not always increase in river communities following spawning of

520 anadromous fishes, this niche space did show consistent movement toward the

521 marine-nutrient source.

522

523 Apex predators are often associated with exerting top-down forces that can initiate

524 trophic cascades within food webs (Brett & Goldman, 1996; McIntosh & Townsend,

525 1996; Ritchie et al., 2012). However, bottom-up forces, such as prey availability, can

526 also influence predator behaviour and dietary preferences, resulting in prey switching

527 and altering predator-prey relationships (Newsome et al., 2014, 2015). For example,

528 human-influenced food subsidies have altered natural predator-prey relationships in

529 terrestrial systems via bottom-up processes (Ripple et al., 2013; Newsome et al.,

530   2014, 2015). These anthropogenic subsidies have been sufficient to maintain the

531   abundance and richness of numerous terrestrial predators, including species of birds,

532   mammals and reptiles (Ripple et al., 2014; Newsome et al., 2015). Here, the provision

533   of an anthropogenic prey subsidy in an aquatic system was via the release of large

534   amounts of angling baits that contained high proportions of MDN. The population

535   benefits of this subsidy for *E. lucius* might have been limited, as it can only be

536   exploited at relatively large sizes. It was beyond this study to determine if there were

537   reproductive and fitness benefits for individuals exploiting these marine prey

538   resources. Nevertheless, the relatively distinct $\delta^{13}C$ signal of the angler bait subsidy,

539   located between the freshwater and anadromous prey $\delta^{13}C$ signal, enabled these

540   nutrients to be traced through successive trophic levels in the food web. Previously,

541   MDN subsidies from aquaculture and angling have only been detected as being

542   assimilated directly by freshwater fishes (Jackson et al., 2013; Bašić et al., 2015;

543   Gutmann Roberts et al., 2017). Thus, a novel outcome of this study was the

544   demonstration that this anthropogenic marine subsidy was transferred to higher

545   trophic levels in the freshwater food web via piscivory. Notwithstanding, this result

546   was detected in only one river reach. Given the characteristics of the study system,

547   this was unavoidable, as the two marine prey pathways were only present in the

548   downstream Severn reach. Although sample sizes were often small in some reaches,

549   these were not considered to have been a major impediment to data analysis and

550   interpretation due to some of the considerable differences in the stable isotope data of

551   both prey and *E. lucius*. However, it would be beneficial to identify whether this

552   transfer of angling MDN though riverine food webs is apparent elsewhere, especially

553   in reaches where they are released in high quantities.

554

555   Angling baits have been argued as acting as a very strong allochthonous subsidy

556   compared to inputs of, for example, terrestrial invertebrates (Bašić et al., 2015;

557   Mehner et al., 2018). Here, their use in the River Severn basin created a novel MDN

558   energy pathway involving cypriniform consumers and the piscivorous *E. lucius*. The

559   dietary contribution of this MDN pathway was generally predicted to be higher than

560   that of the anadromous MDN pathway. This anadromous prey resource was, however,

561   still an important dietary component. Its presence was also consistent with a large

562   body of research that demonstrates the importance of anadromous fishes for

563   maintaining the productivity, diversity, and community structure of many freshwater

564   systems (e.g. Schindler et al., 2005; Richardson et al., 2016). Indeed, apex predatory

565   fishes have been shown to regularly predate upon anadromous fishes when they enter

566   freshwaters to spawn (MacAvoy et al., 2000; Guillerault et al., 2017).

567

568   In summary, the diet composition and isotopic niches of *E. lucius* populations was

569   influenced by the spatial variation of novel marine prey resources. Whilst body size

570   had a strong influence on the ability of *E. lucius* to exploit these marine prey

571   resources, there was considerable variability in the MDN dietary contributions to

572   larger fish. Notwithstanding, that angling bait based on marine resources could be

573   traced through successive trophic levels is a novel finding and highlights how human

574   subsidies can affect the trophic dynamics of apex predators.

575   **Acknowledgments**

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584

585 **References**

586

587 Amat Trigo F., Gutmann Roberts C. & Britton J.R. (2017) Spatial variability in the

588 growth of invasive European barbel *Barbus barbus* in the River Severn basin,

589 revealed using anglers as citizen scientists. *Knowledge & Management of*

590 *Aquatic Ecosystems*, 17.

591 Antognazza C.M., Andreou D., Zaccara S. & Britton R.J. (2016) Loss of genetic

592 integrity and biological invasions result from stocking and introductions of

593 *Barbus barbus*: insights from rivers in England. *Ecology and Evolution* **6**,

594 1280–1292.

595 Aprahamian M.W. (1988) The biology of the twaite shad, *Alosa fallax fallax*

596 (Lacépède), in the Severn Estuary. *Journal of Fish Biology* **33**, 141–152.

597 Araújo M.S., Bolnick D.I. & Layman C.A. (2011) The ecological causes of individual

598 specialisation. *Ecology Letters* **14**, 948–958.

599 Arlinghaus R. & Mehner T. (2003) Socio-economic characterisation of specialised

600 common carp (Cyprinus carpio L.) anglers in Germany, and implications for

601 inland fisheries management and eutrophication control. *Fisheries Research*

602 **61**, 19–33.

603   Barnes C., Sweeting C.J., Jennings S., Barry J.T. & Polunin N.V.C. (2007) Effect of

604   temperature and ration size on carbon and nitrogen stable isotope trophic

605   fractionation. *Functional Ecology* **21**, 356–362.

606   Bašić T. & Britton J.R. (2015) Utility of fish scales from stock assessment surveys in

607   stable isotope analysis for initial assessments of trophic relationships in

608   riverine fish communities. *Journal of Applied Ichthyology* **31**, 296–300.

609   Bašić T., Britton J.R., Jackson M.C., Reading P. & Grey J. (2015) Angling baits and

610   invasive crayfish as important trophic subsidies for a large cyprinid fish.

611   *Aquatic Sciences* **77**, 153–160.

612   Beaudoin C.P., Tonn W.M., Prepas E.E. & Wassenaar L.I. (1999) Individual

613   specialization and trophic adaptability of northern pike (*Esox lucius*): an

614   isotope and dietary analysis. *Oecologia* **120**, 386–396.

615   Bolnick D.I., Svanbäck R., Fordyce J.A., Yang L.H., Davis J.M., Hulsey C.D., *et al.*

616   (2002) The ecology of individuals: incidence and implications of individual

617   specialization. *The American Naturalist* **161**, 1–28.

618   Brett M.T. & Goldman C.R. (1996) A meta-analysis of the freshwater trophic

619   cascade. *Proceedings of the National Academy of Sciences* **93**, 7723–7726.

620   Busst G. & Britton J.R. (2017) Comparative trophic impacts of two globally invasive

621   cyprinid fishes reveal species-specific invasion consequences for a threatened

622   native fish. *Freshwater Biology* **62**, 1587–1595.

623   Busst G.M.A., Bašić T. & Britton J.R. (2015) Stable isotope signatures and trophic-

624   step fractionation factors of fish tissues collected as non-lethal surrogates of

625   dorsal muscle: Non-lethal tissue surrogates for fish isotope studies. *Rapid*

626   *Communications in Mass Spectrometry* **29**, 1535–1544.

627 Busst G.M.A. & Britton J.R. (2016) High variability in stable isotope diet–tissue

628 discrimination factors of two omnivorous freshwater fishes in controlled *ex*

629 *situ* conditions. *The Journal of Experimental Biology* **219**, 1060–1068.

630 Chapman L.J., Mackay W.C. & Wilkinson C.W. (1989) Feeding flexibility in

631 northern pike (Esox lucius): fish versus invertebrate prey. *Canadian Journal*

632 *of Fisheries and Aquatic Sciences* **46**, 666–669.

633 Clavero M., Blanco-Garrido F. & Prenda J. (2004) Fish fauna in Iberian

634 Mediterranean river basins: biodiversity, introduced species and damming

635 impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems* **14**, 575–

636 585.

637 Craig J.F. (2008) A short review of pike ecology. *Hydrobiologia* **601**, 5–16.

638 Grey J., Waldron S. & Hutchinson R. (2004) The utility of carbon and nitrogen

639 isotope analyses to trace contributions from fish farms to the receiving

640 communities of freshwater lakes: a pilot study in Esthwaite Water, UK.

641 *Hydrobiologia* **524**, 253–262.

642 Guillerault N., Bouletreau S., Iribar A., Valentini A. & Santoul F. (2017) Application

643 of DNA metabarcoding on faeces to identify European catfish *Silurus glanis*

644 diet. *Journal of Fish Biology* **90**, 2214–2219.

645 Gutmann Roberts C., Bašić T., Amat Trigo F. & Britton J.R. (2017) Trophic

646 consequences for riverine cyprinid fishes of angler subsidies based on marine-

647 derived nutrients. *Freshwater Biology* **62**, 894–905.

648 Heady W.N. & Moore J.W. (2013) Tissue turnover and stable isotope clocks to

649 quantify resource shifts in anadromous rainbow trout. *Oecologia* **172**, 21–34.

650 Hickley P. & Chare S. (2004) Fisheries for non-native species in England and Wales:

651 angling or the environment? *Fisheries Management and Ecology* **11**, 203–212.

652   Hutchinson J.J. & Trueman C.N. (2006) Stable isotope analyses of collagen in fish

653   scales: limitations set by scale architecture. *Journal of Fish Biology* **69**, 1874–

654   1880.

655   Jackson A.L., Inger R., Parnell A.C. & Bearhop S. (2011) Comparing isotopic niche

656   widths among and within communities: SIBER - Stable Isotope Bayesian

657   Ellipses in R: Bayesian isotopic niche metrics. *Journal of Animal Ecology* **80**,

658   595–602.

659   Jackson M.C., Allen R., Pegg J. & Britton J.R. (2013) Do trophic subsidies affect the

660   outcome of introductions of a non-native freshwater fish? *Freshwater Biology*

661   **58**, 2144–2153.

662   Jackson M.C., Donohue I., Jackson A.L., Britton J.R., Harper D.M. & Grey J. (2012)

663   Population-level metrics of trophic structure based on stable isotopes and their

664   application to invasion ecology. *PLoS ONE* **7**, e31757.

665   Jardine T.D., Gray M.A., McWilliam S.M. & Cunjak R.A. (2005) Stable isotope

666   variability in tissues of temperate stream fishes. *Transactions of the American*

667   *Fisheries Society* **134**, 1103–1110.

668   Kobler A., Klefoth T., Mehner T. & Arlinghaus R. (2009) Coexistence of behavioural

669   types in an aquatic top predator: a response to resource limitation? *Oecologia*

670   **161**, 837–847.

671   MacAvoy S.E., Macko S.A., McIninch S.P. & Garman G.C. (2000) Marine nutrient

672   contributions to freshwater apex predators. *Oecologia* **122**, 568–573.

673   Marcarelli A.M., Baxter C.V., Mineau M.M. & Hall R.O. (2011) Quantity and

674   quality: unifying food web and ecosystem perspectives on the role of resource

675   subsidies in freshwaters. *Ecology* **92**, 1215–1225.

676 Marczak L.B., Thompson R.M. & Richardson J.S. (2007) Meta-analysis: trophic

677   level, habitat, and productivity shape the food web effects of resource

678   subsidies. *Ecology* **88**, 140–148.

679 Matich P., Heithaus M.R. & Layman C.A. (2011) Contrasting patterns of individual

680   specialization and trophic coupling in two marine apex predators:

681   Specialization in top marine predators. *Journal of Animal Ecology* **80**, 294–

682   305.

683 Matthews B. & Mazumder A. (2004) A critical evaluation of intrapopulation variation

684   of $\delta^{13}C$ and isotopic evidence of individual specialization. *Oecologia* **140**,

685   361–371.

686 McIntosh A.R. & Townsend C.R. (1996) Interactions between fish, grazing

687   invertebrates and algae in a New Zealand stream: a trophic cascade mediated

688   by fish-induced changes to grazer behaviour? *Oecologia* **108**, 174–181.

689 Mehner T., Rapp T., Monk C.T., Beck M.E., Trudeau A., Kiljunen M., *et al.* (2018)

690   Feeding Aquatic Ecosystems: Whole-Lake Experimental Addition of Angler's

691   Ground Bait Strongly Affects Omnivorous Fish Despite Low Contribution to

692   Lake Carbon Budget. *Ecosystems*, 1–17.

693 Newsome T.M., Ballard G.-A., Fleming P.J., van de Ven R., Story G.L. & Dickman

694   C.R. (2014) Human-resource subsidies alter the dietary preferences of a

695   mammalian top predator. *Oecologia* **175**, 139–150.

696 Newsome T.M., Dellinger J.A., Pavey C.R., Ripple W.J., Shores C.R., Wirsing A.J.,

697   *et al.* (2015) The ecological effects of providing resource subsidies to

698   predators. *Global Ecology and Biogeography* **24**, 1–11.

699 Niesar M., Arlinghaus R., Rennert B. & Mehner T. (2004) Coupling insights from a

700   carp, Cyprinus carpio, angler survey with feeding experiments to evaluate

701   composition, quality and phosphorus input of groundbait in coarse fishing.

702   *Fisheries Management and Ecology* **11**, 225–235.

703   Nilsson P.A. & Brönmark C. (2000) Prey vulnerability to a gape-size limited

704   predator: behavioural and morphological impacts on northern pike piscivory.

705   *Oikos* **88**, 539–546.

706   Ovidio M. & Philippart J.-C. (2002) The impact of small physical obstacles on

707   upstream movements of six species of fish. In: *Aquatic Telemetry*, Thorstad

708   E.B., Fleming I.A., Næsje T.F. (eds). pp. 55–69. Springer.

709   Pedreschi D., Mariani S., Coughlan J., Voigt C.C., O'Grady M., Caffrey J., *et al.*

710   (2015) Trophic flexibility and opportunism in pike *Esox lucius*. *Journal of*

711   *Fish Biology* **87**, 876–894.

712   Phillips D.L. & Gregg J.W. (2003) Source partitioning using stable isotopes: coping

713   with too many sources. *Oecologia* **136**, 261–269.

714   Phillips D.L., Newsome S.D. & Gregg J.W. (2005) Combining sources in stable

715   isotope mixing models: alternative methods. *Oecologia* **144**, 520–527.

716   Polis G.A., Anderson W.B. & Holt R.D. (1997) Toward an integration of landscape

717   and food web ecology: the dynamics of spatially subsidized food webs.

718   *Annual review of ecology and systematics* **28**, 289–316.

719   Post D.M., Layman C.A., Arrington D.A., Takimoto G., Quattrochi J. & Montana

720   C.G. (2007) Getting to the fat of the matter: models, methods and assumptions

721   for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179–189.

722   R Core Team. 2018. R: A language and environment for statistical computing. R

723   Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-

724   project.org/.

725   Rasmussen J.B., Trudeau V. & Morinville G. (2009) Estimating the scale of fish

726   feeding movements in rivers using δ^{13}C signature gradients. *Journal of animal*

727   *ecology* **78**, 674–685.

728   Richardson D.P., Kohler A.E., Hailemichael M. & Finney B.P. (2016) The fate of

729   marine-derived nutrients: tracing δ^{13}C and δ^{15}N through oligotrophic

730   freshwater and linked riparian ecosystems following salmon carcass analog

731   additions. *Canadian Journal of Fisheries and Aquatic Sciences* **74**, 41–55.

732   Ripple W.J., Estes J.A., Beschta R.L., Wilmers C.C., Ritchie E.G., Hebblewhite M.,

733   *et al.* (2014) Status and ecological effects of the world's largest carnivores.

734   *Science* **343**, 1241484.

735   Ripple W.J., Wirsing A.J., Wilmers C.C. & Letnic M. (2013) Widespread

736   mesopredator effects after wolf extirpation. *Biological Conservation* **160**, 70–

737   79.

738   Ritchie E.G., Elmhagen B., Glen A.S., Letnic M., Ludwig G. & McDonald R.A.

739   (2012) Ecosystem restoration with teeth: what role for predators? *Trends in*

740   *Ecology & Evolution* **27**, 265–271.

741   Rooney N., McCann K.S. & Moore J.C. (2008) A landscape theory for food web

742   architecture. *Ecology Letters* **11**, 867–881.

743   Samways K.M., Soto D.X. & Cunjak R.A. (2018) Aquatic food-web dynamics

744   following incorporation of nutrients derived from Atlantic anadromous fishes.

745   *Journal of Fish Biology* **92**, 399–419.

746   Sandlund O.T., Museth J. & Øistad S. (2016) Migration, growth patterns, and diet of

747   pike (*Esox lucius*) in a river reservoir and its inflowing river. *Fisheries*

748   *Research* **173**, 53–60.

749 Schindler D.E., Leavitt P.R., Brock C.S., Johnson S.P. & Quay P.D. (2005) Marine-

750 derived nutrients, commercial fisheries, and production of salmon and lake

751 algae in Alaska. *Ecology* **86**, 3225–3231.

752 Sorel M.H., Hansen A.G., Connelly K.A., Wilson A.C., Lowery E.D. & Beauchamp

753 D.A. (2016) Predation by Northern Pikeminnow and Tiger Muskellunge on

754 Juvenile Salmonids in a High-Head Reservoir: Implications for Anadromous

755 Fish Reintroductions. *Transactions of the American Fisheries Society* **145**,

756 521–536.

757 Stock B.C., Jackson A.L., Ward E.J., Parnell A.C., Phillips D.L. & Semmens B.X.

758 (2018) Analyzing mixing systems using a new generation of Bayesian tracer

759 mixing models. *PeerJ PrePrints*, e5096.

760 Stock B.C. & Semmens B.X. (2016) Unifying error structures in commonly used

761 biotracer mixing models. *Ecology* **97**, 2562–2569.

762 Takimoto G., Iwata T. & Murakami M. (2002) Seasonal subsidy stabilizes food web

763 dynamics: balance in a heterogeneous landscape. *Ecological Research* **17**,

764 433–439.

765 Ventura M. & Jeppesen E. (2010) Evaluating the need for acid treatment prior to $\delta^{13}C$

766 and $\delta^{15}N$ analysis of freshwater fish scales: effects of varying scale mineral

767 content, lake productivity and CO2 concentration. *Hydrobiologia* **644**, 245–

768 259.

769 Venturelli P.A. & Tonn W.M. (2005) Invertivory by northern pike (*Esox lucius*)

770 structures communities of littoral macroinvertebrates in small boreal lakes.

771 *Journal of the North American Benthological Society* **24**, 904–918.

772   Wheeler A. & Jordan D.R. (1990) The status of the barbel, *Barbus barbus* (L.)

773   (Teleostei, Cyprinidae), in the United Kingdom. *Journal of Fish Biology* **37**,

774   393–399.

775   Wipfli M.S., Hudson J.P., Caouette J.P. & Chaloner D.T. (2003) Marine subsidies in

776   freshwater ecosystems: salmon carcasses increase the growth rates of stream-

777   resident salmonids. *Transactions of the American Fisheries Society* **132**, 371–

778   381.

779   Zhang Y., Negishi J.N., Richardson J.S. & Kolodziejczyk R. (2003) Impacts of

780   marine-derived nutrients on stream ecosystem functioning. *Proceedings of the*

781   *Royal Society of London B: Biological Sciences* **270**, 2117–2123.

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Table 1. Prey resources included in mixing models for each reach and *E. lucius* size category, including their length range (mm) and carbon and nitrogen stable isotope ratios (‰).Cypriniform fishes as prey resources are separated to include those with a freshwater diet and those specialising on marine fishmeal bait

River reach	*E. lucius* size category	Prey resource	n	Prey Length range (mm)	Mean δ^{13}C (‰)	Mean δ^{15}N (‰)
L. W. Avon	≥400 < 650 mm	Macroinvertebrates	10		-30.23 ± 1.47	15.90 ± 1.33
		Cypriniforms – freshwater	18	77 to 330	-26.69 ± 2.10	15.09 ± 1.69
	≥650 < 850 mm	Macroinvertebrates	10		-30.23 ± 1.47	15.90 ± 1.33
		Cypriniforms – freshwater	21	77 to 420	-26.50 ± 2.08	15.08 ± 1.85
	≥850 mm	Macroinvertebrates	10		-30.23 ± 1.47	15.90 ± 1.33
		Cypriniforms – freshwater	22	77 to 510	-26.45 ± 2.04	15.08 ± 1.81
Downstream Severn	≥400 < 650 mm	Macroinvertebrates	9		-29.67 ± 1.19	9.59 ± 0.81
		Cypriniforms – freshwater	15	60 to 316	-26.08 ± 1.38	12.49 ± 1.30
		Cypriniforms – marine	NA			
		Alosa spp.	9		-13.30 ± 0.62	12.52 ± 0.90
	≥650 < 850 mm	Macroinvertebrates	9		-29.67 ± 1.19	9.59 ± 0.81
		Cypriniforms – freshwater	20	60 to 401	-25.94 ± 1.36	12.84 ± 1.37
		Cypriniforms – marine	5	380 to 450	-22.26 ± 0.19	11.88 ± 0.88

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	Alosa spp.	9		-13.30 ± 0.62	12.52 ± 0.90
≥850 mm	Macroinvertebrates	9		--29.67 ± 1.19	9.59 ± 0.81
	Cypriniforms – freshwater	32	60 to 570	-25.56 ± 1.34	12.85 ± 1.21
	Cypriniforms – marine	21	380 to 565	-21.80 ± 0.98	11.73 ± 0.61
	Alosa spp.	9		-13.30 ± 0.62	12.52 ± 0.90

Table 2. Mean (± SD) carbon and nitrogen stable isotope ratios of *Esox lucius* by reach and size category, including the number of individuals analysed and their length range (mm).

River reach	Size category	Length range (mm)	n	Mean $\delta13C$ (‰)	Range $\delta^{13}C$ (‰)	Mean $\delta^{15}N$ (‰)	Range $\delta^{15}N$ (‰)
Warwickshire Avon	≥400 < 650	455 to 640	7	-26.23 ± 1.24	-28.30 to -25.15	19.08 ± 1.36	16.58 to 21.24
	≥651 < 850	680 to 840	6	-24.83 ± 1.82	-26.63 to -21.47	18.25 ± 1.71	15.67 to 19.78
	≥850	860 to- 1020	6	-24.96 ± 0.22	-25.39 to -24.81	19.23 ± 0.30	18.76 to 19.49
Upstream Severn	≥400 < 650	420 to 480	2	-24.48 ± 0.35	-24.73 to -24.23	15.02 ± 0.55	14.63 to 15.41
	≥651 < 850	660 to 774	3	-23.80 ± 0.53	-24.33 to -23.28	15.66 ± 0.55	15.14 to 16.24
	≥850	880 to 901	3	--23.24 ± 0.29	-23.49 to -22.93	16.43 ± 0.57	15.99 to 17.07
Downstream Severn	≥400 < 650	508 to 635	5	-24.35 ± 0.46	-24.74 to -23.69	15.80 ± 0.58	14.86 to 16.28
	≥651 < 850	660 to 838	10	-21.51 ± 1.44	-23.64 to -19.45	16.13 ± 0.56	15.41 to 16.92
	≥850	864 to 1060	15	-19.96 ± 2.02	-22.49 to -16.34	16.18 ± 0.61	15.03 to 16.96

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Table 3. Isotopic niche metrics for *Esox lucius* by reach and size categories, where TA: the total area of the convex hull encompassing the data points, SEA: the Standard Ellipse Area containing 40% of the data, SEA_C: Correction applied to SEA to account for small sample sizes, SEA_B: The Bayesian estimate and 95% credible intervals.

Groupings	TA	SEA	SEA_C	SEA_B	95% CI
Warwickshire Avon	14.21	4.21	4.45	4.21	2.63, 6.85
Upstream Severn	1.45	1.06	1.24	1.03	0.51, 2.35
Downstream Severn	11.79	4.09	4.23	3.96	2.77, 5.82
Warwickshire Avon ≥400 < 650 mm	5.28	3.59	4.31	3.57	1.59, 8.68
Warwickshire Avon ≥650 <850 mm	9.07	7.18	8.98	5.41	1.76, 13.93
Warwickshire Avon ≥850 mm	0.22	0.19	0.23	0.11	0.05, 0.31
Downstream Severn ≥400 < 650 mm	0.58	0.54	0.72	0.29	0.11, 0.89
Downstream Severn ≥650 <850 mm	4.49	2.52	2.83	2.18	1.09, 4.31
Downstream Severn ≥850 mm	7.29	3.87	4.17	3.07	2.01, 5.88

Table 4. Estimated dietary prey contributions from MixSIAR models to *Esox lucius* by reach and size category, group mean % ± SD with 5% and 95% Bayesian credible intervals in parentheses and individual mean % ± SD with predicted % contribution range in parentheses. Cypriniform fishes as prey resources are separated to include those with a freshwater diet and those specialising on marine fishmeal bait

River reach	MixSIAR	Resource	≥400 < 650 mm	≥650 < 850 mm	≥850 mm
Warwickshire Avon	*Group*	Macroinvertebrates	0.73 ± 0.14 (0.47, 0.95)	0.43 ± 0.20 (0.13, 0.78)	0.57 ± 0.13 (0.35, 0.78)
		Cypriniforms – freshwater	0.27 ± 0.14 (0.05, 0.52)	0.57 ± 0.20 (0.22, 0.88)	0.43 ± 0.13 (0.22, 0.65)
	Individual	Macroinvertebrates	0.73 ± 0.02 (0.66 to 0.84)	0.45 ± 0.05 (0.25 to 0.58)	0.58 ± 0.01 (0.56 to 0.59)
		Cypriniforms – freshwater	0.27 ± 0.02 (0.16 to 0.33)	0.54 ± 0.05 (0.42 to 0.75)	0.42 ± 0.01 (0.40 to 0.44)
Downstream Severn	*Group*	Macroinvertebrates	0.33 ± 0.13 (0.11, 0.53)	0.15 ± 0.13 (0.04, 0.44)	0.06 ± 0.05 (0.01, 0.15)
		Cypriniforms – freshwater	0.62 ± 0.14 (0.39, 0.85)	0.54 ± 0.11 (0.36, 0.71)	0.61 ± 0.09 (0.46, 0.75)
		Cypriniforms – marine	NA	0.24 ± 0.13 (0.04, 0.44)	0.20 ± 0.14 (0.02, 0.46)
		Alosa spp.	0.05 ± 0.04 (0.01, 0.13)	0.07 ± 0.05 (0.01, 0.17)	0.13 ± 0.06 (0.03, 0.23)
	Individual	Macroinvertebrates	0.29 ± 0.01 (0.26 to 0.33)	0.13 ± 0.01 (0.09 to 0.20)	0.06 ± 0.01 (0.04 to 0.09)
		Cypriniforms – freshwater	0.66 ± 0.01 (0.63 to 0.69)	0.52 ± 0.02 (0.41 to 0.62)	0.55 ± 0.03 (0.37 to 0.71)
		Cypriniforms – marine	NA	0.29 ± 0.02 (0.19 to 0.41)	0.27 ± 0.01 (0.18 to 0.33)
		Alosa spp.	0.04 ± 0.01 (0.04 to 0.04)	0.05 ± 0.01 (0.03 to 0.07)	0.12 ± 0.02 (0.06 to 0.25)

Figure captions

Figure 1. Western Europe showing the position (inset) of the study area (a), the location of the main rivers (inset) within the Severn River basin (b) and locations of the study reaches within the lower River Severn basin (c), where the areas of river covered by the reaches are represented as the areas between solid lines.

Figure 2. Relationship between length (mm) and (a) $\delta^{13}C$ and (b) $\delta^{15}N$ of *Esox lucius* from all reaches showing linear fit for the Warwickshire Avon (open circle, short-dashed line); Upstream Severn (cross, long-dashed line); Downstream Severn (solid circle, solid line) with 95% confidence intervals shown around the fitted values.

Figure 3. *Esox lucius* $\delta^{13}C$ and $\delta^{15}N$ stable isotope bi-plots and the 40% standard ellipse area (SEAc) for the Warwickshire Avon (open circle, short- dashed line), Upstream Severn (cross, long-dashed line) and Downstream Severn (solid circle, solid line).

Figure 4. Stable isotope bi-plots for (a) the Warwickshire Avon and (b) Downstream Severn showing prey resources as invertebrates (cross), cypriniforms with freshwater diet (x), cypriniforms with marine diet (open square) and *Alosa* spp. (solid square). The *E. lucius* isotopic niche for the sample population (solid grey line) and by size categories (400 - 650 mm (dashed line), 651 - 850 mm (dotted line) and > 850 mm (solid line) enclosing the 40% standard ellipse area (SEAc) are also shown. Mean ± SD of resource points are displayed with symbols corresponding as above.

Figure 5. Estimated dietary prey contributions (0 – 1) from MixSIAR models to the diet of individual *Esox lucius* by body length at (a) the Warwickshire Avon and (b) downstream Severn. Prey resources are represented as overall means in a stacked bar plot for *Alosa* spp (dark grey), 'Cypriniform-marine' (light grey), 'Cypriniform-freshwater' (white) and Invertebrates (black).
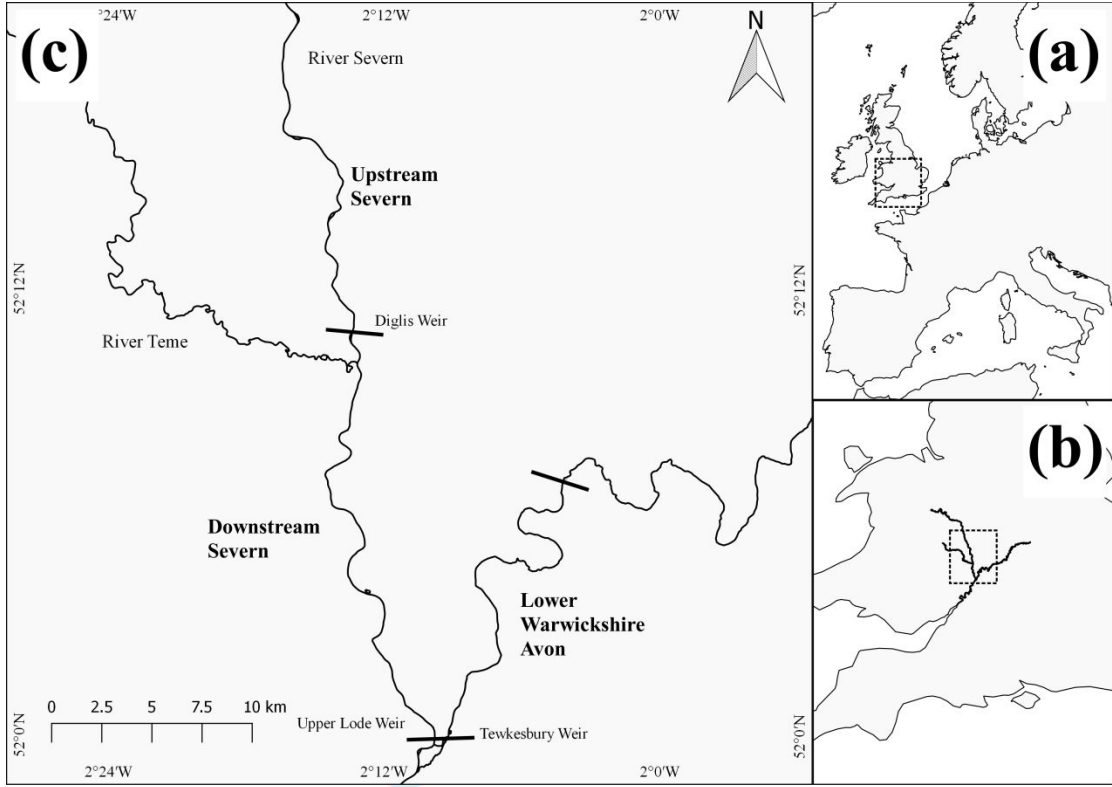
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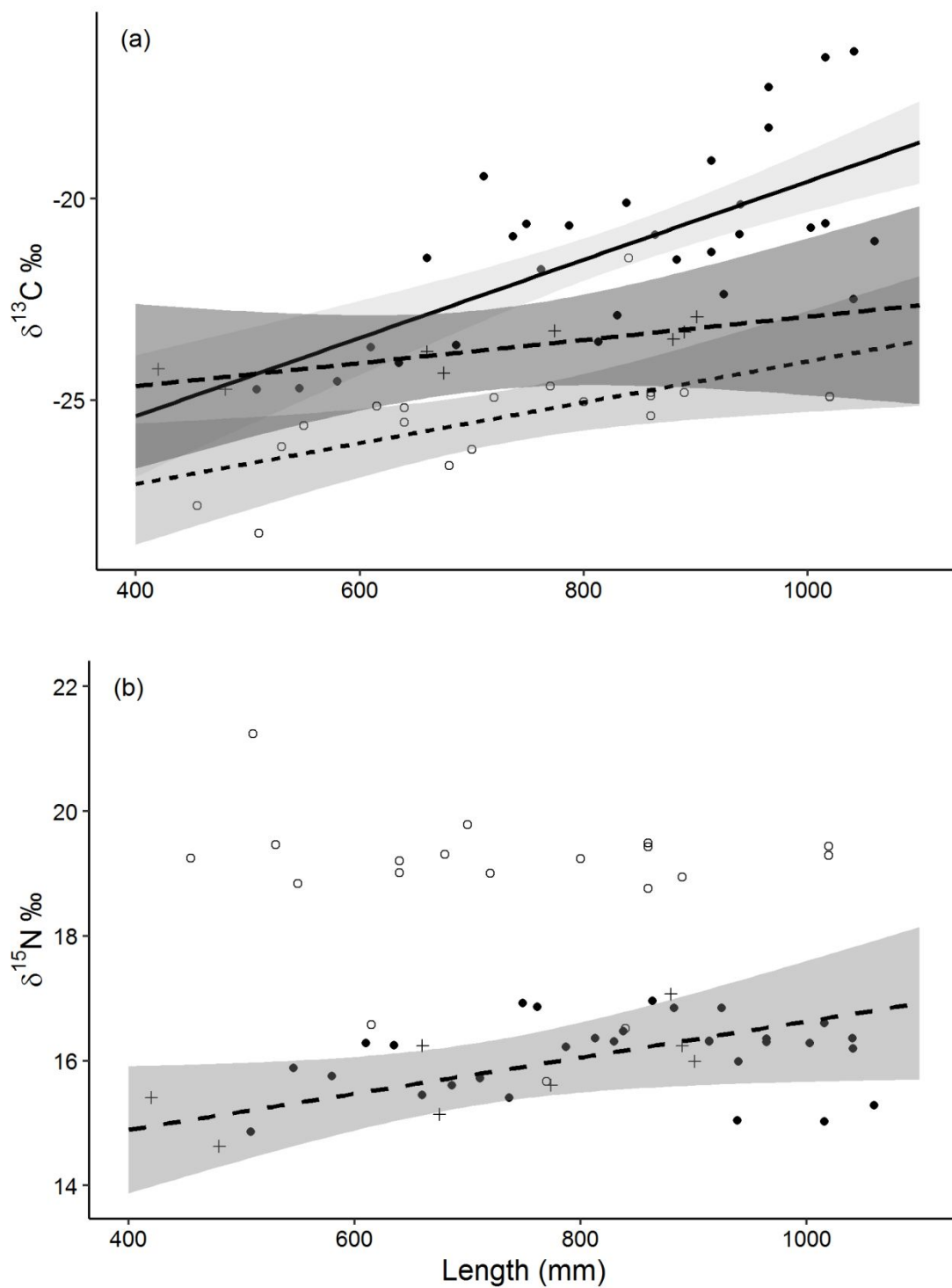
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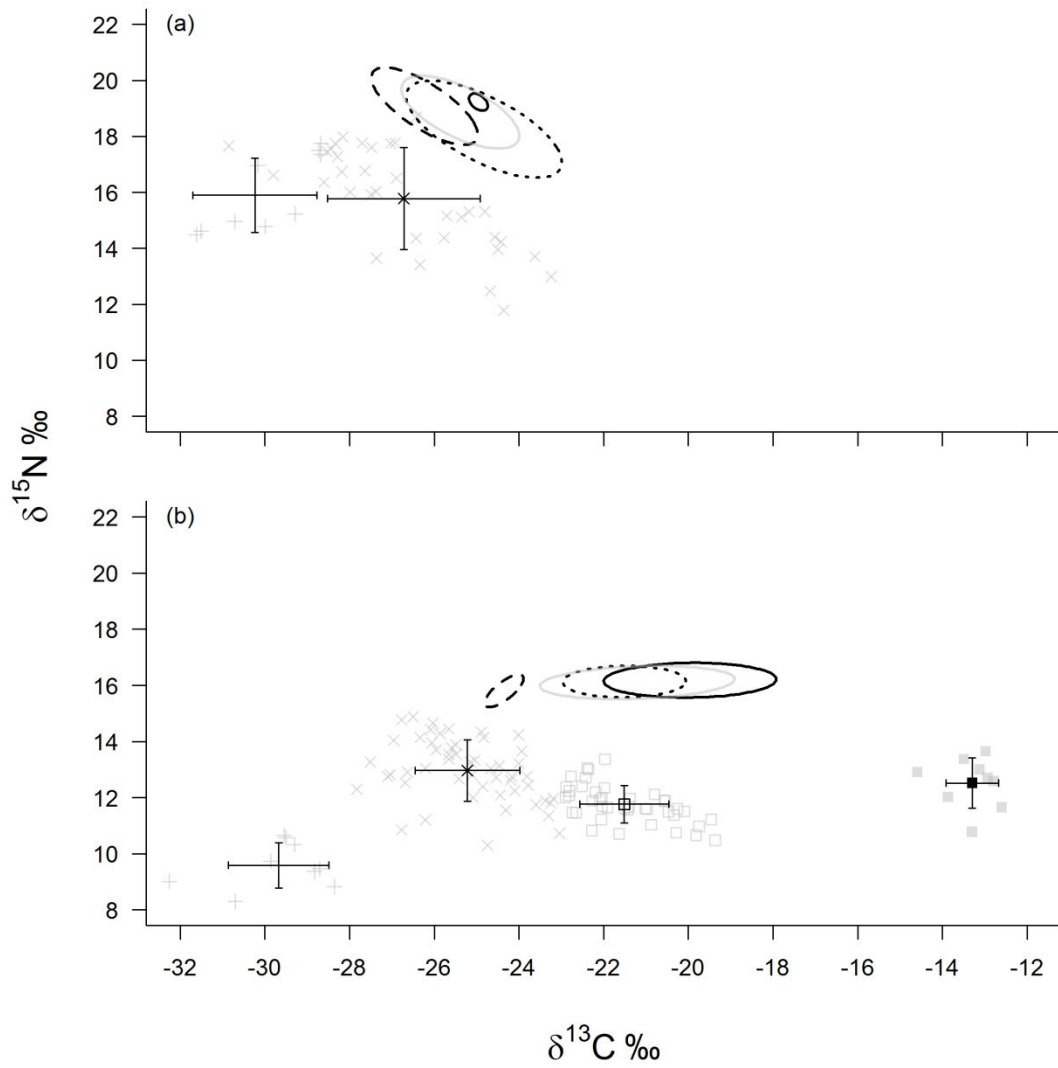45
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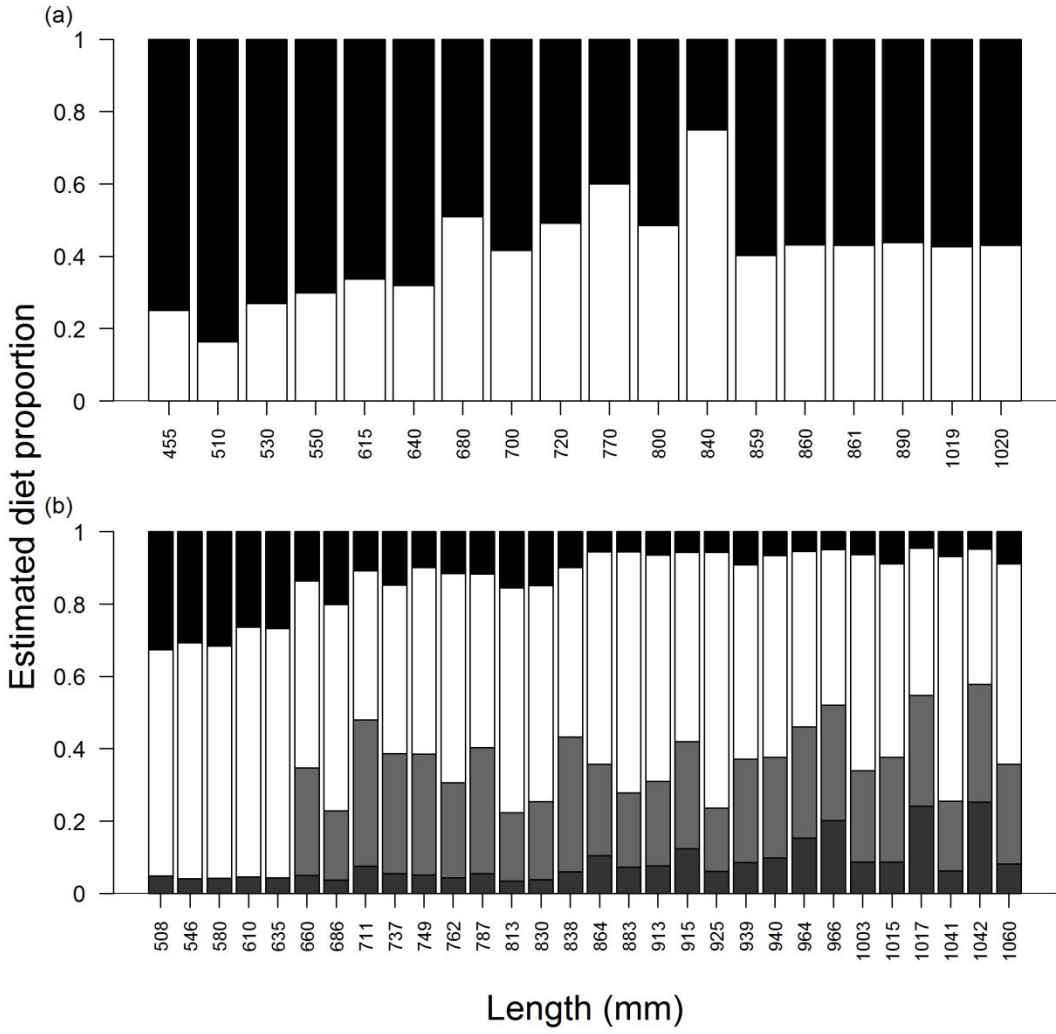48
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FIG.3.

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FIG. 4

FIG. 5.

Supplementary material

Table S1. Individual *E. lucius* sample data including date sampled, location, fork length (mm), weight (g) and carbon and nitrogen stable isotope ratios (‰)

Date Sampled	Location	Length (mm)	Weight (g)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
27/01/2015	Warwickshire Avon	890	7730	18.94	-24.81
06/02/2015	Warwickshire Avon	700	2320	19.78	-26.22
02/03/2015	Warwickshire Avon	1020	9090	19.44	-24.92
04/03/2015	Warwickshire Avon	770	5200	15.67	-24.66
11/03/2015	Warwickshire Avon	1020	9099	19.29	-24.91
03/07/2015	Warwickshire Avon	860	4750	19.43	-24.81
14/07/2015	Warwickshire Avon	720	3300	19	-24.94
20/07/2015	Warwickshire Avon	640	1400	19.01	-25.19
22/07/2015	Warwickshire Avon	550	960	18.84	-25.64
24/07/2015	Warwickshire Avon	860	5500	19.49	-25.39
22/08/2015	Warwickshire Avon	680	1525	19.31	-26.63
24/08/2015	Warwickshire Avon	530	960	19.46	-26.16
14/11/2015	Warwickshire Avon	860	7260	18.76	-24.9
20/02/2016	Warwickshire Avon	510	1400	21.24	-28.3
20/02/2016	Warwickshire Avon	840	5950	16.52	-21.47
27/02/2016	Warwickshire Avon	615	1632	16.58	-25.15
22/06/2017	Warwickshire Avon	455	NA	19.25	-27.62
20/07/2017	Warwickshire Avon	640	NA	19.2	-25.56
25/07/2017	Warwickshire Avon	800	NA	19.24	-25.04
20/09/2014	Downstream Severn	925	5981.7	16.85	-22.37
30/10/2014	Downstream Severn	838	5103	16.47	-20.11
28/11/2014	Downstream Severn	830	5900	16.31	-22.89
05/12/2014	Downstream Severn	737	2948.4	15.41	-20.94
24/01/2015	Downstream Severn	864	6577	16.96	-20.89
24/01/2015	Downstream Severn	940	8278	15.99	-20.15
24/01/2015	Downstream Severn	965	8165	16.3	-17.23
15/02/2015	Downstream Severn	508	1247	14.86	-24.74
15/02/2015	Downstream Severn	711	4649	15.72	-19.45
05/03/2015	Downstream Severn	686	3430.3	15.61	-23.64
05/03/2015	Downstream Severn	914	6463.7	16.31	-19.06
06/03/2015	Downstream Severn	635	1899.4	16.25	-24.08
06/03/2015	Downstream Severn	939	6633.8	15.04	-20.88
10/03/2015	Downstream Severn	660	3459	15.45	-21.48
12/03/2015	Downstream Severn	610	3345.2	16.28	-23.69
12/03/2015	Downstream Severn	1060	9043.5	15.29	-21.06
02/08/2015	Downstream Severn	787	4876	16.22	-20.67
07/09/2015	Downstream Severn	813	3799	16.36	-23.55
04/10/2015	Downstream Severn	546	1247	15.88	-24.71
05/10/2015	Downstream Severn	914	7711	16.32	-21.33

31/10/2015	Downstream Severn	1016	9072	15.03	-20.62
31/10/2015	Downstream Severn	1041.4	9724	16.2	-16.34
05/11/2015	Downstream Severn	1041	12105	16.36	-22.49
13/11/2015	Downstream Severn	580	2070	15.75	-24.54
23/01/2016	Downstream Severn	965	7541	16.35	-18.24
22/02/2016	Downstream Severn	762	3742	16.86	-21.75
01/03/2016	Downstream Severn	1016	9525	16.6	-16.49
02/03/2016	Downstream Severn	749	3515	16.92	-20.63
17/03/2016	Downstream Severn	883	6861	16.85	-21.52
13/11/2016	Downstream Severn	1003	8391.5	16.28	-20.72
31/08/2014	Upstream Severn	774	3160	15.61	-23.28
16/09/2014	Upstream Severn	480	880	14.63	-24.73
29/11/2014	Upstream Severn	420	460	15.41	-24.23
29/11/2014	Upstream Severn	880	5750	17.07	-23.49
29/11/2014	Upstream Severn	901	4280	15.99	-22.93
03/12/2014	Upstream Severn	660	3650	16.24	-23.8
20/12/2014	Upstream Severn	890	3680	16.24	-23.31
24/02/2015	Upstream Severn	675	2420	15.14	-24.33

Table S2. Carbon and nitrogen stable isotope ratios (mean ‰ ± SD) for *E. lucius* at each reach and year showing analysis of variance statistics

River reach	Year	n	Mean δ^{13}C (‰) ± SD	Mean δ^{15}N (‰) ± SD	ANOVA
L. W. Avon	2015	13	-25.32 ± 0.17	18.95 ± 0.29	δ^{13}C (‰) $F_{(2,16)} = 0.49$, P = 0.61
	2016	3	-24.97 ± 1.97	18.11 ± 1.56	δ^{15}N (‰) $F_{(2,16)} = 0.64$, P = 0.54
	2017	3	-26.07 ± 0.79	19.23 ± 0.02	
Downstream Severn	2014	4	-21.58 ± 0.64	16.26 ± 0.31	δ^{13}C (‰) $F_{(2,27)} = 1.28$, P = 0.29
	2015	20	-21.53 ± 0.54	15.91 ± 0.12	δ^{15}N (‰) $F_{(2,27)} = 4.81$, P = 0.02*
	2016	6	-19.89 ± 0.85	16.64 ± 0.11	
Upstream Severn	2014	7	-23.68 ± 0.23	15.88 ± 0.29	δ^{13}C (‰) $F_{(1, 6)} = 0.95$, P = 0.37
	2015	1	-24.33	15.14	δ^{15}N (‰) $F_{(1, 6)} = 0.82$, P = 0.40

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Section S2. Rationale of putative prey resources in mixing models

At the upstream and downstream Severn reaches, the SI data for *S. cephalus* and invasive *B. barbus* were highly similar and so they were combined as a single prey resource in mixing models ('Cypriniforms'). However, in their combined data, $\delta^{13}C$ had high variation (-19.37 to -27.04 ‰) resulting from some individuals specialising on MDN baits and others on macro-invertebrates (Gutmann Roberts et al*.,* 2017). Thus, this 'Cypriniform' prey resource was split into two groups based on their $\delta^{13}C$ data: (1) -19.37 to -22.9 ‰; where diets comprised of a relatively high proportion of MDN ('Cypriniform marine'; mixing model: mean ± SE = 0.50 ± 0.17; Table S3); and (2) -23.04 to -27.04 ‰; where diets were relatively low in MDN ('Cypriniform-freshwater'; mean ± SE = 0.25 ± 0.11; Supplementary material, Table S3). The two groups were entered as separate prey resources in the mixing models. The differences in MDN dietary contributions between these two groups were significant (t-test; *t* = -5.66*,* P < 0.001).

Table S3. Individual carbon and nitrogen stable isotope ratios, lengths and marine derived nutrient contributions for cypriniform fish *S. cephalus* and *B. barbus* used as resources 'Cypriniform freshwater' and 'Cypriniform marine' in Bayesian mixing models as derived from Gutmann-Roberts et al. (2017)

Cypriniform Freshwater				Cypriniform Marine				
Species	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Length (mm)	MDN (%)	Species	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Length (mm)	MDN (%)
B. barbus	-27.04	12.82	510	0.089	*B. barbus*	-22.89	12.37	740	0.359
B. barbus	-26.5	14.88	397	0.11	*B. barbus*	-22.81	12.24	690	0.396
B. barbus	-26.09	14.42	364	0.151	*B. barbus*	-22.74	11.47	520	0.514
B. barbus	-26.03	14.65	660	0.094	*B. barbus*	-22.43	12.71	680	0.411
B. barbus	-25.66	13.54	520	0.375	*B. barbus*	-22.27	11.89	529	0.285
B. barbus	-25.65	13.38	800	0.148	*B. barbus*	-22.04	12	520	0.583
B. barbus	-25.49	13.89	401	0.169	*B. barbus*	-21.98	12.35	670	0.457
B. barbus	-25.41	12.67	580	0.185	*B. barbus*	-21.91	11.65	591	0.607
B. barbus	-25.11	12.81	660	0.231	*B. barbus*	-21.5	11.61	520	0.1
B. barbus	-25.04	13.34	580	0.212	*B. barbus*	-21.4	11.67	630	0.582
B. barbus	-24.85	12.4	770	0.275	*B. barbus*	-21.02	11.61	565	0.584
B. barbus	-24.66	13.03	750	0.215	*B. barbus*	-20.88	11.03	557	0.614

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B. barbus	-24.46	13.14	620	0.241	*B. barbus*	-20.55	11.88	800	0.535
B. barbus	-24.31	11.56	530	0.177	*B. barbus*	-20.29	10.75	800	0.671
B. barbus	-24.1	12.24	630	0.328	*B. barbus*	-20.1	11.51	602	0.835
B. barbus	-24	13.22	593	0.335	*B. barbus*	-19.37	10.48	790	0.776
B. barbus	-23.81	12.76	480	0.226	*B. barbus*	-22.36	13.01	450	0.339
B. barbus	-23.37	11.89	698	0.371	*S. cephalus*	-22.09	11.92	400	0.422
B. barbus	-23.25	11.81	545	0.329	*S. cephalus*	-20.8	12.12	540	0.378
S. cephalus	-24.74	10.3	104	0.463	*S. cephalus*	-19.82	10.66	510	0.655
S. cephalus	-23.6	11.75	300	0.333					
S. cephalus	-23.04	10.73	190	0.417					
Mean ± SE	-24.83 ± 1.09	12.78 ± 1.17		0.25 ± 0.11	Mean ± SE	-21.46 ± 1.06	11.75 ± 0.66		0.50 ± 0.17

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