SPATIO-TEMPORAL CHANGES IN AQUATIC MACRO-INVERTEBRATE ASSEMBLAGES OF CONVENTIONAL RICE FIELDS IN THE CAMARGUE (RHÔNE-DELTA, FRANCE)

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AQUATIC MACRO-INVERTEBRATES
RICE FIELDS
MEDITERRANEAN WETLANDS
CAMARGUE

ABSTRACT. – Mediterranean rice fields constitute temporary marshes artificially kept flooded throughout spring and summer, when natural wetlands dry up. These ecosystems can play an important role as a surrogate habitat for many organisms (*e.g.* invertebrates, amphibians), and as a foraging habitat for others (*e.g.* birds). The macro-invertebrate assemblages of three conventional rice fields, *i.e.* treated with pesticides and mineral fertilizers were studied in Camargue (Rhône delta, French Mediterranean coast) in 1999 and 2000, with a focus on spatio-temporal variability. A total of 70 taxa was recorded, represented by 42 families. Gastropods were dominant in numbers, representing up to 93% of macro-invertebrates in some fields. Arthropods were mainly represented by Diptera, that can form more than 54% of total numbers. Our study showed some changes in Camargue rice fields since the 60's, such as the absence of *Triops cancriformis* and the abundance of an exotic Planorbidae from Asia, *Giraulus chinensis*. Over the cultural season, taxonomic richness rapidly increased soon after flooding and stabilized after a few months. Rice field macro-invertebrate community dynamics could be divided into three main periods, each characterized by the dominance of specific groups. Although inter-field and inter-year differences in mean density of each group were observed, the seasonal succession of species always followed the same pattern. The influence of different biotic and abiotic factors on this animal community is discussed.

INTRODUCTION

In the northern Mediterranean region, the development of agriculture and urbanisation has led to the loss and reduction of numerous natural wetlands by drainage (Hollis 1992). In this context the conversion of natural wetlands into aquatic cultural lands, as rice fields, which changes the structure and functioning of habitats but maintains the area as a wetland, is often considered as a lesser damage.

Mediterranean rice fields constitute temporary marshes artificially kept flooded throughout spring and summer, in complete contrast to the majority of natural wetlands which usually dry up at this time of the year (Pont 1977). These artificial ecosystems can thus play an important role as a surrogate habitat for many organisms such as invertebrates and amphibians (Bigot & Aguesse 1984, Cabral *et al.* 1998). Thus they provide vital feeding resources for local fauna, especially waterbirds (Fasola & Ruiz 1996). This was also highlighted in Camargue, where spatio-temporal use of rice-fields by waterbirds could be accounted for by food availability, especially large invertebrates and amphibian larvae (Tourenq 2000).

Several faunistic inventories of Camargue rice fields were undertaken in the 50's (e.g. Schachter & Conat 1951a, Conat 1952), while quantitative studies were later carried out on specific groups such as chironomids (Tourenq 1975) and micro-crustaceans (Pont 1977, Pont & Vaquer 1986). However the structure and variability of macro-invertebrate assemblages in this habitat are still poorly known. More recently, the impacts of two pesticides on some ricefield macro-invertebrate taxa were experimentally investigated in the same area (Suhling *et al.* 2000). Direct and indirect environmental effects of pesticides generally associated with irrigated culture, were worldwide exemplified in rice fields (see review in Lawler 2001). Pesticides not only affect target species but also the whole community *in situ* (Takamura & Yasuno 1985, Simpson *et al.* 1994 a, b).

We investigated the specific composition of the aquatic macro-invertebrate community in rice fields conventionally run, *i.e.* treated with pesticides and mineral fertilizers. Special attention was given to spatio-temporal variability, over the whole cultural cycle and between two consecutive years. We hypothesized that those communities would be affected, maybe even impoverished, by farming practices, and that there may be major differences among fields and between years, due to differences in the chemicals used. We expected to find major differences with the fauna recorded in the 50's and 60's, given the evolution of field management and cultural practices since then.

MATERIAL AND METHODS

Rice culture in the study area: In Camargue (43°30'N, 4°30'E), rice fields are usually ploughed and harrowed in January. At the end of April-beginning of May, seedling usually takes place on the same day as flooding, or within one week after. Water supplied to rice fields via irrigation systems is pumped from the Rhône river. In conventionally run fields, insecticide application occurs twice during the season: very soon after flooding for chironomid control, and late August to control the rice striped stem borer *Chilo suppressalis* (Pyralid, Lepidoptera). Rice germination takes place 7-10 days after sowing and water level (± 10-15 cm) is periodically lowered (2-5 cm) during application of pesticides or fertilizers. Herbicides are sprayed soon after flooding and then once or twice until mid-June; their main targets are *Echinochloa* spp. and Cyperacea. Fungicides and algicides are added in some plots, at the same period. Fertilization occurs several times across the season, until the end of June approximately. Fields start to dry out at the beginning of September, *i.e.* 3 or 4 weeks before harvest.

Field studies: Three conventional plots named A (2.3 ha), B (4.4 ha) and C (2 ha) respectively, sited in three different rice farms were sampled. Comparing true replicates was impossible, as farming practices do not only differ among farmers, but also between years for a given field; moreover, the planning of farming operations (*e.g.* fertilizers or herbicids application) can be modified overnight, depending on weather conditions and/or crop state. However we selected plots where comparable practices were scheduled (Table I) and which had similar surroundings, as those have a strong impact on the colonization potentialities of rice-fields by various organisms; each of the three study plots was entirely surrounded by other rice plots. The field study was conducted in 1999 and 2000, in the same plots. Annual weather conditions were comparable between years, with an average air temperature of 14.7°C in 1999 and 14.9°c in 2000, an average air temperature during the growing season of 21.5°C in 1999, 21.3°C in 2000, and total rainfall of 556.8mm in 1999 against 509.4 mm in 2000.

Both years, sampling took place at regular intervals during the whole growing season: 15-30 May (period 1), 7-21 June (period 2), 26 June-13 July (period 3), 25 July-9 August (period 4) and 17-29 August (period 5). Invertebrates were collected with a square-sampler (Suhling *et al.* 2000), of which three sides were closed with a 1mm mesh and the fourth with a 0.5 mm sampling net. The frame of the trap (0.1 m^2) was placed over 15 quadrats, distributed every 2 m along a transect line starting around 5 m from the border of the field. The position of transects slightly changed on each sampling date. The inner vegetation was systematically removed, washed within the trap and discarded. Benthos and sediment (the first 2-3 cm of the layer) were pushed into the net using a broom trap. Macro-invertebrates (>1mm) were collected after washing on 5 and 1mm sieves, pre-

Table I. – Main farming operations during the growing season in the three study fields.

	1999			2000		
Fields	**Field A**	**Field B**	**Field C**	**Field A**	**Field B**	**Field C**
Flooding date	28 April	19 April	22 April	25 April	16 April	24 April
Seedling date	30 April	24 April	3 May	25 April	21April	27 April
Fertilization date (N-P-K) : Kg/ha	22 March (11-12-24): 531 27 May (46-00-00): 110 11 June (46-00-00): 116	12 April (22-11-22) : 360 25 May (32-23-00) : 230 28 June (46-00-00) : 80	12 April (20-11-24) : 300 9 June (20-16-00) : 250 10 July (21-00-00) : 150	22 March (15-05-15) : 604 11 May (20-20-00) 10 June (20-20-00) : 250	12 April (18-09-29) :340 30 May (20-20-00) : 350 30 June (46-00-00) : 150	20 April (20-11-24) : 300 26 May (30-25-00) : 170 11 July (30-00-00) : 200
Insecticide application date **Active ingredient : g/ha**	30 April & 6 May alphamethrine : 30 13 August alphamethrine : 15	29 April diazinon : 50 + lindane : 175 25 July & 10 August alphamethrine : 15	12 May diazinon 50 + lindane 175 5 August alphamethrine :15	25 April fipronil : 27.5 10 August alphamethrine : 15	26 April tralomethrin : 16.2 8 August alphamethrine : 15	1 May cyan acide : 0.25 6 August alphamethrine : 15
Herbicide application date **Active ingredient : g/ha**	31 March oxadiazon : 250 + dimethenamid : 747 3 June propanil : 360 + 2,4 MCPA : 400 + bentazone : 1044	29 April molinate :3000 7 May pretilachlore : 1080 + fenclorim : 540 3 June propanil : 1400 + cinosulfuron : 80	6 May molinate : 3600 12 May pretilachlore : 1080 + fenclorim : 540 5 June propanil : 1080 + cinosulfuron : 50 1 July propanil : 1080 + bentazone : 1390 14 June 2,4 MCPA : 320	31 March oxadiazon : 600 31 March dimethenamid : 900 28 May azimsulfuron : 20	26 April molinate : 3000 30 May azimsulfuron : 10	1 May molinate : 3000 6 May pretilachlore: 1200 + fenclorim : 600 31 May azimsulfuron : 20
Fungicide application date **Active ingredient : Kg/ha**	30 April & 6 May - metirame-zinc : 1.6	29 April - chlorothalonil : 0.50	12 May chlorothalonil : 0.50		26 April metirame-zinc : 1.6	1 May chlorothalonil : 1

served in 70% ethanol and brought to the laboratory. They were identified down to species, except for Diptera which were identified to family. Some organisms could only be identified to genus; they appear under "*Genus sp*" in Table II.

Items were grouped into major taxa, and were subjected to statistical analysis. Taxa relative compositions in numbers were compared among sites and between years, using G tests. Density (number m^{-2}) was natural-log transformed, LN (density+1), to normalise residuals. For each taxon (dependant variable), density was measured 5 times throughout the season, with year and site as independent variables. Spatiotemporal changes in macro-invertebrates were analysed by repeated measure anova with pseudoreplication (different samples of the same field cannot be considered as pure replicates). When applicable, pair-wise Bonferroni post hoc tests were performed.

RESULTS

Macro-invertebrate assemblage composition and richness

Over the 1999-2000 sampling period, 70 identifiable taxa of macro-invertebrates distributed over 42 families were recorded (Table II). Taxonomic richness was highest in Coleoptera (9 families and 26 species) although Diptera, which were identified down to family only (11 families), could be more speciose. Total number of identifiable taxa per field and per year ranged between 24 and 45 (Table II). Spatial variation was best exemplified by Coleoptera which counted 11 taxa in field A, 21 in field B and 22 in field C (Table II).

The mean number of identifiable taxa per sample changed across the cultural cycle (repeated anova, F=27.142, p<0.001) with lowest richness observed on period 1, and highest on period 3 (pairwise Bonferroni tests, p<0.001). Mean richness in taxa per sample did not vary between years (repeated anova, F=0.002, p>0.05), but differed among fields (F=3.993, p<0.05), being higher in fields A and B than in field C (pairwise Bonferroni-test, p<0.01). Interactions between site, year and period were significant (repeated anova, F=6.574, p<0.001). According to Bonferroni-tests, in 1999 there was no difference among sites, while in 2000, some differences were observed, but without any clear pattern. There was little year effect on the number of taxa in sites A and B, and none in site C.

Whatever the year or the site, Gastropoda of the Limnophila order were dominant, representing up to 93% of macro-invertebrate abundance in some fields (Fig. 1). Arthropoda were mainly represented by Diptera that could form more than 54% of total numbers; for most other groups, the relative contribution was comprised between 0.1 and

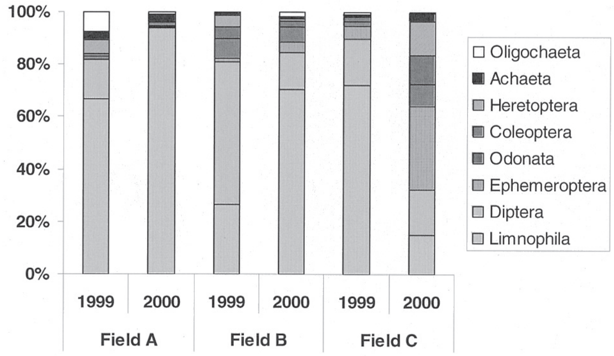

Fig. 1. – Relative composition (% density) of major macro-invertebrates in three Camargue conventional rice fields.

7.7%. The relative contribution in numbers of major taxa highly varied among fields (G test; G = 2429.919 in 1999; G = 4033.828 in 2000; p<0.0001, df = 16). For a given field, taxa relative compositions in numbers significantly differed between 1999 and 2000 (G test; Field A: G = 1563.516, Field B: G = 1014.934, Field C: G = 1632.341; p<0.0001, df = 8).

Difference in mean densities among fields

Mean density varied significantly among the 3 fields, for all orders, except Heteroptera (Table III, Fig. 2). For most groups site A was markedly different from the other two, in which densities were comparable (Bonferroni post-hoc test, p<0.05). Compared with the others, field A was characterized by a higher density of Gastropoda, Achaeta and Oligochaeta, but a lower density of Coleoptera, Odonata and, to less extent, Diptera (Fig.1, Table II). The pattern was slightly different in Ephemeroptera, more abundant in site C than in the other two.

Inter-year differences in mean densities

Annual differences in mean density (Fig. 2) were significant in four groups (Table III). Achaeta, represented by one single family (Erpobdellidae), and Ephemeroptera, mainly represented by Baetidae, were more abundant in 2000 than in 1999. Diptera, mainly Chironomidae, and Oligochaeta, mainly Tubificidae, were more abundant in 1999 than in 2000 (Tables II, III).

Evolution of mean densities over the cultural cycle

For all groups, except Oligochaeta, significant seasonal changes in mean density were observed (Table III, Fig. 2). According to Bonferroni post

Table II. – Number of individuals of each taxon per year and per field.

		Rice field A		Rice field B		Rice field C	
		1999	2000	1999	2000	1999	2000
Taxa		n	n	n	n	n	n
Hirudinea							
Erpobdellidae	*Erpobdella octoculata*	66	227	17	8	15	30
Oligochaeta							
Enchytraeidae		2	0	0	0	0	0
Naïdidae	*Stylaria lacustris*	8	0	2	0	27	0
Tubificidae	*Limnodrilus* sp.	169	0	7	0	2	0
	Branchiura sowerbyi	0	34	0	5	0	0
Unidentified		0	32	0	27	0	5
Limnophila							
Lymnaeidae	*Radix perregra*	0	249	0	8	0	1
Physidae	*Physella acuta*	498	2378	133	525	93	98
Planorbidae	*Gyraulus chinensis*	1017	4571	458	485	2568	41
Succineidae	*Succinea putris*	36	39	17	132	10	2
Heteroptera							
Corixidae	*Corixa* sp.	121	0	95	6	10	97
	Sigara stagnalis	3	0	9	0	3	0
	Micronecta sp	1	0	0	0	0	0
Gerridae	*Gerris lacustris*	1	10	7	6	2	17
Hydrometridae	*Hydrometra* sp.	0	0	0	0	0	1
Mesoveliidae	*Mesovelia* sp.	0	1	0	2	0	1
Naucoridae	*Naucoris* sp.	0	0	0	0	0	1
Nepidae	*Nepa cinerea*	0	0	0	0	0	1
Pleidae		0	0	0	1	0	0
Coleoptera							
Dryopidae	*Dryops* sp.	0	0	0	2	0	0
Dytiscidae	*Coelambus parallelogrammus*	0	0	0	0	0	1
	Colymbetes sp.	0	1	0	2	0	0
	Graphoderus sp.	0	0	1	0	0	0
	Guignotus pusillus	3	80	7	0	30	24
	Hydaticus leander	0	0	0	1	0	1
	Hydaticus sp.	0	0	0	0	0	1
	Hydrovatus cuspidatus	0	0	0	1	0	1
	Ilybius sp	0	0	1	0	1	0
	Laccophilus minutus	1	0	1	11	2	1
	Laccophilus variegatus	0	0	0	1	1	2
	Laccophilus sp	3	0	11	0	7	0
	Rhantus punctatus	3	0	2	2	2	2
	Rhantus larvae	9	0	7	0	18	2
	Unidentified Hydroporinae	0	0	10	0	0	0
Elmidae	*Riolus* sp.	0	0	0	0	0	1
Gyrinidae	*Gyrinus* sp.	0	0	0	0	0	1
Haliplidae	*Haliplus immaculatus*	0	0	0	2	0	3
	Haliplus sp.	0	0	5	1	0	1
Helophoridae	*Helophorus* sp.	0	0	28	3	0	0
Hydrophilidae	*Berosus* sp.	0	1	0	2	1	0
	Enochrus bicolor	1	0	12	2	9	10
	Enochrus testaceus	0	0	0	1	0	11
	Enochrus sp.	2	0	7	0	5	0
	Hydrochara flavipes	0	0	0	0	0	1
	Hydrous piceus	1	0	3	3	1	1
Noteridae	*Noterus clavicornis*	0	1	0	0	1	0
Staphylinidae	*Paederus littoralis*	0	0	0	3	0	0
Unidentified		0	8	0	7	0	41
Odonata							
Aeshnidae	*Anax imperator*	0	0	0	2	0	0
	Anax parthenope	0	0	5	3	0	1
	Anax sp.	0	1	0	1	0	0
Coenagrionidae	*Ischnura* sp.	24	4	119	15	11	30
Libellulidae	*Crocothemis erytraea*	2	2	12	4	18	21
	Orthetrum albistylum	0	0	7	8	1	2
	Orthetrum brunneum	0	0	3	8	15	4
	Orthetrum cancellatum	0	0	27	41	6	9

Table II *(suite)*

	Orthetrum sp.	0	1	0	4	0	2
	Sympetrum fonscolombei	0	1	4	5	7	8
	Sympetrum sp	0	0	1	0	1	0
Ephemeroptera							
Baetidae	*Cloeon dipterum*	2	30	20	4	188	50
Caenidae	*Caenis* sp.	0	0	3	0	0	2
unidentified		0	5	0	64	0	246
Diptera							
Chironomidae		309	26	1066	216	620	60
Culicidae		18	0	25	0	11	0
Dolichopodidae		0	0	0	0	0	71
Ephydridae		1	3	154	0	18	0
Limoniidae		0	1	0	0	0	0
Rhagionidae		0	0	0	1	0	1
Sciomyzidae		1	1	1	3	2	1
Stratiomyidae		0	2	10	8	3	25
Syrphidae		0	0	0	1	1	0
Tabanidae		0	0	2	0	2	1
Tipulidae		12	5	1	1	0	2
unidentified		6	4	0	0	1	1
Amphipoda							
Gammaridae	*Gammarus* sp.	0	0	0	0	1	0
Isopoda							
Asellidae	*Asellus* sp.	0	0	0	2	0	0
	Total number of individuals	2320	7718	2300	1640	3714	937
	Total number of identifiable taxa	26	24	37	43	36	45

Table III. – Results of repeated measure anova for the effect of field, year and sampling period, on mean LN (density+1) of major macro-invertebrate taxa. (* P<0.05, ** P<0.01, *** P<0.001).

Taxa	**F values**			
	Field	**Year**	**Period**	**Period x Field x Year**
ANNELIDA				
Achaeta	47.451 ***	8.539 **	3.357 *	2.697 **
Oligochaeta	45.233 ***	14.811 ***	0.981ns	2.305 *
GASTROPODA				
Limnophila	52.338 ***	0.010 ns	18.811 ***	2.963 **
ARTHROPODA				
Coleoptera	10.262 ***	2.398 ns	12.113 ***	1.202 ns
Heteroptera	1.415 ns	0.039 ns	45.785 ***	6.446 ***
Odonata	44.310 ***	1.527 ns	15.856 ***	8.497 ***
Ephemeroptera	12.953 ***	8.221 **	10.350 ***	13.013 ***
Diptera	5.816 ***	27.294 ***	18.781 ***	5.962 ***

hoc tests, density reached a significant maximum during period 2 in Gastropoda and Diptera, period 3 in Heteroptera, periods 3-4 in Coleoptera, and during periods 3-5 in Odonata which were absent from all sites on the 1st sampling date. In Achaeta, maximum abundance was observed at the beginning of the cultural cycle (period 1), followed by a decrease to a minimum value (periods 3 to 4), and then an increase in period 5, which was especially pronounced in field A. In Ephemeroptera no clear seasonal pattern could be found out.

Interactions between field, year and sampling period were significant for all groups, except Coleoptera (Table III).

DISCUSSION

Macro-invertebrate assemblage in Camargue rice fields

The three conventional rice fields studied in Camargue support a relatively rich macro-invertebrate fauna counting 70 identifiable taxa, represented by 42 families, among which 32 insect families. Macro-crustaceans were poorly represented, with only a few individuals of Amphipoda and Isopoda. The assemblage was largely dominated in numbers by Gastropoda and Diptera larvae, mainly Chironomidae, which was also observed in the Ebro delta conventional rice fields (Gonzalez-Solis & Ruiz 1996). The high abundance of those two herbivorous groups can be partly explained by organic matter left from previous cultures and by blooms of monocellular green algae, due to the inputs of mineral nitrogen (Simpson *et al.* 1994 a, b). Gastropod proliferation could also be indirectly favored by the use of chemicals, to which they are themselves tolerant, which reduces the number of

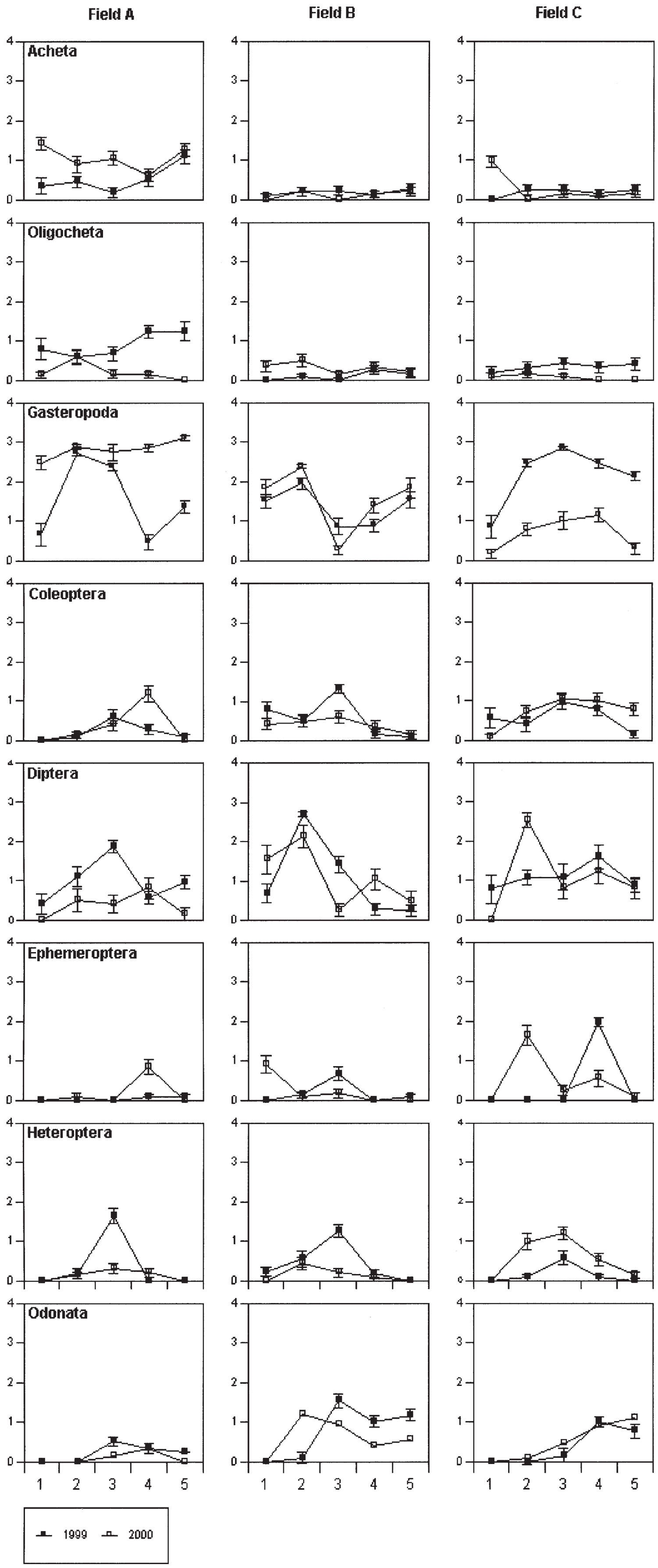

Fig. 2. – Changes in mean density, expressed as LN (density +1), of major macro-invertebrate taxa with year, field and period. Five periods of time are considered: 15-30 Mai (1), 7-21 June (2), 26 June-13 July (3), 25 July-9 August (4) and 17-29 August (5).

their competitors and predators (Suhling *et al* 2000).

The list of macro-invertebrates found in our study is richer than those established in the past in the same area (Schachter & Conat 1951a, Conat 1952, Aguesse 1955, 1957). However no statistical comparison can be carried out, as in those works the sampling effort, frequency and date were not mentioned. More recently, Suhling *et al.* (2000) collected 84 taxa within one single Camargue rice field, but did not provide an exhaustive list. Moreover, their study encompassed both treated and untreated plots, while ours focused on treated ones. Now it was shown that Camargue rice field fauna diversity was limited by the use of chemicals (Bigot & Aguesse 1984, Suhling *et al.* 2000). At the specific scale, our study showed some changes since earlier inventories. For example the gastropodan species recorded in Camargue in the 60s, *i.e. Physa acuta* and four *Lymnaea* species (Marazanof 1964) have been replaced by an exotic Planorbidae from Asia, *Giraulus chinensis*, also abundant in another rice field of the same area (Suhling *et al.* 2000). We did not catch any *Triops cancriformis*, a phyllopodean crustacean that used to be common in Camargue rice fields until the early 70s (Schachter & Conat 1951b). Considered as a pest for cultures, it was the main target of chemical treatments, together with chironomids (Pont & Vaquer 1986).

All taxa found in the study rice-fields are not specific to this habitat, but common in French freshwaters. Considering the classification of France aquatic macro-invertebrate fauna (Usseglio-Polatera *et al.* 2000), based on life history traits and ecological preferences, the taxa collected belong to groups typical of lentic habitats of waterways, stagnant eutrophic waters outside the main river basin and temporary waters. However some species and/or groups can be considered as characteristic of these cultivated systems, such as several Heteroptera families (Aguesse 1957). Rice fields are beneficial for two Odonata, *Ischnura elegans* and *Ischnura punilio*, of which second and/or third generations are linked to this agrosystem (Aguesse 1955). However *I. elegans* may be negatively affected by alphamethrine, currently used in conventional rice fields to control pyralids (Suhling *et al.* 2000).

Variability among fields and years

The relative composition of macro-invertebrate community and the mean density of several orders in field A noticeably differed from those observed in the other two. Although lowest total number of taxa was recorded in this field, mean number of taxa per sample was higher there than in the other sites, as the macro-invertebrate assemblage is mainly composed of abundant species. In this field molluscs and annelids were notably abundant, while several insect groups (especially Odonata, and Coleoptera) were poorly represented.

Inter-year differences were significant for 4 orders in the study fields: Achaeta, Oligochaeta, Diptera and Ephemeroptera. Competition or density-dependent factors could explain those results for the Annelida, as the Achaeta *Erpobdella octoculata* preferentially preys on macro-invertebrates, including Tubificidae (Toman & Dall 1997). For Diptera which are the insecticides (anti chironomids) main target, annual variations could be linked to changes in the active ingredient (Table I), but also to indirect effects on trophic web. Chironomid larvae are an essential element in this habitat, due to their consumption by numerous invertebrates (Odonata, Coleoptera, Heteroptera) and birds (Tourenq 1975). In Ephemeroptera, the pattern of abundance highly varied with site, year and sampling date.

Chemicals use could account for some of the observed inter-site and inter-years differences. Suhling *et al.* (2000) experimentally showed that some Odonata, Coleoptera and Heteroptera, were negatively affected by the same insecticide as that used in fields B and C in 1999, while *Gyraulus chinensis*, *Erpobdella octoculata* and *Laccophilus spp* were more abundant in treated fields. Fipronil, insecticide used as an anti-chironomid, can have long lasting lethal effects on non-target groups, such as Coleoptera (Balança & De Visscher 1997). Lethal effects of propanil on chironomids, microcrustaceans, amphipods, amphibians and fish have been experimentally evidenced (Moore *et al.* 1998). Molinate, an herbicide, is toxic for several aquatic organisms, including fish (Davey *et al.* 1976). However, since pesticide combinations differ both among fields for a given year, and between years for each field (Table I), it is not possible in this study to draw any conclusion on their respective role. It is most likely that synergistic effects between chemicals, biotic interactions and farming practices influence the densities of selected species.

Seasonal succession

Although taxonomic richness varied between years and among fields, it always showed the same seasonal pattern, with a rapid increase at the beginning of the cultural cycle, followed by a plateau. This pattern of fast successions and specific richness changes, observed in many rice fields (Pont 1977, Lawler 2001), is typical of temporary wetlands (Lake *et al.* 1989).

According to our study, rice field cycle can be divided into three main periods, characterized by the dominance of specific macro-invertebrates: (1) Developing of the first invertebrates rapidly after flooding, which reach a peak in abundance early in the season (June). Those are essentially Gastropoda and Diptera (Chironomidae); sometimes Achaeta. (2) Coleoptera and Heteroptera reach a peak around July. (3) Odonata characterise the end of the cultural season.

The first invertebrates colonizing rice fields have developed resistance forms as eggs, larvae or adults, to survive the winter drought in the soil until next flooding. This is the case for example of Diptera, Gastropoda, some Coleoptera and Heteroptera (Bigot & Aguesse 1984). This colonization can be reinforced thanks to passive dispersion of larvae via irrigation waters and by oviposition above the fields (ex Chironomidae) or reproduction within the field (ex gastropods) (Tourenq 1975, Gonzalez-Solis & Ruiz 1996). Most groups which develop later (*e.g.* Coleoptera, Heteroptera Corixidae), immigrate as larvae or adult forms carried in by irrigation waters, or as eggs laid by flying adult forms. Although several Odonata species are able to withstand winter drought as eggs or larvae (Suhling *et al.* 2000), colonization is essentially made by adults from a 1st generation, coming from marshes in the surroundings natural ecosystems to lay eggs in the rice fields (Aguesse 1955). Their low abundance during the first cultural months could be explained by the detrimental effect of ploughing, or by the lack of vegetation. Odonata indeed like to hide in aquatic vegetation, both to be protected from predators and to wait for prey (Darblade & Avignon 1999). In many rice fields, as in fishless temporary ponds, top predators are Odonata, large Hemiptera and Coleoptera (Lawler 2001). This is also the case in Camargue where it seems unlikely that rice fields, given their shallow and hot summer waters, constitute a suitable habitat for fish (Poizat *et al.* 1998). The study fields were dominated by primary consumers throughout the season, but the proportion of predators rose during ricefield phenology. This phenomenon, described in other Camargue rice fields (Pont 1977, Suhling *et al.* 2000), is common in temporary wetlands (Lake *et al.* 1989, Lawler 2001).

The macro-invertebrate community structure of temporary wetlands is influenced by habitat duration, the ability of aquatic species to colonize, their capacity to withstand successive environmental changes and their life history traits (Wiggins *et al.* 1980, Williams 1997). In rice fields, aquatic organisms will have to face additional factors linked to farming practices, such as winter drying out, draining for chemical treatment, pesticide use (Bigot & Aguesse 1984, González-Solís & Ruiz 1996, Lawler 2001). Interestingly, this study in Camargue highlights, beyond the differences observed, the resemblance in the macro-invertebrate communities between past and present rice-fields, and also between rice-fields and natural temporary wetlands. However, to fully comprehend the role of agricultural practices on this ecosystem, organic and conventional plots should be compared in another study.

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