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The influence of fish farming intensification on taxonomic richness and biomass density of macrophyte-dwelling invertebrates in French fishponds

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ABSTRACT

Key-words: *macro-invertebrates, taxonomic richness, biomass density, macrophytes, fish farming*

Fishponds are man-made ecosystems where fish farming may strongly interfere with biodiversity. Intensified practices could be suspected to have a negative impact on animal and plant communities. We investigated the hypothesis that, in French fishponds, taxonomic richness and biomass density of macrophyte-dwelling macro-invertebrates could be influenced by fish stock density and pond fertilization. With a sample of 95 water bodies from three of the most important fishpond regions, studied in 2000, 2001 or 2002, we compared a series of models in which macrophyte cover (in three classes), emergent shore vegetation (in % of pond area) and invertebrate biomass in pond sediment were also considered. Among explanatory variables, macrophyte and helophyte abundance were included in the best models explaining variation in invertebrate taxonomic richness and in biomass density. Taxonomic richness was lower when abundance of both macrophytes and emergent shore vegetation was low ($< 10\%$ and $< 7.5\%$, respectively). Biomass density was higher when macrophyte cover was $\geqslant 10\%$ provided that emergent vegetation was abundant ($\geqslant 7.5\%$). We conclude that fish farming intensification in French fishponds may affect aquatic invertebrate communities, mainly through its impact on the development of aquatic vegetation.

RÉSUMÉ

Influence de l'intensification des pratiques piscicoles sur la richesse taxonomique et la densité de biomasse des invertébrés dans les herbiers de macrophytes des étangs en France

Mots-clés : *macro-invertébrés, richesse taxonomique, densité de biomasse, macrophytes,*

Les étangs piscicoles constituent un écosystème artificiel dans lequel la gestion piscicole est susceptible d'influer fortement sur l'expression de la biodiversité. En particulier, les pratiques intensifiées peuvent influencer négativement les communautés animales et végétales. Nous avons étudié l'hypothèse selon laquelle, dans les complexes d'étangs français, la richesse taxonomique et la densité de biomasse des macro-invertébrés vivant au sein des herbiers de macrophytes pouvaient être influencées par la densité du peuplement piscicole et par la fertilisation des étangs pour la pisciculture. Avec un échantillon de 95 étangs choisis dans trois régions majeures de pisciculture, étudiés en 2000, 2001 ou 2002, nous avons

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pisciculture en étangs

comparé une série de modèles dans lesquels le recouvrement des herbiers de macrophytes, la végétation émergente riveraine et la biomasse des invertébrés du sédiment étaient également pris en considération. Parmi les variables explicatives, seuls le recouvrement des macrophytes et celui des hélophytes sont inclus dans les modèles sélectionnés pour expliquer la variation de la richesse taxonomique et de la densité de biomasse des invertébrés. Nous concluons que l'intensification de la pisciculture dans les systèmes d'étangs français affecte les communautés d'invertébrés principalement par ses impacts sur le développement de la végétation aquatique.

INTRODUCTION

Fishpond complexes are important hot-spots for biodiversity in Europe. In these man-made ecosystems, fish-farming management may strongly interfere with taxonomic richness and abundance of individuals in bird communities (Bukacińska *et al.*, 1996; Lutz, 2001), threatened plants (Broyer *et al.*, 1997; Spalek, 2006), or amphibians (Joly *et al.*, 2001; Hartel *et al.*, 2007).

Aquatic invertebrates play a central role in the fishpond ecosystem as a major food resource for many predatory organisms (Broyer and Curtet, 2010). Moreover, legally protected species included in appendices of the Bern Convention or the E.U. Habitats Directive may occur in this ecosystem (Jolivet, 2006; Buczyńska *et al.*, 2007, Broyer *et al.*, 2009). Since fish predation is likely to influence abundance and composition of invertebrate communities (Thorp *et al.*, 1997; Reshetnikov, 2003; Fisher, 2005), invertebrate biomass or taxonomic richness in fishponds could be expected to be negatively affected by fish stock density. Pond managers may also increase the water volume by scrapping shallow littoral areas and then reduce surface areas where emergent shore vegetation might develop. Pond fertilization implemented by fish farmers may increase phytoplankton biomass, thereby altering water transparency and conditions for macrophyte development. This tends to be followed by an increase in zooplankton prey for carps (Wurts, 2004) and macro-invertebrates.

Our objective was to assess the influence of fish farming intensification on macrophyte-dwelling macro-invertebrates in French fishpond systems. Generally, carps *Cyprinus carpio* form the bulk of fish production and invertebrates constitute an important part of the carp's diet (Juget *et al.*, 1972). Macrophytes may however act as physical refuges for invertebrates and thus potentially reduce the predation effect (Diehl and Kornijów, 1998). To investigate the impact of fish farming on invertebrate taxonomic richness and biomass density, this study aims at answering the following question: are quantitative and qualitative variations in macro-invertebrate communities across fishponds mainly influenced by fish density or pond fertilization?

MATERIAL AND METHODS

> *FISHPOND SELECTION*

The study was carried out in three of the most important fishpond complexes in France: Brenne in central France, Dombes and Forez in eastern France. Brenne and Dombes have more than 1000 ponds each, Forez has 250.

We selected 20 ponds per region and per year, in Brenne and Dombes in 2000 and 2001 (n = 80), in Forez in 2002 (n = 20). Ponds were selected so as to avoid extreme characteristics, in size (neither too small nor too large), in management (all ponds were managed according to traditional local fish farming), in surrounding environment (none was totally surrounded by woodland). Moreover, the sample had to capture enough variation in fish stock density and fish farming practices (presence/absence of fertilization). Although fish farming practices were very similar across the study regions, 10.3% of the selected ponds were fertilized in Dombes, and 52.3% in Brenne, with higher fish stock density in fertilized ponds (329 kg·ha^{-1} ± 125 SD *vs*. 195 ± 80 SD). In Forez, ponds were not fertilized but phosphoric industrial residues have been added to the sediments from the 1930s to the late 1980s. Forez fishponds were thus not considered in the study relating to the influence of fertilization. We also discarded five ponds (one from Dombes, two from Forez, two from Brenne) that had no macrophytes. The total sample was therefore made up of 95 waterbodies. Mean surface areas were 22 ha (± 17 SD) in Dombes, 13 ha (± 9 SD) in Brenne, 14 ha (± 11 SD) in Forez.

> INVERTEBRATE SAMPLING AND DESCRIPTION

Invertebrate taxonomic richness and biomass density in submerged and floating leaves of macrophytes were studied once macrophyte beds were fully grown (mid-June). The vegetation (mainly *Potamogeton* sp., *Chara* sp., *Callitriche* sp., *Ranunculus peltatus, Najas marina* and *N. minor*, *Myriophyllum spicatum* and *Ceratophyllum demersum*) was sampled by two operators with a square (25 cm × 25 cm) landing net (0.1 mm mesh) to collect the plant parts found in the upper first 25 cm of the water column. Floating and submerged vegetation was collected in the landing net, which was kept vertically, at a constant depth and over a maximum distance of 1 m. The net was plunged vertically, very slowly in the middle of the selected macrophyte stands, then swiftly pulled forward and extracted from the water in horizontal position with collected vegetation hanging inside. The latter was then cut with scissors so as to fall either inside or outside the net. The operation was done as quickly as possible to prevent invertebrates from escaping (Downing and Cyr, 1985). Despite the fact that invertebrate biomass and taxa richness could be higher along the edge than inside the macrophyte beds when vegetation density is high (Sloey *et al.*, 1997, but see Strayer *et al.*, 2003), we collected plant samples in the centre of the beds, where the impact of fish predation was expected to be lower (but see Fisher, 2005). Indeed, fish predation is selective and large taxa are generally more vulnerable (Crowder and Cooper, 1982; Morin, 1984; Blois-Heulin *et al.*, 1990; Diehl, 1992). Three samples of the most representative aquatic vegetation were collected in each pond and pooled. The collected vegetation volume was measured by water displacement in a test tube and the shifted volume of water after the introduction of plant material was directly used as a reference to compare invertebrate biomass density between different sites (in mg·L^{-1} of macrophytes *i.e.* in mg·L^{-1} of water displaced by plant material in the test tube). Species specific composition of macrophyte beds was not taken into account (see Deák *et al.*, 2008; Broyer and Curtet, 2010).

Invertebrates were separated from plants under a water flow and sorted by successive sieving (2 mm mesh, then a 0.5 mm one). According to Morin *et al.* (2004), a 1-mm sieve retains on average > 90% of the invertebrate biomass. Invertebrates were identified at the family level (Tachet *et al.*, 2000).

Invertebrate biomass density in sediments was also measured as one of the explanatory variables. A 10-cm-thick layer of sediment was collected in a 225-cm^2 area with an Ekman dredge. For each pond, samples were taken at three different places at the upper extremity (opposite to the outlet) of the water body at a depth of less than one metre: i) in clear aquatic vegetation, ii) at the interface between aquatic vegetation and open water *i.e.* non vegetated areas, iii) in open water. The three samples were pooled prior to invertebrate biomass measurements. Collected sediments were sub-sampled in a squared box with 49 compartments. Analysed compartments were randomly selected until at least 200 individuals were found.

Biomass (dry weight) was measured after desiccation for 24 h at 60 °C. Invertebrate biomass density in sediment was expressed in g·m^{-2}.

> FISHPOND DESCRIPTION

Macrophyte abundance was visually estimated during the sample collection and separated into three classes of bed surface area (1 = < 10% of pond area, 2 = [10–30%[, 3 = ⩾ 30%), after a systematic search for vegetated areas while walking: 1) along the whole pond perimeter and 2) across water bodies, wearing waders. The surface area of littoral emergent vegetation (*Phragmites communis, Typha angustifolia* and *T. lalifolia, Carex* sp*., Scirpus lacustris, Juncus effusus* and *J. conglomeratus, Phalaris arundinacea, Glyceria maxima*) was measured from aerial photographs and transformed into percentages of the total pond area. Data on fish stock density and information about fertilization (presence/absence) were obtained by questioning fish farmers. Fish stock data, which corresponded to harvest in winter following the invertebrate study, were not available for 19 ponds (6 in Dombes, 7 in Brenne and 6 in Forez).

> *DATA ANALYSIS*

To explain inter-fishpond variation in taxonomic richness and biomass density of macrophyte-dwelling invertebrates, we used a set of variables selected to describe pond characteristics and management: fish stock density (continuous), fertilization (nominal), macrophyte abundance (ordinal), helophyte abundance (continuous), invertebrate biomass density in sediment (continuous). The influence of fish stock density and that of fertilization were investigated separately with different samples of 76 and 77 fishponds, respectively, because the two variables were strongly correlated (Mann Whitney test: $Z = -4.051$, $P < 0.001$) and to avoid the addition of missing data (all Forez ponds for fertilization and 13 ponds from Dombes or Brenne for fish stock density). For both dependent variables, generalised linear models (GLMs) were used to compare a series of models specified *a priori*, including one or two explanatory variables with or without interactions. Invertebrate biomass density in macrophytes was square-root transformed beforehand for normalization. We selected the best models with Akaike's information criterion (AIC) as recommended by Burnham and Anderson (2002), by retaining the models with the lowest AIC values. Adding the effects of regions (Dombes, Brenne, Forez), years (2000, 2001, 2002) or pond size (in ha) never improved model fit; those variables were thus not included in the presentation of our results. The influence of explanatory variables that were included in the best models was finally analysed graphically with the 95 fish pond sample. In order to analyse the cross-influence of continuous variables, they were transformed into binomial data: $<$ or $\geqslant$ the median value of the sample.

RESULTS

> *RELATIONSHIP BETWEEN TAXONOMIC RICHNESS AND BIOMASS DENSITY*

A positive logarithmic relationship was observed between invertebrate taxonomic richness and biomass density ($r^2 = 0.15$, $P < 0.001$). Actually, taxonomic richness only decreased at very low biomass densities (Figure 1). Neither taxonomic richness nor biomass density were related to pond surface area (Spearman $r_s = -0.015$, $P = 0.89$ and $r_s = -0.1$, $P = 0.29$). Taxonomic richness did not vary across the three study regions ($F_{2,92} = 0.043$, $P = 0.96$) (Table I) but biomass density was higher in Forez ponds ($F_{2,92} = 6.033$, $P = 0.003$) (Table II).

> *VARIATION IN TAXONOMIC RICHNESS*

The best models explaining the variation of invertebrate richness in fishponds included macrophyte abundance and helophyte abundance. Macrophyte abundance alone had a significant effect. The models including fish stock or fertilization only obtained the highest AIC values (Tables III and IV).

Invertebrate taxonomic richness in macrophytes was lower in ponds where macrophytes and helophytes were not abundant ($<$ 10% and 7.5% respectively) (Figure 2).

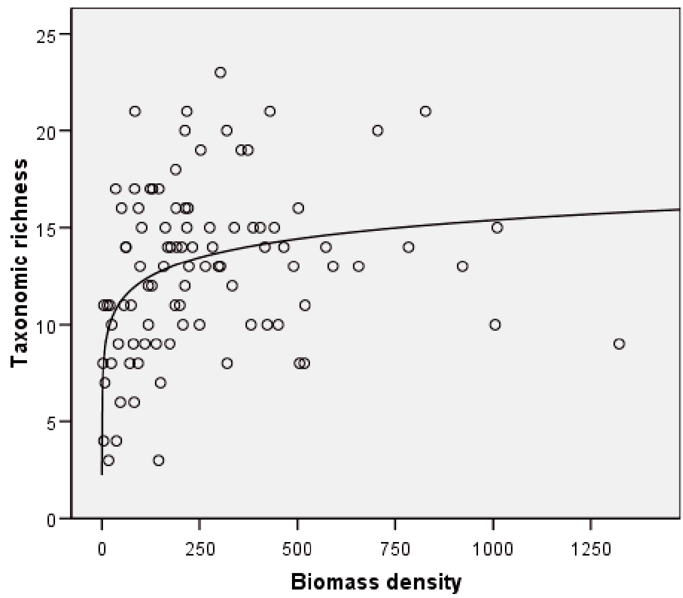

Figure 1
*Relationship between taxonomic (*i.e. *family) richness and biomass density (in mg·L*$^{-1}$ *of macrophyte) of epiphytic invertebrates in French fishponds (2000–2002).*

Figure 1
Relation entre la richesse taxonomique et la densité de biomasse (en mg·L^{-1} de macrophyte) des invertébrés épiphytes dans les étangs piscicoles en France (2000–2002).

> *VARIATION IN BIOMASS DENSITY*

Again, the best models contained macrophyte abundance and helophyte abundance with a significant effect of macrophyte abundance, and the models including fish stock or fertilization only had the highest AIC values (Tables V and VI).

Invertebrate biomass density in macrophytes was higher in ponds where macrophyte beds covered ⩾ 10% of the total surface area, provided that helophytes were abundant (⩾ 7.5%) (Figure 3).

Higher invertebrate biomass density in ponds where both helophytes and macrophytes were abundant could contribute to explain the highest biomass densities found in Forez (Table II). Helophyte abundance was ≥ 7.5% in 72.2% of Forez ponds, 65.7% of Brenne ponds and 21.0% of Dombes ponds. Macrophyte cover was ⩾ 30% in 88.9% of Forez ponds, 42.1% of Brenne ponds and 53.8% of Dombes ponds. It should be noted that the influence of aquatic vegetation (macrophytes + helophytes) on invertebrate biomass density was also observed when Forez fishponds were excluded from the analysis (Table V).

DISCUSSION

In French fishponds, taxonomic richness of macrophyte-dwelling invertebrates decreased only at very low biomass densities. No relationship was found between invertebrate richness and pond surface area. Similarly in Switzerland, pond size did not influence invertebrate richness, except in Odonata (Oertli *et al.*, 2002). Confirming the difference generally found between taxonomic composition of benthic and epiphytic faunas (Kornijów *et al.*, 1990, Kornijów and Kairesalo, 1994), invertebrate biomass found in macrophytes was not correlated with that found in the sediment.

Taxonomic richness and biomass density both depended primarily on the abundance of aquatic vegetation: the former was lower in ponds with fewer macrophytes (total cover <10%)

Table I
Taxa occurrence (presence in n ponds).

Tableau I
Fréquence observée des taxons dans les étangs.

			Brenne		Dombes		Forez
			2000	2001	2000	2001	2002
	Order	Taxa	(*n* = 20)	(*n* = 18)	(*n* = 20)	(*n* = 19)	(*n* = 18)
Bryozoa	*Bryozoa*	*Bryozoa*	14	4	9	14	
Cnidaria	*Cnidaria*	*Cnidaria*	13	10	9	7	
Nemathelminthes	*Nemathelminthes*	*Nemathelminthes*	1	8	7	15	
Platyhelminthes	*Tricladida*	*Dugesiidae*	2	4	2	2	
Annelida	*Hirudinea*	*Erpobdellidae*	3	8	2	5	
		Glossiphoniidae	12	4	8	5	6
		Piscicolidae	4				1
	Oligochaeta	*Oligochaeta*	20	16	18	20	16
Arachnida	*Hydracarina*	*Hydracarina*	17	16	13	16	16
Mollusca	*Veneroida*	*Sphaeriidae*		1		1	
	Basommatophora	*Acroloxidae*	1				
	Gastropoda	*Ferrissiidae*	9	8	4	12	
		Lymnaeidae	17	7	14	19	9
		Physidae	19	15	13	18	12
		Planorbidae	4	6	14	12	6
Crustacea	*Arguloida*	*Argulidae*	1	2	1		1
Crustacea	*Isopoda*	*Asellidae*					1
Crustacea	*Decapoda*	*Cambaridae*			1		
Hexapoda	*Collembola*	*Collembola*		2			1
Hexapoda	*Coleoptera*	*Chrysomelidae*		2		2	3
		Dryopidae		1			
		Dytiscidae	1	5	1	3	10
		Elmidae		2		2	
		Haliplidae		3	3	3	2
		Helophoridae	2				
		Hydrochidae			1		
		Hydrophilidae	3	4	1	5	5
		Hygrobiidae		1			
Hexapoda	*Diptera*	*Anthomyidae*				1	
		Ceratopogonidae	8	9	6	10	10
		Chaoboridae	3	2	2	3	7
		Chironomidae	20	17	19	20	18
		Culicidae		2	2	7	6
		Diptera unident.				1	1
		Ephrydidae					1
		Psychodidae		1			1
		Stratiomyidae			1	2	
		Tipulidae				1	
Hexapoda	*Ephemeroptera*	*Baetidae*	9	8	9	9	12
		Caenidae	17	11	12	15	12
		Ephemeroptera		3		1	
Hexapoda	*Heteroptera*	*Corixidae*	17	16	16	19	14
		Gerridae	5		2	2	1
		Mesoveliidae		2		7	1
		Naucoridae	15	8	9	8	4
		Nepidae	1	2		2	
		Notonectidae		1	1	2	
		Pleidae	11	5	13	12	10
		Veliidae		5		7	3
Hexapoda	*Lepidoptera*	*Pyralidae*	10	4	2	4	8
Hexapoda	*Odonata*	*Aeshnidae*	1	2	1	1	
		Coenagrionidae	20	12	9	17	10
		Lestidae	2				8

Table I
Continued.

Tableau I
Suite.

			Brenne		Dombes		Forez
			2000	2001	2000	2001	2002
	Order	Taxa	(*n* = 20)	(*n* = 18)	(*n* = 20)	(*n* = 19)	(*n* = 18)
Hexapoda	*Plecoptera*	*Plecoptera*		1		1	
Hexapoda	*Trichoptera*	*Ecnomidae*	3	2	1	3	
		Hydroptilidae	8	6	13	3	4
		Leptoceridae		2	1	5	6
		Polycentropodidae	1	1		2	2
		Trichoptera		1		3	1

Table II
Invertebrate taxonomic richness, biomass density (in mg·0.1 L^{-1} of macrophyte) and fish stock density (in kg·ha^{-1}) (means (SD)) in Dombes (39 ponds), Brenne (38 ponds) and Forez (18 ponds).

Tableau II
Richesse taxonomique et densité de biomasse (en mg·0,1 L^{-1} de macrophyte) des invertébrés et densité du peuplement piscicole (en kg·ha^{-1}) (moyennes (écarts-types)) en Dombes (39 étangs), Brenne (38 étangs) et Forez (18 étangs).

	Dombes	Brenne	Forez
Inv. taxonomic richness	12.87 (4.67)	12.97 (4.06)	12.61 (4.12)
Inv. biomass density	209.7 (192.3)	251.1 (206.9)	441.1 (360.8)
Fish stock density	202.1 (80.4)	269.4 (137.3)	295.9 (190.9)

Table III
Model selection analysis of the influence of fish stock density or fertilization, macrophyte abundance, littoral helophyte abundance and invertebrate biomass density in pond sediment, on epiphytic invertebrate taxonomic richness in French fishponds (2000–2002).

Tableau III
Sélection de modèles analysant l'influence de la densité du peuplement piscicole ou de la fertilisation des étangs, de l'abondance des macrophytes, des hélophytes présents sur les berges et de la densité de biomasse des invertébrés dans le sédiment, sur la richesse taxonomique des invertébrés épiphytes dans les étangs piscicoles en France (2000–2002).

Models	AIC	ΔAIC	*w*
Macrophyte abundance + helophyte abundance	427.87	0	0.93
Macrophyte abundance + fish stock + interaction	434.09	6.22	0.04
Helophyte abundance	436.37	8.50	0.01
Helophyte abundance + fish stock	437.85	9.98	0.006
Macrophyte abundance	438.71	10.84	0.004
Macrophyte abundance + fish stock	439.88	12.01	0.002
Macrophyte abundance + invert. biomass in sediment	440.67	12.80	0.002
Fish stock	448.72	20.85	0.000
Macrophyte abundance + helophyte abundance	418.18	0	0.95
Helophyte abundance	424.81	6.63	0.03
Helophyte abundance + fertilization	426.71	8.53	0.01
Helophyte abundance + fertilization + interaction	439.23	21.05	0
Macrophyte abundance	440.01	21.83	0
Macrophyte abundance + fertilization	441.87	23.69	0
Macrophyte abundance + invert. biomass in sediment	441.98	23.80	0
Fertilization	449.81	31.63	0

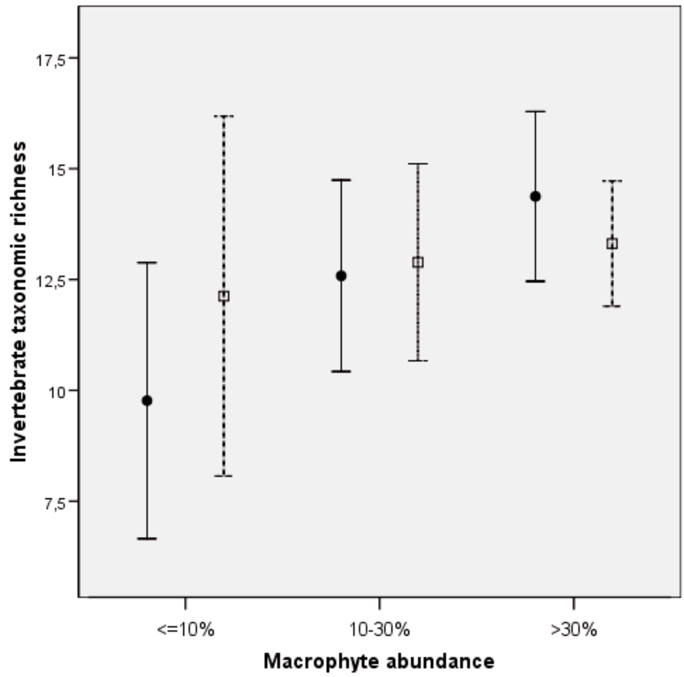

Figure 2
Variation of invertebrate taxonomic richness (mean and 95% confidence interval) with macrophyte cover, in ponds with helophyte abundance < 7.5% *(black dots and full lines) or* ⩾ 7.5% *(white squares and dashed lines) (n* = 13 + 8 + 12 + 9 + 24 + 29 = 95 *ponds).*

Figure 2
Variation de la richesse taxonomique des invertébrés (moyenne et intervalle de confiance à 95 %) en fonction du recouvrement des herbiers de macrophytes, dans les étangs où les hélophytes occupent < 7,5 % (points noirs et ligne pleine) ou ⩾ 7,5 % (carrés blancs et tiretés) de la surface totale en eau (*n* = 13 + 8 + 12 + 9 + 24 + 29 étangs).

Table IV
Estimates and s.e. for the variables included in the best model explaining epiphytic invertebrate taxonomic richness in French fishponds (2000–2002).

Tableau IV
Estimation des paramètres et erreur standard pour les variables incluses dans le meilleur modèle explicatif de la richesse taxonomique des invertébrés épiphytes dans les étangs piscicoles en France (2000–2002).

Model	Estimate	s.e.	*P*
Macrophyte abundance	1.721	0.581	0.004
Helophyte abundance	–0.045	0.033	0.175
Intercept	9.582	1.386	1.8 e –09

when emergent shore vegetation was not abundant either (< 7.5% of total pond area) and the latter was higher in ponds with macrophyte cover ⩾ 10%, provided that emergent vegetation was abundant (⩾ 7.5%). Such a positive relationship between invertebrate taxonomic richness and macrophyte cover was also observed in farm water storages in Australia (Markwell and Fellows, 2008). In West Wales, invertebrate richness in ponds was found to increase with vegetated area but the relationship was weak (Gee *et al.*, 1997). The relationship between invertebrate abundance or richness and plant biomass may differ among macrophyte taxa (Keast, 1984; Hanson, 1990; Humphries, 1996), through the influence of plant density (Linhart *et al.*, 1998; Papas, 2007), richness (Nicolet *et al.*, 2004) or leaf architecture (Dvorak and Best, 1982; Cheruvelil *et al.*, 2001; Balci and Kennedy, 2003; Sidinei *et al.*, 2007).

Table V
Model selection analysis of the influence of fish stock density or fertilization, macrophyte abundance, littoral helophyte abundance and invertebrate biomass density in pond sediment, on epiphytic invertebrate biomass density in French fishponds (2000–2002).

Tableau V
Sélection de modèles analysant l'influence de la densité du peuplement piscicole ou de la fertilisation des étangs, de l'abondance des macrophytes, des hélophytes présents sur les berges et de la densité de biomasse des invertébrés dans le sédiment, sur la densité de biomasse des invertébrés épiphytes dans les étangs piscicoles en France (2000–2002).

Models	AIC	ΔAIC	*w*
Macrophyte abundance + helophyte abundance	511.02	0	0.94
Helophyte abundance	517.50	6.48	0.04
Helophyte abundance + fish stock	518.58	7.56	0.02
Macrophyte abundance	523.64	12.62	0
Macrophyte abundance + fish stock	523.83	12.81	0
Macrophyte abundance + fish stock + interaction	524.75	13.73	0
Macrophyte abundance + invert. biomass in sediment	525.34	14.32	0
Fish stock	532.07	21.05	0
Macrophyte abundance + helophyte abundance	494.73	0	0.65
Helophyte abundance	497.06	2.33	0.20
Helophyte abundance + fertilization	497.63	2.90	0.15
Macrophyte abundance + fertilization	519.74	25.01	0
Macrophyte abundance	520.29	25.56	0
Macrophyte abundance + invert. biomass in sediment	520.64	25.91	0
Macrophyte abundance + fertilization + interaction	521.24	26.51	0
Fertilization	524.98	30.25	0

Table VI
Estimates and s.e. for the variables included in the best model explaining epiphytic invertebrate biomass density in French fishponds (2000–2002).

Tableau VI
Estimation des paramètres et erreur standard pour les variables incluses dans le meilleur modèle explicatif de la densité de biomasse des invertébrés épiphytes dans les étangs piscicoles en France (2000–2002).

Model	Estimate	s.e.	*P*
Macrophyte abundance	2.724	0.928	0.004
Helophyte abundance	0.095	0.084	0.26
Intercept	8.286	2.233	0.0004

Despite the fact that fish might strongly interfere with the abundance and the composition of macro-invertebrate communities (Morin, 1984; Osenberg and Mittelbach, 1989; Zambrano *et al.*, 2001; Scheffer *et al.*, 2006), the model selection led us to consider that fish density and pond fertilization were not major factors explaining the variation in invertebrate biomass density and taxonomic richness in French fishponds. This result suggests that macrophytes and helophytes may provide effective refuges against carp predation. In Dombes, vegetated shore areas could provide *Leucorrhinia pectoralis* (*Odonata*, *Libellulidae*) with safe breeding conditions in ponds where fish stock density was as high as 800 kg·ha^{-1} (Broyer *et al.*, 2009), although this species usually uses aquatic habitats where fish are absent (Wildermuth, 1992). Fertilization contributed to an increase in fish stock density, which was however much lower in our sample (245 kg·ha^{-1} ± 129 SD) than the mean density in Czech fishponds (> 800 kg·ha^{-1}), for example (Pechar, 1995). Fertilization in French fishponds may thus possibly compensate for the negative effect of fish predation by improving trophic conditions for macro-invertebrates without hampering macrophyte development by decreasing water transparency.

In conclusion, macrophyte-dwelling invertebrates might be affected by fish farming intensification in French fishponds, but mainly through its negative impacts on aquatic vegetation.

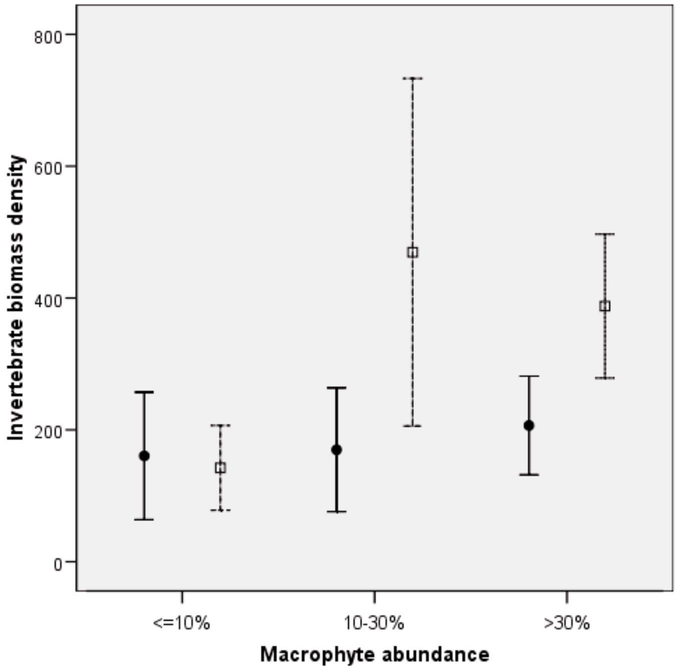

Figure 3
Variation of invertebrate biomass density (in mg·L^{-1} of macrophyte, mean and 95% confidence interval) with macrophyte cover in ponds with helophyte abundance $< 7.5\%$ *(black dots and full lines) or* $\geqslant 7.5\%$ *(white squares and dashed lines) (*$n = 13 + 8 + 12 + 9 + 24 + 29 = 95$ *ponds).*

Figure 3
Variation de la densité de biomasse des invertébrés (en mg·L^{-1} de macrophyte, moyenne et intervalle de confiance à 95 %) en fonction du recouvrement des herbiers de macrophytes, dans les étangs où les hélophytes occupent < 7,5 % (points noirs et ligne pleine) ou ⩾ 7,5 % (carrés blancs et tiretés) de la surface totale en eau ($n = 13 + 8 + 12 + 9 + 24 + 29$ étangs).

This finding supports the idea that fishery business in fishponds can be balanced with the conservation of aquatic invertebrate diversity through management methods that preserve the existence of vegetated microhabitats (Buczyńska *et al.*, 2007). Fishpond management should therefore allow the existence of shallow littoral areas for helophyte development ($<$ 0.60 m) and control the nutrient loading of sediment and water to keep the water clear (Van Donk *et al.*, 1993), *i.e.* to avoid an alternative stable turbid state dominated by phytoplankton (Scheffer, 1990).

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