



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

Journal:	<i>Freshwater Biology</i>
Manuscript ID	FWB-P-Jan-19-0010.R1
Manuscript Type:	Standard Paper
Date Submitted by the Author:	13-Mar-2019
Complete List of Authors:	Nolan, Emma; Bournemouth University, School of Conservation Sciences Gutmann-Roberts, Catherine; Manchester Metropolitan University, ; Bournemouth University, Britton, Rob; Bournemouth University, School of Conservation Sciences
Keywords:	Fisheries < Applied Issues, Running water / rivers / streams < Habitat, Predation < Process / Approach / Methods, Stable isotopes < Process / Approach / Methods, Fish < Taxonomic Group / Assemblage

SCHOLARONE™
Manuscripts

1
2
3 **1 Predicting the contributions of novel marine prey resources from angling and**
4
5 **2 anadromy to the diet of a freshwater apex predator**
6
7
8
9

10 4 Emma T. Nolan; Catherine Gutmann Roberts; J. Robert Britton
11
12
13 5

14 6 Department of Life and Environmental Sciences, Faculty of Science and Technology,
15
16
17 7 Bournemouth University, BH12 5BB, United Kingdom
18
19
20 8

21 9 **Running head:** Marine derived prey in freshwater
22
23
24 10

25
26 11 **Keywords:** *Esox lucius*; individual specialisation; isotopic niche, marine derived
27
28 12 nutrients; stable isotope analysis
29
30
31 13

32
33 14 **Corresponding author:** Robert Britton. Department of Life and Environmental
34
35 15 Sciences, Faculty of Science and Technology, Bournemouth University, BH12 5BB,
36
37 16 United Kingdom. Email: rbritton@bournemouth.ac.uk
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 **17 Abstract**
4
5
6 **18**
7
8 **19** 1. Anadromous fishes can be important prey resources for piscivorous fauna in
9
10 **20** lowland rivers. Freshwater anglers exploiting large-bodied cypriniform fishes
11
12 **21** use high quantities of pelletized marine fishmeal baits that can contribute
13
14 **22** substantially to fish diets. This marine-derived energy pathway also
15
16 **23** potentially provides a marine prey resource for freshwater piscivores.
17
18 **24** However, large-bodied cypriniform fishes are often in a size refuge against
19
20 **25** predation due to their large sizes.
21
22
23
24 **26**
25
26 **27** 2. Stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analysis assessed how novel marine prey
27
28 **28** resources influenced the diet of a freshwater apex predator, Northern pike
29
30 **29** *Esox lucius*, in an impounded river basin (lower River Severn, Western
31
32 **30** England). Up to three groups of prey resources were present: anadromous
33
34 **31** European shad (*Alosa* spp.), cypriniform fishes with dietary specialisms based
35
36 **32** on marine fishmeal baits, and freshwater prey. The availability of these prey
37
38 **33** resources to *E. lucius* varied according to river connectivity and levels of
39
40 **34** angling exploitation in different river reaches.
41
42
43
44 **35**
45
46 **36** 3. Where the three prey groups were present, *E. lucius* were more enriched in
47
48 **37** $\delta^{13}\text{C}$ values (range: -24.74 to -16.34 ‰) compared to river reaches where
49
50 **38** aspects of the marine prey groups were absent. (range: -28.30 to -21.47) In all
51
52 **39** reaches, $\delta^{13}\text{C}$ increased as *E. lucius* length increased. In the reach where all
53
54 **40** prey groups were present, the isotopic niches of three *E. lucius* size categories
55
56
57
58
59
60

1
2
3 41 were strongly partitioned; this was not apparent in reaches where the marine
4
5 42 pathways were unavailable.
6
7
8 43

9
10 44 4. Stable isotope mixing models suggested that freshwater prey were the most
11
12 45 important prey item, contributing between 42 and 96 % to the diet of
13
14 46 individual *E. lucius*. However, where present, anadromous fishes and
15
16 47 cypriniform fishes specialising on marine fishmeal baits were also important
17
18 48 prey items, contributing substantially to the diet of larger *E. lucius* (length >
19
20 49 650 mm). The total dietary contributions of the marine resources varied
21
22 50 considerably among the individual larger fish (22 to 58 % of total diet).
23
24
25
26 51

27
28 52 5. The presence of two marine resource pathways in a lowland river thus
29
30 53 strongly influenced the diet of an apex predator, but with contributions being a
31
32 54 function of their spatial availability, *E. lucius* body size and individual trophic
33
34 55 specialisations. These results emphasise how the anthropogenic activities of
35
36 56 river engineering and human subsidies can affect the trophic dynamics of apex
37
38 57 predators.
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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).

81

1
2
3 82 Fishery management activities often enhance freshwater angling experiences by
4
5 83 diversifying the species available through the release of large-bodied invasive species,
6
7 84 such as carp *Cyprinus carpio* and European barbel *Barbus barbus* (Hickley & Chare,
8
9 85 2004). To target these fishes, catch-and-release anglers can release large amounts of
10
11 86 ‘groundbait’ to attract fish (Jackson et al., 2013), with the quantities used often
12
13 87 exceeding 1 kg of bait per day (Niesar et al., 2004). These baits are increasingly based
14
15 88 on marine fishmeal, with the intensive use of pelletised marine fishmeal now common
16
17 89 in freshwater angling in Western Europe (Arlinghaus & Mehner, 2003; Bašić et al.,
18
19 90 2015; Gutmann Roberts et al., 2017). This MDN subsidy can alter the trophic
20
21 91 interactions between consumers (Bašić et al., 2015), assist invasions (Jackson et al.,
22
23 92 2013), and are increasingly recognised as an important dietary resource to
24
25 93 benthivorous and omnivorous fishes (Gutmann Roberts et al., 2017; Mehner et al.,
26
27 94 2018). Where high concentrations of marine fishmeal have been released into
28
29 95 freshwaters, it can be traced through food webs using stable isotope analyses (SIA),
30
31 96 with $\delta^{13}\text{C}$ differentiating between freshwater (depleted $\delta^{13}\text{C}$) and marine energy
32
33 97 sources (enriched $\delta^{13}\text{C}$) (Grey, Waldron & Hutchinson, 2004; Jardine et al., 2005;
34
35 98 Rasmussen, Trudeau & Morinville, 2009).
36
37
38
39
40
41
42
43

44
45 100 The presence of both anadromous fishes and freshwater fishes with diets comprising
46
47 101 mainly of marine fishmeal thus potentially provide apex predators in lowland rivers
48
49 102 with additional prey resources to freshwater prey. However, the ability of these
50
51 103 predators to exploit these marine derived resources will at least partially depend on
52
53 104 their ability to consume large bodied prey. This is because anadromous fishes entering
54
55 105 freshwater to spawn tend to be relatively large, with even the smallest *Alosa* spp.
56
57 106 migrants to European rivers generally being above 300 mm body length (Aprahamian,
58
59
60

1
2
3 107 1988). Cypriniform fishes that have diets specialising on pelletised fishmeal also tend
4
5 108 to be relatively large (> 380 mm) (Amat Trigo, Gutmann Roberts & Britton, 2017;
6
7 109 Gutmann Roberts et al. 2017). Given that freshwater apex fish predators, such as
8
9 110 Northern pike *Esox lucius*, are gape-limited in their prey selection (Craig, 2008;
10
11 111 Nilsson & Brönmark, 2000) then these marine derived resources might only be
12
13 112 available to the larger individuals in their populations. This influence of predator body
14
15 113 size on their prey sizes is important, as apex predator populations often couple
16
17 114 multiple energetic pathways in aquatic food webs through their exploitation of a wide
18
19 115 range of prey resources (e.g. Rooney, McCann, & Moore, 2008). Thus, traits that
20
21 116 influence prey size in apex predators will influence their ability to couple these energy
22
23 117 pathways (Nilsson & Brönmark, 2000; Rooney et al., 2008).
24
25
26
27
28
29
30

31 119 Correspondingly, the aim here was to quantify how spatial variation in the availability
32
33 120 of marine prey resources (large bodied anadromous fish and cypriniform fishes
34
35 121 consuming MDN angler baits) influenced the diet of a gape-limited apex predator in a
36
37 122 lowland river. Where present, the exploitation of marine energy pathways by a
38
39 123 freshwater apex predator should lead to enriched $\delta^{13}\text{C}$ values and distinct population
40
41 124 dietary niches versus those fish that forage where the marine energy pathways are
42
43 125 absent (MacAvoy et al., 2000; Samways et al., 2018). The apex predator was *E.*
44
45 126 *lucius*, with their populations studied in the River Severn basin, Western England
46
47 127 (Fig. 1), where individuals grow to relatively large sizes (body lengths > 1 m; mass $>$
48
49 128 12 kg). In this basin, there is considerable spatial variation in the availability of
50
51 129 marine prey resources. Impoundments affect the upstream access of migrating
52
53 130 anadromous fishes (mainly *Alosa* spp.; Arahamian, 1988); inputs of MDN based
54
55 131 angling bait are affected by spatial differences in fish community structure and
56
57
58
59
60

1
2
3 132 varying levels of angling activity (Gutmann Roberts et al., 2017). Using SIA to test
4
5 133 the influence of the presence/ absence of these MDN subsidies on *E. lucius* diet, the
6
7 134 objectives were to (1) assess the spatial variability in stable isotope data of the marine
8
9 135 and non-marine prey resources; (2) quantify the relationships between *E. lucius* body
10
11 136 length (as a proxy of gape size) and their stable isotope data; (3) determine the
12
13 137 influence of the marine prey resources on *E. lucius* trophic niche sizes (as isotopic
14
15 138 niches); and (4) assess how the diet composition of *E. lucius* at individual and
16
17 139 population levels are influenced by differences in the spatial availability of the marine
18
19 140 prey resources.
20
21
22
23
24
25

141

142 **Methods**

143

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

1
2
3 157 lower reach of the Warwickshire Avon ('Warwickshire Avon'; 51.9955°, -2.1579° to
4
5 158 52.1152°, -2.0702°; Fig. 1c) was up to 20 m wide, with depths to 4 m and is separated
6
7
8 159 from the Severn by the presence of flow regulation structures (two separate weirs).
9

10 160

11
12 161

13
14
15 162 *Sampling of *Esox lucius**

16
17 163 The habitat characteristics of the study reaches resulted in fish sampling by traditional
18
19 164 methods (electric fishing, seine netting, fyke netting) being inefficient or unfeasible,
20
21 165 other than within limited off-channel areas provided by boat marinas. Consequently,
22
23 166 sample collection of *E. lucius* was primarily via catch and release angling. This was
24
25 167 facilitated by the Environment Agency, the inland fishery regulatory body of England,
26
27 168 who established an *E. lucius* angling network within the Severn catchment. Within
28
29 169 this network, participating anglers recorded their catches and were trained in
30
31 170 collecting scale samples. Whilst the primary purpose of scale collection was for fish
32
33 171 age determination for management purposes, they concomitantly provided material
34
35 172 suitable for stable isotope analysis in this study (Hutchinson & Trueman, 2006; Bašić
36
37 173 & Britton, 2015). Scales tend to have a longer stable isotope half-life than muscle and
38
39 174 fin tissue (Busst & Britton, 2017). Consequently, between August 2014 and July
40
41 175 2017, anglers collected scales from captured *E. lucius* and recorded the location and
42
43 176 date of capture and fish fork length (Supplementary material, Table S1). Note, angling
44
45 177 effort for *E. lucius* was variable between reaches, being highest in the downstream
46
47 178 Severn reach and lowest in the upstream Severn reach, resulting in spatial variation in
48
49 179 *E. lucius* sample sizes. Due to this method of sample collection, there was no
50
51 180 opportunity for the collection of complementary data, such as stomach contents via
52
53 181 stomach flushing or gape size measurements. Angling for *E. lucius* is also not
54
55
56
57
58
59
60

1
2
3 182 permitted on the river between mid-March and mid-June, a period covering the
4
5 183 majority of the *Alosa* spawning season.
6
7

8 184

9
10 185 *Spatial and temporal variation in the availability of putative prey of *Esox lucius**

11
12 186 Upper Lode weir is passable by anadromous *Alosa* spp. that enter the river each year

13
14 187 to spawn between April and June, generally at lengths between 300 and 450 mm

15
16 188 (Arahamian, 1988). Diglis weir and the weirs leading into the River Warwickshire

17
18 189 Avon are, however, considered impassable to *Alosa* spp. Therefore, the downstream

19
20 190 Severn reach was considered as the only reach within the study where this

21
22 191 anadromous energy pathway was present for *E. lucius*. Although anadromous Atlantic

23
24 192 salmon *Salmo salar* adults also enter the River Severn to spawn they are not resident

25
26 193 in the study reaches or available as a prey resource as they can ascend all weirs on the

27
28 194 main river during their upstream migration to spawning grounds located in the upper

29
30 195 catchment. The Warwickshire Avon is inaccessible to migrating *S. salar* due to

31
32 196 impassable engineering structures in the lower river (Tewkesbury weir).

33
34 197 Quantification of the levels of use of pelletized marine fishmeal baits by anglers

35
36 198 within each reach could not be assessed directly (e.g. by creel census). However,

37
38 199 large-bodied cypriniform fishes (mainly *B. barbus*, but also chub *Squalius cephalus*)

39
40 200 in the downstream Severn reach have already been identified as specialising on

41
42 201 pelletised fishmeal (Gutmann Roberts et al., 2017). Correspondingly, all reaches

43
44 202 could potentially contain prey resources that include cypriniform fish specialising on

45
46 203 marine fishmeal baits, but with the downstream Severn reach the only reach where

47
48 204 both marine prey resource groups could be present (i.e. *Alosa* spp. and cypriniform

49
50 205 fishes specialising on fishmeal baits). Note that throughout the catchment, whilst *B.*

1
2
3 206 *barbus* populations were present and targeted by anglers, they were invasive, having
4
5 207 been introduced in 1956 (Wheeler & Jordan, 1990; Antognazza et al., 2016).
6
7
8 208

9
10 209 *Sampling for putative prey species of Esox lucius*

11
12 210 Samples for stable isotope analysis of the putative prey species of *E. lucius* were
13
14 211 collected throughout the study period from the downstream Severn and Warwickshire
15
16 212 Avon reaches only, as logistical constraints prevented the collection of comparative
17
18 213 putative prey species from the upstream Severn reach. The putative prey samples
19
20 214 from the downstream Severn and Warwickshire Avon reaches were small cypriniform
21
22 215 fishes (< 400 mm; *R. rutilus*, *S. cephalus*, *B. barbus*), and macro-invertebrates
23
24 216 (Gammaridae, Chironomidae and Asellidae), as macro-invertebrates can be important
25
26 217 prey resources for *E. lucius*, especially where individuals are less than 600 mm
27
28 218 (Chapman, Mackay & Wilkinson, 1989; Venturelli & Tonn, 2005; Pedreschi et al.,
29
30 219 2015). Fish were sampled by angling in the main river channels and by seine netting
31
32 220 in boat marinas, while macroinvertebrates were sampled by sweep netting in littoral
33
34 221 areas. Samples of larger (> 400 mm) *B. barbus* and *S. cephalus* were collected via
35
36 222 angling (Gutmann Roberts et al., 2017), ensuring that the putative prey resources of *E.*
37
38 223 *lucius* included larger cypriniform fish that can specialise on pelletised fishmeal
39
40 224 (Gutmann Roberts et al., 2017). In addition, scale samples of *Alosa* spp. in the
41
42 225 downstream Severn reach were collected opportunistically and non-invasively during
43
44 226 their spawning periods (April to June), such as by collecting scales from carcasses
45
46 227 from otter *Lutra lutra* predation. For all putative prey fish, identification was to
47
48 228 species, with measurement (fork length, nearest mm) and the collection of 3 to 5
49
50 229 scales from the body area between the dorsal fin and lateral line. For macro-
51
52 230 invertebrates, identification was to family.
53
54
55
56
57
58
59
60

231

232 *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 $\delta^{13}\text{C}$ (\pm SD) of
241 0.18 ± 0.12 and in $\delta^{15}\text{N}$ 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).

255

1
2
3 256 *Data analyses*
4

5 257 As samples were collected across years, data were first subject to analysis of variance
6
7 258 (ANOVA) to test for differences in *E. lucius* $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values among years at
8
9 259 each reach. As these results did not show consistent significant differences within
10
11 260 reach (Supplementary material, Table S2), the stable isotope data were combined
12
13 261 across all years without correction. The relationship between *E. lucius* body length
14
15 262 and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were determined for each reach using linear regression. Analysis of
16
17 263 covariance (ANCOVA) was then used to test for independent and interactive effects
18
19 264 of both reach and fish length on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Both models included reach as a
20
21 265 factor (fixed, 3 levels: Warwickshire Avon, upstream Severn, downstream Severn)
22
23 266 and fish length as a covariate, together with their interaction. Thus, a significant ($\alpha =$
24
25 267 0.05) interaction term would indicate that the relationship between the respective
26
27 268 isotope value and body length varied according to reach. Where there was a
28
29 269 significant main effect of reach, Tukey's post-hoc tests were used for pairwise
30
31 270 comparisons between factor levels. In addition, differences in the SI data of all
32
33 271 putative prey were tested between the downstream Severn and Warwickshire Avon
34
35 272 reaches using t-tests. Prior to analyses, normality and homoscedasticity of data were
36
37 273 assessed by visual inspection of the residual plots
38
39
40
41
42
43
44
45

274

46 275 The *E. lucius* stable isotope data were then analysed in two ways. First, the isotopic
47
48 276 niche of *E. lucius* was estimated using metrics based on standard ellipses obtained by
49
50 277 applying the data within a Bayesian framework, completed within the package 'Stable
51
52 278 Isotope Bayesian Ellipses in R' (SIBER; Jackson et al., 2011). Niche metrics were
53
54 279 first assessed for all *E. lucius* at each reach and then, for the downstream Severn and
55
56 280 Warwickshire Avon reaches where sample sizes were highest by three distinct size
57
58
59
60

1
2
3 281 categories: $\geq 400 < 650$ mm; $\geq 650 < 850$ mm; and ≥ 850 mm. SIBER metrics were
4
5 282 only calculated for sample sizes greater than or equal to five (Table 2). Isotopic niche
6
7 283 sizes were calculated as standard ellipse areas (SEA), with these representing the core
8
9 284 40 % of the isotopic data (Jackson et al., 2011). This bivariate measure of the
10
11 285 distribution of individuals in isotopic space thus is a representation of a population's
12
13 286 typical resource use (Jackson et al., 2011; Jackson et al., 2012). Additional
14
15 287 calculations were the total area of the convex hull encompassing the data points (TA),
16
17 288 the correction applied to SEA to account for small sample sizes (SEA_C), and the
18
19 289 Bayesian standard ellipse areas (SEA_B) and their 95% credible intervals. For SEA_B ,
20
21 290 significant differences in the size of isotopic niches were identified when $\geq 95\%$ of
22
23 291 posterior draws for one area were smaller than the other. The area of niche overlap
24
25 292 between two or more ellipses was also calculated where appropriate.
26
27
28
29
30
31
32

33 294 Then, for *E. lucius* at the downstream Severn and Warwickshire Avon reaches, their
34
35 295 SI data were applied to Bayesian mixing models to predict the relative proportions (as
36
37 296 posterior probability distributions) of the putative prey resources that contributed to
38
39 297 their diet. This was not completed for the upstream Severn due to the low *E. lucius*
40
41 298 sample size ($n < 5$) and lack of SI data on their putative prey. The mixing models
42
43 299 were completed in the package 'Mixing Models for Stable Isotope Analysis in R'
44
45 300 (MixSIAR; Stock et al., 2018). MixSIAR was used to assess the proportional prey
46
47 301 contributions to *E. lucius* diet in the two reaches according to the three size categories
48
49 302 outlined above for the niche metrics (to assess group level contributions), and then
50
51 303 individually, by including individual as a covariate to explain variability in mixture
52
53 304 proportions. This enabled assessment of differences in individual level contributions
54
55 305 versus group level contributions. All models were run using 'normal' run length
56
57
58
59
60

1
2
3 306 (chain length: 100,000 iterations with burn-in of 50,000, with posterior thinning (thin:
4
5 307 50) and 3 chains). Model diagnostics were based on Gelman-Rubin and Geweke, with
6
7 308 sufficient convergence to accept the results (Stock & Semmens, 2016). The isotopic
8
9 309 fractionation values between the prey resources and *E. lucius* ($\delta^{15}\text{N}$ 3.35 ± 0.25 ‰;
10
11 310 $\delta^{13}\text{C}$ 3.49 ± 0.25 ‰) were based on values obtained for other piscivorous fish through
12
13 311 controlled feeding experiments (Barnes et al., 2007), with correction for scales from
14
15 312 dorsal muscle (Heady & Moore, 2013; Busst, Bašić & Britton, 2015; Busst & Britton,
16
17 313 2016). Mixing model outputs were reported as means of all feasible solutions with
18
19 314 standard deviation and the 5th to 95th credible intervals of the distribution ranges.
20
21
22
23
24
25

26 316 Before the mixing models were run, there was consideration of how the putative prey
27
28 317 data were entered. For the larger bodied (> 380 mm) cypriniform prey (*B. barbuis* and
29
30 318 *S. cephalus*), there was considerable range in their $\delta^{13}\text{C}$ isotope values (-28.4 to -19.4
31
32 319 ‰), with individuals with enriched $\delta^{13}\text{C}$ the result of their dietary specialisation on
33
34 320 pelletised fishmeal released by anglers (Gutmann Roberts et al., 2017). Due to this
35
36 321 considerable $\delta^{13}\text{C}$ range, this 'Cypriniform' prey resource was split into two groups
37
38 322 ('marine' and 'freshwater'). This grouping was based on the Bayesian stable isotope
39
40 323 mixing model results of Gutmann Roberts et al. (2017), where cypriniform prey
41
42 324 resources with $\delta^{13}\text{C}$ of -22.90 to -19.40 ‰ had relatively high predicted proportions of
43
44 325 MDN to their diet (predicted mean \pm SE MDN contribution to diet: 0.50 ± 0.17 ;
45
46 326 Supplementary material, Table S3). These fish were thus grouped as 'Cypriniform-
47
48 327 marine' in the mixing models. Cypriniform prey resources with $\delta^{13}\text{C}$ of -28.04 to -
49
50 328 23.04 ‰ had relatively low proportions of MDN in their diet (mean \pm SE MDN
51
52 329 contribution to diet: = 0.24 ± 0.11 ; Table S3). These fish were then grouped as
53
54 330 'Cypriniform-freshwater' in the mixing models. The differences in MDN dietary
55
56
57
58
59
60

1
2
3 331 contributions between the two groups were significant (t-test; $t = -5.66$, $P < 0.001$;
4
5 332 Supplementary material, Table S3). Smaller bodied (< 380 mm) cypriniform fishes
6
7 333 (*R. rutilus*, *B. barbatus* and *S. cephalus*) were then all assigned to the appropriate group
8
9 334 based on their isotope value and thus were incorporated within the ‘Cypriniform-
10
11 335 freshwater’ group. This was due to the high similarity of their SI data with the larger
12
13 336 non-MDN cypriniforms. Importantly, this also reduced the overall number of prey
14
15 337 resources used in the mixing models, enhancing model performance and reducing
16
17 338 prediction uncertainty (Phillips & Gregg, 2003; Phillips, Newsome & Gregg, 2005).
18
19
20
21
22
23

24 340 The putative prey resources that could be entered into each mixing model were thus
25
26 341 macro-invertebrates (combined data for Gammaridae, Chironomidae and Asellidae,
27
28 342 due to similarity of SI data; cf. Results), *Alosa* spp., ‘Cypriniform-freshwater’ fish and
29
30 343 ‘Cypriniform-marine’ fish, with the prey resources analysed separately for each reach.
31
32 344 However, the use of all of these resources in the models for each *E. lucius* size
33
34 345 category was not appropriate. This was because of the *E. lucius* size-specific gape
35
36 346 limitations, where smaller individuals are limited in their ability to consume larger-
37
38 347 bodied prey items (Nilsson & Brönmark, 2000). The use of angler-captured fish
39
40 348 meant the gape sizes of *E. lucius* could not be measured directly. Therefore, for each
41
42 349 individual *E. lucius* analysed, their maximum ingestible prey size (MP) was estimated
43
44 350 as a function of their fork length (FL) ($MP = (0.13FL)+0.40$; Nilsson & Brönmark,
45
46 351 2000). To incorporate these maximum prey lengths into the analysis, mixing models
47
48 352 were run for three size categories of *E. lucius* outlined earlier. The mean MP was
49
50 353 determined for each reach and size category, and only prey resources under the mean
51
52 354 MP were entered into their mixing model (Table 1). Although this meant that the
53
54 355 mixing models differed between the size categories, it ensured the final models were
55
56
57
58
59
60

1
2
3 356 parsimonious and ecologically realistic.
4
5

6 357

7
8 358 All statistical analysis and graphical outputs were performed using R (Version 3.5.2;

9
10 359 R Development Core Team 2018). Where error is expressed around the mean, it

11
12 360 represents \pm 95% confidence limits unless otherwise stated.
13
14

15 361

16 17 362 **Results**

18
19 363

20 21 364 *Stable isotope relationships with length in *Esox lucius**

22
23 365 There was a significant increase in $\delta^{13}\text{C}$ with increasing length for *E. lucius* within

24
25 366 reaches (Fig. 2; Table 2; Warwickshire Avon: $R^2 = 0.34$, $F_{1,17} = 10.08$; $P < 0.01$,

26
27 367 upstream Severn: $R^2 = 0.71$, $F_{1,6} = 17.76$, $P < 0.01$; downstream Severn: $R^2 = 0.47$,

28
29 368 $F_{1,28} = 24.75$, $P < 0.001$). This increase was also independent of reach (ANCOVA:

30
31 369 $F_{1,51} = 75.21$, $P < 0.001$). The $\delta^{13}\text{C}$ values also differed significantly between reaches

32
33 370 (ANCOVA: $F_{2,51} = 33.24$, $P < 0.001$), where *E. lucius* from the Warwickshire Avon

34
35 371 had depleted $\delta^{13}\text{C}$ versus both the downstream Severn (-3.49 ‰, $t = -7.87$, $P < 0.001$)

36
37 372 and upstream Severn (-1.80 ‰, $t = -2.91$, $P = 0.01$). Fish from the downstream Severn

38
39 373 reach also had significantly enriched $\delta^{13}\text{C}$ values versus the upstream Severn reach

40
41 374 ($+1.70$ ‰, $t = 2.84$, $P = 0.02$). The interaction between length and reach was not

42
43 375 significant (ANCOVA: $F_{2,51} = 2.86$, $P = 0.06$).
44
45

46
47 376

48
49 377 The relationship between $\delta^{15}\text{N}$ and fish length was not significant in the Warwickshire

50
51 378 Avon ($R^2 = 0.04$, $F_{1,17} = 0.29$; $P = 0.60$) and downstream Severn ($R^2 = 0.01$, $F_{1,28} =$

52
53 379 1.29 , $P = 0.28$) (Fig. 2; Table 2). There was, however, a significant increase in $\delta^{15}\text{N}$

54
55 380 with fish length at upstream Severn (Fig. 2; Table 2; $R^2 = 0.51$, $F_{1,6} = 6.12$, $P = 0.04$).
56
57
58
59
60

1
2
3 381 The relationship between $\delta^{15}\text{N}$ and fish length was not significant independent of
4
5 382 reach (ANCOVA: $F_{1,51} = 1.78$, $P = 0.19$), but $\delta^{15}\text{N}$ did differ significantly between
6
7 383 reaches (ANCOVA: $F_{2,51} = 63.38$, $P < 0.001$). Fish in the Warwickshire Avon had
8
9 384 significantly higher $\delta^{15}\text{N}$ than at the other reaches (downstream Severn $+2.81$ ‰, $t =$
10
11 385 10.27 , $P < 0.01$; upstream Severn $+3.06$ ‰, $t = 8.04$, $P < 0.01$).
12
13
14
15 386

16
17 387 *Isotopic niche of *Esox lucius**

18
19 388 The isotopic niche size (as SEA_B) of *E. lucius* was largest for the Warwickshire Avon,
20
21 389 followed by downstream Severn and was smallest at upstream Severn (Table 3). The
22
23 390 position, size and location of the ellipses varied in niche space, where *E. lucius*
24
25 391 isotopic niche from the Warwickshire Avon occupied more space on the $\delta^{15}\text{N}$ axis
26
27 392 and less space on the $\delta^{13}\text{C}$ axis compared with the downstream Severn reach that
28
29 393 showed the opposite pattern (Fig. 3).
30
31
32
33 394

34
35 395 Isotopic niche sizes (as SEA_B) by the three size categories of *E. lucius* revealed that in
36
37 396 the Warwickshire Avon, the largest niche was in fish of 651 to 850 mm and the
38
39 397 smallest niche for fish > 850 mm (Table 3; Fig. 4). These niches also showed a high
40
41 398 degree of overlap across all size categories with, for example, the niche of the largest
42
43 399 size category (> 850 mm) sitting entirely within the niche for fish of 651 to 850 mm
44
45 400 (Fig. 4). By contrast, the isotopic niches by size category in the downstream Severn
46
47 401 reach had greater separation along the $\delta^{13}\text{C}$ axis (Table 3; Fig. 4). The niche size for
48
49 402 fish of 400 to 650 mm was relatively small compared to the two larger size categories
50
51 403 and did not overlap (Table 3; Fig. 4). The isotopic niche for fish of > 850 mm was the
52
53 404 largest within the downstream Severn reach and was considerably $\delta^{13}\text{C}$ enriched,
54
55
56
57
58
59
60

1
2
3 405 resulting in it sharing only 40 % of its niche space with that for fish of 651 to 850 mm
4
5 406 (Table 2; Fig. 4).
6
7
8 407

9
10 408 *Spatial and temporal variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of putative prey resources*

11
12 409 The $\delta^{13}\text{C}$ values of macro-invertebrates did not differ between reaches (Warwickshire
13
14 410 Avon: -30.23 ± 0.46 ‰; downstream Severn: -29.67 ± 0.39 ‰; *t-test*: $t = -0.92$, *d.f.* =
15
16 411 17, $P = 0.37$; Table 1; Fig. 4). There was, however, significant $\delta^{13}\text{C}$ enrichment in the
17
18 412 putative prey resources between the reaches (*t-test*: $t = 7.82$, *d.f.* = 168.67, $P < 0.001$;
19
20 413 Table 1; Fig 4). This significant $\delta^{13}\text{C}$ enrichment was thus due to significant
21
22 414 differences in the fish prey resources (Warwickshire Avon: -26.48 ± 0.31 ;
23
24 415 downstream Severn: -22.78 ± 0.34 ; *t-test*: $t = -8.01$, *d.f.* = 145.62, $P < 0.001$; Table 1;
25
26 416 Fig. 4).
27
28
29
30
31
32 417

33 418 The putative prey resources were significantly enriched in $\delta^{15}\text{N}$ in the Warwickshire
34
35 419 Avon (16.02 ± 0.24 ‰) versus the Severn (12.28 ± 0.13 ‰) reaches (*t-test*: $t = -7.81$,
36
37 420 *d.f.* = 168.67, $P < 0.001$; Table 1; Fig. 4). Differences were in both
38
39 421 macroinvertebrates and fish prey resources (macroinvertebrates: *t-test*: $t = 12.64$, *d.f.*
40
41 422 = 15.10, $P < 0.001$; prey fish: *t-test*: $t = -8.0$, *d.f.* = 145.62, $P < 0.001$; Table 1; Fig.
42
43 423 4).
44
45
46
47 424

48
49 425 *Stable isotope mixing model predictions of *Esox lucius* diet composition*

50
51 426 At both the Warwickshire Avon and downstream Severn reaches, *E. lucius* isotopic
52
53 427 niches across all size categories were positioned between the putative prey resources
54
55 428 (Fig. 4). At the Warwickshire Avon, whilst the cypriniform fishes specialising on
56
57 429 marine fishmeal baits were present, the gape limitations in the size range of the
58
59
60

1
2
3 430 analysed *E. lucius* meant none were considered as available prey in mixing models.
4
5 431 Thus, all dietary contributions in this reach were of freshwater origin (Table 1), with
6
7 432 predictions that macro-invertebrate prey resources were contributing substantially to
8
9 433 the diet of *E. lucius* < 650 mm (Table 4). Freshwater fishes and macroinvertebrates
10
11 434 were then important prey items at sizes > 650 mm (Table 4).
12
13
14
15 435

16
17 436 In the downstream Severn reach, whilst freshwater fish were predicted as the most
18
19 437 important prey resource in all size categories, the two marine prey resources were
20
21 438 increasingly important prey items as *E. lucius* body length increased. Overall, the
22
23 439 proportions dietary contributions of *Alosa* spp. increased from 0.05 ± 0.04 in fish <
24
25 440 650 mm to 0.13 ± 0.06 in fish of length > 850 mm (Table 4). Whilst gape limitations
26
27 441 precluded cypriniform fishes specialising on marine fishmeal bait from diet
28
29 442 predictions for *E. lucius* < 650 mm, in the larger size categories, the predicted
30
31 443 contributions were 0.24 ± 0.13 for 650 to 850 mm and 0.20 ± 0.14 for fish > 850 mm
32
33 444 (Table 4).
34
35
36
37
38 445

39
40 446 When predicted at the individual level, there was less dietary variability in *E. lucius* in
41
42 447 the Warwickshire Avon than in the downstream Severn reach (Table 4; Fig. 5). At the
43
44 448 downstream Severn reach, individual variability in diet increased with increasing gape
45
46 449 size, with the highest individual variability apparent for fish > 850 mm (Table 4). For
47
48 450 these fish, the 'Cypriniform-freshwater' prey had an estimated range of between 0.37
49
50 451 and 0.71 contribution to individual diet, *Alosa* spp. between 0.06 and 0.25 and
51
52 452 cypriniform fishes specialising on marine fishmeal bait between 0.18 and 0.33 (Table
53
54 453 4; Fig. 5b). The highest mean proportional contribution of marine resources to the diet
55
56 454 of an individual fish was 58 % (Fig. 5b).
57
58
59
60

1
2
3 4554
5 456 **Discussion**6
7 457

8 458 Stable isotope analysis revealed the presence of marine subsidies within an
9
10 459 impounded lowland river resulted in their substantial contribution to the assimilated
11
12 460 diet of large-bodied *E. lucius*. Results showed considerable dietary niche partitioning
13
14 461 between *E. lucius* size categories when anadromous *Alosa* spp. and cypriniform fish
15
16 462 specialising on marine fishmeal bait were available as prey. Where these resources
17
18 463 were not available, this niche partitioning was not evident. Stable isotope mixing
19
20 464 models revealed that in the downstream Severn reach, up to 33 % of *E. lucius*
21
22 465 population diet could be attributed to the marine subsidies at the population level,
23
24 466 with the greatest proportion of this marine resource contributed by cypriniform fishes
25
26 467 (20 % of total population diet). There was, however, considerable variation among
27
28 468 individuals, with between 22 and 58 % of individual diets consisting of the two
29
30 469 marine resources.

31
32 470

33 471 These results are consistent with studies on individual specialisation that suggest long
34
35 472 term differences in the diet of consumers can result in considerable variation of $\delta^{13}\text{C}$
36
37 473 within populations (Matthews & Mazumder, 2004). Other apex predators have also
38
39 474 been reported to couple distinct energetic pathways within complex food webs. For
40
41 475 example, Matich, Heithaus & Layman (2011) revealed that two pelagic shark species
42
43 476 coupled distinct food webs through dietary variations resulting from one species being
44
45 477 dietary specialists and the other being generalists. Individual specialisation in *E.*
46
47 478 *lucius* has also been previously documented (Beaudoin et al., 1999; Kobler et al.,
48
49 479 2009). It has been hypothesised as a potentially important mechanism in reducing
50
51
52
53
54
55
56
57
58
59
60

1
2
3 480 intraspecific competition, with Kobler et al., (2009) showing substantial behavioural
4
5 481 diversification in individual *E. lucius* that helped to reduce intra-specific competitive
6
7 482 interactions. Here, the diet diversification in the larger *E. lucius* was through their
8
9 483 specialisation on the marine prey subsidies that were all lengths >280 mm. Although
10
11 484 it could not be tested whether the fish specialising on these subsidies had different
12
13 485 behavioural traits to those that primarily consumed freshwater prey, they did require
14
15 486 functional traits that enabled the capture and handling of large prey. Whilst it could
16
17 487 also not be tested whether the consumption of these larger prey was a response to
18
19 488 intra-specific competition, the exploitation of marine subsidies by these individuals
20
21 489 resulted in higher intrapopulation variation and individual specialisation, as has been
22
23 490 shown elsewhere (e.g. Beaudoin et al., 1999; Bolnick et al., 2002; Araújo, Bolnick &
24
25 491 Layman, 2011). In doing so, the two marine energy pathways present in the
26
27 492 downstream Severn reach were coupled with those from non-marine sources at the
28
29 493 apex of this riverine food web.
30
31
32
33
34
35
36
37

38 495 The $\delta^{13}\text{C}$ of *E. lucius* differed significantly between the reaches, but with the effect of
39
40 496 the interaction of reach and fish length on $\delta^{13}\text{C}$ not being significant. There was,
41
42 497 however, high variability in $\delta^{13}\text{C}$ of larger *E. lucius* in the downstream Severn reach
43
44 498 that could potentially have strongly influenced this non-significant result. There was
45
46 499 also considerable variability in the contribution of marine resources to the diet of the
47
48 500 larger fish in the downstream Severn reach. Nevertheless, within this reach, the
49
50 501 dietary contributions of the two marine subsidies did increase with *E. lucius* body
51
52 502 length, explained by their prey selection being dependent on gape size, with this a
53
54 503 function of their body length. This finding is important, as in the dietary analyses of
55
56 504 *E. lucius*, individual diets tend to primarily consist of smaller prey (e.g. < 200 mm
57
58
59
60

1
2
3 505 length), irrespective of whether that fish can consume larger prey (Craig, 2008;
4
5 506 Sandlund, Museth & Øistad, 2016). This results from both a limited availability of
6
7 507 larger prey and larger prey having higher handling times that incurs an increased risk
8
9 508 of kleptoparasitism (Nilsson & Brönmark, 2000; Craig, 2008). Here, the stable
10
11 509 isotope data suggested that individual *E. lucius* over 650 mm could consume
12
13 510 relatively large fishes, with, for example, the approximate sizes of *Alosa* spp. in the
14
15 511 River Severn during their spawning period being > 300 mm (Aprahamian, 1988).
16
17 512 Moreover, the MDN prey resource from angling bait comprised of fishes of only
18
19 513 above 380 mm length. The presence of anadromous *Alosa* spp. in diet was also
20
21 514 interesting given they are only available for a relatively short period each year,
22
23 515 generally April to June, a period coincident with the post-spawning period of *E. lucius*
24
25 516 (Craig, 2008). Utilisation of these gape dependent resources resulted in isotopic niche
26
27 517 differences between populations with and without MDN pathways. This finding is
28
29 518 also consistent with Samways et al. (2018), who found that whilst the total ecological
30
31 519 niche space did not always increase in river communities following spawning of
32
33 520 anadromous fishes, this niche space did show consistent movement toward the
34
35 521 marine-nutrient source.
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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.,

1
2
3 530 2014, 2015). These anthropogenic subsidies have been sufficient to maintain the
4
5 531 abundance and richness of numerous terrestrial predators, including species of birds,
6
7 532 mammals and reptiles (Ripple et al., 2014; Newsome et al., 2015). Here, the provision
8
9 533 of an anthropogenic prey subsidy in an aquatic system was via the release of large
10
11 534 amounts of angling baits that contained high proportions of MDN. The population
12
13 535 benefits of this subsidy for *E. lucius* might have been limited, as it can only be
14
15 536 exploited at relatively large sizes. It was beyond this study to determine if there were
16
17 537 reproductive and fitness benefits for individuals exploiting these marine prey
18
19 538 resources. Nevertheless, the relatively distinct $\delta^{13}\text{C}$ signal of the angler bait subsidy,
20
21 539 located between the freshwater and anadromous prey $\delta^{13}\text{C}$ signal, enabled these
22
23 540 nutrients to be traced through successive trophic levels in the food web. Previously,
24
25 541 MDN subsidies from aquaculture and angling have only been detected as being
26
27 542 assimilated directly by freshwater fishes (Jackson et al., 2013; Bašić et al., 2015;
28
29 543 Gutmann Roberts et al., 2017). Thus, a novel outcome of this study was the
30
31 544 demonstration that this anthropogenic marine subsidy was transferred to higher
32
33 545 trophic levels in the freshwater food web via piscivory. Notwithstanding, this result
34
35 546 was detected in only one river reach. Given the characteristics of the study system,
36
37 547 this was unavoidable, as the two marine prey pathways were only present in the
38
39 548 downstream Severn reach. Although sample sizes were often small in some reaches,
40
41 549 these were not considered to have been a major impediment to data analysis and
42
43 550 interpretation due to some of the considerable differences in the stable isotope data of
44
45 551 both prey and *E. lucius*. However, it would be beneficial to identify whether this
46
47 552 transfer of angling MDN through riverine food webs is apparent elsewhere, especially
48
49 553 in reaches where they are released in high quantities.
50
51
52
53
54
55
56
57
58
59
60

1
2
3 555 Angling baits have been argued as acting as a very strong allochthonous subsidy
4
5 556 compared to inputs of, for example, terrestrial invertebrates (Bašić et al., 2015;
6
7 557 Mehner et al., 2018). Here, their use in the River Severn basin created a novel MDN
8
9 558 energy pathway involving cypriniform consumers and the piscivorous *E. lucius*. The
10
11 559 dietary contribution of this MDN pathway was generally predicted to be higher than
12
13 560 that of the anadromous MDN pathway. This anadromous prey resource was, however,
14
15 561 still an important dietary component. Its presence was also consistent with a large
16
17 562 body of research that demonstrates the importance of anadromous fishes for
18
19 563 maintaining the productivity, diversity, and community structure of many freshwater
20
21 564 systems (e.g. Schindler et al., 2005; Richardson et al., 2016). Indeed, apex predatory
22
23 565 fishes have been shown to regularly predate upon anadromous fishes when they enter
24
25 566 freshwaters to spawn (MacAvoy et al., 2000; Guillerault et al., 2017).

30 567

31
32
33 568 In summary, the diet composition and isotopic niches of *E. lucius* populations was
34
35 569 influenced by the spatial variation of novel marine prey resources. Whilst body size
36
37 570 had a strong influence on the ability of *E. lucius* to exploit these marine prey
38
39 571 resources, there was considerable variability in the MDN dietary contributions to
40
41 572 larger fish. Notwithstanding, that angling bait based on marine resources could be
42
43 573 traced through successive trophic levels is a novel finding and highlights how human
44
45 574 subsidies can affect the trophic dynamics of apex predators.

49 575 **Acknowledgments**

50
51 576

52
53
54 577 We thank the anglers of the Severn Basin Predator study for their assistance in the
55
56 578 collection of scale samples. We also thank Brecht Morris and Laura Bullock of the
57
58 579 Environment Agency for their help in establishing the angler network and for field
59
60

1
2
3 580 assistance. EN was supported by a studentship funded by the Severn Rivers Trust, the
4
5 581 Environment Agency and Bournemouth University. Permission for sampling of fish
6
7
8 582 was given by the Environment Agency. Regulated procedures on live fish were
9
10 583 completed only by licenced individuals under UK Home Office licence 70/8063.

11
12 584

13
14
15 585 **References**

16
17 586

18
19 587 Amat Trigo F., Gutmann Roberts C. & Britton J.R. (2017) Spatial variability in the
20
21 588 growth of invasive European barbel *Barbus barbus* in the River Severn basin,
22
23 589 revealed using anglers as citizen scientists. *Knowledge & Management of*
24
25 590 *Aquatic Ecosystems*, 17.

26
27
28 591 Antognazza C.M., Andreou D., Zaccara S. & Britton R.J. (2016) Loss of genetic
29
30 592 integrity and biological invasions result from stocking and introductions of
31
32 593 *Barbus barbus*: insights from rivers in England. *Ecology and Evolution* **6**,
33
34 594 1280–1292.

35
36
37 595 Aprahamian M.W. (1988) The biology of the twaite shad, *Alosa fallax fallax*
38
39 596 (Lacépède), in the Severn Estuary. *Journal of Fish Biology* **33**, 141–152.

40
41
42 597 Araújo M.S., Bolnick D.I. & Layman C.A. (2011) The ecological causes of individual
43
44 598 specialisation. *Ecology Letters* **14**, 948–958.

45
46
47 599 Arlinghaus R. & Mehner T. (2003) Socio-economic characterisation of specialised
48
49 600 common carp (*Cyprinus carpio* L.) anglers in Germany, and implications for
50
51 601 inland fisheries management and eutrophication control. *Fisheries Research*
52
53 602 **61**, 19–33.

- 1
2
3 603 Barnes C., Sweeting C.J., Jennings S., Barry J.T. & Polunin N.V.C. (2007) Effect of
4
5 604 temperature and ration size on carbon and nitrogen stable isotope trophic
6
7 605 fractionation. *Functional Ecology* **21**, 356–362.
8
9
10 606 Bašić T. & Britton J.R. (2015) Utility of fish scales from stock assessment surveys in
11
12 607 stable isotope analysis for initial assessments of trophic relationships in
13
14 608 riverine fish communities. *Journal of Applied Ichthyology* **31**, 296–300.
15
16
17 609 Bašić T., Britton J.R., Jackson M.C., Reading P. & Grey J. (2015) Angling baits and
18
19 610 invasive crayfish as important trophic subsidies for a large cyprinid fish.
20
21 611 *Aquatic Sciences* **77**, 153–160.
22
23
24 612 Beaudoin C.P., Tonn W.M., Prepas E.E. & Wassenaar L.I. (1999) Individual
25
26 613 specialization and trophic adaptability of northern pike (*Esox lucius*): an
27
28 614 isotope and dietary analysis. *Oecologia* **120**, 386–396.
29
30
31 615 Bolnick D.I., Svanbäck R., Fordyce J.A., Yang L.H., Davis J.M., Hulseley C.D., *et al.*
32
33 616 (2002) The ecology of individuals: incidence and implications of individual
34
35 617 specialization. *The American Naturalist* **161**, 1–28.
36
37
38 618 Brett M.T. & Goldman C.R. (1996) A meta-analysis of the freshwater trophic
39
40 619 cascade. *Proceedings of the National Academy of Sciences* **93**, 7723–7726.
41
42
43 620 Busst G. & Britton J.R. (2017) Comparative trophic impacts of two globally invasive
44
45 621 cyprinid fishes reveal species-specific invasion consequences for a threatened
46
47 622 native fish. *Freshwater Biology* **62**, 1587–1595.
48
49
50 623 Busst G.M.A., Bašić T. & Britton J.R. (2015) Stable isotope signatures and trophic-
51
52 624 step fractionation factors of fish tissues collected as non-lethal surrogates of
53
54 625 dorsal muscle: Non-lethal tissue surrogates for fish isotope studies. *Rapid*
55
56 626 *Communications in Mass Spectrometry* **29**, 1535–1544.
57
58
59
60

- 1
2
3 627 Busst G.M.A. & Britton J.R. (2016) High variability in stable isotope diet–tissue
4
5 628 discrimination factors of two omnivorous freshwater fishes in controlled *ex*
6
7 629 *situ* conditions. *The Journal of Experimental Biology* **219**, 1060–1068.
8
9
10 630 Chapman L.J., Mackay W.C. & Wilkinson C.W. (1989) Feeding flexibility in
11
12 631 northern pike (*Esox lucius*): fish versus invertebrate prey. *Canadian Journal*
13
14 632 *of Fisheries and Aquatic Sciences* **46**, 666–669.
15
16
17 633 Clavero M., Blanco-Garrido F. & Prenda J. (2004) Fish fauna in Iberian
18
19 634 Mediterranean river basins: biodiversity, introduced species and damming
20
21 635 impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems* **14**, 575–
22
23 636 585.
24
25
26 637 Craig J.F. (2008) A short review of pike ecology. *Hydrobiologia* **601**, 5–16.
27
28 638 Grey J., Waldron S. & Hutchinson R. (2004) The utility of carbon and nitrogen
29
30 639 isotope analyses to trace contributions from fish farms to the receiving
31
32 640 communities of freshwater lakes: a pilot study in Esthwaite Water, UK.
33
34 641 *Hydrobiologia* **524**, 253–262.
35
36
37 642 Guillerault N., Bouletreau S., Iribar A., Valentini A. & Santoul F. (2017) Application
38
39 643 of DNA metabarcoding on faeces to identify European catfish *Silurus glanis*
40
41 644 diet. *Journal of Fish Biology* **90**, 2214–2219.
42
43
44 645 Gutmann Roberts C., Bašić T., Amat Trigo F. & Britton J.R. (2017) Trophic
45
46 646 consequences for riverine cyprinid fishes of angler subsidies based on marine-
47
48 647 derived nutrients. *Freshwater Biology* **62**, 894–905.
49
50
51 648 Heady W.N. & Moore J.W. (2013) Tissue turnover and stable isotope clocks to
52
53 649 quantify resource shifts in anadromous rainbow trout. *Oecologia* **172**, 21–34.
54
55
56 650 Hickley P. & Chare S. (2004) Fisheries for non-native species in England and Wales:
57
58 651 angling or the environment? *Fisheries Management and Ecology* **11**, 203–212.
59
60

- 1
2
3 652 Hutchinson J.J. & Trueman C.N. (2006) Stable isotope analyses of collagen in fish
4
5 653 scales: limitations set by scale architecture. *Journal of Fish Biology* **69**, 1874–
6
7 654 1880.
- 8
9
10 655 Jackson A.L., Inger R., Parnell A.C. & Bearhop S. (2011) Comparing isotopic niche
11
12 656 widths among and within communities: SIBER - Stable Isotope Bayesian
13
14 657 Ellipses in R: Bayesian isotopic niche metrics. *Journal of Animal Ecology* **80**,
15
16 658 595–602.
- 17
18
19 659 Jackson M.C., Allen R., Pegg J. & Britton J.R. (2013) Do trophic subsidies affect the
20
21 660 outcome of introductions of a non-native freshwater fish? *Freshwater Biology*
22
23 661 **58**, 2144–2153.
- 24
25
26 662 Jackson M.C., Donohue I., Jackson A.L., Britton J.R., Harper D.M. & Grey J. (2012)
27
28 663 Population-level metrics of trophic structure based on stable isotopes and their
29
30 664 application to invasion ecology. *PLoS ONE* **7**, e31757.
- 31
32
33 665 Jardine T.D., Gray M.A., McWilliam S.M. & Cunjak R.A. (2005) Stable isotope
34
35 666 variability in tissues of temperate stream fishes. *Transactions of the American*
36
37 667 *Fisheries Society* **134**, 1103–1110.
- 38
39
40 668 Kobler A., Klefoth T., Mehner T. & Arlinghaus R. (2009) Coexistence of behavioural
41
42 669 types in an aquatic top predator: a response to resource limitation? *Oecologia*
43
44 670 **161**, 837–847.
- 45
46
47 671 MacAvoy S.E., Macko S.A., McIninch S.P. & Garman G.C. (2000) Marine nutrient
48
49 672 contributions to freshwater apex predators. *Oecologia* **122**, 568–573.
- 50
51
52 673 Marcarelli A.M., Baxter C.V., Mineau M.M. & Hall R.O. (2011) Quantity and
53
54 674 quality: unifying food web and ecosystem perspectives on the role of resource
55
56 675 subsidies in freshwaters. *Ecology* **92**, 1215–1225.
- 57
58
59
60

- 1
2
3 676 Marczak L.B., Thompson R.M. & Richardson J.S. (2007) Meta-analysis: trophic
4
5 677 level, habitat, and productivity shape the food web effects of resource
6
7 678 subsidies. *Ecology* **88**, 140–148.
- 8
9
10 679 Matich P., Heithaus M.R. & Layman C.A. (2011) Contrasting patterns of individual
11
12 680 specialization and trophic coupling in two marine apex predators:
13
14 681 Specialization in top marine predators. *Journal of Animal Ecology* **80**, 294–
15
16 682 305.
- 17
18
19 683 Matthews B. & Mazumder A. (2004) A critical evaluation of intrapopulation variation
20
21 684 of $\delta^{13}\text{C}$ and isotopic evidence of individual specialization. *Oecologia* **140**,
22
23 685 361–371.
- 24
25
26 686 McIntosh A.R. & Townsend C.R. (1996) Interactions between fish, grazing
27
28 687 invertebrates and algae in a New Zealand stream: a trophic cascade mediated
29
30 688 by fish-induced changes to grazer behaviour? *Oecologia* **108**, 174–181.
- 31
32
33 689 Mehner T., Rapp T., Monk C.T., Beck M.E., Trudeau A., Kiljunen M., *et al.* (2018)
34
35 690 Feeding Aquatic Ecosystems: Whole-Lake Experimental Addition of Angler's
36
37 691 Ground Bait Strongly Affects Omnivorous Fish Despite Low Contribution to
38
39 692 Lake Carbon Budget. *Ecosystems*, 1–17.
- 40
41
42 693 Newsome T.M., Ballard G.-A., Fleming P.J., van de Ven R., Story G.L. & Dickman
43
44 694 C.R. (2014) Human-resource subsidies alter the dietary preferences of a
45
46 695 mammalian top predator. *Oecologia* **175**, 139–150.
- 47
48
49 696 Newsome T.M., Dellinger J.A., Pavey C.R., Ripple W.J., Shores C.R., Wirsing A.J.,
50
51 697 *et al.* (2015) The ecological effects of providing resource subsidies to
52
53 698 predators. *Global Ecology and Biogeography* **24**, 1–11.
- 54
55
56 699 Niesar M., Arlinghaus R., Rennert B. & Mehner T. (2004) Coupling insights from a
57
58 700 carp, *Cyprinus carpio*, angler survey with feeding experiments to evaluate
59
60

- 1
2
3 701 composition, quality and phosphorus input of groundbait in coarse fishing.
4
5 702 *Fisheries Management and Ecology* **11**, 225–235.
6
7
8 703 Nilsson P.A. & Brönmark C. (2000) Prey vulnerability to a gape-size limited
9
10 704 predator: behavioural and morphological impacts on northern pike piscivory.
11
12 705 *Oikos* **88**, 539–546.
13
14 706 Ovidio M. & Philippart J.-C. (2002) The impact of small physical obstacles on
15
16 707 upstream movements of six species of fish. In: *Aquatic Telemetry*, Thorstad
17
18 708 E.B., Fleming I.A., Næsje T.F. (eds). pp. 55–69. Springer.
19
20
21 709 Pedreschi D., Mariani S., Coughlan J., Voigt C.C., O’Grady M., Caffrey J., *et al.*
22
23 710 (2015) Trophic flexibility and opportunism in pike *Esox lucius*. *Journal of*
24
25 711 *Fish Biology* **87**, 876–894.
26
27
28 712 Phillips D.L. & Gregg J.W. (2003) Source partitioning using stable isotopes: coping
29
30 713 with too many sources. *Oecologia* **136**, 261–269.
31
32
33 714 Phillips D.L., Newsome S.D. & Gregg J.W. (2005) Combining sources in stable
34
35 715 isotope mixing models: alternative methods. *Oecologia* **144**, 520–527.
36
37
38 716 Polis G.A., Anderson W.B. & Holt R.D. (1997) Toward an integration of landscape
39
40 717 and food web ecology: the dynamics of spatially subsidized food webs.
41
42 718 *Annual review of ecology and systematics* **28**, 289–316.
43
44
45 719 Post D.M., Layman C.A., Arrington D.A., Takimoto G., Quattrochi J. & Montana
46
47 720 C.G. (2007) Getting to the fat of the matter: models, methods and assumptions
48
49 721 for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179–189.
50
51 722 R Core Team. 2018. R: A language and environment for statistical computing. R
52
53 723 Foundation for Statistical Computing, Vienna, Austria. URL [https://www.R-](https://www.R-project.org/)
54
55 724 [project.org/](https://www.R-project.org/).

- 1
2
3 725 Rasmussen J.B., Trudeau V. & Morinville G. (2009) Estimating the scale of fish
4
5 726 feeding movements in rivers using $\delta^{13}\text{C}$ signature gradients. *Journal of animal*
6
7 727 *ecology* **78**, 674–685.
- 8
9
10 728 Richardson D.P., Kohler A.E., Hailemichael M. & Finney B.P. (2016) The fate of
11
12 729 marine-derived nutrients: tracing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ through oligotrophic
13
14 730 freshwater and linked riparian ecosystems following salmon carcass analog
15
16 731 additions. *Canadian Journal of Fisheries and Aquatic Sciences* **74**, 41–55.
- 17
18
19 732 Ripple W.J., Estes J.A., Beschta R.L., Wilmers C.C., Ritchie E.G., Hebblewhite M.,
20
21 733 *et al.* (2014) Status and ecological effects of the world's largest carnivores.
22
23 734 *Science* **343**, 1241484.
- 24
25
26 735 Ripple W.J., Wirsing A.J., Wilmers C.C. & Letnic M. (2013) Widespread
27
28 736 mesopredator effects after wolf extirpation. *Biological Conservation* **160**, 70–
29
30 737 79.
- 31
32
33 738 Ritchie E.G., Elmhagen B., Glen A.S., Letnic M., Ludwig G. & McDonald R.A.
34
35 739 (2012) Ecosystem restoration with teeth: what role for predators? *Trends in*
36
37 740 *Ecology & Evolution* **27**, 265–271.
- 38
39
40 741 Rooney N., McCann K.S. & Moore J.C. (2008) A landscape theory for food web
41
42 742 architecture. *Ecology Letters* **11**, 867–881.
- 43
44
45 743 Samways K.M., Soto D.X. & Cunjak R.A. (2018) Aquatic food-web dynamics
46
47 744 following incorporation of nutrients derived from Atlantic anadromous fishes.
48
49 745 *Journal of Fish Biology* **92**, 399–419.
- 50
51
52 746 Sandlund O.T., Museth J. & Øistad S. (2016) Migration, growth patterns, and diet of
53
54 747 pike (*Esox lucius*) in a river reservoir and its inflowing river. *Fisheries*
55
56 748 *Research* **173**, 53–60.
- 57
58
59
60

- 1
2
3 749 Schindler D.E., Leavitt P.R., Brock C.S., Johnson S.P. & Quay P.D. (2005) Marine-
4
5 750 derived nutrients, commercial fisheries, and production of salmon and lake
6
7 751 algae in Alaska. *Ecology* **86**, 3225–3231.
- 8
9
10 752 Sorel M.H., Hansen A.G., Connelly K.A., Wilson A.C., Lowery E.D. & Beauchamp
11
12 753 D.A. (2016) Predation by Northern Pikeminnow and Tiger Muskellunge on
13
14 754 Juvenile Salmonids in a High-Head Reservoir: Implications for Anadromous
15
16 755 Fish Reintroductions. *Transactions of the American Fisheries Society* **145**,
17
18 756 521–536.
- 19
20
21 757 Stock B.C., Jackson A.L., Ward E.J., Parnell A.C., Phillips D.L. & Semmens B.X.
22
23 758 (2018) Analyzing mixing systems using a new generation of Bayesian tracer
24
25 759 mixing models. *PeerJ PrePrints*, e5096.
- 26
27
28 760 Stock B.C. & Semmens B.X. (2016) Unifying error structures in commonly used
29
30 761 biotracer mixing models. *Ecology* **97**, 2562–2569.
- 31
32
33 762 Takimoto G., Iwata T. & Murakami M. (2002) Seasonal subsidy stabilizes food web
34
35 763 dynamics: balance in a heterogeneous landscape. *Ecological Research* **17**,
36
37 764 433–439.
- 38
39
40 765 Ventura M. & Jeppesen E. (2010) Evaluating the need for acid treatment prior to $\delta^{13}\text{C}$
41
42 766 and $\delta^{15}\text{N}$ analysis of freshwater fish scales: effects of varying scale mineral
43
44 767 content, lake productivity and CO_2 concentration. *Hydrobiologia* **644**, 245–
45
46 768 259.
- 47
48
49 769 Venturelli P.A. & Tonn W.M. (2005) Invertebrate communities of littoral macroinvertebrates in small boreal lakes.
50
51 770
52
53 771 *Journal of the North American Benthological Society* **24**, 904–918.
- 54
55
56
57
58
59
60

- 1
2
3 772 Wheeler A. & Jordan D.R. (1990) The status of the barbel, *Barbus barbus* (L.)
4
5 773 (Teleostei, Cyprinidae), in the United Kingdom. *Journal of Fish Biology* **37**,
6
7 774 393–399.
8
9
10 775 Wipfli M.S., Hudson J.P., Caouette J.P. & Chaloner D.T. (2003) Marine subsidies in
11
12 776 freshwater ecosystems: salmon carcasses increase the growth rates of stream-
13
14 777 resident salmonids. *Transactions of the American Fisheries Society* **132**, 371–
15
16 778 381.
17
18
19 779 Zhang Y., Negishi J.N., Richardson J.S. & Kolodziejczyk R. (2003) Impacts of
20
21 780 marine-derived nutrients on stream ecosystem functioning. *Proceedings of the*
22
23 781 *Royal Society of London B: Biological Sciences* **270**, 2117–2123.
24
25
26 782
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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	<i>E. lucius</i> size category	Prey resource	n	Prey Length range (mm)	Mean $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)
L. W. Avon	$\geq 400 < 650$ 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
	$\geq 650 < 850$ 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	$\geq 400 < 650$ 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			
	$\geq 650 < 850$ mm	<i>Alosa</i> spp.	9		-13.30 ± 0.62	12.52 ± 0.90
		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	

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46

		<i>Alosa</i> 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
		<i>Alosa</i> spp.	9		-13.30 ± 0.62	12.52 ± 0.90

Copy for Review

Table 2. Mean (\pm 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 $\delta^{13}\text{C}$ (‰)	Range $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	Range $\delta^{15}\text{N}$ (‰)
Warwickshire Avon	$\geq 400 < 650$	455 to 640	7	-26.23 ± 1.24	-28.30 to -25.15	19.08 ± 1.36	16.58 to 21.24
	$\geq 651 < 850$	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	$\geq 400 < 650$	420 to 480	2	-24.48 ± 0.35	-24.73 to -24.23	15.02 ± 0.55	14.63 to 15.41
	$\geq 651 < 850$	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	$\geq 400 < 650$	508 to 635	5	-24.35 ± 0.46	-24.74 to -23.69	15.80 ± 0.58	14.86 to 16.28
	$\geq 651 < 850$	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

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 $\geq 400 < 650$ mm	5.28	3.59	4.31	3.57	1.59, 8.68
Warwickshire Avon $\geq 650 < 850$ 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 $\geq 400 < 650$ mm	0.58	0.54	0.72	0.29	0.11, 0.89
Downstream Severn $\geq 650 < 850$ 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 % \pm SD with 5% and 95% Bayesian credible intervals in parentheses and individual mean % \pm 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	$\geq 400 < 650$ mm	$\geq 650 < 850$ mm	≥ 850 mm
Warwickshire Avon	<i>Group</i>	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)
	<i>Individual</i>	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	<i>Group</i>	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)
	<i>Individual</i>	<i>Alosa spp.</i>	0.05 ± 0.04 (0.01, 0.13)	0.07 ± 0.05 (0.01, 0.17)	0.13 ± 0.06 (0.03, 0.23)
		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)
		<i>Alosa spp.</i>	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) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ 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* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 \pm SD of resource points are displayed with symbols corresponding as above.

1
2
3 Figure 5. Estimated dietary prey contributions (0 – 1) from MixSIAR models to the
4 diet of individual *Esox lucius* by body length at (a) the Warwickshire Avon and (b)
5 downstream Severn. Prey resources are represented as overall means in a stacked bar
6 plot for *Alosa* spp (dark grey), ‘Cypriniform-marine’ (light grey), ‘Cypriniform-
7 freshwater’ (white) and Invertebrates (black).
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Copy for Review

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

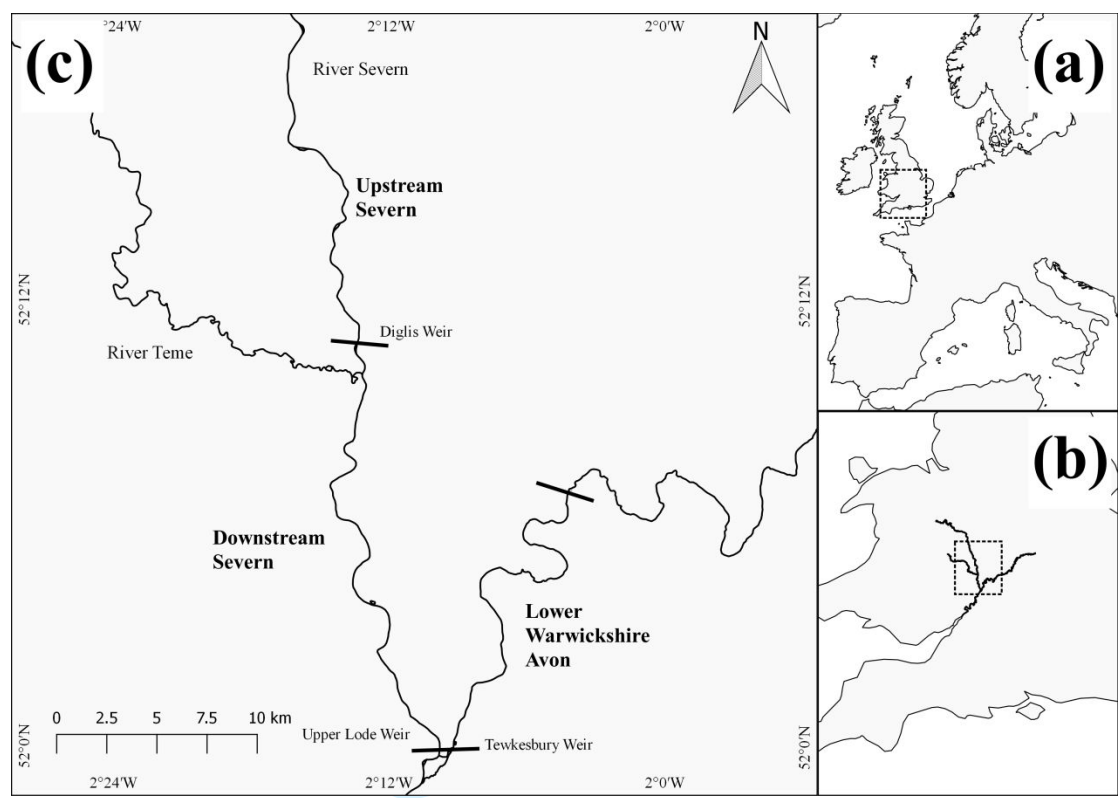


FIG. 1.

For Review

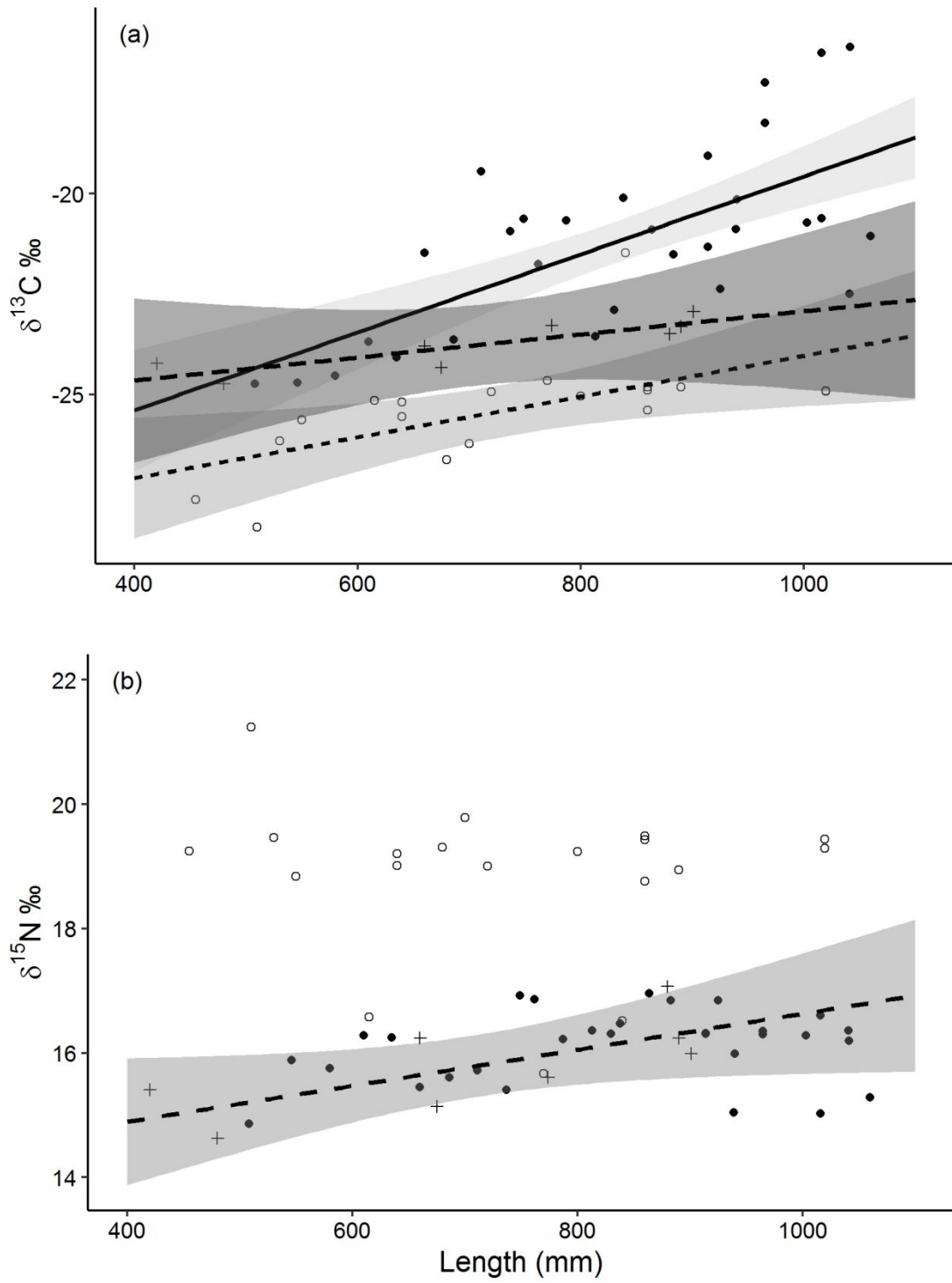


FIG. 2.

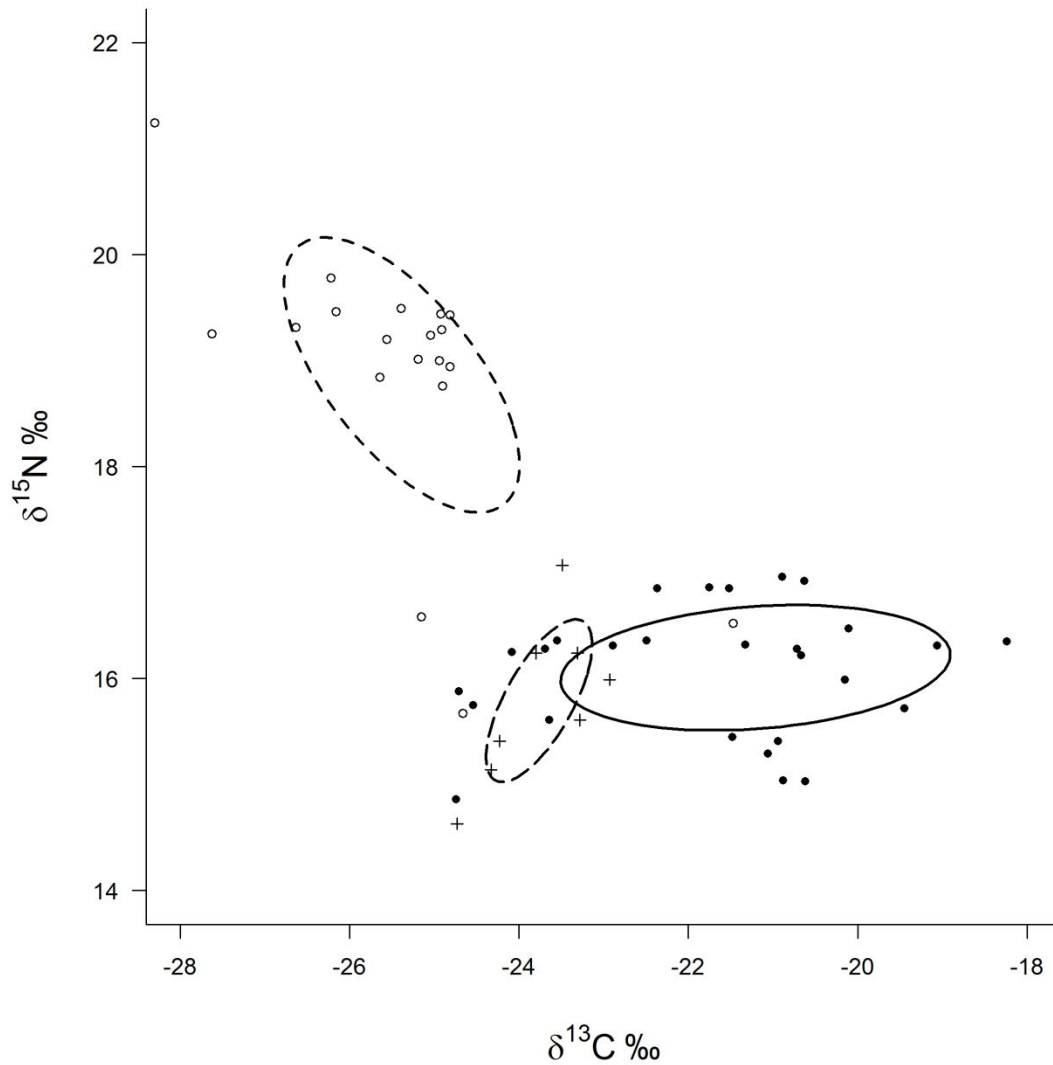


FIG.3.

iew

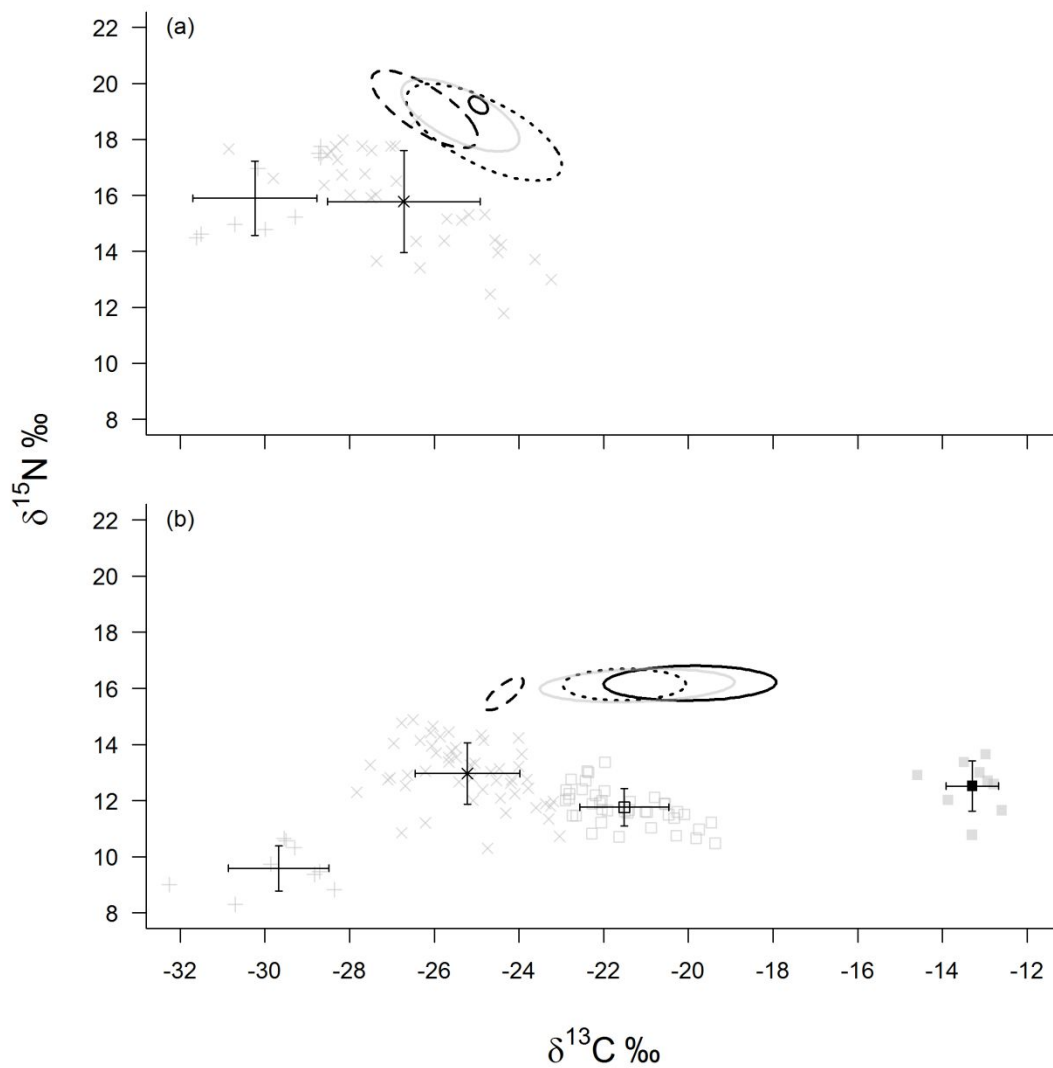


FIG. 4

iew

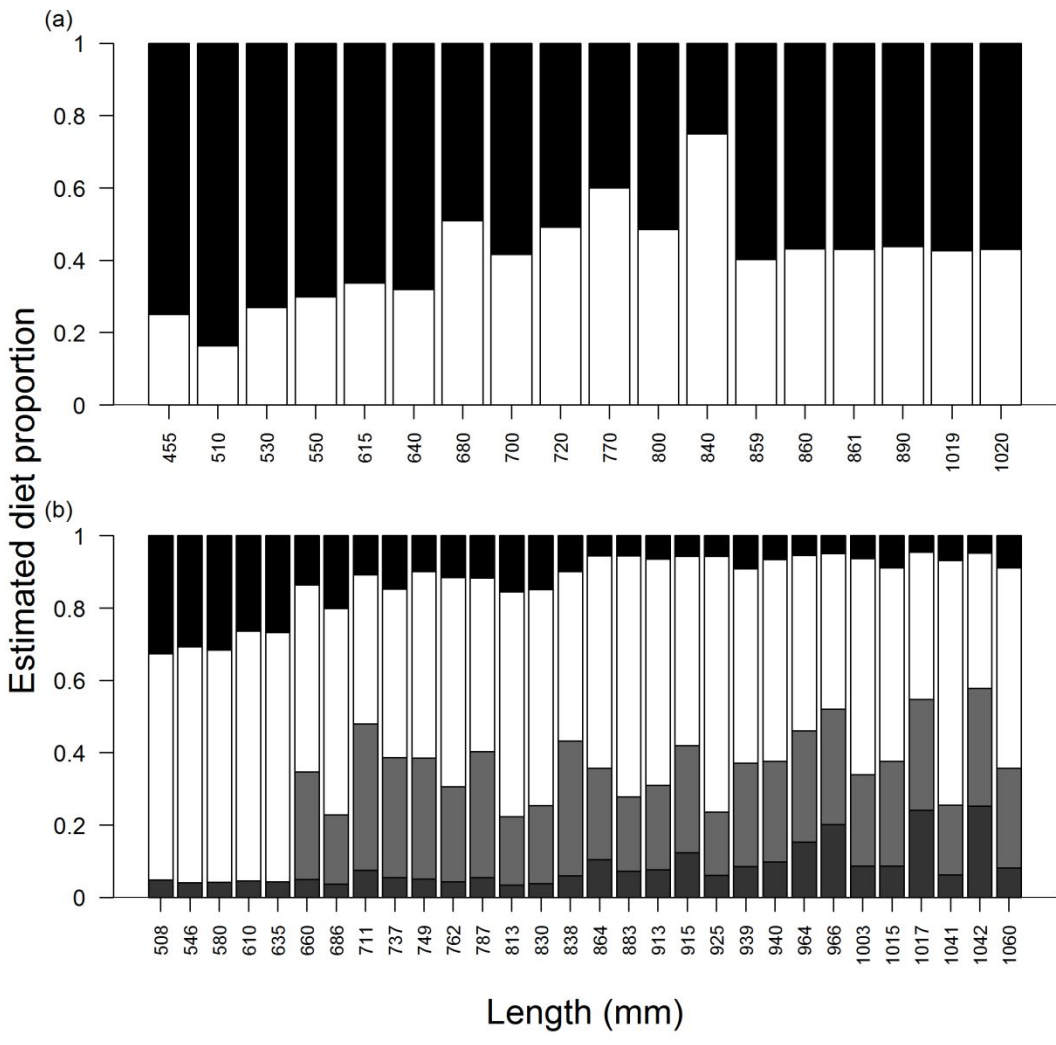


FIG. 5.

iew

Supplementary materialTable 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)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
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

3	31/10/2015	Downstream Severn	1016	9072	15.03	-20.62
4	31/10/2015	Downstream Severn	1041.4	9724	16.2	-16.34
5	05/11/2015	Downstream Severn	1041	12105	16.36	-22.49
6	13/11/2015	Downstream Severn	580	2070	15.75	-24.54
7	23/01/2016	Downstream Severn	965	7541	16.35	-18.24
8	22/02/2016	Downstream Severn	762	3742	16.86	-21.75
9	01/03/2016	Downstream Severn	1016	9525	16.6	-16.49
10	02/03/2016	Downstream Severn	749	3515	16.92	-20.63
11	17/03/2016	Downstream Severn	883	6861	16.85	-21.52
12	13/11/2016	Downstream Severn	1003	8391.5	16.28	-20.72
13	31/08/2014	Upstream Severn	774	3160	15.61	-23.28
14	16/09/2014	Upstream Severn	480	880	14.63	-24.73
15	29/11/2014	Upstream Severn	420	460	15.41	-24.23
16	29/11/2014	Upstream Severn	880	5750	17.07	-23.49
17	29/11/2014	Upstream Severn	901	4280	15.99	-22.93
18	03/12/2014	Upstream Severn	660	3650	16.24	-23.8
19	20/12/2014	Upstream Severn	890	3680	16.24	-23.31
20	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 $\delta^{13}\text{C}$ (‰) ± SD	Mean $\delta^{15}\text{N}$ (‰) ± SD	ANOVA
L. W. Avon	2015	13	-25.32 ± 0.17	18.95 ± 0.29	$\delta^{13}\text{C}$ (‰) $F_{(2,16)} = 0.49$, $P = 0.61$
	2016	3	-24.97 ± 1.97	18.11 ± 1.56	$\delta^{15}\text{N}$ (‰) $F_{(2,16)} = 0.64$, $P = 0.54$
	2017	3	-26.07 ± 0.79	19.23 ± 0.02	
Downstream Severn	2014	4	-21.58 ± 0.64	16.26 ± 0.31	$\delta^{13}\text{C}$ (‰) $F_{(2,27)} = 1.28$, $P = 0.29$
	2015	20	-21.53 ± 0.54	15.91 ± 0.12	$\delta^{15}\text{N}$ (‰) $F_{(2,27)} = 4.81$, $P = 0.02^*$
	2016	6	-19.89 ± 0.85	16.64 ± 0.11	
Upstream Severn	2014	7	-23.68 ± 0.23	15.88 ± 0.29	$\delta^{13}\text{C}$ (‰) $F_{(1,6)} = 0.95$, $P = 0.37$
	2015	1	-24.33	15.14	$\delta^{15}\text{N}$ (‰) $F_{(1,6)} = 0.82$, $P = 0.40$

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. barbuis* were highly similar and so they were combined as a single prey resource in mixing models ('Cypriniforms'). However, in their combined data, $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ data: (1) -19.37 to -22.9 ‰; where diets comprised of a relatively high proportion of MDN ('Cypriniform marine'; mixing model: mean \pm SE = 0.50 \pm 0.17; Table S3); and (2) -23.04 to -27.04 ‰; where diets were relatively low in MDN ('Cypriniform-freshwater'; mean \pm SE = 0.25 \pm 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. barbuis* 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	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Length (mm)	MDN (%)	Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Length (mm)	MDN (%)
<i>B. barbuis</i>	-27.04	12.82	510	0.089	<i>B. barbuis</i>	-22.89	12.37	740	0.359
<i>B. barbuis</i>	-26.5	14.88	397	0.11	<i>B. barbuis</i>	-22.81	12.24	690	0.396
<i>B. barbuis</i>	-26.09	14.42	364	0.151	<i>B. barbuis</i>	-22.74	11.47	520	0.514
<i>B. barbuis</i>	-26.03	14.65	660	0.094	<i>B. barbuis</i>	-22.43	12.71	680	0.411
<i>B. barbuis</i>	-25.66	13.54	520	0.375	<i>B. barbuis</i>	-22.27	11.89	529	0.285
<i>B. barbuis</i>	-25.65	13.38	800	0.148	<i>B. barbuis</i>	-22.04	12	520	0.583
<i>B. barbuis</i>	-25.49	13.89	401	0.169	<i>B. barbuis</i>	-21.98	12.35	670	0.457
<i>B. barbuis</i>	-25.41	12.67	580	0.185	<i>B. barbuis</i>	-21.91	11.65	591	0.607
<i>B. barbuis</i>	-25.11	12.81	660	0.231	<i>B. barbuis</i>	-21.5	11.61	520	0.1
<i>B. barbuis</i>	-25.04	13.34	580	0.212	<i>B. barbuis</i>	-21.4	11.67	630	0.582
<i>B. barbuis</i>	-24.85	12.4	770	0.275	<i>B. barbuis</i>	-21.02	11.61	565	0.584
<i>B. barbuis</i>	-24.66	13.03	750	0.215	<i>B. barbuis</i>	-20.88	11.03	557	0.614

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46

<i>B. barbuis</i>	-24.46	13.14	620	0.241	<i>B. barbuis</i>	-20.55	11.88	800	0.535
<i>B. barbuis</i>	-24.31	11.56	530	0.177	<i>B. barbuis</i>	-20.29	10.75	800	0.671
<i>B. barbuis</i>	-24.1	12.24	630	0.328	<i>B. barbuis</i>	-20.1	11.51	602	0.835
<i>B. barbuis</i>	-24	13.22	593	0.335	<i>B. barbuis</i>	-19.37	10.48	790	0.776
<i>B. barbuis</i>	-23.81	12.76	480	0.226	<i>B. barbuis</i>	-22.36	13.01	450	0.339
<i>B. barbuis</i>	-23.37	11.89	698	0.371	<i>S. cephalus</i>	-22.09	11.92	400	0.422
<i>B. barbuis</i>	-23.25	11.81	545	0.329	<i>S. cephalus</i>	-20.8	12.12	540	0.378
<i>S. cephalus</i>	-24.74	10.3	104	0.463	<i>S. cephalus</i>	-19.82	10.66	510	0.655
<i>S. cephalus</i>	-23.6	11.75	300	0.333					
<i>S. cephalus</i>	-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