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SELECTIVE USE AND SPATIAL DISTRIBUTION OF NATIVE AND NON-NATIVE FISH IN WETLAND HABITATS

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ABSTRACT

Wetland habitats are crucial for many fish species as spawning, feeding or nursery areas, but the major factors that govern their use by fish are poorly identified. In the present study, we aim to investigate the selective use and the spatial distribution of native and non-native fish species in different types of wetland habitats (grasslands and reed beds) in a large freshwater marsh (North Western France). The selective use was measured by comparing the community that uses wetland habitats to the total community of the marsh (sampled in the permanent aquatic habitats (canals) during the low water period). The spatial distribution was studied by analyzing the presence probability of fish in wetland habitats as a function of the distance from adjacent canals. All sampled wetland habitats were occupied by fish, and the fish community in wetland habitats was dominated by three native (*Abramis brama*, *Scardinius erythrophthalmus* and *Anguilla anguilla*) and three non-native (*Ameiurus melas*, *Gambusia holbrooki* and *Lepomis gibbosus*) species. Species richness and total fish abundance differed between canals and wetland habitats as a consequence of a variable propensity to use wetland habitats by native (avoidance and preference) and non-native (no preference) species. Non-native species were also more abundant in reed beds than in grassland while no differences were observed for native species. Universally, the presence probability of fish always decreased in wetland habitats as the distance from the canals increased and only a narrow area, close to canals (50–80 m), was well used by fish. However, non-native fish species used over greater distances in reed beds than in grasslands while no differences were observed for native species. Variable interpretations related to species tolerance, reproductive guilds or diet are proposed to understand the mechanisms that might explain the widespread success of non-native species in this spatially varying environment. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: temporary waters; fish community; habitat use; flooded areas; grassland; reed bed; colonization

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INTRODUCTION

Wetland habitats, defined here as habitats that are seasonally inundated and connected to permanent aquatic habitats by surface waters, are very varied (e.g. river floodplain, freshwater marsh, oxbow), and widely distributed, occurring across virtually all continents (see review in Williams, 2006). They have been reported as playing fundamental roles for a broad range of plant and animal communities (Williams, 2006), including many fish species (e.g. King *et al*., 2003; DeAngelis *et al*., 2005; Trexler *et al*., 2005; Nunn *et al*., 2007). Depending on their life history, some fish species are restricted to permanent habitats whereas other species can use wetland habitats as spawning, feeding or nursery areas (Snodgrass *et al*., 1996; Baber *et al*., 2002; Williams, 2006). Based on their behavioural responses to flooding regimes (magnitude, frequency and duration), fish species that use wetland habitats have been classified into two groups by Welcomme (1979): (1) fish that avoid environmental fluctuations by migrating to and from the main river channel (permanent habitat being used as a refuge and feeding area during the low water period, Gozlan *et al*., 1998; Magoulick and Kobza, 2003), and (2) fish that are able to survive widely fluctuating conditions and even drought (Sayer, 2005).

Although many species belong to this latter category, very few of them are adapted to survive complete loss of water from their habitat in temperate environments (Sayer, 2005; Williams, 2006), and temperate fish species

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exploit wetland habitats during floods and emigrate before droughts as environmental conditions decline (Poizat and Crivelli, 1997; Cucherousset *et al*., 2007b). Several studies have already addressed the composition of the fish community in wetland habitats at a given moment and its changes throughout flooding events, or the intensity of fish exchanges between wetland habitats and adjacent permanent habitats (e.g. Poizat and Crivelli, 1997; Baber *et al*., 2002; Hohausová *et al*., 2003; Crain *et al*., 2004). However, the major factors that govern the use of wetland habitats by fish species are poorly identified (Baber *et al*., 2002). For instance, the selective use of different types of wetland habitats by fish and their spatial distribution in these habitats have been rarely addressed. For the latter matter, the role of the distance to permanent habitat has been recently suggested (Rehage and Trexler, 2006).

As most aquatic habitats, wetland habitats are often submitted to various anthropogenic disturbances. In recent decades, aquatic habitats have suffered severe degradation due to resource exploitation and harvesting, urban and agricultural encroachment and global change (Tockner and Stanford, 2002; Williams, 2006). These drastic changes have undoubtedly modified the composition and functioning of fish communities (Pont *et al*., 2006; Welcomme *et al*., 2006). More precisely, it has been suggested that these human-caused environmental disturbances have facilitated the decline of some native species, and conversely, the establishment of self-sustaining populations of more tolerant non-native fish species (Moyle and Light, 1996; Marchetti *et al*., 2004; Alcaraz *et al*., 2005; Garcia-Berthou, 2007), but these aspects have been investigated rarely in wetland habitats.

The general objective of the present study is to investigate the selective use and the spatial distribution of fish in different types of wetland habitats in a large freshwater marsh in North Western France. The selective use of wetland habitats was measured by comparing the fish community that uses wetland habitats during the flooding period with the total fish community of the marsh (i.e. inhabiting permanent habitats during the low water period). The spatial distribution of fish in wetland habitats was studied by analyzing the presence probability of fish in wetland habitats as a function of the distance from the adjacent permanent habitat. Furthermore, these processes were investigated for different species, notably according to their origin (native vs non-native).

MATERIALS AND METHODS

Study area

The study was carried out in the Grande Brière Mottière marsh (7000 ha, North Western France, 47°22′N, 02°11′W, Cucherousset *et al*., 2006). It is composed of a complex web of canals (i.e. 144 km of permanent habitats that cover 206 ha) and a large patchwork of wetland habitats, i.e. reed beds (5500 ha) and grasslands (1000 ha), that flood in winter and progressively dry out in spring and summer as a result of the rainfall regime and water level regulations by a sluice located at the outlet (Figure 1). A drastic decrease in agricultural practices (mainly grazing and peat extraction) has occurred during the last century. This has favoured the development and rapid expansion of reed beds mainly composed of the common reed (*Phragmites australis*). In the last 50 years, the surface area covered by reed beds has increased from 2% to 85% of the total area of the marsh, to the detriment of natural grasslands that have decreased from 83% to currently 10% of the marsh (Bernard and Rolland, 1990).

Fish sampling

To compare the fish community that uses wetland habitats (accessible only during the flooding period) with the total pool of species of the marsh, that is, fish community in the network of canals during the low water period (hereafter called ‘comparison between wetland habitats and canals’), fish sampling was carried out at two key periods over two years (2004 and 2005, Figure 1). Fish sampling was performed using the point abundance sampling approach (PAS, see Nelva *et al*., 1979; Persat and Copp, 1990; Janác and Jurajda, 2005) with an electric fishing apparatus (EFKO F.E.G. 8000, 30 cm anode diameter, 400–600 V, 6–10 A). However, the efficiency of electric fishing is limited in deep waters (e.g. Lucas and Baras, 2000) and is restricted to the superficial water layers (≤1 m depth in Copp and Penaz, 1988). Fish communities in wetland habitats are known to change throughout the flooding period (Baber *et al*., 2002). Several studies have already shown that highest abundances and dispersions of fish on wetland habitats occur in the middle of the flooding period (Crain *et al*., 2004; Cucherousset *et al*., 2007a). Consequently and despite some differences in flooding patterns between the two years, fish sampling operations

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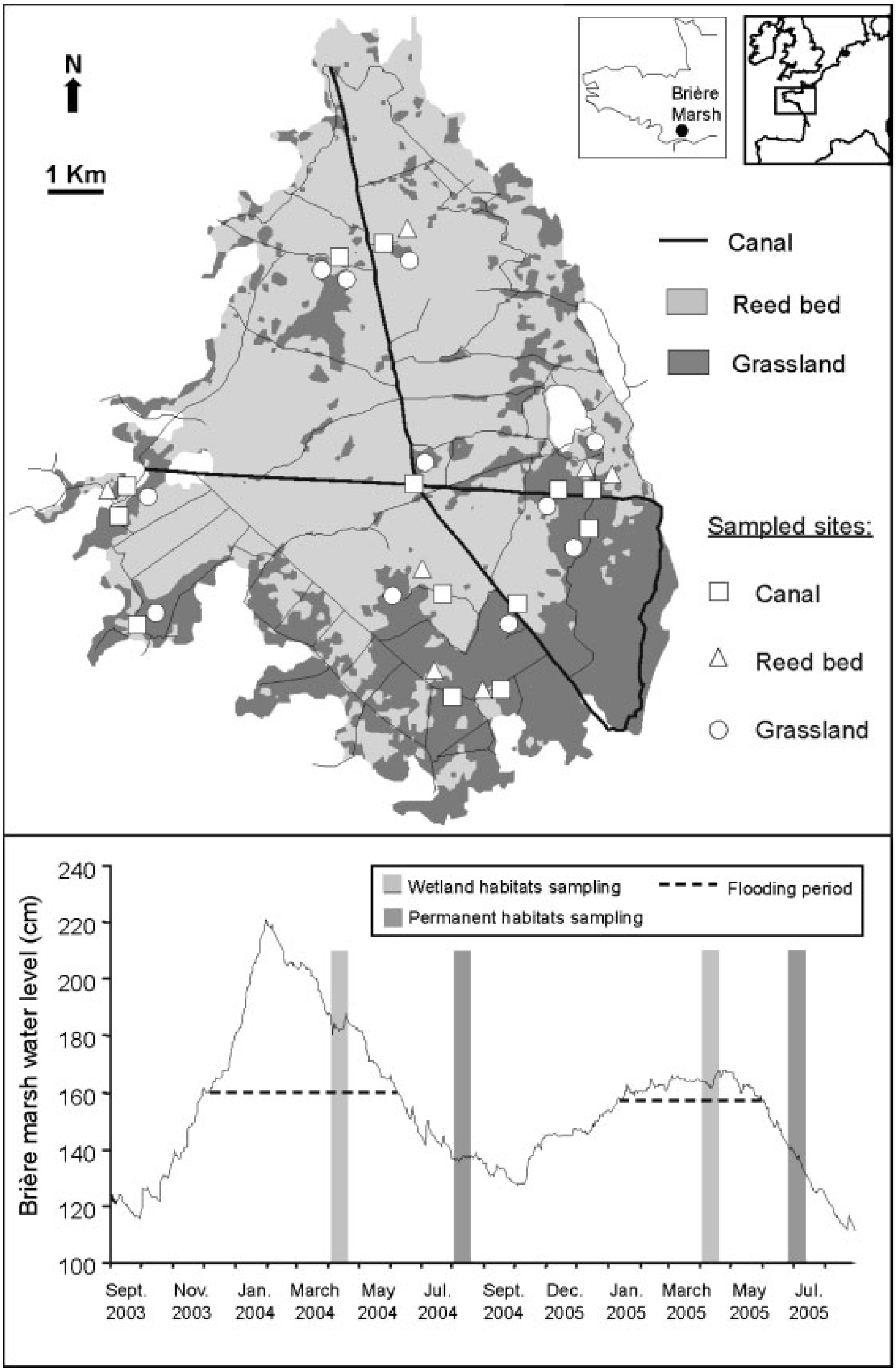

Figure 1. Map of the Brière marsh showing the canal network, the two types of wetland habitats (grassland and reed bed) and the location of sites sampled in 2004 and 2005 (top). Water levels (French General Level, cm) in the Brière marsh from September 2003 to August 2005 and an indication of the sampling periods of wetland habitats (clear grey, flooding period) and canals (dark grey, low water period) (bottom). The horizontal dotted line represents the minimal threshold of water level required to inundate the temporarily flooded habitats (*source*: Parc naturel régional de Brière)

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were carried out on wetland habitats (eleven grasslands and seven reed beds) from early to mid-April in 2004 and 2005 (mean water depth of 46.6 (± 13.7 SD) and 26.9 (± 8.4 SD) cm, respectively). That period corresponded to the middle of the flooding period during the spring recession stage of water levels (Figure 1). To address the aim of the study and to avoid potential biases associated with electrofishing efficiency, 13 canals adjacent to the monitored wetland habitats (Figure 1) were sampled in the summer (low water period) when depth was similar to the depth in wetland habitats (mean water depth of 47.1 (± 24.3 SD) and 36.5 (± 17.1 SD) cm in 2004 and 2005, respectively).

The presence and/or movement of the operator may cause disturbance during sampling (Cowx *et al*., 2001; Janac and Jurajda, 2005). To reduce this potential bias, the anode was thrown from a boat or by wading depending upon site accessibility (e.g. Persat and Copp, 1990; Janac and Jurajda, 2005), to a distance of 8–10 m from the operator in a haphazard fashion and in all accessible habitats (from the connection with the canal up to about 300 m in wetland habitats). In addition, sampling was always carried out 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 the comparison of sampling points, within and between sites as long as sufficient samples are taken from a range of habitats (Copp, 1989; Perrow *et al*., 1996; Garner, 1997). Consequently, a total of 665 PAS were performed in canals (25.6 ± 3.8 SD per site) and 1156 PAS in wetland habitats (32.1 ± 6.0 SD per site) to standardize the sampling effort between sites (≈ 0.4 PAS.100 m^{-2}, Cucherousset *et al*., 2007a). Fish were collected with a net, identified for species, measured to the nearest mm and always released back into the water immediately and behind the operators. Fish abundance was expressed in catch per unit effort (CPUE), that is, the number of individuals caught per PAS. To investigate the spatial distribution of fish in wetland habitats, each PAS was located with a Global Positioning System to calculate the distance from the nearest adjacent canal (to the nearest metre) using a Geographical Information System (source: Parc naturel regional de Brière).

Statistical analysis

As sampling in wetland habitats was carried out in spring, all fish species (except northern pike, *Esox lucius*) had not yet reproduced and all individuals sampled in wetland habitats were thus used for statistical analyses. In canals, young-of-the-year (YOY) individuals were removed from the dataset after inspection of the distribution of specific size-classes (*as per* Carpentier *et al*., 2004) to permit comparisons with wetland habitats sampled at a different season. Preliminary analyses showed that no difference occurred in species richness, mean total fish abundance and mean abundance for each dominant species (see section ‘Results’) in each habitat between years (Wilcoxon signed rank test, $p > 0.05$). Therefore, no distinction was made between years in the analyses.

The selective use of wetland habitats by fish was analysed at the site level (each wetland habitat vs its adjacent canal containing the pool of species during the low water period). Since deviations from normality were detected in the dataset, the non-parametric Mann–Whitney U test was used to compare species richness and fish abundance between habitats. Spearman correlation was used to compare the composition of the fish community (dominant species, i.e. relative abundance >5% in at least one of the two types of wetland habitats) between canals and the two types of wetland habitats. To describe the propensity of each dominant species to use wetland habitats relative to canals, the Jacob’s electivity index (log Q, Jacobs, 1974 and review in Lechowicz, 1982) was calculated for each fish species in each wetland habitat/canal pair using the following formula: $\log Q_i = [WH_i(1-C_i)]/[C_i(1-WH_i)]$ where WH_i and C_i are the relative abundance of species$_i$ in wetland habitats and canals, respectively. The mean Jacob’s electivity index was then compared to a predicted mean value of 0 using the non-parametric Wilcoxon-signed rank test. When a statistically significant difference occurs, a positive mean $\log Q_i$ value indicates a ‘preference’ of species$_i$ to wetland habitat whereas a negative mean $\log Q_i$ value indicates an ‘avoidance’ of species$_i$ to wetland habitat.

The spatial distribution of fish in wetland habitats was analysed at the PAS level (the sampling unit at which the distances from canals were measured) using fish presence/absence data. Analyses were performed using logistic regression (i.e. presence/absence response curve; see Trexler and Travis, 1993). We estimated the probability (p) of a fish species or a group of species (i.e. native and non-native) being present as a function of a measured variable (see details for example in Pont *et al*., 2005). This can be extended to include more than one explanatory variable. In the present study, the distance from canal and the type of wetland habitats (grassland/reed bed) were used as

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explanatory variables. For all tests, significance was set at $p = 0.05$, but probabilities >0.05 and <0.1 were included for heuristic purposes.

RESULTS

Fish communities in permanent and wetland habitats

In total, 496 individuals belonging to fifteen species were caught in canals during the low water period. The mean species richness was 8.73 (±1.31 SD) species per canal (range: 6 to 11 species) and the mean fish abundance was 14.62 (±8.67 SD) CPUE (range: 3.36–37.35). Seven species largely dominated the fish community: black bullhead (*Ameiurus melas*), bream (*Abramis brama*), mosquitofish (*Gambusia holbrooki*), roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus*), European eel (*Anguilla anguilla*) and pumpkinseed (*Lepomis gibbosus*). They accounted for 99.1% of the total number of fish sampled (Table I). Bream, rudd and European eel are native species whereas black bullhead, mosquitofish and pumpkinseed are non-native species. In total, the other species accounted for less than 0.9% of the total number of fish sampled (Table I). All sampled wetland habitats contained fish, resulting in the capture of 927 individuals belonging to twelve species (Table I). Only three species sampled in canals were not found in wetland habitats [perch (*Perca fluviatilis*), three-spined stickleback (*Gasterosteus aculeatus*) and pikeperch (*Sander lucioperca*)]. The mean species richness was 4.66 (±2.10 SD) species per wetland habitat (range: 1–9 species) and the mean fish abundance was 0.81 (±0.77 SD) CPUE (range: 0.02–3.00). The mean species richness was 1.9 times lower in wetland habitats than in canals (Mann–Whitney test, $U = 884$, $p < 0.001$, $n = 62$) and the mean fish abundance was 18 times lower in wetland habitats than in canals (Mann–Whitney test, $U = 936$, $p < 0.001$, $n = 62$). Nevertheless, no differences were found in mean species richness (Mann–Whitney test, $U = 131$, $p = 0.451$, $n = 36$) and in mean fish abundance (Mann–Whitney test, $U = 121$, $p = 0.284$, $n = 36$) between grasslands and reed beds. Six species largely dominated the fish communities

Table I. Fish species (scientific name), number of individuals (*N*) and occurrence (number of sites where the species was recorded/number of sites sampled, in %) in the permanent habitats during low water period (canals, $n = 26$) and in the two types of wetland habitats during the flooding period, that is grasslands ($n = 22$) and reed beds ($n = 14$), sampled in 2004 and 2005 in the Brière marsh

Species	Permanent habitats		Wetland habitats			
			Grasslands		Reed beds	
Scientific name	*N*	Occurrence (%)	*N*	Occurrence (%)	N	Occurrence (%)
*Ameiurus melas**	3903	100	105	68	138	100
Abramis brama†	2013	100	95	55	22	50
*Gambusia holbrooki**	1211	100	9	23	32	43
Rutilus rutilus	1040	100	19	36	11	36
Scardinius erythrophthalmus	564	100	222	95	86	100
*Lepomis gibbosus**	398	92	18	32	63	57
Anguilla anguilla	282	100	41	59	33	71
*Carassius gibelio**	47	50	8	36	1	7
*Cyprinus carpio**	18	42	8	18	2	7
Esox lucius	7	19	8	18	2	14
Perca fluviatilis	5	19	0	0	0	0
Gasterosteus aculeatus	4	12	0	0	0	0
Tinca tinca	2	8	0	0	3	14
*Micropterus salmoides**	1	4	0	0	1	7
*Sander lucioperca**	1	4	0	0	0	0

*Denotes non-native species based on Keith and Allardi (2001).

†Some *Blicca bjoerkna* individuals were grouped with *Abramis brama* as they were not reliably identifiable in the field.

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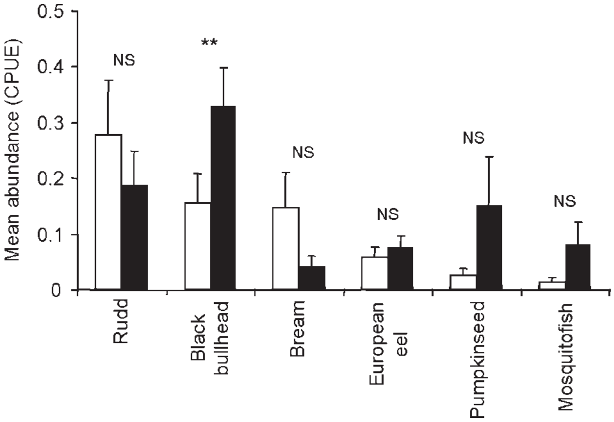

Figure 2. Mean abundance (CPUE = number of individuals per PAS) of the six most abundant species sampled in the grasslands (white bars, $n = 22$) and reed beds (black bars, $n = 14$) in 2004 and 2005 in the Brière marsh. Error-bars are standard error. NS: not significant and $^{**}p < 0.01$ for Mann–Whitney U tests for between-temporarily flooded habitat comparisons

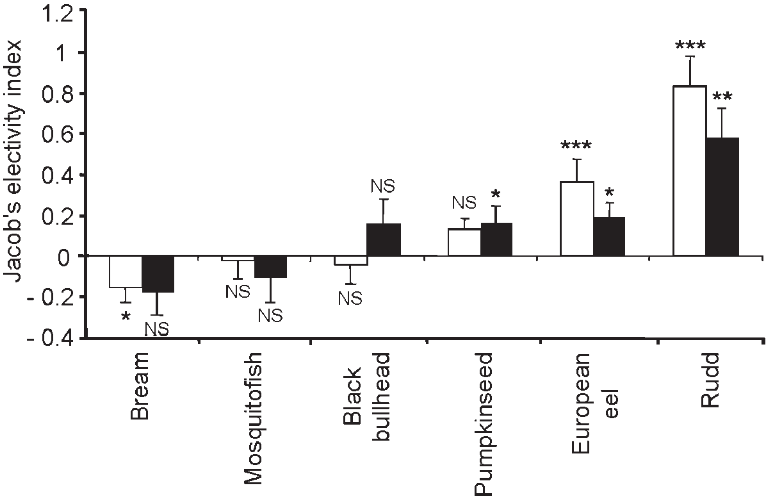

Figure 3. Selective use of the two types of wetland habitats based on Jacob's index of electivity for the six dominant species in grasslands (white bars, $n = 22$) and reed beds (black bars, $n = 14$) relative to the adjacent canals in 2004 and 2005 in the Brière marsh. Error-bars are standard errors. NS: not significant, $^{*}p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$ for Wilcoxon-signed rank tests

in the two types of wetland habitats (i.e. black bullhead, bream, mosquitofish, rudd, pumpkinseed and European eel) and represented 93.2% of the total catches (Table I). The numerical importance of these six dominant species was different between canals and the two types of wetland habitats (Spearman correlation, $R\text{s} = 0.314$, $p = 0.544$, $n = 6$ for grasslands and $R\text{s} = 0.257$, $p = 0.622$, $n = 6$ for reed beds). Mean abundance of black bullhead was significantly higher in reed beds than in grasslands (Mann–Whitney test, $U = 71$, $p = 0.007$, $n = 36$) and nearly significantly higher for pumpkinseed ($U = 106$, $p = 0.082$, $n = 36$, Figure 2).

Fish propensity to use wetland habitats

Investigations based on Jacob's electivity index yielded three types of fish species response (Figure 3). The first type corresponded to species that did not selectively use wetland habitats: mosquitofish and black bullhead for the two types of wetland habitats (Wilcoxon signed rank test, $Z > 0.284$, $p > 0.500$, $n = 22$ grasslands and $Z = 1.153$

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and -0.847 respectively, $p > 0.249$ $n = 14$ reed beds), and bream in reed beds ($Z = 1.183$, $p > 0.237$ $n = 14$, Figure 3). The second type was composed of bream that avoided grasslands (Wilcoxon signed rank test, $Z = 2.118$, $p = 0.034$, $n = 22$, Figure 3). Three species belonged to the third response type where a significant positive electivity index was found (i.e. a preference for wetland habitats). Pumpkinseed preferentially used reed beds whereas European eel and rudd preferentially used the two types of wetland habitats compared to canals ($Z < -2.293$, $p < 0.022$, Figure 3). A nearly significant preferential use of grassland was also observed for pumpkinseed ($Z = -1.859$, $p = 0.063$, $n = 22$).

Spatial distribution of fish on wetland habitats

Universally, the presence probability curve of the six most abundant species always decreased as the distance from canals increased in grasslands and reed beds but this trend was not similar for all species between the two types of wetland habitats (Figure 4 and Table II). The distances from canals where non-native fish species (black bullhead, pumpkinseed, mosquitofish) were sampled in wetland habitats (data analysed either at the species level or at the species group level) were greater in reed beds than in grasslands. For native species, bream reached greater distances in grasslands than in reed beds, and patterns of use of the two types of wetland habitats by rudd, European eel and the native species group were similar (Table II). In grasslands, rudd used the furthest areas, followed by black bullhead, bream, pumpkinseed, European eel and mosquitofish. In reed beds, black bullhead and rudd used the furthest areas, followed by pumpkinseed, European eel, bream and mosquitofish (Figure 4).

DISCUSSION

The present study provides new insights into the selective use and spatial distribution of native and non-native fish species in different types of wetland habitats. Here, all sampled wetland habitats supported fish while other studies have demonstrated that temporary wetland habitats are partially occupied by fish (site occupancy rate ranging from 21 to 71%, Snodgrass *et al*., 1996; Baber *et al*., 2002). This result suggests that wetland habitats in the Brière marsh are relatively attractive for fish, at least in terms of fish presence. The comparison of the fish community between wetland habitats and adjacent permanent habitats has been poorly investigated (but see Trexler *et al*., 2000; Rehage and Trexler, 2006). Here, we found that differences between the fish communities of these two habitats were very large (species richness, ranks of species and total fish abundance): wetland habitats were only used by some fish species of the marsh (i.e. sampled in canals during the low water period). Furthermore, we found variable responses among species (abundance and spatial distribution) to the type of wetland habitats, and this will be discussed below with regards to species origin.

We also found that fish species exhibited variable propensities to use the two types of wetland habitats, certainly in relation to differences in the functional roles played by wetland habitats for these species. For example, rudd preferentially used both types of wetland habitats compared to canals. This species reproduces in shallow vegetated areas from April to June (Keith and Allardi, 2001) and it probably uses wetland habitats to reproduce. The same preferences were observed for the European eel, a catadromous species. This species may use wetland habitats because they provide higher quantities of food resources than canals and support a limited number of predators (Snodgrass *et al*., 1996; Corti *et al*., 1999), at least until a certain threshold of water level is attained (Kushlan, 1976). In contrast, bream avoided the use of grasslands and reed beds, while roach was abundant in canals and rare in wetland habitats. These species reproduce later in the season and in deeper waters (along canal banks) than the other species and are classified as bottom feeders (Keith and Allardi, 2001). Environmental conditions in wetland habitats might not provide the ecological requirements for spawning and feeding of these species. Non-native species (except pumpkinseed) exhibited the same absence of propensity to use wetland habitats and did not selectively use them. Although little is known about their ability to use wetland habitats outside their native range, these species exhibited an opportunistic use of the two types of habitats (Cucherousset, 2006).

Our results on the relationship between fish presence probability in wetland habitats and the distance from permanent habitats are in agreement with previous studies (Carpentier *et al*., 2004; Rehage and Trexler, 2006). These studies have demonstrated that fish presence probability decreases with increasing distance from permanent habitats. Here, only a narrow area, relatively close to canals (50–80 m, Figure 4), was well used by fish, but fish

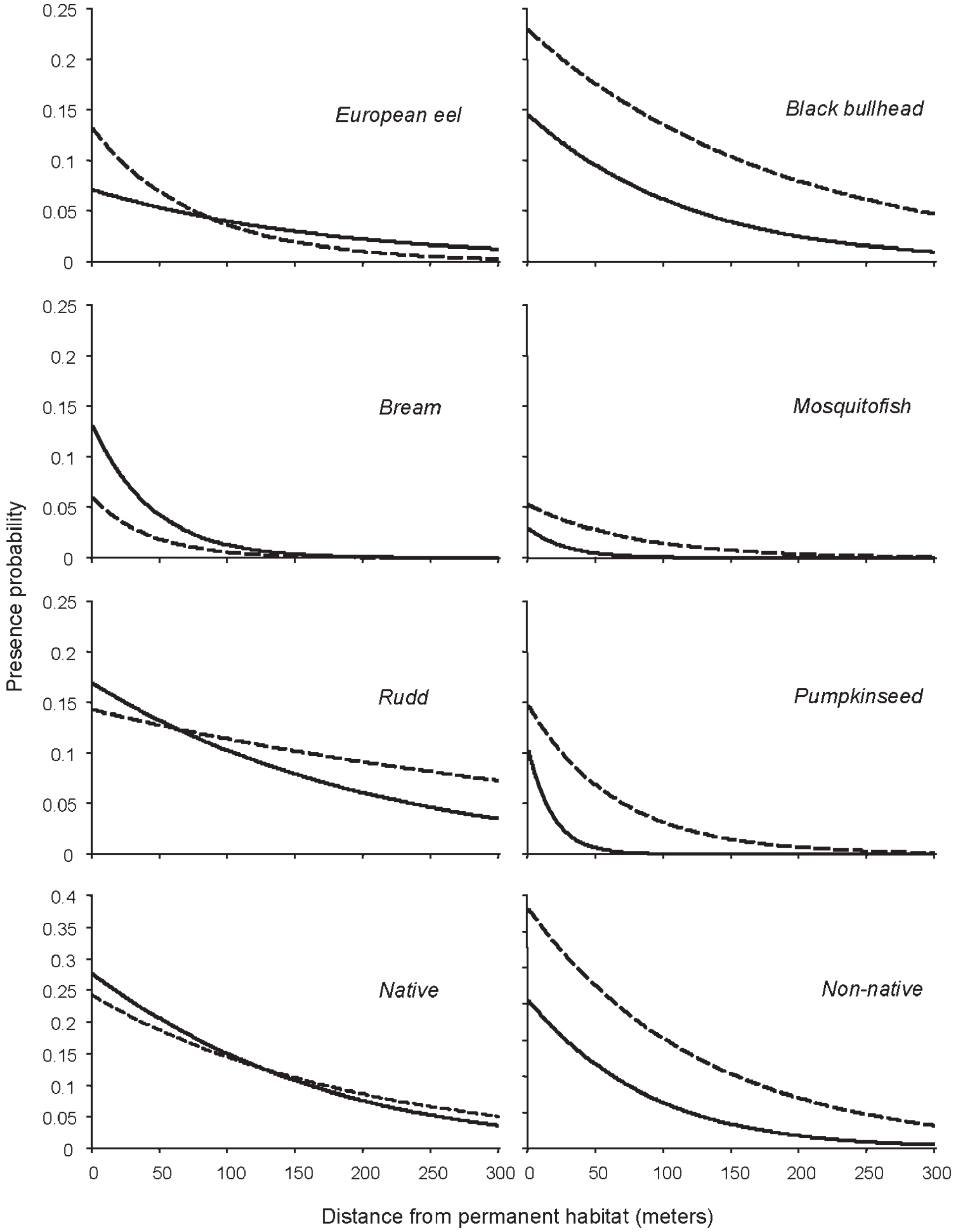

Figure 4. Probability curves (logistic regression) of fish species presence in wetland habitats relative to the distance from permanent habitats (canal, in metres). Models were performed for the six dominant fish species and for the two species groups (i.e. native (left) and non-native (right), and in grasslands (full lines) and reed beds (dotted lines)). See details in Table II for parameters of the models and statistics

presence probability rapidly decreased beyond these distances from canals. We also found that non-native species reached greater distances in reed beds than in grasslands while no differences were observed for native species. Wetland habitats are harsh and spatially varying environments and their use by fish can be interpreted as a trade-off which occurs when physiological, behavioral or ecological traits (e.g. use of wetland habitats) that confer an advantage for performing one function (e.g. reproduction or growth), simultaneously confer a disadvantage for performing another function (e.g. survival or physiological maintenance) due to the reduction of habitats in space,

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Table II. Results of logistic regressions modelling the presence of fish on wetland habitats in relation to the distance from permanent habitats (canals) and the type of wetland habitat (model information and p-values). The models were performed for the six dominant species and for the two species groups (native and non-native) in grasslands ($n = 730$ PAS) and reed beds ($n = 426$ PAS) in 2004 and 2005 in the Brière marsh

Model fitting information and testing global null hypothesis $\beta = 0$

Species	Intercept only	Intercept and covariates	χ^2 for covariates
European eel	−252.569	−245.285	7.284 with 2 d.f. ($p = 0.026$)
Bream	−176.879	−157.916	18.963 with 2 d.f. ($p < 0.0001$)
Rudd	−425.672	−421.263	4.409 with 2 d.f. ($p = 0.1103$)
Native	−550.685	−538.330	12.355 with 2 d.f. ($p = 0.021$)
Black bullhead	−417.710	−397.894	19.816 with 2 d.f. ($p < 0.001$)
Mosquitofish	−88.487	−79.469	9.018 with 2 d.f. ($p = 0.011$)
Pumpkinseed	−189.866	−162.150	27.716 with 2 d.f. ($p < 0.0001$)
Non-native	−488.381	−449.536	38.845 with 2 d.f. ($p < 0.001$)

p-values

Species	Intercept	Habitat	Distance
European eel	<**0.00001**	0.1680	**0.0024**
Bream	<**0.00001**	**0.00002**	**0.0235**
Rudd	<**0.00001**	0.9969	**0.0055**
Native	<**0.00001**	0.8081	<**0.00001**
Black bullhead	<**0.00001**	**0.00003**	**0.0001**
Mosquitofish	<**0.00001**	**0.01918**	**0.0099**
Pumpkinseed	<**0.00001**	**0.00009**	<**0.00001**
Non-native	<**0.00001**	<**0.00001**	<**0.00001**

Differences between the models (with variables and intercept) and the global null model (intercept only) were tested using the likelihood-ratio based on the difference in deviance ($D = -2 \log$ (likelihood ratio)) between the two models. The significance of reduction in deviance was tested by comparing the observed value with a χ^2 distribution (bolded values are significant).

time and quality during drought (Magoulick and Kobza, 2003; Cucherousset *et al*., 2007b). In the wetland habitats, we studied, the availability of resources (i.e. food or spawning substrate) does not decrease as a function of the distance from canals (Cucherousset, 2006), and fish would probably increase their benefits by using less exploited habitats (i.e. far from permanent habitats). At the same time, by exploiting areas far away from refuges (permanent habitats), fish would increase the cost of physiological maintenance and the risk of being trapped in isolated pools as the season progresses. Being trapped would incur adverse costs, such as low survival rates (Poizat and Crivelli, 1997). Our findings showed that the probability of fish presence rapidly decreases as the distance from canals increases. Consequently, the costs of exploiting wetland habitats far from the adjacent permanent habitats are probably higher than the benefits and are variable between species (see the case of non-native species on reed beds and grasslands). These results suggest that non-native species might obtain higher benefits in reed beds than native species. Non-native species (e.g. black bullhead and pumpkinseed) may benefit from some advantages provided by reed beds such as food availability due to the high abundance of invertebrates (Bedford and Powell, 2005). Furthermore, non-native species have generally higher physiological tolerance (e.g. temperature, oxygen concentration) than native species (Marchetti *et al*., 2004; Cucherousset *et al*., 2007b). Mosquitofish and black bullhead are able to tolerate higher water temperatures and lower oxygen levels by using aerial surface respiration (Otto, 1973; McKinsey and Chapman, 1998; Sargent and Galat, 2002). These characteristics might permit non-native species to exploit larger areas on reed beds than native species. Since reed beds have drastically colonized the Grande Brière Mottière marsh during the last 50 years and currently dominate the landscape (Bernard and Rolland, 1990), the capacity of non-native species to exploit reed beds may explain their widespread invasive success observed in the study site.

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