

Durham Research Online

Deposited in DRO:

01 April 2016

Version of attached file:

Accepted Version

Peer-review status of attached file:

Peer-reviewed

Citation for published item:

Bolland, J.D. and Nunn, A.D. and Lucas, M.C. and Cowx, I.G. (2015) 'The habitat use of young-of-the-year fishes during and after floods of varying timing and magnitude in a constrained lowland river.', *Ecological engineering.*, 75 . pp. 434-440.

Further information on publisher's website:

<http://dx.doi.org/10.1016/j.ecoleng.2014.12.009>

Publisher's copyright statement:

© 2014 This manuscript version is made available under the CC-BY-NC-ND 4.0 license
<http://creativecommons.org/licenses/by-nc-nd/4.0/>

Additional information:

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in DRO
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full DRO policy](#) for further details.

1 The habitat use of young-of-the-year fishes during and after floods of varying
2 timing and magnitude in a constrained lowland river

3
4 **Version accepted for publication by Ecological Engineering**

5
6 J.D. Bolland^{a,b*}, A.D. Nunn^a, M.C. Lucas^b and I.G. Cowx^a

7 ^a *University of Hull International Fisheries Institute, Cottingham Road, Hull, HU6 7RX, UK*

8 ^b *School of Biological and Biomedical Sciences, Durham University, Durham, DH1 3LE, UK*

9
10 * Correspondence to: J.D. Bolland, University of Hull International Fisheries Institute,
11 Cottingham Road, Hull. HU6 7RX. Tel: +44(0)1482 466435. Fax: +44 (0)1482 470129. E-mail:

12 J.Bolland@hull.ac.uk

23 The habitat use of young-of-the-year fishes during and after floods of varying
24 timing and magnitude in a constrained lowland river

25

26 ABSTRACT

27

28 Globally, channelisation and artificial levee construction have reduced rivers to single-thread
29 channels isolated from their floodplains. These modifications may be particularly detrimental to
30 fish during floods, because of increased severity of conditions in the main river channel,
31 prevention of fish finding refuge in floodplain habitats, and stranding of fish when floodwaters
32 recede after artificial levees are ‘over-topped’. Notwithstanding, few studies have examined the
33 habitat use by young-of-the-year (YoY; age 0+ year) fish in constrained lowland rivers during
34 floods in slackwaters (main channel with little or no discernible current) and after floods on
35 floodplains. This study investigated the community structure and density of 0+ fish species
36 before (main river), during and after floods of varying timing and magnitude in the River
37 Yorkshire Ouse, a constrained lowland river in north-east England. Slackwaters provided refuge
38 for high densities of mainly eurytopic 0+ fishes during floods and high densities of 0+ fishes
39 were found stranded on floodplains after floods. Community composition in slackwaters during
40 floods and on floodplains after floods was significantly different to the main river catches during
41 average daily flows, possibly related to species-specific morphology and behavioral responses to
42 elevated flow. Despite there being floods of greater magnitude during the winter, peak densities
43 of 0+ fish stranded on floodplains occurred in the summer, and probably related to habitat use
44 immediately prior to floods. Fish were also found stranded on floodplains actively managed to
45 store floodwater to protect property and are presumed to permit safe egress for fish. The results

46 are discussed in relation to lowland river rehabilitation, which is particularly important because
47 of potential conflicts between obligations under various European directives to improve the
48 status of fish populations in degraded rivers (Water Framework Directive) whilst at the same
49 time minimise flooding of societal assets (Flood Directive).

50

51 *Key words:* Backwater; disturbance; flood timing; lateral connectivity; mortality; river-
52 floodplain ecosystem.

53

54 **1. Introduction**

55

56 Natural lowland river-floodplain ecosystems have a complex gradient of aquatic and riparian
57 habitats that collectively contribute high structural diversity (Welcomme, 1979; Junk *et al.*,
58 1989). In addition, natural rivers are characterised by high hydrological connectivity during
59 floods that cause lateral expansion of the main river channel onto the floodplain (Welcomme,
60 1979), connecting various landscape patches and determining the availability of previously
61 isolated habitats to fish. Specifically, river-floodplain connectivity allows fish to disperse freely
62 and take advantage of different floodplain habitats for refuge, spawning, nursery and feeding.
63 Thus, lateral connections are essential for the functioning and integrity of natural floodplain
64 ecosystems (Amoros and Bornette, 2002).

65 To prevent damage to property caused by flooding many rivers have been subjected to
66 channelisation and artificial levee construction reducing them to single-thread channels and
67 isolating them from their floodplains (Ward and Stanford, 1995; Cowx and Welcomme, 1998).
68 Reduced floodplain habitat has been reported to affect fish species that are adapted to use

69 periodically-inundated floodplains as spawning and nursery habitats (Kwak, 1988; Lucas and
70 Baras, 2001; Grift *et al.*, 2003). Such modifications can also have adverse consequences for
71 fishes during floods and high flow events because of increased severity of conditions (e.g.
72 increased water velocity and bedload transport) in the main channel (Lusk *et al.*, 1998; Poff *et*
73 *al.*, 2006), prevention of fish finding floodplain habitats for refuge (Ross and Baker, 1983;
74 Kwak, 1988), and the stranding of fish when floodwaters recede after artificial levees are ‘over-
75 topped’. This is of particular importance to young-of-the-year (YoY; age 0+) fish because of
76 their poor swimming capabilities (Harvey, 1987; Mann and Bass, 1997). Although river
77 discharge and the timing of floods are increasingly being recognised as an important cause of
78 inter-annual variability in the recruitment success of cyprinid fishes (Nunn *et al.*, 2007), the
79 influence of floods on 0+ fish habitat use during and after floods in modified lowland rivers is
80 poorly known. In addition, flood frequency and magnitude are predicted to increase under the
81 influence of climate change (Kundzewicz, 2007) and interact with existing riverine alterations
82 and further impact ecosystem functioning (Peterson and Kwak, 1999; Gibson *et al.*, 2005).

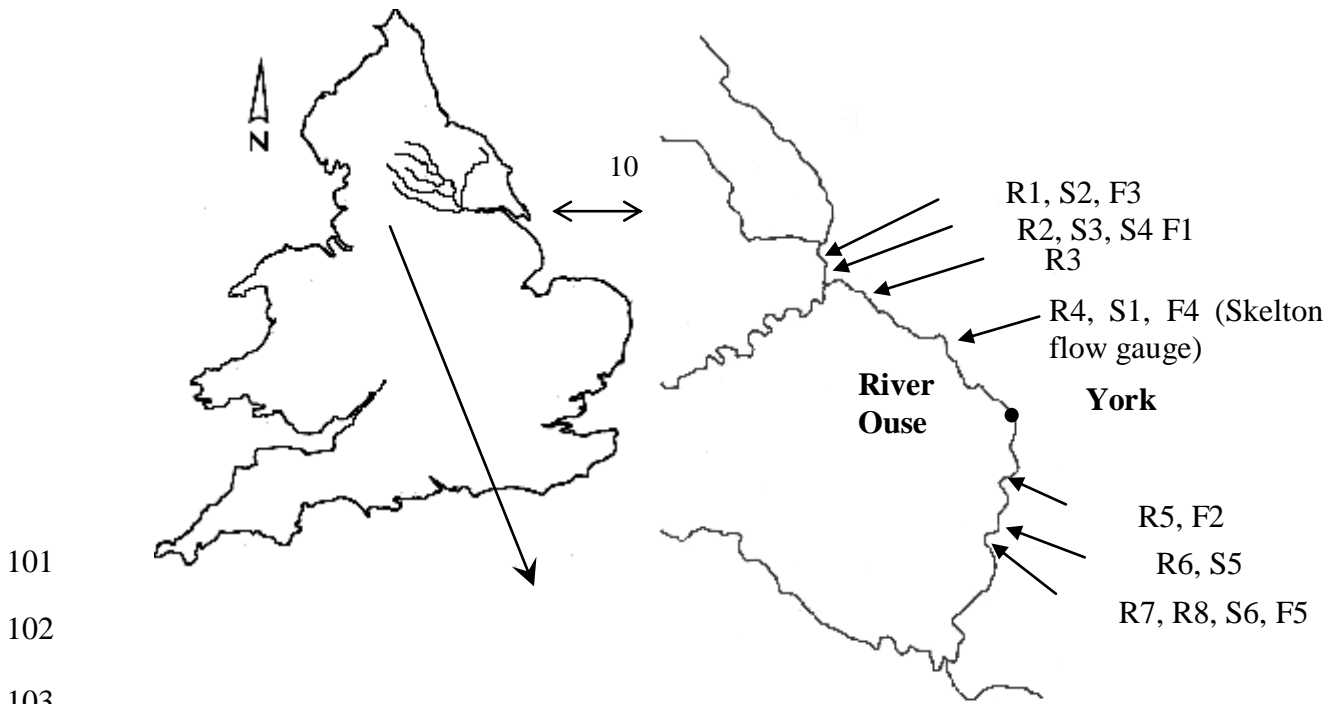
83 The aim of this study was to determine the habitat use of 0+ fishes during (slackwaters; main
84 channel with little or no discernible current, Humphries *et al.*, 2006) and after (floodplains
85 isolated from the main river) floods of varying timing and magnitude in a constrained lowland
86 river, the River Yorkshire Ouse, in north-east England. Specifically, the objectives were to: (1)
87 compare fish community structure in slackwaters during floods with that in the main river during
88 average flows; (2) evaluate the community structure of fish stranded on floodplains isolated from
89 the main river by artificial levees after floods; and (3) assess the propensity for fish stranding on
90 floodplains with differing floodwater ingress and egress routes.

91

92 **2. Study area**

93

94 The Yorkshire Ouse (Figure 1) is one of the UK's largest single-thread rivers and has been
95 isolated from its floodplain by channelisation and levee construction. The river drains 10 000
96 km² of predominantly rural catchment, has an average width of 50 m and a depth of 3-4 m; water
97 quality is generally good (Neal and Robson, 2000). Precipitation run-off from the Pennines often
98 results in elevated river levels and out-of-bank floods, such as those which occurred in August,
99 October and December 2004, October 2005, March and December 2006, and January 2007
100 (Figure 2).

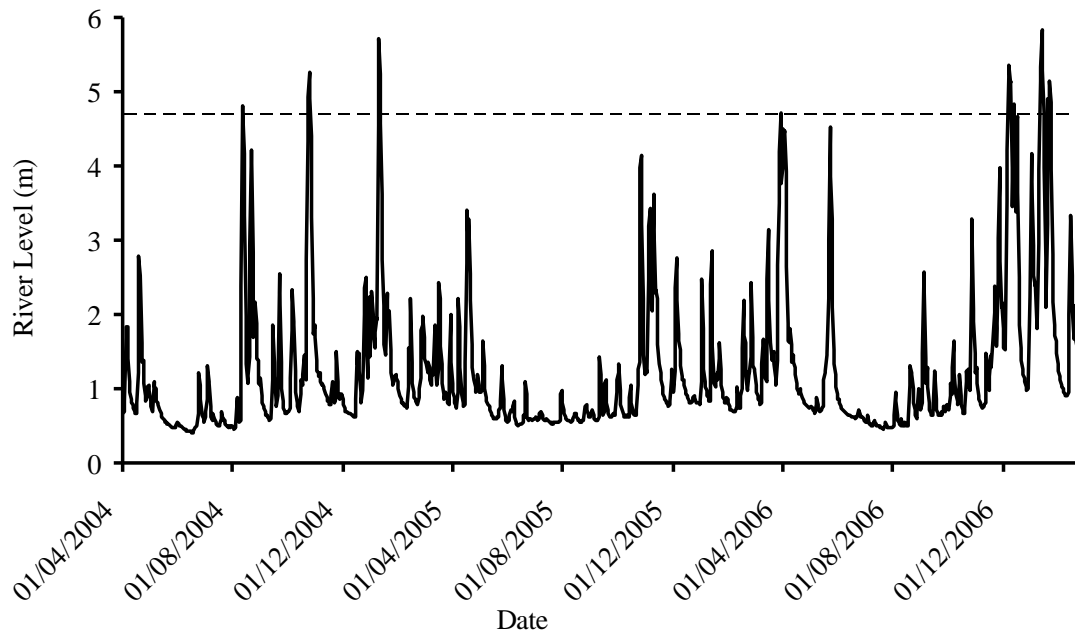


101

102

103

104 Figure 1. A map of England showing the location of the Ouse catchment, and a more
105 detailed catchment map showing river, slackwater and floodplain sampling sites, and Skelton
106 flow gauge. Site codes are as in Table I.



107

108 Figure 2. Mean daily river level (m) in the Yorkshire Ouse at Skelton from April 2004 to
 109 February 2007. River level when 'out-of-bank' floods occur (---).

110

111 3. Materials and methods

112

113 3.1. 0+ fish surveys

114 Sampling occurred at eight river sites (during average daily flows), six slackwater sites
 115 (during elevated flows) and five floodplain sites (after floods) (Table I). The river sites were in
 116 the margins of the main channel in areas devoid of large woody debris, in water ≤ 1.5 m deep,
 117 where water velocity was slow and where 0+ fishes tend to aggregate. 0+ fish aggregations were
 118 surveyed at river sites from April 2004 to February 2007 (fortnightly during May to July and
 119 monthly during August to April), inclusive, in daylight hours. The slackwater areas sampled only
 120 existed during elevated river levels and floods, and consisted of plateaus between the main river
 121 channel and levees (S1, S2 and S3), a 'backed-up' tributary (S4), a slipway between two

122 buildings (S5) and a bay downstream of some large marginal willows (*Salix* spp.) (S6).
123 Floodplains were sampled after flood events as soon as areas of water became isolated from the
124 main river channel. Four of the floodplain sites flooded because levees overtopped. Two of these
125 (F1 and F2) drained through underground pipes, one (F3) drained via a ‘flap-gated’ ditch but left
126 a substantial area of water isolated from the main river, and one (F4) emptied through a sluice
127 with any residual water extracted by pumping. The fifth floodplain site (F5) was flooded by a
128 manually operated sluice (upstream end) and was drained through a sluice (downstream end)
129 after river levels receded; any residual water was extracted by pumping.

130 All samples were collected using a micromesh seine net (25-m long by 3-m deep, 3-mm
131 hexagonal mesh) set in a rectangle parallel to the bank by wading or pulled between two people
132 stood at the upstream and downstream end of where the net was set using a rope when it was too
133 deep to wade along the river. All sites sampled, except a small area of S4, were shallower than
134 the depth of the seine net (Table I) and thus sampling efficiency was assumed to be comparable.
135 The seine net captured larvae as small as 5 mm, although its efficiency was reduced for fish
136 smaller than ~15 mm (Cowx *et al.*, 2001). Captured fish were identified to species (Pinder,
137 2001), separated into six larval (L1-L6) and one 0+ juvenile (J) developmental step (Copp, 1990;
138 Peñáz, 2001), and measured for standard length (SL, nearest mm). 0+ fishes were aged by
139 analysis of length-frequency distributions or by scale reading (Bagenal & Tesch, 1978).

140

141 Table I. Details of sites surveyed for 0+ fishes in the Yorkshire Ouse river (R), slackwaters (S) and floodplains (F), including
 142 substratum and number of times sampled (*n*).

Site name	Habitat	Code	Dimensions	Substrate	<i>n</i>
Linton	Main river	R1	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Sand/clay	31
Newton	Main river	R2	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Sand/clay	19
Beningbrough	Main river	R3	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Sand/clay	28
Clifton	Main river	R4	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Sand/clay	19
Fulford	Main river	R5	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Mud/silt	30
Naburn	Main river	R6	River width 50 m, max. depth 3-4 m, sampling depth 1.5 m	Sand/clay	19
Acaster Malbis	Main river	R7	River width 50 m, max. depth 3-4 m, sampling depth 1.5 m	Concrete	31
Naburn weir	Main river	R8	River width 70 m, max. depth 3-4 m, sampling depth 1.5 m	Sand/clay	19
Clifton	Slackwater	S1	River width 100 m, max. depth 9-10 m, sampling depth 2 m	Grass	8
Linton carpark	Slackwater	S2	River width 150 m, max. depth 10-12 m, sampling depth 1 m	Concrete	3
Newton	Slackwater	S3	River width 100 m, max. depth 9-10 m, sampling depth 1 m	Grass	3
River Kyle	Slackwater	S4	River width 30 m, max. depth 9-10 m, sampling depth up to 10 m	Grass	2
Naburn	Slackwater	S5	River width 100 m, max. depth 9-10 m, sampling depth 1 m	Concrete	3
Naburn weir	Slackwater	S6	River width 100 m, max. depth 10-12 m, sampling depth 2-3 m	Grass	2
Newton Ings	Floodplain	F1	Ings surface area 3 ha, drained down sampling area 0.5 ha, depth 0.5 m	Grass	6
Nun Ings	Floodplain	F2	Ings surface area 1 ha, drained down sampling area 0.15 ha, depth 0.5 m	Grass	5
South Ings	Floodplain	F3	Ings surface area 25 ha, drained down sampling area 0.5 ha, depth 0.5 m	Grass	1
Linton Ings	Floodplain	F4	Ings surface area 20 ha, drained down sampling area 0.2 ha, depth 0.5 m	Grass	2
Rawcliffe Ings	Floodplain	F5	Ings surface area 20 ha, drained down sampling area 0.3 ha, depth 0.5 m	Grass	4

143 3.2. *Data analysis*

144 At each site, the frequency of occurrence and relative abundance of each fish species
145 was calculated from all surveys (Hynes, 1950), and the Shannon-Wiener diversity index
146 (H'), Margalef's species richness index (d) (Washington, 1984) and the relative density
147 (fish m^{-2}) of 0+ fishes (all species combined) was calculated for each sampling occasion.
148 Frequency of occurrence of a given species was defined as the number of surveys in which
149 the species occurred, expressed as a percentage of the total number of surveys carried out.
150 Relative abundance of a species was defined as the percentage of total catches (numbers) in
151 all surveys contributed by the given species.

152 Mann-Whitney U -tests were used to test the null hypothesis that the mean H' and d of
153 0+ fishes for all surveys at each site did not differ significantly between the river and
154 slackwater / floodplain sampling units. Non-parametric Multi Dimensional Scaling (MDS,
155 Clarke and Warwick, 2001), based on Bray-Curtis similarity (Bray and Curtis, 1957) of
156 mean percentages of each 0+ fish species was carried out to investigate similarity in 0+ fish
157 species composition between sites. One-way, *a priori* Analysis of Similarities (ANOSIM,
158 Clarke and Warwick, 1994) was used to test the null hypothesis that there was no
159 significant difference in 0+ fish species composition between main river (R), slackwater (S)
160 and floodplain (F). SIMPER (Similarity Percentages – species contributions, Clarke and
161 Warwick, 1994) analysis was used to calculate the percentage contribution of each key
162 species to the overall dissimilarity of 0+ fish communities caught in the main river to those
163 in slackwaters and on floodplains.

164 All statistical analyses were performed with SPSS version 16. Multivariate analysis
165 were carried out using PRIMER (Plymouth Routines In Multivariate Ecological Research)
166 (version 6.1).

167

168 **4. Results**

169

170 *4.1. Fishes caught in slackwaters*

171 During elevated flow and flood events, high densities of 0+ fishes congregated in
172 slackwaters (S1-S6; total >25 000 individuals, mean = 30 ± 43 fish m⁻²). At the site level,
173 the maximum density of 0+ fishes in slackwaters during specific floods was 147 fish m⁻² at
174 S5 (January 2007), followed by 104 fish m⁻² at S4 (December 2006) and 38 fish m⁻² at S2
175 (August 2004).

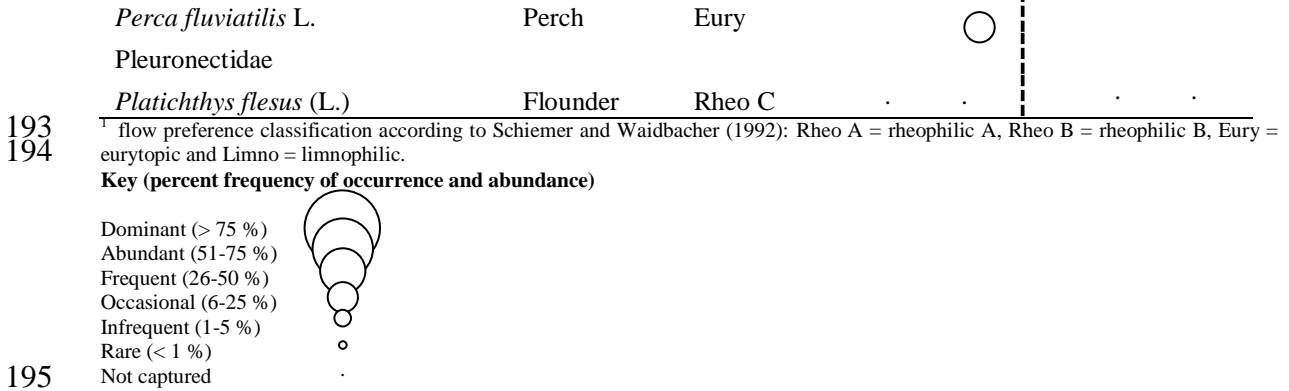
176 The community composition of the main river was significantly different to
177 slackwaters (ANOSIM: $r = 0.43$, $p = 0.004$; Figure 3) and median H' was significantly
178 lower in slackwaters (Mann-Whitney U -test: $Z = -2.160$, $n = 13$, $P = 0.031$), but not median
179 richness (Mann-Whitney U -test: $Z = -0.154$, $n = 13$, $P = 0.877$). The main river catches
180 were dominated (relative abundance) by eurytopic and rheophilic species (all samples from
181 R1-R8; roach = 36%, gudgeon = 22%, chub = 18% and bleak = 14%; Table II and III).
182 Catches from slackwaters were dominated by eurytopic species (bleak = 53% and roach =
183 29%), with rheophilic species less prevalent (chub = 10%; Table II and III). Community
184 dissimilarity between the main river and slackwaters was 49%, mainly caused by the shift
185 in the dominant species to bleak and lack of gudgeon in slackwaters (Table III), i.e. the

186 relative abundance of bleak was highest in slackwaters, whereas gudgeon, roach, chub and
 187 dace were most abundant in the main river.

188

189 Table II. Frequency of occurrence (percentage of surveys in which the species
 190 occurred) and relative abundance (percentage of total catches (numbers) in all surveys) (see
 191 key) of 0+ fish captured from the Yorkshire Ouse river (R), slackwater (S) and floodplain
 192 (F) from April 2004 to February 2007, including their flow preference classification¹.

Family <i>Species</i>	Vernacular name	Flow pref. ¹	Occurrence			Abundance		
			R	S	F	R	S	F
Cyprinidae								
<i>Abramis bjoerkna</i> (L.)	Silver bream	Eury	○	.	.	○	.	.
<i>Abramis brama</i> (L.)	Bream	Eury	○	○	○	○	○	○
<i>Alburnus alburnus</i> (L.)	Bleak	Eury	○	○	○	○	○	○
<i>Barbus barbus</i> (L.)	Barbel	Rheo A	○	○	.	○	○	.
<i>Gobio gobio</i> (L.)	Gudgeon	Rheo B	○	○	○	○	○	○
<i>Leuciscus cephalus</i> (L.)	Chub	Rheo A	○	○	○	○	○	○
<i>Leuciscus leuciscus</i> (L.)	Dace	Rheo A	○	○	○	○	○	○
<i>Phoxinus phoxinus</i> (L.)	Minnow	Rheo A	○	○	○	○	○	○
<i>Rutilus rutilus</i> (L.)	Roach	Eury	○	○	○	○	○	○
<i>Scardinius erythrophthalmus</i> (L.)	Rudd	Limno	.	○	.	.	○	.
Balitoridae								
<i>Barbatula barbatula</i> (L.)	Stone loach	Rheo A	○	○	.	○	○	.
Esocidae								
<i>Esox lucius</i> L.	Pike	Eury	○	○	○	○	○	○
Thymallidae								
<i>Thymallus thymallus</i> (L.)	Grayling	Rheo A	○	.	.	○	.	.
Gasterosteidae								
<i>Gasterosteus aculeatus</i> L.	Three-spined stickleback	Eury	○	○	○	○	○	○
<i>Pungitius pungitius</i> (L.)	Ten-spined stickleback	Limno	○	.	○	○	.	○
Cottidae								
<i>Cottus gobio</i> L.	Bullhead	Rheo A	○	.	.	○	.	.
Percidae								
<i>Gymnocephalus cernuus</i> (L.)	Ruffe	Eury	○	○	○	○	○	○
			○	○		○	○	○
			○			○		



197 Table III. Similarity percentages (SIMPER) analysis of the mean relative abundances

198 of key fish species and their contributions (%) to dissimilarities in main river and

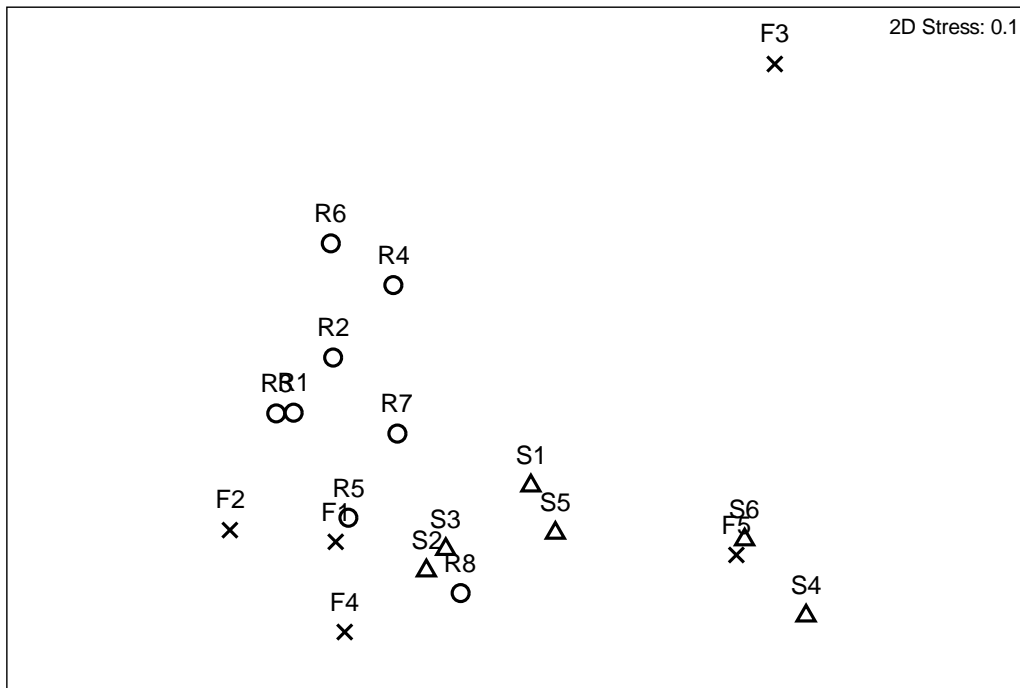
199 slackwater 0+ fish community composition. Minor species (<5% cumulative dissimilarity)

200 were excluded from the table.

Species	Mean relative abundance (%)		Cumulative dissimilarity (%)
	Main river	Slackwater	
Bleak	14	53	39
Gudgeon	22	4	58
Roach	36	29	77
Chub	18	10	89
Dace	6	1	94

201

202



203

204 Figure 3. MDS plot (centroids) comparing 0+ fish communities from Yorkshire Ouse
 205 river (○), slackwater (△) and floodplain (×). Site codes are the same as in Table I.

206

207 *4.2. Fishes caught on floodplains*

208 The community composition of 0+ fishes captured on floodplains was significantly
 209 different to the main river (ANOSIM: $r = 0.37$, $p = 0.009$; Figure 3) and the median H' and
 210 d were significantly lower on floodplains than in the main river (Mann Whitney U -test: H' :
 211 $Z = -2.623$, $n = 13$, $P = 0.009$; d : $Z = -2.006$, $n = 13$, $P = 0.045$). Roach, bleak and chub
 212 occurred most frequently on floodplains after floods and also dominated catches (roach =
 213 34%, bleak = 24% and chub = 22%; Table II and IV). Community dissimilarity between the
 214 main river and floodplains was 54%, which was caused by variability in roach abundance
 215 between floodplains, and a decline in gudgeon abundance and an increase in bleak
 216 abundance on floodplains compared with the main river (Table IV).

217

218 Table IV. Similarity percentages (SIMPER) analysis of the mean relative abundances
219 of key fish species and their contributions (%) to dissimilarities in main river and
220 floodplain 0+ fish community composition. Minor species (<5% cumulative dissimilarity)
221 were excluded from the table.

Species	Mean relative abundance (%)		Cumulative dissimilarity (%)
	Main river	Floodplain	
Roach	36	34	21
Gudgeon	22	0	41
Bleak	14	24	59
Chub	18	22	74
Three-spined stickleback	0	14	87
Dace	6	0	93

222

223 More than 20 000 fishes were captured at floodplain sites and substantial temporal
224 variations in fish densities were observed. During the August 2004 flood, mean densities of
225 8 and 11 fish m⁻² were recorded at F1 and F2, respectively. Extrapolating those densities for
226 the area of floodwater during sampling (F1 = 2.0 ha and F2 = 0.4 ha) equates to
227 approximately 16 000 and 4400 stranded fish, respectively. Although there were floods of
228 greater magnitude during the winter months (October 2004, January 2005, December 2006
229 and January 2007; Figure 2), densities of fishes stranded on floodplains (F1 and F2) were
230 significantly lower than during the August 2004 flood (Mann-Whitney *U*-test: F1 (1 fish m⁻²
231 ²): $Z = -2.518$, $n = 12$, $P = 0.012$; F2 (<1 fish m⁻²): $Z = -2.334$, $n = 9$, $P = 0.020$). The large
232 numbers of 0+ fish stranded at F1 and F2 after the August 2004 flood was possibly related
233 to habitat use of fish prior to the flood. Indeed, the density of fish in the margins of the
234 main channel prior to floods during winter months (October 2004, January 2005, December

235 2006 and January 2007; Figure 2) were significantly lower than prior to the August 2004
236 flood (Mann-Whitney U -test: $Z = -1.980$, $n = 27$, $P = 0.048$).

237 Floodwater at F1 and F2 returned to the main river through underground pipes,
238 therefore all stranded fish inevitably died. The three other floodplains (F3, F4 and F5) are
239 managed to return a large majority of floodwater to the main river after the flood pulse has
240 receded, and are presumed to permit safe egress for fish. Despite this, stranded fish were
241 captured at F3 (1 fish m^{-2}) and F4 (8 fish m^{-2}) after the floods in March 2006 and August
242 2004, respectively. F5, unlike all other floodplain sites surveyed, was flooded by a
243 manually operated sluice (upstream end), and fish were probably “washed-in”, reflected by
244 a density of 10 fish m^{-2} after a high flow event in October 2005.

245

246 **5. Discussion**

247

248 Individual fish species have variable resilience to floods based on differences in life
249 history strategies, behaviour during floods and body morphology. In rivers with an
250 aseasonal flood pulse (seemingly independent of season, i.e. the UK; Winemiller, 2004),
251 riverine fish species have evolved life-history strategies to survive floods based upon
252 seasonal timing and predictability (Poff and Allan, 1995), i.e. spawning is timed so that
253 hatching coincides with low flood probability (‘low flow recruitment hypothesis’ *sensu*
254 Humphries *et al.*, 1999). Therefore, atypical summer floods that coincide with larval and
255 juvenile life stages of fish are more likely to cause displacement and mortality because of
256 their poor swimming capabilities (Harvey, 1987; Mann and Bass, 1997; Nunn *et al.*, 2007).
257 Behavioural adaptations enable fish to respond directly to individual high flow and flood

258 events by dispersing into slackwaters (Humphries *et al.*, 2006) and onto floodplains (Grift
259 *et al.*, 2003; Schwartz and Herricks, 2005) to avoid mortality, physical damage or
260 displacement. The problem of flushing and mortality associated with summer flood events
261 is potentially exacerbated in industrialised nations, because construction of artificial levees
262 has reduced rivers to single-thread channels and impeded lateral connectivity with
263 floodplains. Unfortunately, the resilience of 0+ fishes to floods of irregular timing in
264 heavily-modified lowland rivers are largely unknown.

265 During all the floods surveyed, areas of slackwater provided refuge for high densities of
266 0+ fishes. Pearsons *et al.* (1992) reported that fish populations were more stable in
267 physically complex habitats because of the increased availability of flow refugia. 0+ fish
268 community structure differed between the main river at low flow and in slackwaters during
269 floods. Specifically, the proportion of bleak in slackwaters increased and the proportion of
270 gudgeon decreased, probably related to species-specific morphological and behavioral
271 responses to elevated flow (Tew *et al.*, 2002). Bleak are a slender, eurytopic fish that
272 probably lack the physiological ability to maintain station in the main channel (Clough *et*
273 *al.*, 2004), although this was not empirically investigated. Gudgeon are benthic-dwelling
274 rheophilic species that probably use hydrodynamic properties of the body and interstitial
275 spaces of the river bed as refuge.

276 After floods, 0+ fishes were found stranded on floodplains isolated from the main river
277 after artificial levees were ‘over-topped’. Flood timing was a critical driver of lateral
278 displacement of 0+ fishes, as a significantly higher number of fish were found stranded
279 after the flood in August 2004 than after winter floods of greater magnitude. King *et al.*
280 (2003) similarly documented stranding of larval and juvenile cyprinids after a summer

281 flood. While YoY fish abundance is obviously higher in summer months compared to the
282 winter, habitat use of 0+ fish prior to summer floods in the current study probably elevated
283 their susceptibility to lateral displacement as the flood water dispersed over levees onto the
284 floodplain. Indeed, juvenile fish select marginal habitat during summer, probably in relation
285 to optimal temperature, feeding and predator avoidance (Garner, 1997a, b; Baras and
286 Nindaba, 1999a, b).

287 Fish were also found stranded in managed floodplains, i.e. ‘over-topped’ levees that
288 drain through flap gates, and sluice-filled and -drained water storage areas that are pumped
289 dry after floods recede. Although densities of 10 fish m⁻² were found stranded in these
290 areas, the majority probably successfully returned to the main river through flap gates and
291 sluices. Halls *et al.* (2008) documented that sluice gates permitted lateral migrations of fish
292 in Bangladesh. Consequently, future floodplain rehabilitation or floodwater management
293 structures should be sympathetically designed for fish by allowing all water to drain back
294 into the river, thus removing the potential for fish mortality from stranding. Furthermore,
295 water, and thus fish, should be quickly returned to the main river to reduce potential
296 predation by piscivorous and scavenging birds, and mortality from low dissolved oxygen
297 and high levels of tannins (Lusk *et al.*, 1998; Fontenot *et al.*, 2001; Henning *et al.*, 2007).

298 Cowx and Gerdeaux (2004) emphasised the need to recreate functional habitats for
299 spawning, feeding, nursery (growth) and resting (self protection) areas, and the connectivity
300 between these habitats, i.e. improving the ecological functioning of the river system
301 (Schiemer *et al.*, 1999). This study identified that slackwaters provided refuge for high
302 densities of 0+ fishes and substantial numbers of 0+ fishes were stranded behind artificial
303 levees, thus providing empirical evidence for the need to recreate riverine habitat diversity

304 and channel morphology and reinstate lowland river lateral connectivity (Cox and
305 Welcomme 1998). It is also important to recognize that floodplain rehabilitation increase
306 system biodiversity, provides spawning and nursery areas for juvenile fish and benefit
307 society from the natural functional attributes of river landscapes for flood protection (Poff,
308 2002; Tockner and Stanford, 2002; Brenner *et al.*, 2003). Therefore, floodplain
309 rehabilitation can improve the ecological status of rivers, as is required in Europe under the
310 European Union, Water Framework Directive (2000/60/EEC) whilst at the same time
311 enabling societal obligations for flood mitigation under the EU Floods Directive
312 (2007/60/EC) to be met.

313

314 **Acknowledgements**

315

316 The authors would like to thank Dr Jonathan Harvey, Dr Richard Noble, Darren Rollins
317 and Ryan Taylor for their assistance in data collection, and Barry Byatt, Michael Lee and
318 other Environment Agency staff for their assistance during flood events, and knowledge of
319 the river and surrounding floodplains. Funding was provided by the Environment Agency
320 under Science Project SC030215 'Dispersal Behaviour of Coarse Fish'. We are grateful to
321 Dr Graeme Peirson for his assistance with project support and all landowners for
322 permission to access the river.

323

324 **References**

325

- 326 Amoros C, Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine
327 floodplains. *Freshwater Biology* **47**: 761-776.
- 328 Bagenal TB, Tesch FW. 1978. Age and growth. In: *Methods for the Assessment of Fish*
329 *Production in Fresh Waters*. Bagenal TB, ed. Oxford: Blackwell Scientific
330 Publications, pp. 101-136.
- 331 Baras E, Nindaba J. 1999a. Diel dynamics of habitat use by riverine young-of-the-year
332 *Barbus barbus* and *Chondrostoma nasus* (Cyprinidae). *Archiv für Hydrobiologie* **146**:
333 431-448.
- 334 Baras E, Nindaba J. 1999b. Seasonal and diel utilisation of inshore microhabitats by larvae
335 and juveniles of *Leuciscus cephalus* and *Leuciscus leuciscus*. *Environmental Biology*
336 *of Fishes* **56**: 183–197.
- 337 Bray JR, Curtis JT. 1957. An ordination of upland forest communities of southern
338 Wisconsin. *Ecological Monographs* **27**: 325-349.
- 339 Brenner T, Buijse AD, Lauff M, Luquet JF, Staub E. 2003. The Present Status of the River
340 Rhine with Special Emphasis on Fisheries Development. Pages 121-148 in
341 Welcomme R.L, Petr T., editors. Proceedings of the Second International Symposium
342 on the Management of Large Rivers for Fisheries, Volume I.
- 343 Clarke KR, Warwick RM. 1994. Change in marine communities: an approach to statistical
344 analysis and interpretation. Natural Environment Research Council, UK: p. 144.
- 345 Clarke KR, Warwick RM. 2001. Change in Marine Communities: an Approach to
346 Statistical Analysis and Interpretation. Second Edition. PRIMER-E, Plymouth.

347 Clough SC, Lee-Elliott IE, Turnpenny AWH, Holden SDJ, Hinks C. 2004. Swimming
348 speeds in fish: Phase 2. Bristol: Environment Agency, R & D Technical Report W2-
349 049/TR1.

350 Copp GH. 1990. Recognition of cohorts and growth of larval and juvenile roach *Rutilus*
351 *rutilus* (L.), using size-class ordination of developmental steps. *Journal of Fish*
352 *Biology* **36**: 803-819.

353 Cowx IG, Gerdeaux D. 2004. The effects of fisheries management practises on freshwater
354 ecosystems. *Fisheries Management and Ecology* **11**: 145-151.

355 Cowx IG, Nunn AD, Harvey JP. 2001. Quantitative sampling of 0-group fish populations in
356 large lowland rivers: point abundance sampling by electric fishing versus micromesh
357 seine netting. *Archiv für Hydrobiologie* **151**: 369-382.

358 Cowx IG, Welcomme RL (eds). 1998. Rehabilitation of Rivers for Fish. Oxford: Fishing
359 News Books, Blackwell Science, 260 pp.

360 Fontenot QC, Rutherford DA, Kelso WE. 2001. Effects of environmental hypoxia
361 associated with the annual flood pulse on the distribution of larval sunfish and shad in
362 the Atchafalaya River Basin, Louisiana. *Transactions of the American Fisheries*
363 *Society* **130**: 107–116.

364 Garner P. 1997a. Habitat use by 0+ cyprinid fish in the River Great Ouse, East Anglia.
365 *Freshwater Forum* **8**: 2-27.

366 Garner P. 1997b. Seasonal variation in the habitat available for 0+ *Rutilus rutilus* (L.) in a
367 regulated river. *Aquatic Conservation: Marine and Freshwater Ecosystems* **7**: 199-
368 210.

369 Gibson CA, Meyer JL, Poff NL, Hay LE, Georgakakos A. 2005. Flow regime alterations
370 under changing climate in two river basins: Implications for freshwater ecosystems.
371 *River Research and Applications* **21**: 849-864.

372 Grift RE, Buijse AD, Van Densen WLT, Machiels MAM, Kranenbarg J, Breteler JPK,
373 Backx JJGM. 2003. Suitable habitats for 0-group fish in rehabilitated floodplains
374 along the lower River Rhine. *River Research and Applications* **19**: 353-374.

375 Halls AS, Payne AI, Alam SS, Barman SK. 2008. Impacts of flood control schemes on
376 inland fisheries in Bangladesh: guidelines for mitigation. *Hydrobiologia* **609**: 45-58.

377 Harvey BC. 1987. Susceptibility of young-of-the-year fishes to downstream displacement
378 by flooding. *Transactions of the American Fisheries Society* **116**: 851-855.

379 Henning JA, Gresswell RE, Fleming IA. 2007. Use of seasonal freshwater wetlands by
380 fishes in a temperate river floodplain. *Journal of Fish Biology* **71**: 476-492.

381 Humphries P, Cook RA, Richardson AM, Serafini LG. 2006. Creating a disturbance:
382 manipulating slackwaters in a lowland river. *River Research and Applications* **22**:
383 525-542.

384 Humphries P, King AJ, Koehn JD. 1999. Fish, flows and flood plains: links between
385 freshwater fishes and their environment in the Murray-Darling River system,
386 Australia. *Environmental Biology of Fishes* **56**: 129-151.

387 Hynes HBN 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and
388 *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes.
389 *Journal of Animal Ecology* **19**: 36-58.

- 390 Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river–floodplain
391 systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**, 110–
392 127.
- 393 King AJ, Humphries P, Lake PS. 2003. Fish recruitment on floodplains: the roles of
394 patterns of flooding and life history characteristics. *Canadian Journal of Fisheries
395 and Aquatic Sciences* **60**: 773-786.
- 396 Kundzewicz ZW, Mata LJ, Arnell NW, Döll P, Kabat P, Jiménez B, Miller KA, Oki T, Sen Z,
397 Shiklomanov IA. 2007. *Freshwater resources and their management. Climate Change
398 2007: Impacts, Adaptation and Vulnerability*. Contribution of Working Group II to the
399 Fourth Assessment Report of the Intergovernmental Panel on Climate Change. (eds ML
400 Parry, OF Canziani, J.P. Palutikof, PJ van der Linden, CE Hanson): Cambridge
401 University Press, Cambridge, UK.
- 402 Kwak TJ 1988. Lateral movement and use of floodplain habitat by fishes of the Kankakee
403 River, Illinois. *American Midland Naturalist* **120**: 241–249.
- 404 Lucas MC, Baras E. 2001. *Migration of Freshwater Fishes*. Oxford: Blackwell Science.
- 405 Lusk S, Halacka K, Luskova V. 1998. The effect of an extreme flood on the fish
406 communities in the upper reaches of the Ticha Orlice river (the Labe drainage area).
407 *Czech Journal of Animal Science* 43: 531-536.
- 408 Mann RHK, Bass JAB. 1997. The critical water velocities of larval roach (*Rutilus rutilus*)
409 and dace (*Leuciscus leuciscus*) and implications for river management. *Regulated
410 Rivers: Research and Management* **13**: 295-301.

411 Neal C, Robson AJ. 2000. A summary of river water quality data collected within the Land-
412 Ocean Interaction Study: core data for eastern UK rivers draining to the North Sea.
413 *The Science of the Total Environment* **251/252**: 585-665.

414 Nunn AD, Harvey JP, Britton JR, Frear PA, Cowx IG. 2007. Fish, climate and the Gulf
415 Stream: the influence of abiotic factors on the recruitment success of cyprinid fishes
416 in lowland rivers. *Freshwater Biology* **52**: 1576-1586.

417 Pearsons TN, Li HW, Lamberti GA. 1992. Influence of habitat complexity on resistance to
418 flooding and resilience of stream fish assemblages. *Transactions of the American*
419 *Fisheries Society* **121**: 427–436.

420 Peñáz M. 2001. A general framework of fish ontogeny: a review of the ongoing debate.
421 *Folia Zoologica* **50**: 241-256.

422 Peterson JT, Kwak TJ. 1999. Modeling the effects of land use and climate change on
423 riverine Smallmouth Bass. *Ecological Applications* **9**: 1391–1404.

424 Pinder AC. 2001. Keys to Larval and Juvenile Stages of Coarse Fishes from Fresh Waters
425 in the British Isles. Scientific Publication No. 60, Freshwater Biological Association:
426 Ambleside.

427 Poff NL, Allan JD. 1995. Functional organization of stream fish assemblages in relation to
428 hydrological variability. *Ecology* **76**: 606–627.

429 Poff NL, Olden JD, Pepin DM, Bledsow BP. 2006. Placing global stream flow variability
430 in geographic and geomorphic contexts. *River Research and Applications* **22**: 149-
431 166.

432 Poff NL. 2002. Ecological response to and management of increased flooding due to
433 climate change. *Proceedings of the Royal Society of London (A)* **360**: 1497-1510.

- 434 Ross ST, Baker JA. 1983. The response of fishes to periodic spring floods in a Southeastern
435 Stream. *American Midland Naturalist* **109**: 1–14.
- 436 Schiemer F, Baumgartner C, Tockner K. 1999. Restoration of floodplain rivers: the Danube
437 restoration project. *Regulated Rivers: Research and Management* **15**: 231–244.
- 438 Schwartz JS, Herricks EE. 2005. Fish use of stage-specific fluvial habitats as refuge patches
439 during a flood in a low-gradient Illinois stream. *Canadian Journal of Fisheries and*
440 *Aquatic Sciences* **62**: 1540-1552.
- 441 Tew KS, Han CC, Chou WR, Fang LS. 2002. Habitat and fish fauna structure in a
442 subtropical mountain stream in Taiwan before and after a catastrophic typhoon.
443 *Environmental Biology of Fishes* **65**: 457-462.
- 444 Tockner K, Stanford JA. 2002. Riverine floodplains: present state and future trends.
445 *Environmental Conservation* **29**: 308-330.
- 446 Ward JV, Stanford JA. 1995. Ecological connectivity in alluvial river ecosystems and its
447 disruption by flow regulation. *Regulated Rivers: Research & Management* **11**: 105–
448 119.
- 449 Washington HG 1984. Diversity, biotic and similarity indices: a review with special
450 relevance to aquatic ecosystems. *Water Research* **18**: 653-694.
- 451 Welcomme RL. 1979. *Fisheries Ecology of Floodplain Rivers*. London: Longman, 325 pp.
- 452 Winemiller KO. 2004. Floodplain river food webs: generalizations and implications for
453 fisheries management. In: *Proceedings of the Second International Symposium on the*
454 *Management of Large Rivers for Fisheries Volume II*. Welcomme R, Petr T., Eds.,
455 FAO Regional Office for Asia and the Pacific, Bangkok, Thailand. RAP Publication
456 2004/17, pp. 285-309.

