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

J.D. Bolland[a,b*], A.D. Nunn[a], M.C. Lucas[b] and I.G. Cowx[a]

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

[b] *School of Biological and Biomedical Sciences, Durham University, Durham, DH1 3LE, UK*

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

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ABSTRACT

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

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

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

1. Introduction

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

To prevent damage to property caused by flooding many rivers have been subjected to channelisation and artificial levee construction reducing them to single-thread channels and isolating them from their floodplains (Ward and Stanford, 1995; Cowx and Welcomme, 1998). Reduced floodplain habitat has been reported to affect fish species that are adapted to use periodically-inundated floodplains as spawning and nursery habitats (Kwak, 1988; Lucas and Baras, 2001; Grift *et al*., 2003). Such modifications can also have adverse consequences for fishes during floods and high flow events because of increased severity of conditions (e.g. increased water velocity and bedload transport) in the main channel (Lusk *et al*., 1998; Poff *et al*., 2006), prevention of fish finding floodplain habitats for refuge (Ross and Baker, 1983; Kwak, 1988), and the stranding of fish when floodwaters recede after artificial levees are ‘over-topped’. This is of particular importance to young-of-the-year (YoY; age 0+) fish because of their poor swimming capabilities (Harvey, 1987; Mann and Bass, 1997). Although river discharge and the timing of floods are increasingly being recognised as an important cause of inter-annual variability in the recruitment success of cyprinid fishes (Nunn *et al*., 2007), the influence of floods on 0+ fish habitat use during and after floods in modified lowland rivers is poorly known. In addition, flood frequency and magnitude are predicted to increase under the influence of climate change (Kundzewicz, 2007) and interact with existing riverine alterations and further impact ecosystem functioning (Peterson and Kwak, 1999; Gibson *et al*., 2005).

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

2. Study area

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

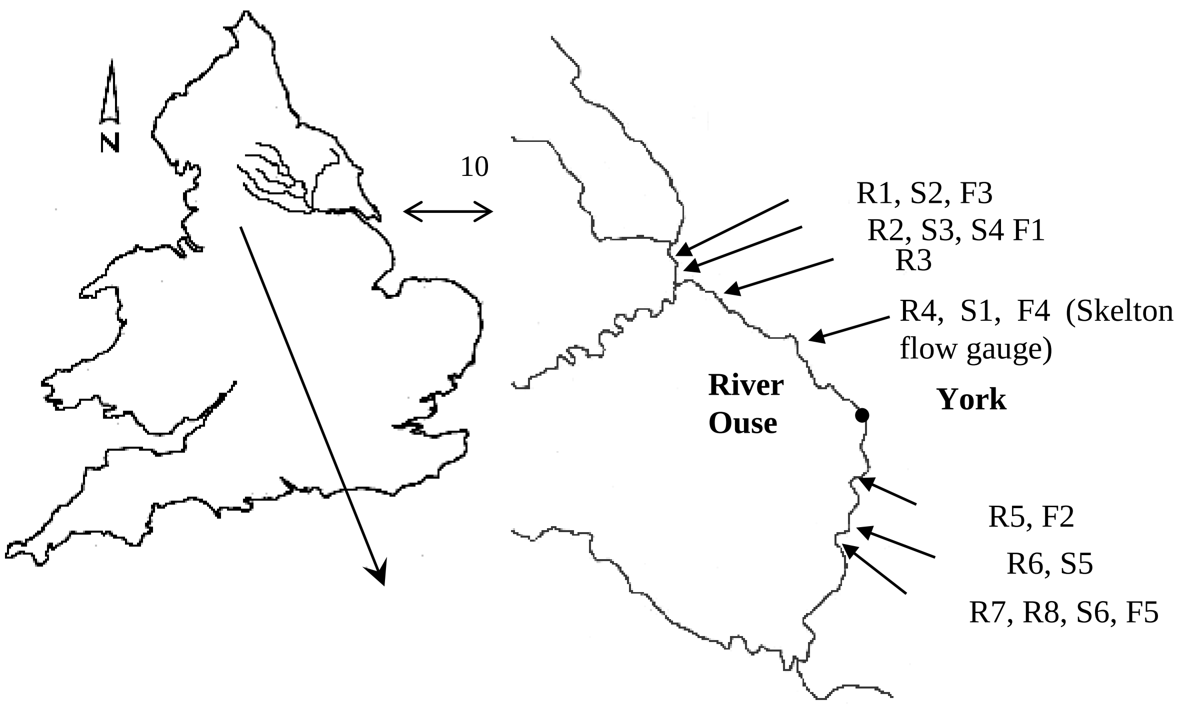


Figure 1. A map of England showing the location of the Ouse catchment, and a more detailed catchment map showing river, slackwater and floodplain sampling sites, and Skelton flow gauge. Site codes are as in Table I.

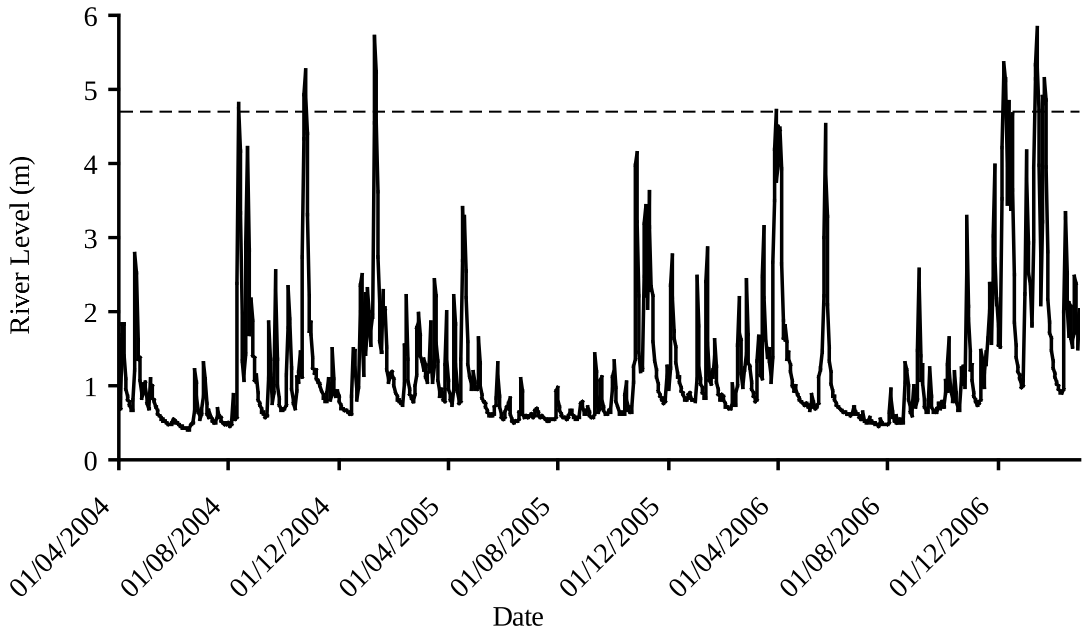


Figure 2. Mean daily river level (m) in the Yorkshire Ouse at Skelton from April 2004 to February 2007. River level when 'out-of-bank' floods occur (‒ ‒ ‒).

3. Materials and methods

3.1. 0+ fish surveys

Sampling occurred at eight river sites (during average daily flows), six slackwater sites (during elevated flows) and five floodplain sites (after floods) (Table I). The river sites were in the margins of the main channel in areas devoid of large woody debris, in water ≤1.5 m deep, where water velocity was slow and where 0+ fishes tend to aggregate. 0+ fish aggregations were surveyed at river sites from April 2004 to February 2007 (fortnightly during May to July and monthly during August to April), inclusive, in daylight hours. The slackwater areas sampled only existed during elevated river levels and floods, and consisted of plateaus between the main river channel and levees (S1, S2 and S3), a 'backed-up' tributary (S4), a slipway between two buildings (S5) and a bay downstream of some large marginal willows (*Salix* spp.) (S6). Floodplains were sampled after flood events as soon as areas of water became isolated from the main river channel. Four of the floodplain sites flooded because levees overtopped. Two of these (F1 and F2) drained through underground pipes, one (F3) drained via a 'flap-gated' ditch but left a substantial area of water isolated from the main river, and one (F4) emptied through a sluice with any residual water extracted by pumping. The fifth floodplain site (F5) was flooded by a manually operated sluice (upstream end) and was drained through a sluice (downstream end) after river levels receded; any residual water was extracted by pumping.

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

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

Site name	Habitat	Code	Dimensions	Substrate	*n*
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

3.2. Data analysis

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

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

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

4. Results

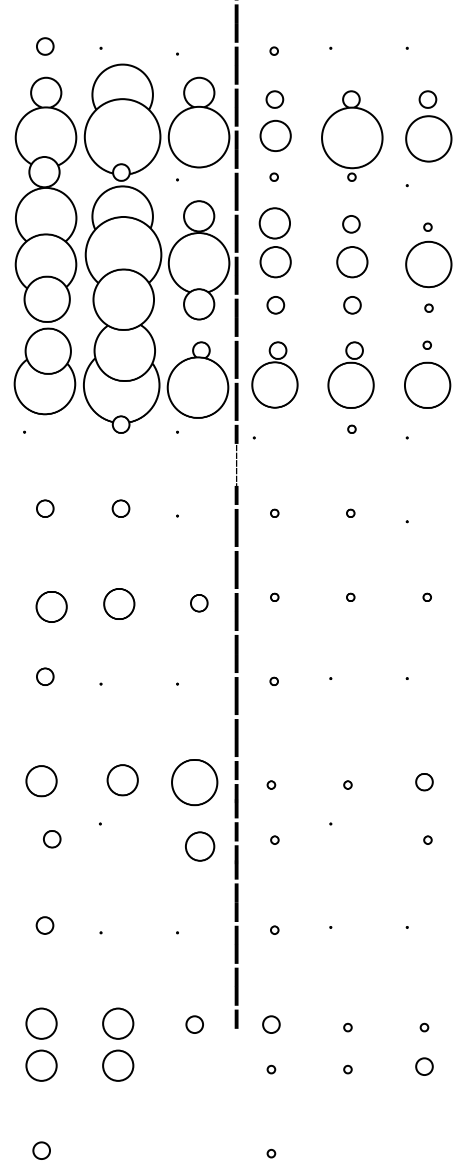
4.1. Fishes caught in slackwaters

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

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

Table II. Frequency of occurrence (percentage of surveys in which the species occurred) and relative abundance (percentage of total catches (numbers) in all surveys) (see key) of 0+ fish captured from the Yorkshire Ouse river (R), slackwater (S) and floodplain (F) from April 2004 to February 2007, including their flow preference classification[1].

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



Perca fluviatilis L.	Perch	Eury
Pleuronectidae		
Platichthys flesus (L.)	Flounder	Rheo C

[1] flow preference classification according to Schiemer and Waidbacher (1992): Rheo A = rheophilic A, Rheo B = rheophilic B, Eury = eurytopic and Limno = limnophilic.

Key (percent frequency of occurrence and abundance)

Dominant (> 75 %)
Abundant (51-75 %)
Frequent (26-50 %)
Occasional (6-25 %)
Infrequent (1-5 %)
Rare (< 1 %)
Not captured

Table III. Similarity percentages (SIMPER) analysis of the mean relative abundances of key fish species and their contributions (%) to dissimilarities in main river and slackwater 0+ fish community composition. Minor species (<5% cumulative dissimilarity) 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

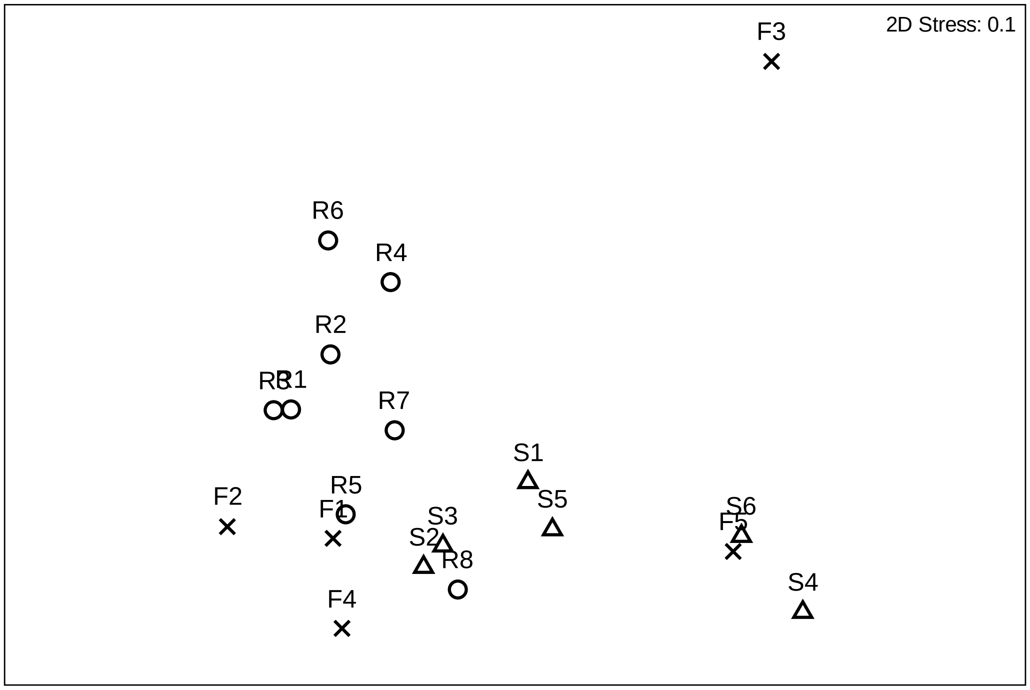


Figure 3. MDS plot (centroids) comparing 0+ fish communities from Yorkshire Ouse river (○), slackwater (Δ) and floodplain (×). Site codes are the same as in Table I.

4.2. Fishes caught on floodplains

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

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

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

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

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

5. Discussion

Individual fish species have variable resilience to floods based on differences in life history strategies, behaviour during floods and body morphology. In rivers with an aseasonal flood pulse (seemingly independent of season, i.e. the UK; Winemiller, 2004), riverine fish species have evolved life-history strategies to survive floods based upon seasonal timing and predictability (Poff and Allan, 1995), i.e. spawning is timed so that hatching coincides with low flood probability ('low flow recruitment hypothesis' *sensu* Humphries *et al*., 1999). Therefore, atypical summer floods that coincide with larval and juvenile life stages of fish are more likely to cause displacement and mortality because of their poor swimming capabilities (Harvey, 1987; Mann and Bass, 1997; Nunn *et al*,, 2007). Behavioural adaptations enable fish to respond directly to individual high flow and flood events by dispersing into slackwaters (Humphries *et al*., 2006) and onto floodplains (Grift *et al*., 2003; Schwartz and Herricks, 2005) to avoid mortality, physical damage or displacement. The problem of flushing and mortality associated with summer flood events is potentially exacerbated in industrialised nations, because construction of artificial levees has reduced rivers to single-thread channels and impeded lateral connectivity with floodplains. Unfortunately, the resilience of 0+ fishes to floods of irregular timing in heavily-modified lowland rivers are largely unknown.

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

After floods, 0+ fishes were found stranded on floodplains isolated from the main river after artificial levees were 'over-topped'. Flood timing was a critical driver of lateral displacement of 0+ fishes, as a significantly higher number of fish were found stranded after the flood in August 2004 than after winter floods of greater magnitude. King *et al*. (2003) similarly documented stranding of larval and juvenile cyprinids after a summer flood. While YoY fish abundance is obviously higher in summer months compared to the winter, habitat use of 0+ fish prior to summer floods in the current study probably elevated their susceptibility to lateral displacement as the flood water dispersed over levees onto the floodplain. Indeed, juvenile fish select marginal habitat during summer, probably in relation to optimal temperature, feeding and predator avoidance (Garner, 1997a, b; Baras and Nindaba, 1999a, b).

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

Cowx and Gerdeaux (2004) emphasised the need to recreate functional habitats for spawning, feeding, nursery (growth) and resting (self protection) areas, and the connectivity between these habitats, i.e. improving the ecological functioning of the river system (Schiemer *et al*., 1999). This study identified that slackwaters provided refuge for high densities of 0+ fishes and substantial numbers of 0+ fishes were stranded behind artificial levees, thus providing empirical evidence for the need to recreate riverine habitat diversity and channel morphology and reinstate lowland river lateral connectivity (Cowx and Welcomme 1998). It is also important to recognize that floodplain rehabilitation increase system biodiversity, provides spawning and nursery areas for juvenile fish and benefit society from the natural functional attributes of river landscapes for flood protection (Poff, 2002; Tockner and Stanford, 2002; Brenner *et al*., 2003). Therefore, floodplain rehabilitation can improve the ecological status of rivers, as is required in Europe under the European Union, Water Framework Directive (2000/60/EEC) whilst at the same time enabling societal obligations for flood mitigation under the EU Floods Directive (2007/60/EC) to be met.

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