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CONSEQUENCES OF FISH FARMING DEMISE FOR BIRD AND ODONATE SPECIES RICHNESS IN FRENCH FISHPONDS

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RÉSUMÉ.— *Conséquences de la déprise piscicole sur la richesse spécifique des oiseaux et des Odonates dans des étangs de pisciculture français*.— Les étangs piscicoles sont des écosystèmes artificiels au sein desquels la biodiversité a été modelée par la pisciculture traditionnelle. Les conséquences d'une déprise piscicole y ont été peu étudiées. Ce travail décrit la variabilité de la richesse spécifique des oiseaux nicheurs et des Odonates, sur des étangs 1) encore gérés par des pisciculteurs, 2) abandonnés depuis 4-10 ans, ou 3) abandonnés depuis plus de 10 ans, en Sologne (région Centre Val-de-Loire ; départements : Cher, Loir-et-Cher, Loiret). La richesse de l'avifaune s'avère être principalement favorisée par le développement des ceintures de végétation aquatique, mais cet effet positif n'a pas été constaté sur les étangs abandonnés depuis plus de dix ans. Quatre espèces, le Fuligule milouin *Aythya ferina*, le Fuligule morillon *Aythya fuligula,* le Grèbe à cou noir *Podiceps nigricollis* et le Phragmite des joncs *Acrocephalus schoenobaenus* ont été plus fréquemment trouvées sur les étangs encore gérés pour la pisciculture. Trois d'entre elles sont des benthivores, ce constat pouvant refléter un effet de la présence des Cyprinidés sur la productivité primaire de l'écosystème aquatique. Nos résultats suggèrent donc que la déprise piscicole peut être défavorable à l'avifaune, même si des sites de nidification *a priori* accueillants sont disponibles. Mais l'on doit souligner que les étangs solognots sont de faible productivité piscicole (≤ 150 kg/ha). Nos observations ne sauraient donc être extrapolées à des étangs de pisciculture intensive. La richesse en Odonates semble dépendre de l'étendue des formations végétales riveraines peu élevées. Aucune des espèces observées ne semble être favorisée par l'absence de Cyprinidés. La préservation des ceintures d'hélophytes bas suffit à maintenir la richesse des étangs, indépendamment de la présence/absence de la pisciculture.

SUMMARY.— Fishponds are anthropogenic aquatic ecosystems where biodiversity is shaped by fish farming practices. Little is known on the consequences of fish farming cessation. This study describes the variation of species richness in breeding birds and Odonates, between ponds either managed for fish farming, or abandoned, for 4-10 years or > 10 years, in Sologne (Centre Val-de-Loire region, central France). Bird species richness was primarily favoured by the extent of littoral helophyte belts but this positive effect was not recorded in ponds without fish farming for more than ten years. Four species: the Pochard *Aythya ferina*, the Tufted Duck *Aythya fuligula,* the Black-necked Grebe *Podiceps nigricollis* and the Sedge Warbler *Acrocephalus schoenobaenus* were more frequently found in ponds still stocked with Carp *Cyprinus carpio*. Three of them were benthivorous divers. We hypothesized that this could reflect a carp effect on the ecosystem productivity. Our results therefore suggest that fish farming demise may be detrimental to birds even though adequate nesting sites remain available. It should be emphasized however that fish farming productivity is low in Sologne (≤ 150 kg/ha). Our observations therefore could not be extrapolated to fish ponds with intensive fish farming. Odonate richness seems to depend on the development of low emergent vegetation. The absence of carp stocking did not correlate with higher frequency for any species. Conservation of low helophyte belts then seems to be the proper management to meet Odonate requirements.

Fishponds constitute an important wetland category for wildlife. They provide an example of a man-made aquatic ecosystem in which biodiversity may be positively or negatively affected by their management. Some direct or indirect effects of fish farming intensification have been described as a major constraint for diverse taxa of invertebrates (Weir, 1972; Foster, 1991; Fairchild, 2000), vascular plants (Crivelli, 1983; Meijer *et al*., 1990; Crowder & Painter, 1991; Lougheed *et al*., 1998) or birds (Bouffard & Hanson, 1997; Musil, 2006; Haas *et al*., 2007). In fact, through the effects of fertilization (used to increase primary productivity), more stable water levels, regular drying out periods and control of aquatic vegetation, fish farming management may diversely affect habitat conditions for wildlife (Broyer *et al*., 2016b). Cyprinids may also mobilise both phosphorus through sediment re-suspension and nitrogen through excretion and therefore contribute to enhance the primary productivity of the aquatic ecosystem (Lamarra, 1975; Breukelaar *et al*., 1994; Driver *et al*., 2005; Chumchal *et al*., 2005). While acknowledging that the abundance of zooplankton, aquatic macro-invertebrates, and submersed and emergent vascular plants may be negatively related to fish density in Belgian ponds, Lemmens *et al*. (2013) did not recommend the "zero management" scenario, which may involve a risk of negative alteration of ecosystem functioning in the long term. Hassall *et al*. (2012) underlined the dynamic nature of plant communities in pond systems, some species becoming prevalent at later stages of succession at the expense of certain other taxa such as the charophytes. In Poland, ponds without management for fish farming are characterized in late stages of succession by the lack of certain vascular flora species (Falkowski *et al*., 2009).

Traditional fish farming in European fishpond systems usually relies on temporal draining of water bodies as a method for fish harvesting. Emergent plant species and aquatic macro-invertebrates may be positively affected by this regular frequency of drainage (Lemmens *et al*., 2015). High richness in plant species that are protected by the French legislation similarly depends in the Dombes (eastern France) on drying out periods usually implemented by fish farmers (Broyer & Curtet, 2012). Moreover, the lack of care for controlling bank vegetation after fish farming demise, or for maintaining regular spring water level, may lead to the overgrowth of willows *Salix* sp. to the detriment of helophyte belts and thereby to unfavourable nesting conditions for certain aquatic birds (Petkov, 2006). Mabry and Dettman (2010) postulated that, without active management of aquatic vegetation, some wetlands may not provide suitable habitats for many species of Odonates, particularly those of conservation concern.

Active management of ponds by fish farmers may therefore theoretically affect biodiversity either positively or negatively. European fishpond regions are important hotspots for biodiversity, providing large units of favourable habitats at a scale which is rarely found in other wetland categories. Several centuries of fish farming practices have shaped here communities of aquatic invertebrates and birds. In many regions however, low economic returns on a fish production which is nowadays often rather extensive increase the risk of fish farming abandonment (Falkowski *et al*., 2009; Broyer *et al*., 2015). In French fishpond systems, this recent trend is likely to negatively affect duck breeding conditions (Broyer *et al*., 2016a, b). The objective of this study was to describe the effect of fish farming interruption on the taxonomic richness of breeding birds and Odonates in pond habitats. Scrub succession resulting from the dynamics of uncontrolled willows at the expense of reedbeds or other emergent helophyte stands was considered separately since vegetation control may be achieved through alternative management, independently from fish farming, for hunting purposes or for biodiversity conservation. The study was carried out in Sologne (central France, Centre Val-de-Loire region).

METHODS

STUDY REGION AND SAMPLING METHOD

In Sologne (47° 37'N, 01° 55'E), nearly 3 000 ponds (total surface area: 11 000 ha) were set up on granitic sands and clay, *i.e.* on poor soils favourable to the forest rather than to agriculture (Guellec, 1987). Low primary productivity resulting from soil conditions leads to usually low fish biomass density (≤ 150 kg/ha). Fish farming has strongly declined over the last twenty years and, according to local fish farmers, only 25 % of fishponds are still regularly stocked and harvested.

The data were collected in a sample of 61 ponds, 30 of which (category FF1) being regularly stocked with Carp *Cyprinus carpio* and harvested every year or at least every 2 or 3 years (surface area: 1.9 to 36.8 ha, median = 7.1 ha), and 31 not stocked with fish for at least 4 years. The subsample of abandoned ponds was split into two subequal categories:

FF2 with 15 ponds not stocked with carp for 4-10 years (surface area: 2.9 to 30.5 ha, median = 5.6 ha), FF3 with 16 ponds not stocked for more than 10 years (surface area: 2.1 to 15.9 ha, median = 5.1 ha). All studied ponds were shallow (mean depth of about 1 metre). As a rule, they are not fertilized in Sologne and fish is not artificially fed. Abandoned ponds nevertheless differed by the absence of carp stocking, *vs.* 100-150 kg/ha in fish farming ones. Fish in abandoned ponds was either absent or only present with low population density of smaller non-commercial species. These ponds also differed by the absence of water level control and drying out periods. In principle, the absence of management led in the long term to a scrub succession at the expense of helophyte belts. In order to unravel the specific consequences of *Salix* encroachment from the other, more direct, effects of fish farming absence (no carp stocking, no water level control, no drying out periods), the studied ponds were selected so as to obtain in each fish farming category (FF1 to FF3) a similar proportion of ponds with prevailing high or low emergent helophyte development at the edge of water bodies (> 10 m wide belts in ≥ 25 % of the perimeter) and ponds with *Salix* growth immediately near water in > 50 % of the perimeter (Tab. I). Our results therefore did not represent the actual regional reality since the shores of abandoned ponds most often become fully overgrown by woody vegetation. Direct human disturbance caused by fish farming or by waterfowl hunting cannot be considered here as potential limiting factors for Odonates and for birds during their breeding time. Hunting pressure in particular is usually low and starts after the end of waterfowl breeding period. Moreover, pond access is strictly controlled by the owners and no recreational activity is allowed.

In principle, there is a spatial component for explaining the structure of bird or Odonate communities throughout a pond complex, with fewer species in water bodies situated too far from other source habitats (Mc Cauley, 2006). For Odonates, Raebel *et al*. (2011) found that the presence of another wetland in the surroundings of a pond (within 1600 m for Anisoptera, within 100 to 400 m for Zygoptera) could be a necessary condition for reaching high species richness. For each studied pond, we therefore measured the distance to the closest neighbouring water body.

The objective of this study was to explain inter-pond variability in bird and Odonate species richness with diverse environmental variables and across the fish farming categories. Birds and Odonates were selected as biodiversity indicators because of assumed contrasting tolerance for fish presence and distinct patterns of aquatic vegetation as breeding habitat (Broyer & Curtet 2012).

ENVIRONMENTAL VARIABLES

Sediment samples were collected for physicochemical analysis in March 2014, before the early growth of aquatic vegetation, with a Van Veen dredge (collecting a 5-7 cm layer) in 3 different areas of each pond (near the upper extremity of the water body). The 3 samplings per pond were pooled before analysis of exchangeable calcium, magnesium and potassium, phosphorus (Joret-Hebert method), total Kjeldahl nitrogen and organic carbon. Aquatic vegetation: littoral belts of emergent helophytes and floating or submersed macrophyte stands, was mapped in the field over two successive years, 2014 (half of the sample) and 2015 (the remaining ponds). Transects across water bodies with waders enabled us to assess macrophyte cover in each pond. With the help of aerial photographs, we measured the proportion of pond perimeter with > 10 m wide littoral belts: i) of low helophytes (< 1m high, usually *Juncus* or *Carex*), ii) of high helophytes (> 1 m high, usually *Phragmites*). We measured at the same time water pH as well as water transparency with a Secchi disk.

BREEDING BIRD SPECIES RICHNESS

Species richness indeed is a simple biological indicator. Assessing abundance however would require species-specific methods whereas species richness proved to be a relevant indicator of habitat quality in pond ecosystems for different animal categories, birds included (Hartel *et al*. 2009). Potentially breeding bird species were censused in each pond by a method derived from the Counting Points (Blondel *et al*., 1970). A static observer was situated close to the most vegetated part of the pond edge (most developed helophyte stands) with the possibility left to fully check with a telescope the open water area, without obstacles. During 20 minute-sessions, all birds seen or heard were censused and territorial, nuptial or breeding behaviour, nests or juveniles, were systematically recorded. Three successive censuses were carried out within the periods 15 April-15 May, 15 May-15 June, 15 June-15 July. For each pond, non-passerine species were considered as potentially breeding when adults were observed in at least two sessions or if the presence of chicks was recorded. The presence of favourable nesting habitat (wooded edge or reed bed) was also required for the Ardeidae. Passerine species were included in the list when they were seen or heard in at least 2 sessions or when a singing male was heard in one of the two last records. Of course, the observation of a nest was a conclusive information. This method was applied in 2013 (n = 57 ponds), 2014 (n = 61) and 2015 (n = 58).

ODONATE SPECIES RICHNESS

We searched for Odonate species along transects across and around littoral emergent vegetation. Transect length was 100 m or 2x50 m in small vegetation units. The number of transects was defined so that the different categories of helophyte stands (height, dominant flora) found in each pond were all studied: at least 2 transects per pond, up to 3 or 4 in case of large helophyte belts or diverse habitat categories. The time devoted to observation varied therefore in proportion of habitat complexity. Each one of the 58 ponds (30 in 2014 and 28 in 2015) was visited twice, in May and in July, to establish a list of species observed at least in one visit. The year effect was controlled by the fact that half of the ponds were studied in 2014 or in 2015 in each fish farming category. For each pond, Odonates and aquatic vegetation were described the same year.

DATA ANALYSIS

The main variable of interest to explain the observed variations in our biodiversity indicators was fish farming management. Before modelling the variation in bird and Odonate species richness with diverse explanatory variables, it was necessary to compare the environmental characteristics of the ponds from each fish farming category. We used ANOVAs with Bonferroni correction. The data on aquatic vegetation were collected over two successive years, 2014 for half of the sampled ponds, 2015 for the others. Odonate richness was measured the same way in the same ponds. Bird richness was measured on the complete sample annually in 2013, 2014 and 2005. We retained for each pond the highest annual score.

To explain the variations in bird or Odonate species richness, we used GLMs with the following explanatory variables: fish farming categories (FF) (n = 3), the distance to the closest pond (CP), the abundance of high helophytes (HH), of low helophytes (LH), of high + low helophytes (HLH), macrophyte cover (MA), water pH (PH), water transparency (WT) and the physicochemical characteristics of the sediment. Models were compared with their AICc scores. We only show here the models with the highest AICc scores (n = at least 7 models including all those with AICc weight > 0) + the null model. The finally retained models were those within ΔAICc < 2 (Burnham & Anderson, 2002). The conclusions were validated by graphical plotting of the results.

We also compared with discriminant analyses and with Fisher's exact tests the distribution of each bird species and each Odonate species across the FF categories, provided that it was found in at least five ponds of one category.

All calculations were conducted with R 64 3.0.3.

RESULTS

VARIATION OF ENVIRONMENTAL VARIABLES ACROSS FF CATEGORIES

No significant differences between FF categories were observed for pond surface area, for organic carbon, total nitrogen, phosphorus, potassium, calcium and magnesium in sediments, for water transparency (Tab. 1) (ANOVAs with Bonferroni correction: all P > 0.1). Water pH was higher in FF2 than in FF1 (P = 0.016) but no difference was recorded between FF3 and the two other categories. As a result of the sampling procedure, the percentage of pond perimeter with helophyte stands > 10 m wide did not differ significantly across FF categories (FF1: 47 ± 34 %, FF2: 56 ± 26 %, FF3: 47± 37 %). Macrophyte cover was usually low (FF1: 5.0 ± 9.3 %, FF2: 15.7 ± 27.2 %, FF3: 5.6 ± 18.8 %) and the difference across FF categories was not significant (ANOVA with F = 1.935, P = 0.15).

TABLE I

Results of ANOVAs comparing pond characteristics across the 3 FF categories

	F	P
Water transparency	0.962	*0.39*
Water pH	4.293	*0.02*
Organic carbon	0.166	*0.85*
Calcium	2.286	*0.11*
Total nitrogen	0.442	*0.65*
Phosphorus	1.912	*0.16*
Potassium	1.864	*0.16*
Magnesium	2.849	*0.07*
Total pond area	2.302	*0.11*
Water area	2.091	*0.13*
Macrophyte cover	1.935	*0.15*

As all the chemical variables describing the sediment were highly correlated (all p-values ≤ 0.001), we then used organic carbon (OC) as a unique descriptor of sediment characteristics.

BIRD SPECIES RICHNESS

Bird species richness was positively correlated with pond size and was therefore divided by the square root of surface area to compare ponds of different sizes (no correlation between so-corrected species richness and pond surface area). The most parsimonious model within ΔAICc <2 included the interaction between helophyte (high + low) abundance and fish farming categories (FF), water transparency and organic carbon in the sediment. Only the effects of the HLH*FF interaction and of helophyte abundance were significant in the model (P < 0.005) (Tab. II). Bird species richness increased with helophyte abundance in ponds still managed for fish farming or in ponds abandoned for < 10 years, but the development of helophyte belts did not improve bird richness in ponds abandoned for > 10 years (Fig.1).

TABLE II

Model selection using AICc between GLMs explaining the variation of bird species richness corrected by the square root of pond surface area, with fish farming management (FF in three categories: harvested during the last three years, abandoned for 4-10 years, abandoned for more than 10 years), distance to the closest pond (CP), water transparency (WT), water pH (PH), high helophyte abundance (HH), high + low helophyte abundance (HLH), macrophyte abundance (MA), organic carbon in sediment (OC). Sologne, 2013-2014-2015

	n	k	AICc	ΔAICc	w
HLH*FF+HLH+FF+OC+MA	57	7	148.28	0.08	0.45
HLH*FF+HLH+FF+OC+MA+CP	57	8	148.20	0,00	0.47
HLH*FF+HLH+FF+OC+CP	57	7	153.47	5.27	0.03
HLH+FF+OC+MA+CP	57	6	154.15	5.95	0.02
HLH*FF+HLH+FF+MA+CP	57	7	154.60	6.40	0.02
HLH+FF+OC+MA+CP+WT+PH	57	9	158.93	10.73	0,00
HLH*FF+HLH+FF	57	5	159.33	11.13	0,00
(*)	57	1	224.45	76.25	0,00

	Est.	s.e.	z	p
Intercept	1.503	0.427	3.52	0.0009
HLH*FF	-1.053	0.354	-2.97	0.004
HLH	2.362	0.704	3.35	0.001
FF	0.291	0.209	1.39	0.17
OC	-0.006	0.004	-1.39	0.17
MA	0.875	0.656	1.33	0.19
CP	-0.001	0,00	-1.58	0.12

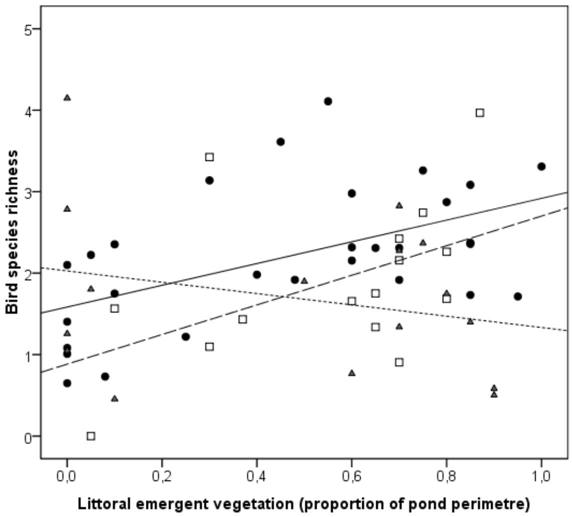

Figure 1.— Bird species richness (number divided by the square root of pond surface area) in relation to the abundance of littoral vegetation (proportion of pond perimeter with high + low helophyte stands > 10m wide), in ponds with active fish farming (black circles and solid line), abandoned for < 10 years (white squares with dashed line), abandoned for > 10 years (grey triangles with dotted line). Sologne, 2013-2014-2015.

Four species were found to be significantly more frequent in ponds with active fish farming than in ponds of the two other categories: the Pochard *Aythya ferina* and the Sedge Warbler *Acrocephalus schoenobaenus* in 2014 and in 2015, the Tufted Duck *Aythya fuligula* and the Black-necked Grebe *Podiceps nigricollis* in 2014 (Fisher's exact tests with P values < 0.05) (Tab. III). The discriminant analysis confirmed the relationship between FF1 and these four species (positive ordinates on the first axis) and suggested a possible link between *Ardea cinerea* and FF2 (negative ordinates on both axes) (Fig. 2).

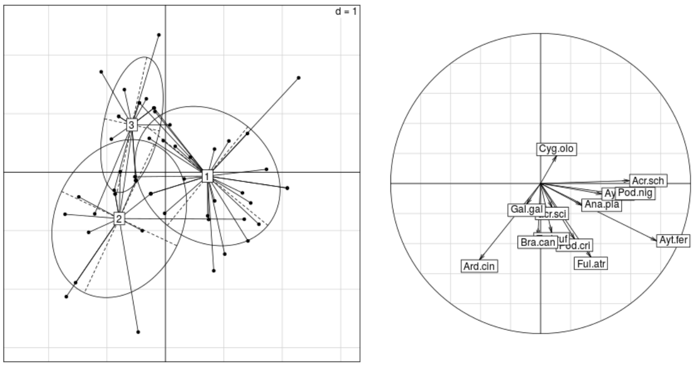

Figure 2.— Bird species coordinates on the two first axes of the discriminant analysis, compared to the distribution of the 3 FF categories. Each species is named by the first 3 letters of their genus and species names (for complete names, see Tab. III). Sologne, 2013-2014-2015.

TABLE III

Bird species occurrence (n ponds, in italics) and frequency (subsample proportion, in roman) in Sologne ponds with fish farming (FF1), abandoned for 4-10 years (FF2) or for > 10 years (FF3)

	FF1						**FF2**						**FF3**					
	2013		**2014**		**2015**		**2013**		**2014**		**2015**		**2013**		**2014**		**2015**	
Acrocephalus schoenobaenus	*10*	0.33	*12*	0.40	*14*	0.47	*1*	0.08	*0*	0,00	*1*	0.08	*1*	0.07	*1*	0.06	*3*	0.19
Acrocephalus scirpaceus	*11*	0.37	*14*	0.47	*16*	0.53	*7*	0.58	*6*	0.40	*4*	0.33	*4*	0.27	*5*	0.31	*8*	0.50
Alcedo atthis	*0*	0.00	*1*	0.03	*5*	0.17	*0*	0.00	*1*	0.07	*1*	0.08	*0*	0.00	*1*	0.06	*1*	0.06
Anas clypeata	*0*	0.00	*2*	0.07	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0,00	*0*	0.00	*0*	0,00	*0*	0,00
Anas crecca	*0*	0.00	*2*	0.07	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0,00	*0*	0.00	*0*	0,00	*0*	0,00
Anas platyrhynchos	*15*	0.50	*24*	0.80	*16*	0.53	*6*	0.50	*9*	0.60	*4*	0.33	*8*	0.53	*9*	0.56	*5*	0.31
Anas querquedula	*0*	0.00	*1*	0.03	*2*	0.07	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00
Anas strepera	*2*	0.07	*3*	0.10	*3*	0.10	*0*	0.00	*0*	0.00	*0*	0.00	*1*	0.00	*0*	0.00	*0*	0.00
Ardea cinerea	*0*	0.00	*1*	0.03	*1*	0.03	*2*	0.13	*5*	0.33	*5*	0.42	*1*	0.07	*1*	0.06	*3*	0.19
Ardea purpurea	*1*	0.03	*1*	0.03	*1*	0.03	*1*	0.08	*0*	0.00	*0*	0.00	*1*	0.07	*1*	0.06	*1*	0.06
Aythya ferina	*13*	0.43	*20*	0.67	*14*	0.47	*3*	0.25	*3*	0.20	*2*	0.17	*2*	0.13	*0*	0.00	*2*	0.13
Aythya fuligula	*8*	0.27	*10*	0.33	*7*	0.23	*0*	0.00	*1*	0.07	*1*	0.08	*1*	0.07	*1*	0.06	*2*	0.13
Branta canadensis	*0*	0.00	*3*	0.10	*0*	0.00	*0*	0.13	*2*	0.13	*3*	0.25	*0*	0.00	*0*	0.00	*0*	0.00
Chlidonias hybrida	*0*	0.00	*3*	0.10	*1*	0.03	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00
Cygnus olor	*6*	0.20	*7*	0.23	*6*	0.20	*3*	0.25	*1*	0.07	*1*	0.08	*3*	0.20	*3*	0.19	*3*	0.19
Egretta garzetta	*0*	0.00	*1*	0.03	*1*	0.03	*0*	0.00	*0*	0.00	*1*	0.08	*1*	0.07	*1*	0.06	*1*	0.06
Emberiza schoeniclus	*4*	0.13	*3*	0.10	*4*	0.13	*0*	0.00	*0*	0.00	*0*	0.00	*1*	0,00	*0*	0.00	*0*	0.00
Fulica atra	*23*	0.77	*24*	0.80	*23*	0.77	*7*	0.58	*10*	0.67	*8*	0.67	*10*	0.67	*6*	0.38	*8*	0.50
Gallinula chloropus	*0*	0.00	*8*	0.27	*8*	0.27	*0*	0.00	*5*	0.33	*3*	0.25	*0*	0.00	*4*	0.25	*6*	0.38
Larus ridibundus	*2*	0.07	*3*	0.10	*1*	0.03	*0*	0.00	*0*	0.00	*0*	0,00	*1*	0.07	*1*	0.06	*0*	0.06
Locustella naevia	*2*	0.07	*1*	0.03	*3*	0.10	*0*	0.00	*1*	0.07	*1*	0.08	*0*	0.07	*0*	0.00	*0*	0.00
Nycticorax nycticorax	*0*	0.00	*1*	0.03	*1*	0.03	*0*	0.00	*1*	0.07	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00
Phalacrocorax carbo	*0*	0.00	*1*	0.03	*1*	0.03	*0*	0.00	*0*	0.00	*0*	0,00	*0*	0.00	*0*	0.00	*1*	0.06
Podiceps cristatus	*18*	0.60	*21*	0.70	*19*	0.63	*9*	0.75	*9*	0.60	*5*	0.42	*6*	0.40	*6*	0.38	*5*	0.31
Podiceps nigricollis	*4*	0.13	*8*	0.27	*6*	0.20	*2*	0.13	*0*	0.00	*0*	0.00	*3*	0.07	*0*	0.00	*1*	0.06
Rallus aquaticus	*0*	0.00	*2*	0.07	*2*	0.07	*0*	0.00	*1*	0.07	*0*	0.00	*1*	0.00	*0*	0.00	*0*	0.00
Tachybaptus ruficollis	*3*	0.10	*5*	0.17	*6*	0.20	*4*	0.33	*2*	0.13	*3*	0.25	*3*	0.20	*0*	0.00	*0*	0.00
Vanellus vanellus	*0*	0.00	*1*	0.03	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00	*0*	0.00

ODONATE SPECIES RICHNESS

No relationship with pond surface area was recorded for Odonate species richness. The selected model included the abundance of low helophytes, macrophyte cover and water pH. Adding FF or CP to this model increased the AICc score so that ΔAICc was >2 (Tab. IV).

TABLE IV

Model selection using AICc between GLMs explaining the variation of odonate species richness, with fish farming management (FF in three categories: harvested during the last three years, abandoned for 4-10 years, abandoned for more than 10 years), distance to the closest pond (CP), water transparency (WT), water pH (PH), low helophyte abundance (LH), high helophyte abundance (HH), macrophyte abundance (MA), organic carbon in sediment (OC). Sologne, 2014-2015

	n	k	AICc	ΔAICc	w
HL+MA+PH	54	4	315.84	0,00	0.60
LH+MA+PH+CP	54	5	318.25	2.41	0.18
LH+MA+PH+FF	54	6	318.81	2.97	0.14
LH+MA	54	3	319.62	4.26	0.07
LH+MA+FF+OC+CP+WT+PH	54	9	326.45	10.61	0,00
LH+HH+FF+OC+MA+CP+WT+PH	54	10	329.42	13.58	0,00
LH	54	2	330.42	14.58	0,00
(*)	54	1	346.00	30.16	0,00

	Est.	s.e.	z	p
Intercept	6.408	5.096	1.26	0.21
LH	7.886	1.988	3.97	0.0002
MA	-0.280	3.079	-0.09	0.93
PH	0.703	0.897	0.78	0.44

Odonate species richness was positively influenced by the abundance of low littoral vegetation (P = 0.0002), without any observed difference between fish farming categories (Fig. 3).

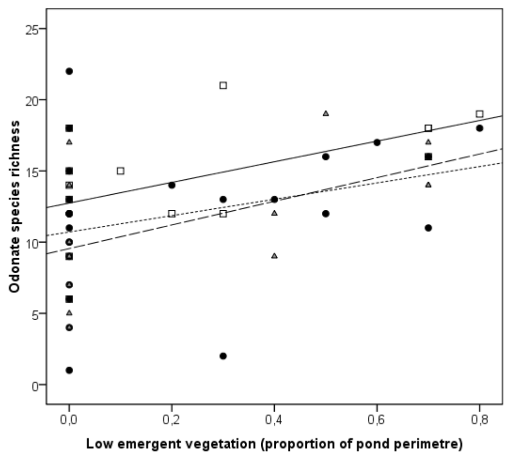

Figure 3.— Odonate species richness in relation to the abundance of low littoral vegetation (proportion of pond perimeter with helophyte stands > 10m wide), in ponds with active fish farming (black circles and solid line), abandoned for < 10 years (white squares with dashed line), abandoned for > 10 years (grey triangles with dotted line). Sologne, 2014-2015

For none of the species found in this study did the frequency differ across FF categories (Fisher's exact tests with all P values > 0.05) (Tab. V). The discriminant analysis showed that virtually all observed species were on the negative ordinates of the first axis, along with high species richness, but without correlation with fish farming presence/absence (Fig. 4).

TABLE V

Odonate species occurrence (n ponds, in italics) and frequency (subsample proportion, in roman) in Sologne ponds with fish farming (FF1), abandoned for 4-10 years (FF2) or for > 10 years (FF3)

	FF1		FF2		FF3	
ZYGOPTERA						
Calopteryx splendens	*3*	0.11	*0*	0.00	*3*	0.19
Calopteryx virgo	*0*	0.00	*3*	0.21	*1*	0.06
Ceriagrion tenellum	*11*	0.39	*0*	0.00	*0*	0.00
Chalcolestes viridis	*9*	0.30	*11*	0.79	*12*	0.75
Coenagrion puella	*18*	0.64	*2*	0.14	*4*	0.25
Coenagrion scitulum	*1*	0.04	*6*	0.43	*5*	0.31
Enallagma cyathigerum	*12*	0.43	*1*	0.07	*1*	0.06
Erythromma lindenii	*2*	0.07	*1*	0.07	*0*	0.00
Erythromma najas	*6*	0.21	*7*	0.50	*6*	0.38
Erythromma viridulum	*5*	0.18	*4*	0.29	*2*	0.13
Ischnura elegans	*26*	0.93	*13*	0.93	*13*	0.81
Lestes barbarus	*2*	0.07	*0*	0.00	*1*	0.06
Lestes dryas	*0*	0.00	*8*	0.57	*10*	0.63
Lestes sponsa	*14*	0.50	*9*	0.06	*5*	0.31
Lestes virens	*4*	0.14	*9*	0.06	*8*	0.50
Platycnemis pennipes	*11*	0.39	*2*	0.14	*0*	0.00
Pyrrhosoma nymphula	*4*	0.14	*1*	0.07	*2*	0.13
Sympecma fusca	*15*	0.54	*8*	0.57	*4*	0.25
ANISOPTERA						
Aeshna affinis	*2*	0.07	*2*	0.14	*0*	0.00
Aeshna isoceles	*7*	0.25	*0*	0.00	*0*	0.00
Aeshna mixta	*1*	0.04	*14*	1.00	*15*	0.94
Anax imperator	*17*	0.61	*2*	0.14	*1*	0.06
Anax parthenope	*5*	0.18	*1*	0.07	*0*	0.00
Brachytron pratense	*8*	0.29	*9*	0.64	*8*	0.50
Cordulia aenea	*19*	0.68	*1*	0.07	*2*	0.13
Crocothemis erythraea	*8*	0.29	*2*	0.14	*2*	0.13
Epitheca bimaculata	*0*	0.00	*3*	0.21	*1*	0.06
Gomphus pulchellus	*2*	0.07	*11*	0.79	*9*	0.56
Leucorrhinia caudalis	*1*	0.04	*12*	0.86	*12*	0.75
Leucorrhinia pectoralis	*4*	0.14	*13*	0.93	*13*	0.81
Libellula depressa	*21*	0.75	*11*	0.79	*11*	0.69
Libellula quadrimaculata	*18*	0.64	*2*	0.14	*1*	0.06
Orthetrum albistylum	*23*	0.82	*5*	0.36	*9*	0.56
Orthetrum cancellatum	*20*	0.71	*3*	0.21	*5*	0.31
Orthetrum coerulescens	*1*	0.04	*1*	0.07	*0*	0.00
Somatochlora flavomaculata	*0*	0.00	*1*	0.07	*0*	0.00
Somatochlora metallica	*0*	0.00	*9*	0.64	*6*	0.38
Sympetrum fonscolombii	*2*	0.07	*1*	0.07	*0*	0.00
Sympetrum meridionale	*7*	0.25	*0*	0.00	*1*	0.06
Sympetrum sanguineum	*19*	0.68	*9*	0.64	*8*	0.50
Sympetrum striolatum	*3*	0.11	*2*	0.14	*0*	0.00

DISCUSSION

Considering that macrophyte and invertebrate diversity was lower in unmanaged ponds in the UK, Sayer *et al*. (2012) advocate the merits of active pond management for biodiversity conservation. Schmidt (1993, 2012), Kalkman and Conze (2015) emphasized the negative consequences on the Odonate species *Sympetrum depressiusculum* of the abandonment of the raising of young carp in temporary flooded conditions before their transfer into permanent ponds. Our results did not point out any negative effect of fish farming on bird or Odonate species richness. No Odonate species was significantly more frequent in ponds after the cessation of carp stocking. Usually low fish biomass density in Sologne (≤ 150 kg/ha) is a possible explanation even though high Odonate specific richness was recorded in the Dombes (centre-east of France) despite fish biomass up to 800 kg/ha (Broyer *et al*., 2009).

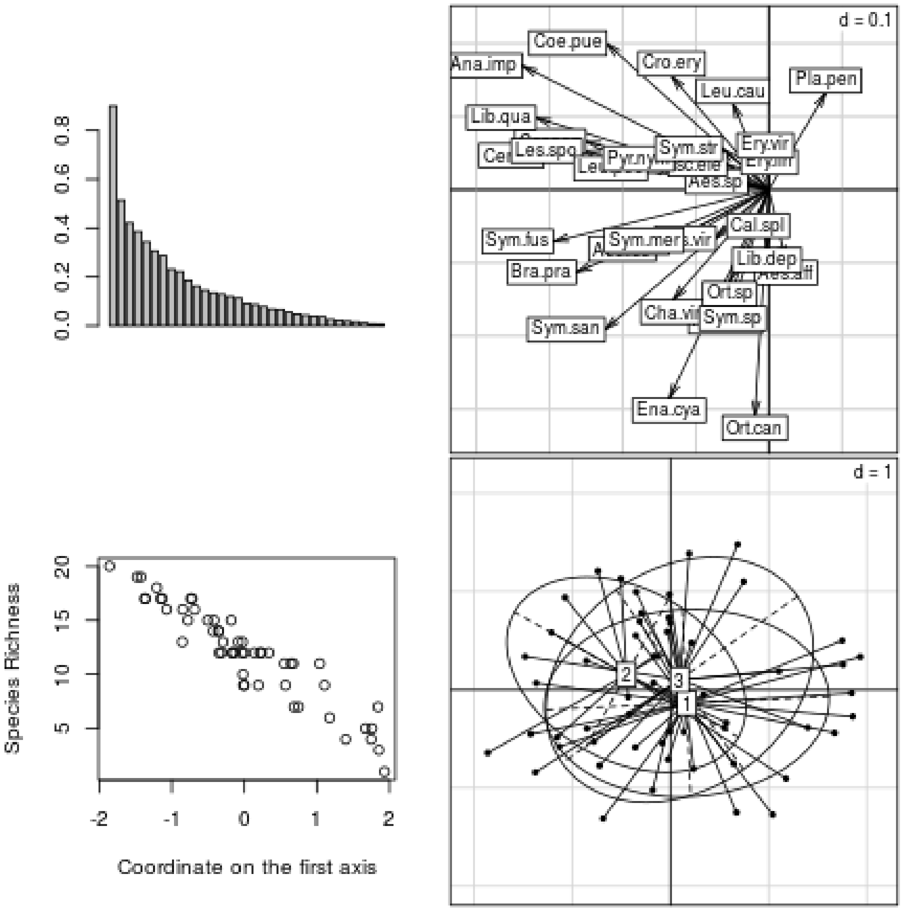

Figure 4.— Odonate species coordinates on the two first axes of the discriminant analysis and variation of species richness per pond on the first axis, compared to the distribution of the 3 FF categories. Each species is named by the first 3 letters of their genus and species names (for complete names, see Table V). Sologne, 2014-2015

Johansson and Brodin (2003) found in Sweden that, while species richness was not affected by the presence of fish, Odonate abundance was higher in waters without fish. In Swedish lakes however, fish is often trout or salmon and such conclusion does not necessarily apply to French fishpond regions. In this study, Odonate species richness was linked to the development of low littoral vegetation, irrespective of fish farming. This result, which points out indirectly the consequences of willow encroachment on helophyte belts in abandoned ponds, suggests strongly that an alternative control of bank vegetation around ponds without fish farming may be adequate for the preservation of Odonate richness.

Similarly, no bird species seemed to benefit from fish farming abandonment. Conversely, four species were found to be more frequent in ponds still managed by fish farmers. Three of them: the Pochard, the Tufted Duck and the Black-necked Grebe are diving (but not primarily fish-eating) birds, which seek for invertebrate-prey under the water surface. This common habit suggests an influence of fish farming on pond carrying capacity for birds through a positive effect on the biomass of aquatic invertebrates, despite the competition for prey between fish and birds (Kloskowski *et al*., 2010). It could be hypothesized that this effect could be linked to a higher productivity of the aquatic ecosystem. Since fishponds are not fertilized here and since the chemical characteristics of their sediment did not differ across FF categories, this effect could possibly be a consequence of the presence of Cyprinids. By stirring the sediment and with their excretions, Carp may indeed contribute to the concentration of nutrients dissolved in water (Lamarra, 1975; Breukelaar *et al*., 1994; Driver *et al*., 2005; Chumchal *et al*., 2005; Matsuzaki *et al*., 2007), thereby elevating pond primary and secondary productivity. Lower attractiveness and lower nesting success for ducks in Forez ponds (centre-east of France) that were abandoned by fish farmers were attributed to the absence of this carp effect on nutrient dynamics (Broyer *et al*., 2016a). The higher frequency of the Sedge Warbler is more difficult to explain. Unlike the other aquatic warblers, this species is not closely associated with emergent littoral vegetation (Thomas, 1984) and the consequences of pond abandonment on terrestrial surroundings (prevalence of forested habitats) should perhaps be taken into account. Bird species richness is nevertheless a positive function of the development of helophyte belts at the edge of water bodies, provided that ponds are still managed for fish farming or abandoned for less than ten years. This positive effect of littoral vegetation was not recorded in case of fish farming cessation in the long term.

In conclusion, our results confirm that:

(*i*) aquatic vegetation is a powerful and cost-effective tool for assessing the ecological status of fishponds and may thereby contribute to the implementation of the E.U. Water Frame Directive (Broyer & Curtet, 2012). Bank helophytes provide nesting places for many waterbird species and Odonates may use emergent aquatic plants as proximate cues of habitat quality or may be attracted by prey abundance in riparian areas with high structural complexity (Remsburg, 2011);

(*ii*) fish stocking does not necessarily impact Odonate species richness. Helophyte belts could limit the exposure to predation on larvae by hampering fish movements in shallow littoral areas and act as refuges before the development of macrophyte beds (Broyer & Curtet, 2011),

(*iii*) fish farming may enhance pond attractiveness for some benthivorous bird species. Extensive fish farming seems therefore to positively contribute to biodiversity in pond systems.

Our results, however, were obtained in ponds with moderate fish biomass density. They cannot obscure the possible negative impacts of fish farming intensification (Broyer & Curtet, 2012).

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