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Letter

Habitat use of an artificial wetland by the invasive catfish *Ameiurus melas*

Abstract – This study examined the distribution and habitat selection of the invasive black bullhead [*Ameiurus melas* (Rafinesque)] in the ditches and surrounded temporary flooded habitats of an artificial wetland in western France. A multiscale approach was used to quantify patterns of *A. melas* abundance in relation to physical habitat characteristics in the ditch network. Young-of-the-year (YOY) and adult *A. melas* largely dominated the local fish assemblage but were highly variable among sites. Although we found evidence for some fine-scale habitat differences for YOY and adult individuals, the abundance of *A. melas* was positively and consistently related to the dominance of reed beds. Furthermore, *A. melas* preferentially used reed beds as opposed to marsh meadows during the flooding period. The results from this study suggest that the invasion of *A. melas* has been facilitated by the expansion of reed beds associated with the diminution of agricultural pressure in recent decades. This study represents an unusual example where human activities can have had an unexpected effect by facilitating an invasive fish species.

**J. Cucherousset[1], J.-M. Paillisson[1],
A. Carpentier[1], M.-C. Eybert[1],
J. D. Olden[2]**

[1]Biologie des Populations et de la Conservation, Université de Rennes 1, Rennes, France, [2]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA

Introduction

Invasive species constitute a major threat to biodiversity and ecosystem integrity and cause substantial economic damage (Vitousek *et al.* 1997; Kolar & Lodge 2001; Lee 2002, Pimentel 2005). Freshwaters are considered one of the most severely degraded ecosystems in industrialised countries (Oberdorff et al. 2002) and have been the recipient of many invasions, in particular by fish species (see Copp et al. 2005; García-Berthou et al. 2005 for review). The success of nonindigenous fish has been widely studied and attributed to several factors including specific life history traits (Olden et al. 2006), phylogeny (Alcaraz et al. 2005) and environmental characteristics including abiotic factors or human use (Moyle & Light 1996; Alcaraz et al. 2005).

Environmental disturbance is known to greatly facilitate fish invasions (Moyle & Light 1996). Habitat modification and fragmentation (e.g., water pollution, construction of dams and water diversions) threaten native fish faunas while favouring the invasion of more tolerant non-native species (Marchetti et al. 2004). In the case of some artificial ecosystems, the decline of traditional human activities can impact local species diversity by favouring the loss and fragmentation of habitat (Wolter 2001). Studies of invasive fish species in artificial environments are particularly rare, although such species often dominate these areas that are now common throughout the landscape. It is the case for the black bullhead [*Ameiurus melas* (Rafinesque)], which was introduced into France from North America in 1871, and is now widespread in Europe (Wheeler 1978), notably with recent records in Spain and Portugal (Elvira 1984; Doadrio 2001; Gante & Santos 2002). Despite its classification as a 'species liable to cause biological disequilibrium' by the French legislation (article R. 232–3 Code rural, see Guevel 1997), few ecological studies have been conducted in its European non-native range (but see Boët 1980).

In the present article, we study the distribution and habitat selection of young-of-the-year (YOY) and adult *A. melas* in an artificial wetland in western

France. We use an integrative approach (Copp 1989; Poizat & Pont 1996) to examine the response of *A. melas* to habitat heterogeneity at two spatial scales: ditch network level and local microhabitat.

Material and methods

Study area

The Brière wetland flows in the estuary of the Loire River (northwest France, 47 °22′N, 02 °11′W) and represents a large freshwater marsh (9000 ha, Fig. 1). It is composed of a complex network of permanently flooded ditches within a patchwork of temporary habitats that flood in winter and progressively dry during spring and summer as a result of the rainfall

regime and water level regulations. Since the last transgression (8000 BP), peat lands have developed and reed beds have progressively settled. Furthermore, the Brière marsh has rapidly changed during the last century as a result of a 3-year flood period during the Second World War and a continuous decrease of many agricultural activities. For instance, grazing decreased greatly (200 bovines and horses in the early 1980s vs. 3000 animals in the early 1900s) and peat extraction ceased completely in the 1950s, whereas 100,000 hl of peat were extracted in the 1880s. The combination of changes in human activities has favoured the development and expansion of reed beds mainly composed of the common reed [*Phragmites australis* (Cav.) Trin. ex Steud.] (Bernard & Rolland 1990). During the last century, the surface area covered by
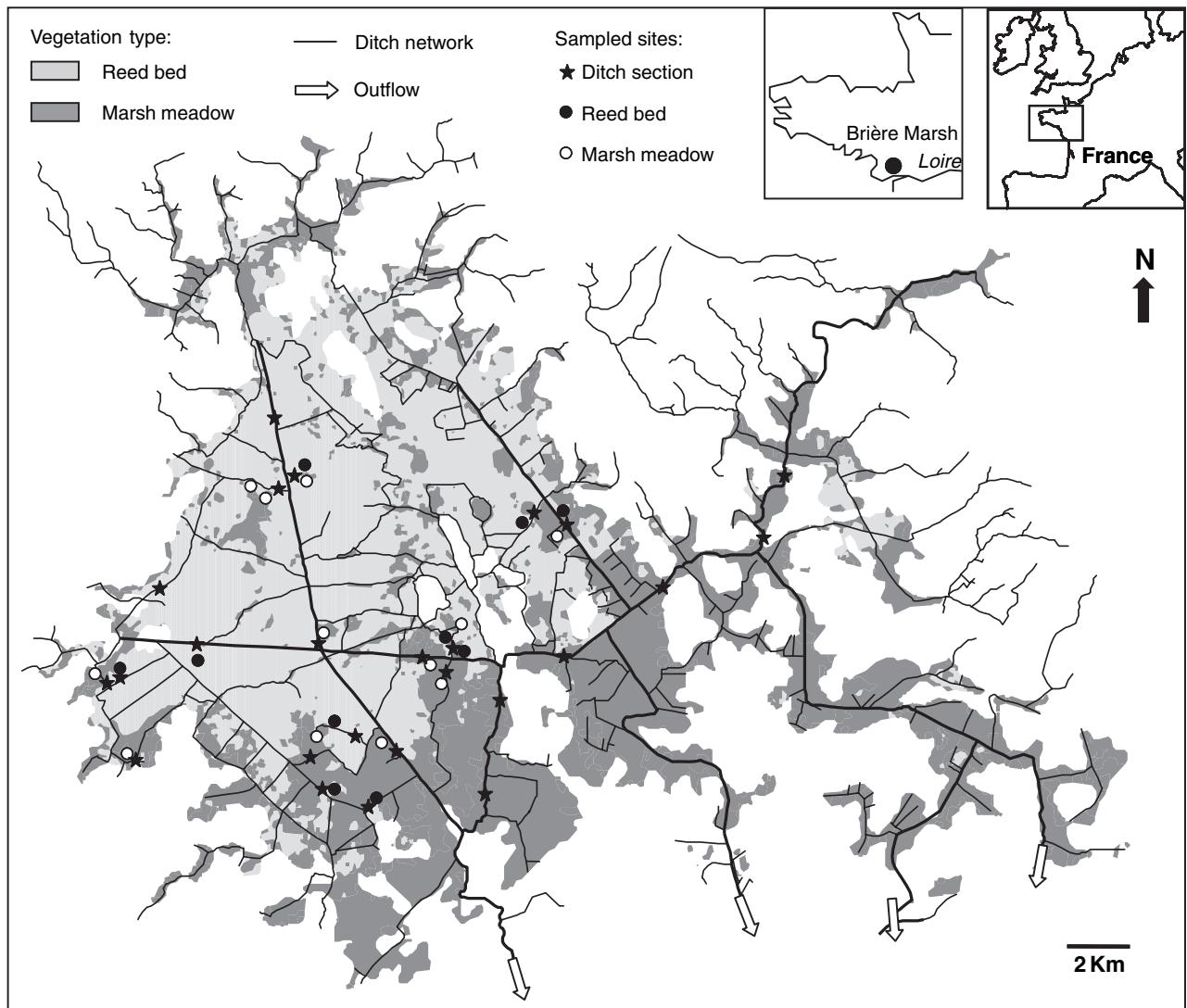

Fig. 1. Map of the Brière marsh illustrating the ditch network and the matrix of temporary habitats (marsh meadow and reed bed). Location of permanent habitats sampled in August 2004 (★) and temporary habitats sampled in April 2004, where reed beds are represented as (●) and marsh meadows as (○).

reed beds increased from 2% to 85% of the total area, and marsh meadows, mainly composed of other Poaceae, decreased from 83% to 10%, the rest being covered by open waters (Bernard & Rolland 1990). These changes in human activities have played a significant role in the loss of native plant and animal species (Bernard & Rolland 1990; Eybert et al. 1998). At the same time, the Brière marsh has experienced several invasion events, and notably that of *A. melas*. Historical data indicate that *A. melas* was introduced in 1929 (Maillard 1972). It is now widely distributed throughout the entire wetland.

Fish sampling

Fish sampling was performed using an electrofishing (FEG 8000, EFKO, Leutkirch, Germany) apparatus (400–600 V and 6–10 A) with a 30-cm diameter anode. This sampling technique was chosen because it is the least destructive, most cost-effective and least biased (good efficiency for capturing all species and most life stages, Persat & Copp 1990). Fish were sampled in two periods of 2004, which were dictated by the pattern of floods, the seasonal configuration of habitats and safety precautions associated with electrofishing. All fish species inhabit the ditch web during drought (hereafter called permanent habitats), and some of them colonise reed beds and meadows (hereafter called temporary habitats) during the flooding season for the purposes of nursery, growing or spawning areas (Carpentier et al. 2004). These latter habitats (10 reed beds and 12 meadows) were sampled in April (Fig. 1) during the recession of water levels (average water depth of 51.0 cm ± 19.1 SD) and before spawning of most species. Given that the efficiency of electrofishing is limited in deeper waters, permanent habitats (25 ditches, Fig. 1) were sampled in August when the water level was low (average water depth of 52.4 cm ± 29.0 SD).

Importantly, fish sampling was performed using the point abundance sampling (PAS) method (Nelva et al. 1979). This procedure involves throwing the anode from a boat to a distance of 5–10 m to limit fish escape and sampling at an interval of ≥50 m. Furthermore, the anode must be thrown in shallow waters to surprise the fish and minimise sampling bias (Persat & Copp 1990). Fish were collected with a net, identified to species, measured to the nearest mm [fork length for all species except total length for European eel *Anguilla anguilla* (Linnaeus)] and immediately released back into water. We followed recommendations of Copp & Garner (1995) concerning the number of PAS per site: 30.0 PAS ± 3.8 per temporary habitat and 26 PAS ± 4.1 per ditch. Each PAS was located using a Global Positioning System to perform spatial analyses. We used size-class distribution profiles to distinguish YOY from adults for each fish species (Carpentier et al. 2004). A threshold of 70 mm was used to distinguish the two age classes in *A. melas*. This fish-size threshold agrees with the findings of Hanchin et al. (2002). Based on specific length–weight relationships defined *in situ* (Cucherousset, unpublished data), we calculated the relative biomass of each fish species.

Environmental characteristics of permanent habitats

We classified ditch size into two categories: those belonging to the primary network (main river or large ditches directly connected to the main river, mean width = 19.7 ± 6.0 m) and those belonging to the secondary network (ditches connected to the primary network level, mean width = 8.9 ± 2.6 m). A set of descriptors of the ditch network in the vicinity of each sampled ditch (ditch network variables) was extracted from a Geographical Information System (ArcView 3.2, Environmental Science Research Institute Inc., Redlands, CA, USA) using land cover and hydrographical network information. These variables represent the degree of connectivity of the ditch network. The number of ditches (ND), number of connections (crossroads between ditches, NC), length of ditches belonging to the primary (LDI) and the secondary (LDII) network levels and total length of ditches (TLD = LDI + LDII) were calculated for each ditch at different radius values (buffer area, calculated at the central part of each site): 200, 400, 600, 800 and 1000 m. This range of radius values corresponds to the mean linear home range values (0.5–2.1 km, Sakaris et al. 2005) for the closely related species, brown bullhead [*Ameiurus nebulosus* (Leseur)].

Four fine-scale (microhabitat) variables were measured at each PAS during fish sampling. Water depth (WD) was transformed into two classes (0–50 cm and >51 cm, after inspection of the distribution frequency of values), substrate (SU) was classified into two types (peat, not peat), vegetation cover (VC) was visually estimated as the percentage of area covered by plants and transformed into two classes (absence or presence) for analyses and adjacent habitat type was categorised as reed beds or marsh meadows.

Data analysis

The PAS from each ditch were analysed collectively at the ditch network scale and punctually at the microhabitat scale (Copp 1989). At the ditch network level, we conducted a series of preliminary analyses to quantify the degree of multicollinearity among continuous variables [length of ditches were $\ln(x + 1)$ transformed]. Next, a principal components analysis was performed on the resulting independent variables

(ND_200, TLD_200, ND_600, TLD_600, 77.5% of the variation in the ditch network descriptors explained by the first two axes) to classify ditches into two groups highlighted by the significant contribution of NC_600 [inertia analysis procedure (Legendre & Legendre 1998), see values in Table 1]. The resulting variable was called 'ditch connectivity' (Table 1). At the same time, we analysed the relationships between three fish descriptors, i.e., abundance (catch per unit effort, CPUE = number of individuals/PAS), relative abundance (%) and relative biomass (%), for YOY and adults of *A. melas* using linear regression analysis.

The relationships between the abundance of each size-class of *A. melas* (dependent variable) and the habitat descriptors at the two spatial scales (independent variables) were analysed separately using general linear models. In these models, a forward selection procedure was applied to the variables with a probability of entry of F of <0.15 and to exclude of >0.20. We also tested for differences in the abundance of

A. melas (CPUE of YOY and adults combined) and for other species in the assemblage (species CPUE and total richness) in the two temporary habitat types (marsh meadows vs. reed beds). Assumptions of normality and homoscedasticity were tested using the Kolmogorov–Smirnov/Lilliefors test and Levene's test, respectively, before performing a t-test. When deviations from normality were detected, nonparametric Mann–Whitney tests were performed. The statistical analyses were performed using STATISTICA (StatSoft Inc., Tulsa, OK, USA) and a critical alpha level of 0.05 was used for all tests.

Results

Distributional patterns of *Ameiurus melas* in permanent habitats

In total, 11,921 individuals (9650 adults and 2271 YOY) belonging to 17 species were captured in permanent habitats (646 PAS), including 5334 individuals of *A. melas* (4524 adults and 810 YOY) (Table 2). *Ameiurus melas* largely dominated the fish assemblage in terms of abundance, relative abundance and relative biomass for both adult and YOY populations followed by bream spp. [silver bream *Blicca bjoerkna* (Linnaeus) and common bream *Abramis brama* (Linnaeus)], roach [*Rutilus rutilus* (Linnaeus)], rudd [*Scardinius erythrophthalmus* (Linnaeus)], mosquitofish (*Gambusia holbrooki* Girard), pumpkinseed [*Lepomis gibbosus* (Linnaeus)] and *A. anguilla* (Table 2). On average, YOY and adults of *A. melas* accounted for 30.3% and 33.8% of the relative abundance and 20.6% and 35.2% of the relative biomass of the fish assemblage, respectively. However, adult abundance varied greatly between sites

Table 1. Summary statistics for the final set of habitat variables used to model *Ameiurus melas* abundance. Reported values are proportions (%) for the categories of the ditch network and microhabitat variables.

Habitat variables	Code	Categories (relative proportion, %)	
Ditch network scale (N = 25 ditches)			
Ditch size	DS	Primary (60.4)	Secondary (39.6)
Ditch connectivity†	DC	Low (68)	High (32.0)
Microhabitat scale (N = 646 PAS)			
Water depth	WD	0–50 cm (55.7)	>51 cm (47.3)
Substrate	SU	Peat (67.6)	Not peat (32.4)
Vegetation cover	VC	Absence (63.6)	Presence (36.4)
Adjacent habitat type	AH	Reed bed (46.1)	Marsh meadow (53.9)

†Ditch connectivity results from a PCA on independent continuous ditch network variables (see the Data Analysis section for more details). The two modalities are mainly derived from NC_600 values (inertia analysis procedure); low: ≤4 ditches in a radius of 600 m around the sampled ditches, high: >4 ditches.

Table 2. Details on fish species sampled in the 25 permanent habitats in the Brière marsh: origin (introduced vs. native), total number, mean (SD) abundance (CPUE), relative abundance (%) and relative biomass (%) for adult and YOY.

Species	Origin†	N		Abundance (CPUE)		Relative abundance (%)		Relative biomass (%)	
		Adults	YOY	Adult	YOY	Adult	YOY	Adult	YOY
Black bullhead, *Ameiurus melas* (Rafinesque)	I	4524	810	7.35 (8.7)	1.19 (0.9)	33.81 (24.4)	30.30 (21.9)	35.20 (24.3)	20.59 (15.9)
Silver bream, *Blicca bjoerkna* (Linnaeus)	N	2015	696	3.05 (2.8)	0.92 (0.7)	22.76 (17.7)	23.57 (17.4)	21.72 (15.2)	19.66 (15.6)
Common bream, *Abramis brama* (Linnaeus)‡									
Roach, *Rutilus rutilus* (Linnaeus)	N	1021	393	1.61 (1.3)	0.79 (0.7)	14.82 (11.1)	19.64 (15.3)	12.36 (10.7)	17.09 (13.9)
Rudd, *Scardinius erythrophthalmus* (Linnaeus)	N	589	130	0.94 (0.9)	0.26 (0.3)	7.15 (5.5)	6.73 (8.0)	4.39 (3.5)	2.59 (3.3)
Mosquitofish, *Gambusia holbrooki* Girard	I	675	§	1.10 (1.3)	§	7.38 (5.8)	§	0.12 (0.1)	§
Pumpkinseed, *Lepomis gibbosus* (Linnaeus)	I	538	49	0.85 (0.7)	0.19 (0.3)	9.97 (13.3)	4.78 (7.3)	6.19 (9.2)	2.01 (3.2)
European eel, *Anguilla anguilla* (Linnaeus)	N	240	123	0.38 (0.3)	0.46 (0.5)	3.50 (3.7)	11.83 (13.5)	11.78 (11.4)	25.23 (23.4)
Others species¶	N–I	48	70	0.07 (0.1)	0.13 (0.2)	0.61 (1.1)	3.15 (5.1)	8.24 (11.4)	12.92 (15.5)

†N for native and I for introduced based on Keith & Allardi (2001).
‡*Blicca bjoerkna* and *Abramis brama* were grouped together because juveniles were not reliably identifiable in the field.
§All *Gambusia holbrooki* were grouped as adult.
¶Others species (mean relative abundance <1%) were Prussian carp *Carassius gibelio* (Bloch) (I), European perch *Perca fluviatilis* Linnaeus (N), northern pike *Esox lucius* Linnaeus (N), common carp *Cyprinus carpio* Linnaeus (I), tench *Tinca tinca* (Linnaeus) (N), largemouth bass *Micropterus salmoides* (Lacepède) (I), bitterling *Rhodeus amarus* (Bloch) (N), three-spined stickleback *Gasterosteus aculeatus* Linnaeus (N) and pikeperch *Sander lucioperca* (Linnaeus) (I).

(range 1.1–84.2%). Because fish abundance (CPUE) was highly correlated with relative abundance (%) and relative biomass (%) for both adults (linear regression, $R^2 = 0.91$, $P < 0.001$ and $R^2 = 0.81$, $P = 0.002$, respectively) and YOY (linear regression, $R^2 = 0.99$, $P < 0.001$ and $R^2 = 0.53$, $P = 0.042$, respectively), we used abundance (CPUE) values to investigate the relationships between *A. melas* abundance and the suite of environmental variables.

Associations between *Ameiurus melas* and environmental characteristics of permanent habitats

At the ditch network level, we found no significant relationship between abundance of YOY and adults and the two habitat descriptors, although *A. melas* abundance was marginally lower in large ditches (Table 3). At the microhabitat scale, YOY and adults were more abundant in locations with peat substrate (Table 4; Fig. 2). We found a number of subtle differences for YOY and adults. Whereas abundance of adults increased with the presence of adjacent reed beds (Fig. 2), this relationship was not observed for YOY (Table 4). YOY abundance was negatively related to water depth (Table 4; Fig. 2), whereas adult abundance was not (Table 4). The VC × WD and WD × SU interactions were significant for adults.

Use of temporary habitats by *Ameiurus melas* and the fish assemblage

In total, we captured 411 individuals (131 *A. melas*) on the temporary habitats (659 PAS), belonging to 13 species. We found no difference in species richness between the two habitat types (marsh meadows vs. reed beds, *t*-test, pooled variance $t = -0.488$, d.f. = 20, $P > 0.05$), whereas more fish (total abundance) were captured in reed beds (Mann–Whitney $U = 24.0$, $P = 0.018$). Abundance (CPUE) of the fish assemblage without *A. melas* was similar between the two types of temporary habitats (Mann–Whitney

Table 3. Results of the general linear model for the abundance (CPUE) of young-of-the-year and adult *Ameiurus melas* [ln($x + 1$) transformed values] performed at the ditch network level ($N = 25$ ditches).

Habitat variable	MS	d.f.	F	P	β
Dependent variable					
Abundance of adult *A. melas*					
DS	0.639	1	3.189	0.089	−0.191
DC	0.007	1	0.034	0.855	−0.019
DS × DC	0.059	1	0.295	0.593	−0.058
Abundance of young-of-the-year *A. melas*					
DS	0.268	1	4.092	0.056	−0.124
DC	0.024	1	0.372	0.549	−0.037
DS × DC	0.101	1	1.547	0.227	0.076

See Table 1 for details on habitat variables.

Table 4. Results of the general linear model for the abundance (CPUE) of young-of-the-year and adult *Ameiurus melas* [ln($x + 1$) transformed values] performed at the microhabitat scale in the 25 sampled ditches ($N = 646$ PAS).

Habitat variable	MS	d.f.	F	P	β
Dependent variable					
Abundance of adult *A. melas*					
AH	4.81	1	19.02	**<0.001**	−0.115
VC	0.02	1	0.09	0.768	0.007
WD	0.40	1	1.59	0.208	−0.029
SU	10.28	1	40.66	**<0.001**	0.157
AH × VC	0.12	1	0.49	0.483	0.016
AH × WD	0.07	1	0.28	0.597	−0.011
AH × SU	0.04	1	0.18	0.675	−0.010
VC × WD	1.49	1	5.88	**0.016**	0.056
VC × SU	0.09	1	0.36	0.548	−0.015
WD × SU	2.17	1	8.57	**0.004**	−0.069
Abundance of young-of-the-year *A. melas*					
AH	0.064	1	0.88	0.350	−0.013
VC	0.083	1	1.13	0.287	−0.014
WD	0.721	1	9.85	**0.002**	0.038
SU	0.807	1	11.02	**0.001**	0.044
AH × VC	0.016	1	0.22	0.642	−0.005
AH × WD	0.105	1	1.44	0.231	−0.014
AH × SU	0.076	1	1.03	0.310	−0.013
VC × WD	0.214	1	2.92	0.088	−0.021
VC × SU	0.057	1	0.78	0.378	−0.011
WD × SU	0.274	1	3.74	0.053	0.024

Significant values are in bold. See Table 1 for details on environmental variables.

$U = 38.5$, $P > 0.05$), but abundance of *A. melas* was significantly higher in reed beds (Mann–Whitney $U = 20.5$, $P = 0.008$) when compared with marsh meadows.

Discussion

In the present study, we found that the contemporary fish assemblage of the Brière marsh is largely dominated by the invasive *A. melas*. Our results provide strong evidence that *A. melas* prefer reed bed habitats, a habitat type that has rapidly invaded the marsh because of the decline of agricultural practices in this artificial ecosystem (Bernard & Rolland 1990). This suggests that *A. melas* may have benefited from the expansion of reed beds in view of (i) the positive relationships found between its abundance and the presence of adjacent reed beds, (ii) the selection of peat substratum in small ditches and (iii) the preferential use of reed beds (vs. marsh meadows) during the flooding period. Although some differences were found between YOY and adult individuals as a consequence of the ontogenetic shift in habitat use from YOY (pelagic habits) to adult (benthic habits) life stages (e.g., Boët 2001). In general, YOY and adult abundance in permanent habitats was both positively correlated with trends derived from the development of reed beds. Indeed, reed beds are highly productive aquatic habitats. They likely affect habitat structure
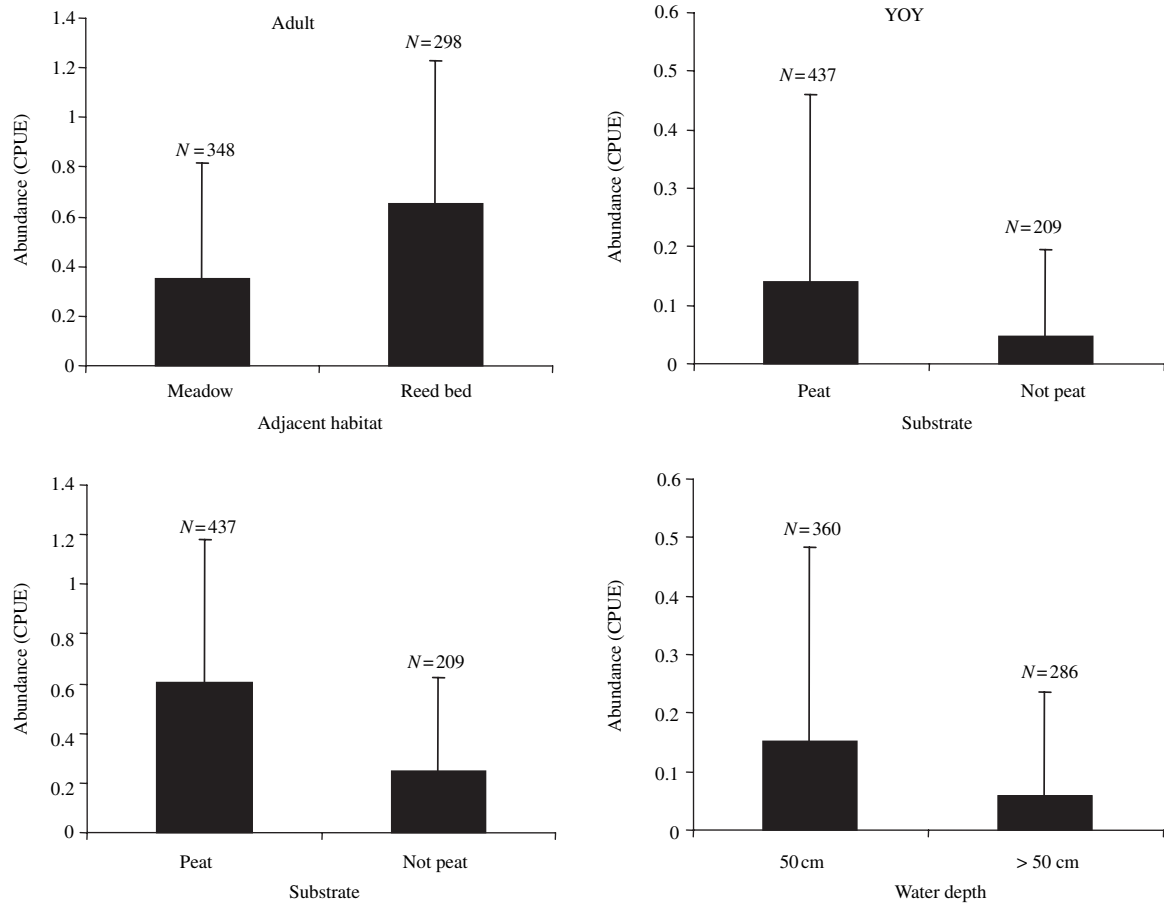
Fig. 2. Adult and young-of-the-year *Ameiurus melas* abundance [mean CPUE ± SD, ln(x + 1) transformation] in permanent habitats in relation to microhabitat variables (N = 646 PAS): adjacent habitat, substrate and water depth. Statistical results are detailed in Table 4. Note different scales on the *y*-axes.

and food resources because of the large amounts of detritus produced, which can remain standing for one or more years in the litter (see details in Mason & Bryant 1975). *Ameiurus melas* may preferentially occupy reed beds during the flooding season for trophic cues, notably the presence of a specific invertebrate assemblage associated with reed bed litter (Bedford & Powell 2005). Moreover, *A. melas* is a species with limnophilic habits (Gante & Santos 2002) and is tolerant to the harsh conditions imposed in many wetlands; therefore, it is likely to benefit from such changes in the abiotic environment. In the same way, we found that *A. melas* illustrates a strong affinity to reed beds as temporary flooded habitats. Furthermore, *A. melas* abundance increases when decreasing water depth (Brown et al. 1999) and the production of a large amount of litter by the reed beds might favour *A. melas* by limiting water depth.

While we are unsure of the specific mechanisms that have led to the invasion success of *A. melas*, it is likely that the presence of other invasive animals has played a facilitative role. For example, we believe that the

recent introduction of the invasive red swamp crayfish [*Procambarus clarkii* (Girard)] in the Brière marsh may have favoured the establishment of *A. melas* by modifying the physical characteristics of the habitat. In fact, *P. clarkii* is known to impact substrate composition (Rodríguez et al. 2005), which may favour limnophilic species like *A. melas* that depend on specific substrate conditions for spawning and nest construction (Braig & Johnson 2003). Moreover, *P. clarkii* might represent a more profitable prey item for *A. melas* compared with smaller invertebrates. Empirical evidence for such patterns would provide support for the invasional meltdown hypothesis of Simberloff & Von Holle (1999), whereby the presence of particular invasive species facilitates the subsequent establishment of other nonindigenous species. Future research addressing these questions is warranted.

During the last 10 years, an active management plan has been undertaken in the Brière wetland to restore marsh meadows through clear-cutting operation and promoting the grazing of reed beds. These restoration activities have already positively affected

the density and species richness of waterfowl assemblage (Eybert et al. 1998). Because physical habitat can mediate biotic resistance to an invader and control invasion success and subsequent impacts (Byers 2002), it would be of interest to investigate whether the restoration of marsh meadows could increase the resistance of this ecosystem to future spread of *A. melas*. Furthermore, the study of the functional use of these temporary flooded habitats and its seasonal variability (Crain et al. 2004) is needed to better evaluate their effects on fish assemblage composition. At the very least, we cite the need to increase our understanding of the autoecology of *A. melas* to better understand the ecological impacts of introduced freshwater fish in artificial environments that are now prevalent across the landscape.

Acknowledgements

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