# How do fish exploit temporary waters throughout a flooding episode?

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**Abstract** Temporary waters are important habitats for many fish species. Nevertheless, determination of which species colonise these habitats, when this occurs and where fish distribute themselves within the temporary waters are rare. The fish assemblage on a temporarily flooded grassland and its adjacent permanent canal, together with environmental variables, were monitored throughout an entire flooding event from February to May 2006 in the Brière marsh (Northwest France). In total, 589 fish belonging to 12 species were captured, but the fish assemblage was dominated by six species in both habitats. Frequency of occurrence of fish was significantly higher in the canal than in the grassland (52.9 $\pm$ 11.9% and 13.0 $\pm$ 2.4%, respectively) and similar result was observed for relative density (1.72 $\pm$ 0.50 and 0.28 $\pm$ 0.08 fish per point sample, respectively). These parameters changed during the flooding event and maximum values were recorded in mid-April, when proliferation of zooplankton and water temperature above 12 °C were observed. The extent of fish colonisation in the grassland was influenced by water level. During the first half of the flooding event, the proportion of grassland occupied by fish represented, on average, 45.9 $\pm$ 3.7% of the available flooded habitat. Afterwards, the extent of fish colonisation in the grassland decreased when water level decreased and fish used only 17.8 $\pm$ 2.1% of the available inundated area and remained close to the canal. A lack of synchronisation in the flood event and water temperature resulted in a mismatch between fish abundance and spatial distribution within the flooded grassland.

KEYWORDS: connectivity, fish community, flooded grassland, flooding regime, spatial distribution.

## Introduction

Temporary waters are highly diverse (e.g. tidal salt marshes, river floodplains, oxbow ponds) and are important components of the landscape (Williams 2006). These habitats play fundamental ecological functions for numerous plant and animal organisms (see review in Williams 2006), and particularly for fish (e.g. Welcomme 1979; Copp 1989; King, Humphries & Lake 2003). Indeed, temporary waters are important areas for reproduction, nursery, feeding and refuge against predators during particular periods depending on species life histories and flooding conditions (Poizat & Crivelli 1997; Baber, Childers, Babbitt & Anderson 2002; King *et al.* 2003). Nevertheless, there are relatively few studies that have examined fish use of temporary waters in relation to the particular environmental features of these habitats (Baber *et al.* 2002; Williams 2006). Some studies have investigated the composition and structure of fish assemblages in temporarily flooded habitats at a given time, occasionally including their changes over time (e.g. King *et al.* 2003; Crain, Whitener & Moyle 2004; Cucherousset, Paillisson, Carpentier, Eybert & Olden 2006). Others have analysed fish exchanges between temporary and adjacent permanent waters (e.g. Poizat & Crivelli 1997; Hohausová, Copp & Jankovský 2003; Cucherousset, Paillisson, Carpentier & Chapman 2007a). The influence of abiotic and biotic environmental variables on the use of temporary waters by fish has also been addressed (e.g. Ostrand & Wilde 2001; Baber *et al.* 2002; Carpentier, Paillisson, Feunteun & Marion 2004). Nevertheless, integrate approaches that address all of these issues throughout an entire flooding event, i.e. responding to the key question 'how do fish exploit temporarily flooded habitats throughout a flooding period?', are rare in temperate waters. The aim of the present study was to examine: (1) which species colonise temporary habitats compared with fish assemblage inhabiting adjacent

permanent waters; (2) when do these species colonise the temporary waters throughout a flooding event; (3) where do these species distribute themselves within the temporary waters and (4) what are the biotic and abiotic environmental variables that influence the use of these habitats by fish.
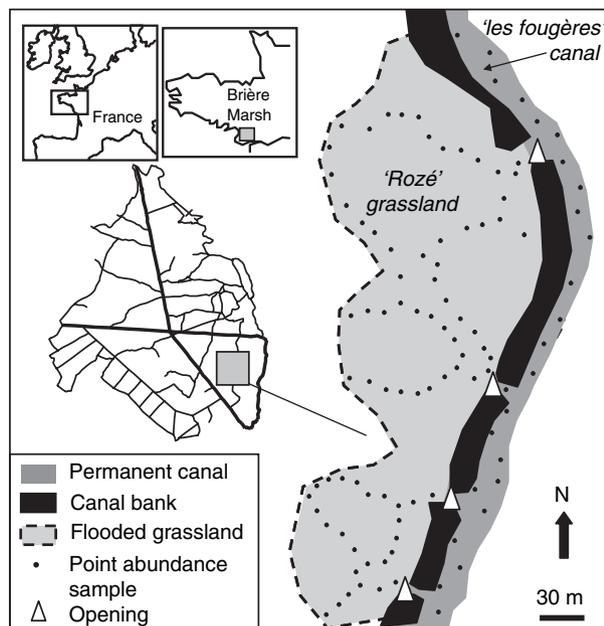
## Materials and methods

### Study area

The Grande Brière Mottière (Loire River drainage, North West France, 47°22' N, 02°11' W) is a 7000-ha, freshwater marsh composed of a complex network of permanently flooded canals (144 km covering 206 ha) within a large mosaic of seasonally flooded reed beds (5500 ha) and grasslands (1000 ha) (Fig. 1). Temporary habitats generally flood in winter and progressively dry out during spring and summer as a result of the rainfall regime and water level management (Fig. 2). The permanent canal network consist of primary and secondary waterways of which the primary canals are large canals directly connected to the main river (mean width = 19.7 ± 6.0 m) and the secondary canals are small canals connected to the primary network level (mean width = 8.9 ± 2.6 m; see details in



**Figure 1.** Map of the Grande Brière Mottière marsh and location of the study site, i.e. the 'les fougères' canal and the 'Rozé' flooded grassland. ● represent a series of fish sampling points (PAS, electric fishing Point Abundance Sampling) performed on 19 April 2006 in the permanent canal and the flooded grassland. △ indicate the openings in the emerged bank (dredging materials).
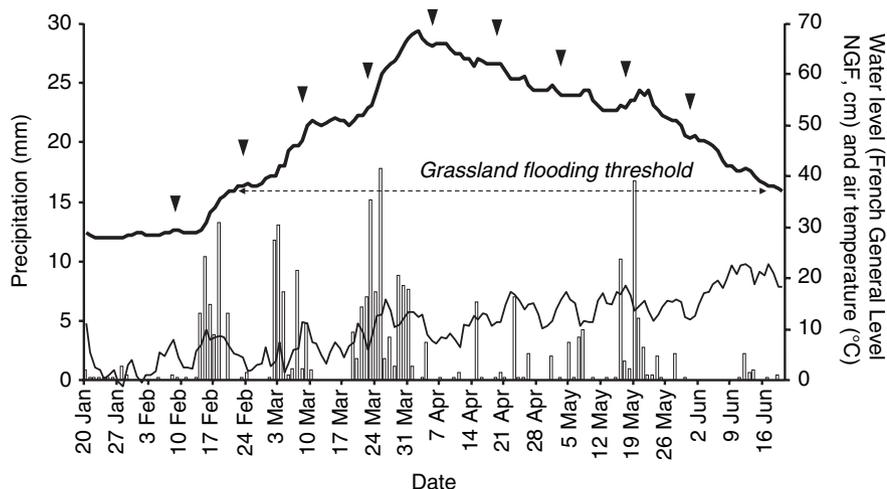
Cucherousset *et al.* 2006). The present study was conducted throughout the flooding period in 2006 (February to May) in a typical sector of the Grande Brière Mottière marsh that includes a permanent canal (the 'fougères' canal, belonging to the secondary level of the network) and its adjacent grassland (the 'Rozé' grassland, Fig. 1). The canal section was 450 m long and 13.2 m (±1.2) wide with low vegetation cover (8.4 ± 2.0%) and a peat substratum. The 5.2 ha area of the inundated grassland was more densely vegetated (72.6 ± 2.2%) than the canal. At the maximum flood event (2 April), mean water level reached 66.5 cm (±1.2) in the canal and 30.6 cm (±0.7) on the grassland (Fig. 2). The canal is separated from the grassland by a bank created from the dredging of the canal (peat and mud piled along the canal). Fish can only colonise the grassland via four openings in the bank (3-5 m wide) that were from 60 to 139 m apart (mean distance = 89.7 ± 24.4 m, Fig. 1).

### Fish sampling and monitoring of environmental variables

Field operations were performed once every 2 weeks from early February (i.e. just after the last frost), when small shallow-watered areas began to form in the grassland, to late May at the end of the flood event when only a few narrow and inaccessible pools were still flooded (Fig. 2). Fish sampling was conducted simultaneously in the two habitats using the point abundance sampling (PAS, Nelva, Persat & Chessel 1979) by electric fishing (EFKO F.E.G. 8000, 30 cm anode diameter, 400–600 V, 6–10 A). This approach was efficient because water level never exceeded 70 cm (see Copp & Penaz 1988; Lucas & Baras 2000) although the presence and/or movement of the operator may cause disturbance during sampling (Cowx, Nunn & Harvey 2001; Jánáč & Jurajda 2005). To reduce this potential bias, the anode was thrown (from a boat or by wading depending upon site accessibility) to a distance of 8–10 m away from the operator in a haphazard fashion in all accessible habitats (e.g. Persat & Copp 1990; Jánáč & Jurajda 2005). In the flooded grassland, sampling was conducted from each opening up to the water's edge (i.e. the extent of flooding in the grassland, Fig. 1). In addition, sampling was always conducted by the same operator and each sample was separated by a minimum of 20 m to limit disturbance. PAS aims to provide semi-quantitative samples, and hence permits comparison of sampling points, within and between sites as long as sufficient samples are taken from a range of habitats (Copp 1989; Perrow, Jowitt & Zambrano González 1996; Garner 1997).

**Figure 2.** Precipitation (vertical bars), daily water level (thick line) and air temperature (fine line) in the Grande Brière Mottière marsh from 20 January to 20 June 2006. ▼ indicate sampling dates and – – – the minimal threshold of water level to flood the grassland.

A total of 225 samples was taken from the permanent canal (25 samples per date) and 670 in the flooded grassland (74.4 ± 5.6 samples per date). Sampling effort was standardised between sites (0.44 ± 0.04 PAS 100 $m^{-2}$ in the flooded grassland and 0.42 ± 0.00 PAS 100 $m^{-2}$ in the permanent canal, respectively; non-parametric ANOVA, Kruskal–Wallis, $KW = 36.0$, $P = 0.671$, $n = 18$) and between dates ($KW = 8.0$, $P = 0.433$, $n = 9$). Shocked fish were collected with a hand net, identified to species, measured to the nearest millimetre and immediately released back into the water. In early spring, all fish species (except pike *Esox lucius* L.) had not yet reproduced and young-of-the-year represented only 1.7% of the fish sampled throughout the study. Consequently, all size classes were pooled for analyses. Three descriptors were used to characterise the fish assemblage in the two habitats: double-normalised species richness (*S*", i.e. number of species divided by the number of samples and fish relative density), frequency of occurrence (number of samples where fish were captured divided by the total number of samples, expressed in %), and relative density [total and for each species, expressed in Catch Per Unit Effort (CPUE), i.e. number of individuals $PAS^{-1}$]. To describe the distribution of fish on the flooded grassland from the permanent canal, the linear distance (in m) between each sample on the grassland and the nearest opening was calculated using a Global Positioning System and a Geographical Information System (source: Parc naturel régional de Brière). The extent of fish colonisation in the grassland (i.e. the mean distance to nearest opening of sampled fish) and the proportion of flooded grassland occupied by fish (i.e. the extent of colonisation weighted the distance between the water's edge and the canal, in %) were reported for each date.

For each date, four environmental variables were measured in the two habitats. Water temperature was recorded every 15 min from 10:00 to 14:00 hours using automatic sensors (Sensor StowAway TidBit, Onset Computer Corporation). The mean and coefficient of variation (standard deviation divided by the mean, expressed in %) of water temperature were calculated. Conductivity ($\mu S$ $cm^{-1}$) and the concentration in dissolved oxygen (mg $L^{-1}$) were measured in the two habitats between 11:00 and 12:00 hours. Changes in food availability in the two habitats were recorded by monitoring zooplankton abundance (mainly *Cladocera* and *Copepoda*), which constitutes the major food source for fish. This was determined by filtering 15 L of water (0.1-mm mesh) and preserving the samples in 70% ethanol. Zooplankton abundance was measured in the laboratory using a Dollfus counting chamber and a binocular microscope, and expressed as the number of individuals per litre of water (ind. $L^{-1}$). All environmental variables were always measured in the same locations in the canal and in the grassland.

*Statistical analyses*

As deviations from normality were detected in the different data sets, non-parametric tests (Wilcoxon signed rank test, Spearman rank correlation and Kruskal–Wallis test) were performed for between-sites and between-dates comparisons in species composition and environmental conditions. A rejection level of $\alpha = 0.05$ was used in all tests. Values are mean ± standard error (SE).
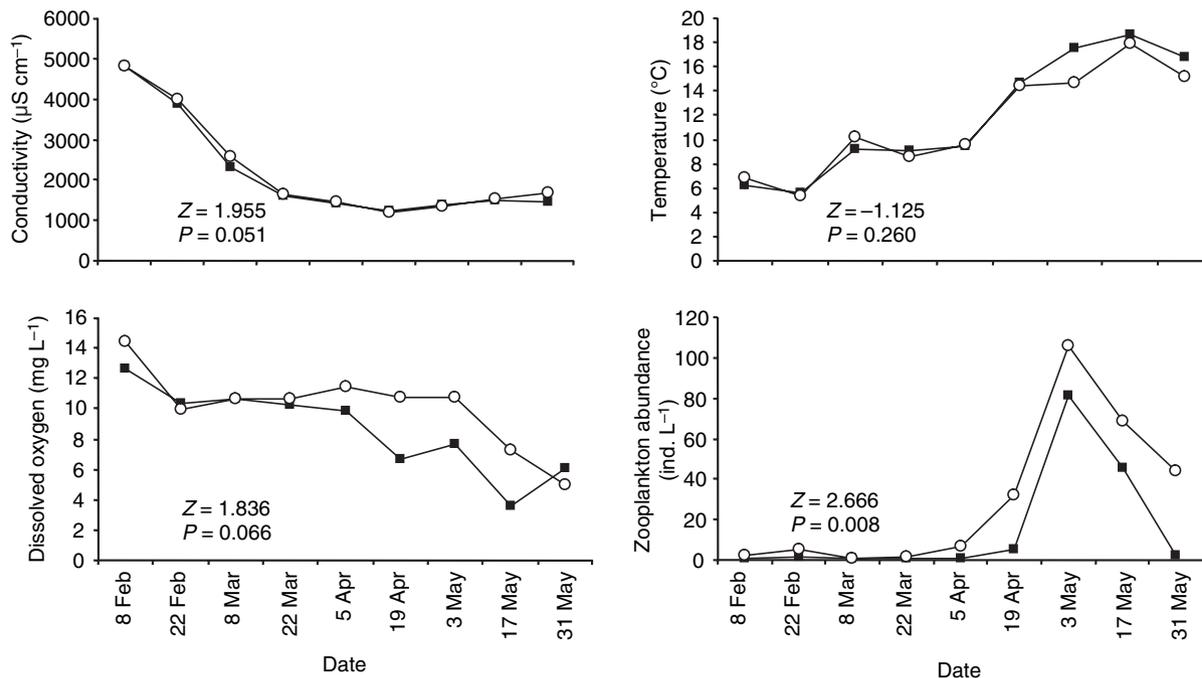
**Figure 3.** Environmental variables in the flooded grassland (○) and in the permanent canal (■) from 8 February to 31 May 2006: conductivity, mean water temperature, dissolved oxygen concentration and zooplankton abundance. Results of between-sites comparisons (Wilcoxon signed rank test) are provided for each environmental variable ($n = 9$ dates).

## Results

### Succession of environmental variables

Water conductivity and concentration of dissolved oxygen decreased in the two habitats during the flood event, while water temperature increased. Water conductivity and concentration of dissolved oxygen were nearly significantly different between the two habitats but mean water temperature was not (see $Z$-statistics in Fig. 3). Water temperatures were more buffered in the canal with a mean value of the coefficient of variation higher in the grassland ($6.9 \pm 1.3\%$) than in the canal ($4.7 \pm 1.1\%$, Wilcoxon-signed rank test, $Z = 2.310$, $P = 0.021, n = 9$). At the start of the survey, zooplankton abundance was low, but increased in early May when water temperature was above 12 °C (Fig. 3). This pattern was similar in the two sites but zooplankton abundance was lower in the permanent canal than in the flooded grassland (see $Z$-statistics in Fig. 3).

### Fish assemblage composition and its succession throughout the flooding event

In total, 589 individuals belonging to 12 species were sampled: 386 individuals (belonging to 11 species) captured in the canal and 203 individuals (11 species)

in the grassland (Table 1). The fish assemblage was dominated by the same six species in the two habitats (Table 1): common bream, *Abramis brama* (L.), black bullhead, *Ameiurus melas* (Rafinesque), roach, *Rutilus rutilus* (L.), rudd, *Scardinius erythrophthalmus* (L.), European eel, *Anguilla anguilla* (L.) and gibel carp, *Carassius gibelio* (Bloch). The other species comprised <5% relative abundance (Table 1). Except for three-spine stickleback, *Gasterosteus aculeatus* L., all the species recorded in the canal were sampled in the grassland. The double-normalised species richness ($S''$) was nearly significantly higher in the grassland than in the canal ($0.39 \pm 0.06$ and $0.24 \pm 0.05$ respectively, see $Z$-statistics in Fig. 4). Patterns of $S''$ were similar in the two habitats throughout the flooding period and highest during the first half of the flood event. Frequency of occurrence of fish was constant and low in the two habitats until 5 April (Fig. 4). On 19 April, it increased in the canal from 28% to 72% followed by high values (92–96%) until the end of the flood event, while a brief peak (25%) was observed in the grassland on 3 May. Frequency of occurrence of fish was significantly higher in the canal than in the grassland ($52.9 \pm 11.9\%$ and $13.0 \pm 2.4\%$, respectively, see $Z$-statistics in Fig. 4). Patterns of fish relative density were similar to those described for the frequency of occurrence throughout the flooding period.

**Table 1.** Details on fish species sampled in the permanent canal and in the flooded grassland from February to May 2006: common and scientific names and abundance

| Species | | Abundance | |
| --- | --- | --- | --- |
| Common name | Scientific name | Canal | Grassland |
| Common bream | *Abramis brama* | 100 | 75 |
| Black bullhead | *Ameiurus melas* | 94 | 27 |
| Roach | *Rutilus rutilus* | 90 | 12 |
| Rudd | *Scardinius erythrophthalmus* | 19 | 38 |
| European eel | *Anguilla anguilla* | 27 | 20 |
| Gibel carp | *Carassius gibelio* | 28 | 16 |
| Northern pike | *Esox lucius* | 10 | 8 |
| Common carp | *Cyprinus carpio* | 6 | 4 |
| Threespine stickleback | *Gasterosteus aculeatus* | 6 | 0 |
| Pumpkinseed | *Lepomis gibbosus* | 4 | 1 |
| Mosquitofish | *Gambusia holbrooki* | 2 | 1 |
| Tench | *Tinca tinca* | 0 | 1 |

Relative density was higher in the canal than in the grassland ($1.72 \pm 0.50$ CPUE and $0.28 \pm 0.08$ CPUE, respectively, see $Z$-statistics in Fig. 4). The strong increase in frequency of occurrence and relative density in the two habitats coincided with the maximum water level of the flood event (Fig. 2), a large increase in water temperature and the proliferation of zooplankton (Fig. 3).

At the species level, variations in relative density occurred between the two habitats (Fig. 5): significantly higher CPUE of bream, black bullhead and roach in the canal than in the grassland, nearly significantly higher CPUE of European eel and gibel carp and no difference in CPUE of rudd. Conversely, the species composition was different in the two habitats on each date (Spearman rank order correlation, $0.06 < r_s < 0.66$, $0.136 < P < 0.919$, $n = 12$ species, Fig. 5). Differences between species were found in the timing of use of the temporary habitat (Fig. 5). For instance, rudd and European eel colonised the grassland early and were recorded in this habitat during the entire flooding event while the other species generally colonised the grassland later (in mid-April, at the maximum water level and when the water temperature increased, Fig. 5).

## Spatial distribution of fish on the grassland throughout the flooding event

The proportion of grassland occupied by fish changed significantly between dates (non-parametric ANOVA, Kruskal–Wallis, $KW = 59.9$, $P < 0.0001$, $n = 203$ fish) and it was also the case for the extent of colonisa-
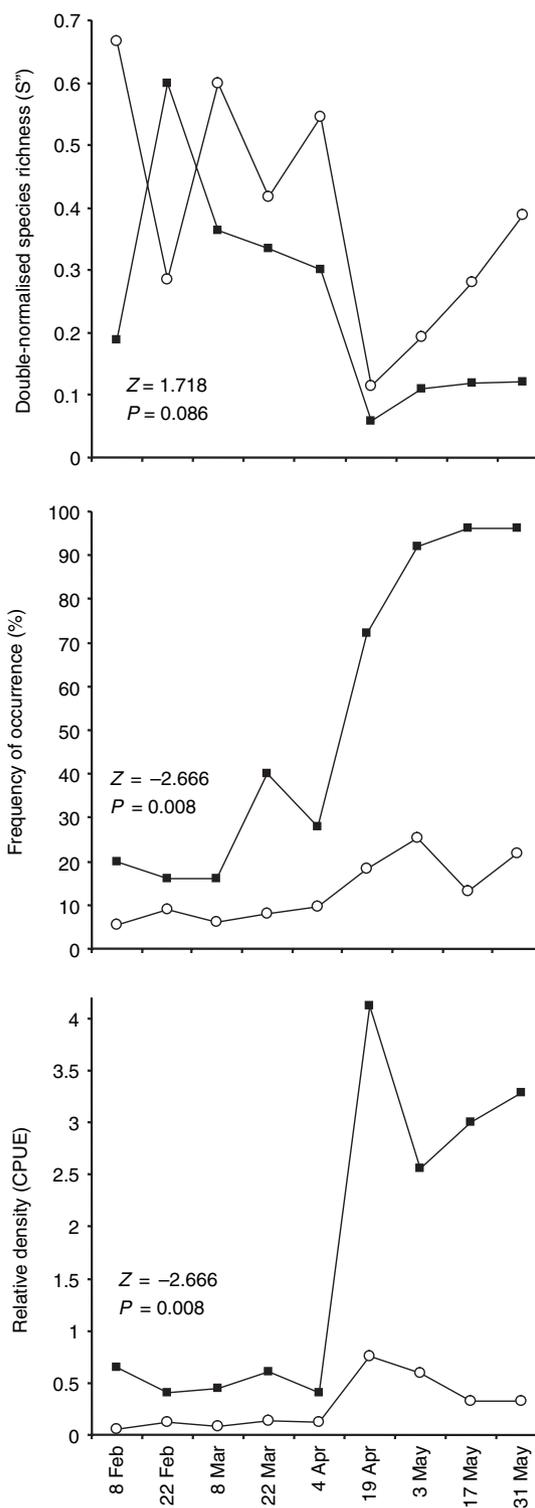


**Figure 4.** Descriptors of the fish assemblage present in the flooded grassland (○) and in the canal (■) throughout the flooding period (8 February to 31 May 2006): double-normalised species richness ($S''$), frequency of occurrence (CPUE) and relative density (%). Results of between-sites comparisons (Wilcoxon signed rank test) are provided for each descriptor ($n = 9$ dates).
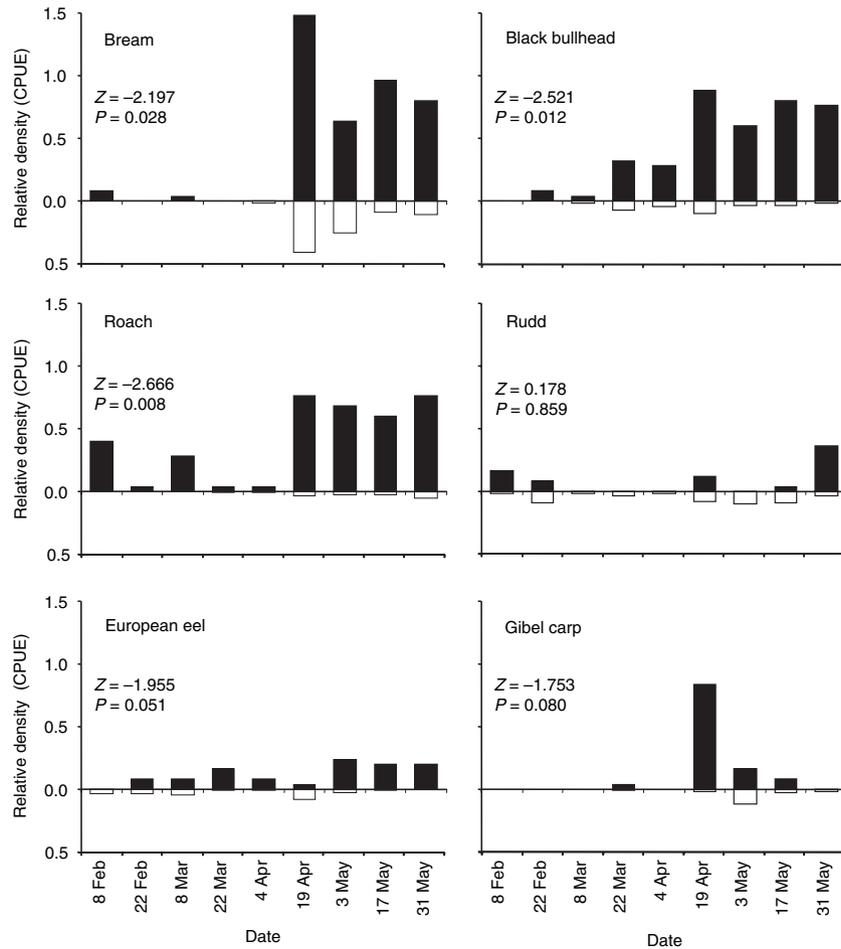
**Figure 5.** Temporal patterns of relative density [in Catch Per Unit Effort (CPUE), ind. PAS$^{-1}$] of the six dominant fish species in the canal (■) and in the flooded grassland (□) throughout the flooding period.

tion ($KW = 59.4$, $P < 0.0001$). During the first half of the inundation, the extent of colonisation increased continuously in conjunction with the increase in water level (Fig. 2), while the relative density of fish in the grassland was still low (Fig. 4). During this period, the proportion of grassland occupied by fish was, on average, $45.9 \pm 3.7\%$ of the available flooded area (Fig. 6). The maximum extent of colonisation corresponded to maximum water level, i.e. on 4 April (Fig. 6). During the second part of the inundation, as water level decreased (Fig. 2) and water temperature increased (Fig. 3), the extent of colonisation significantly decreased (Fig. 6). On average, fish used $17.8 \pm 2.1\%$ of the available flooded grassland during this period, and were mainly located close to the openings.

## Discussion

The use of temporary flooded habitats by fish was highly variable during the period of inundation,

influenced by changes in the fish assemblage of the adjacent canal, governed by environmental variables, and restricted in time and space relatively to the duration of the flood event and the area flooded. The use of temporarily flooded habitats can be interpreted as a trade-off between benefits and costs provided by these habitats to fish (Cucherousset *et al.* 2007a). This trade-off is likely to vary throughout the flooding period as a consequence of changes in environmental variables (here water level, zooplankton abundance, temperature) that modify the ratio of costs (e.g. physiological stress, see in Magoulick & Kobza 2003, Matthews and Marsh-Matthews 2003 and predation pressure, see in Kushlan 1976; Capone & Kushlan 1991) vs benefits (e.g. growing conditions, see in Capone & Kushlan 1991) compared with permanent habitats. Indeed, Williams (2006) stated that the main advantages for fish to colonise temporary waters are the presence of abundant food resources, earlier spring spawning breeding possibilities (the water being often
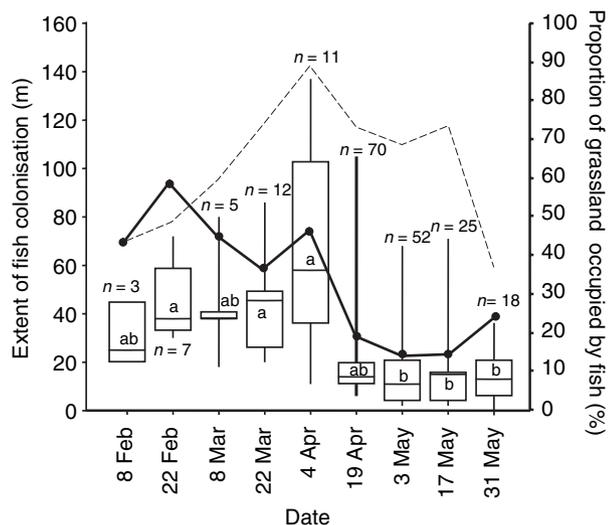
**Figure 6.** Extent of fish colonisation in the grassland (boxes, in m) and proportion of grassland occupied by fish (—●—, in %) throughout the flooding event (8 February to 31 May 2006). Boxes indicate the first and third quartiles, middle lines represent the mean value and the whiskers represent minimum and maximum values. – – – represents the water's edge (extent of flooding) in the grassland. Two different letters indicate significant differences at $P < 0.05$ from pairwise comparisons of the distance to the permanent canal variable between dates.

warmer than in adjacent permanent waters) and reduced predation, notably by large fish. In the present study, no differences in mean water temperature were found between habitats. However, temperature variation amplitude, zooplankton abundance (particularly when considered with respect to the number of fish), vegetation coverage and consequently oxygenation of water were higher in the flooded grassland than in the adjacent permanent canal, particularly during the first phase of the flooding period. At this time, the grassland constituted a high quality and attractive habitat for fish. As water level declines, a decrease in food availability (e.g. Capone & Kushlan 1991), a decline in water quality (low dissolved oxygen concentration and high water temperature, e.g. Magoulick & Kobza 2003), and an increase in predation pressure by birds (e.g. Kushlan 1976) are commonly reported. In the present study, such changes in environmental variables have been measured. Furthermore, the establishment of a black tern, *Chlidonias niger* (L.), colony on the flooded grassland in early May was observed (see also a preliminary assessment of avian predation on flooded grassland in Cucherousset, Paillisson & Roussel 2007b). During the period of water recession, fish present in the grassland moved either nearer to the openings or emigrated from the grassland to the canal, i.e. to deeper habitats being used as refuge

or feeding areas in summer (e.g. Gozlan, Mastrorillo, Dauba, Tourenq & Copp 1998; Magoulick & Kobza 2003).

The extent of fish colonisation in the inundated grassland was influenced by water level. Indeed, the maximum distance colonised in the grassland corresponded to the maximum water level associated with a low water temperature ($<12\ °C$) period (early April), the grassland supporting a low relative density of fish species that used flooded habitat as feeding area (e.g. European eel and black bullhead). Afterwards, the extent of fish colonisation in the grassland decreased while the relative density of fish increased as zooplankton abundance and water temperature increased ($>12\ °C$, mid-April). Furthermore, these fish were mainly mature bream, rudd and gibel carp (Authors, unpublished data), confirming the dependent relationship between water temperature and sequential spawning migrations (Hladík and Kubečka 2003). A lack of synchronisation in flood event and water temperature was observed in the present study, so environmental conditions were certainly not optimum for cyprinid recruitment (King *et al.* 2003). These results also raise the question of accessibility of temporary waters and connectivity with the permanent habitat. Indeed, delays in colonisation of the grassland by many species were observed compared with their pattern of presence in the canal, and a restricted spatial distribution of fish was measured on the grassland. Several authors demonstrated that connectivity between temporary and permanent waters is important for fish movements (e.g. Nicolas & Pont 1995, Baber *et al.* 2002; Hohausová *et al.* 2003). The consequence of dredging (i.e. bank construction and reduction of connectivity) can have adverse effects on fish assemblage by impeding fish movements between temporary and permanent habitats (Baber *et al.* 2002) and this was observed in the present study. Nevertheless, further investigations are needed to understand how variable flooding and connectivity conditions could influence the use of temporary waters by fish.

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