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Habitat variability and space utilization by the amphibian communities of the French Upper-Rhone floodplain

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Key words: amphibian community, spatial-temporal predictability, predation, floodplain, disturbance of water level, life history

Abstract

In order to study the relationship between community organization and spatial-temporal variability, species richness and abundance of amphibian species were estimated in 17 sites of the French Upper Rhone floodplain. These sites were chosen because they were representative of the diversity of successional processes, age and connection with the active channel. Ecological variation among these sites was estimated by the analysis of 14 mesological, hydrological, and biotic variables, by means of correspondence analysis. Level of disturbance, eutrophication, water origin, presence of fish and water persistence were the main determinants of site typology.

Amphibian species richness was highest in temporary sites experiencing intermediate level of disturbance. Three species (*Rana ridibunda, Rana dalmatina, Triturus helveticus*) were ubiquitous, three species (*Hyla arborea, Bufo calamita, Pelodytes punctatus*) were characteristic of habitats with intermediate variability and four (*Triturus cristatus, Triturus alpestris, Bufo bufo, Bombina variegata*) were rare in the floodplain. The most abundant species in the floodplain appeared to be r-selected and most of them showed a temporal flexibility of reproduction. These reproduction traits were assumed to respond to the balance between habitat unpredictability and interspecific constraint by making the adjustment to both availability and suitability of breeding habitats possible.

Introduction

The life cycle of most amphibian species depends on both aquatic and terrestrial habitats. Because larval survival is especially variable, the larval stage is a major key of demography of amphibian populations. In the Upper Rhone floodplain, the amphibians use a wide diversity of aquatic sites for reproduction. According to its location in the floodplain, an aquatic site experiences varying levels of disturbance induced by flood events. Are amphibian community structures influenced by changes in spatial-temporal variability? Consequently, the first problem we have to deal with is the influence of variation in the range of spatial-temporal variability on the structure of amphibian communities.

In such habitats as the aquatic sites of the floodplain, spatial-temporal variability exhibits diverse patterns. We focused more particularly on habitat predictability. A habitat was defined as predictable when the factors such as water level or productivity were either constant or periodical. In such a habitat, interspecific relationships were expected to be the major cause of larval mortality. For instance, in a site where water is permanent, predation by fishes was expected to induce high larval mortality. In contrast, a habitat was defined as unpredictable when water level and productivity varied according to a more stochastic pattern. In such temporary sites where water filling was unpredictable, desiccation probability was expected to be the key factor for larval survival. In contrast, because the presence of predators was more unlikely in such a habitat type, mortality due to predation was expected to be lower than in more predictable habitats.

When spatial-temporal predictability was high, interspecific relationships such as competition and predation were expected to play a major role in community organization, favouring predation avoidance or a high level of specialization (K-selected species), which makes niche partitioning possible; consequently

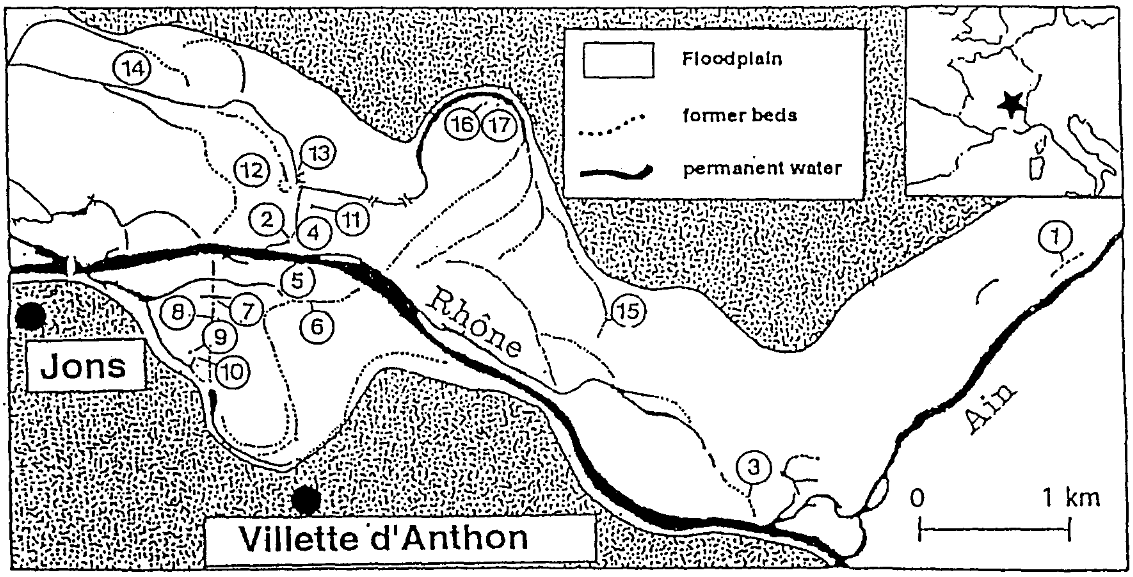

Fig. 1. Map of the Jons sector (Upper-Rhone, France) showing the active channel and the network of old channels. Numbers indicate sites sampled.

(1) species richness was expected to be high in such predictable habitat types and (2) life-history traits were expected to be K-selected. In contrast, in sites where water filling is unpredictable, (1) richness was expected to be low and, (2) species were expected to exhibit traits that favour colonization processes (r-selected species).

The amphibian species were expected to respond to predictability of water filling by different strategies. The relationship between predictability and evolution of biological traits has been largely considered in the literature, particularly by theories dealing with the r-K concept (MacArthur & Wilson, 1967; Pianka, 1970). For example, the relationship between egg size and fecundity has been largely investigated. Number and size of eggs vary greatly from one amphibian species to the other (Salthe, 1969; Salthe & Duellman, 1973; Kaplan & Salthe, 1979) and some species exhibit parental care.

By studying some amphibian biological traits in relation to the ecological distribution of the species in the floodplain, our aim was to identify the traits on which the selective pressure caused by disturbance was highest.

Description of study sites

The Rhone floodplain section studied is located 20 km upstream from Lyon, where the river develops different geomorphological styles: large meanders on the margins of the floodplain and braided channels close to the active channel (Fig. 1). The area has been described by Bravard *et al.* (1986) and Richardot-Coulet *et al.* (1987). Seventeen sites providing examples of all the available habitat types were investigated. These habitat types depended on 1) the type of successional process, 2) age, and 3) connection with the active channel(s). Sites J1 to J4 were located near lotic braided channels and experienced all the flood events. Sites J5 and J6 were more distant from the active channel and were submerged less frequently. The other sites were not submerged by floods and were more or less silted. In sites J7 to J11 water filling mainly depended on water table level. Sites J12 to J17 were located on the border of the floodplain, their water filling depending either on the water table or on rainfall.

Materials and methods

Amphibian sampling

Amphibian species differ both in their behaviour and in habitat use. Consequently they cannot be censused

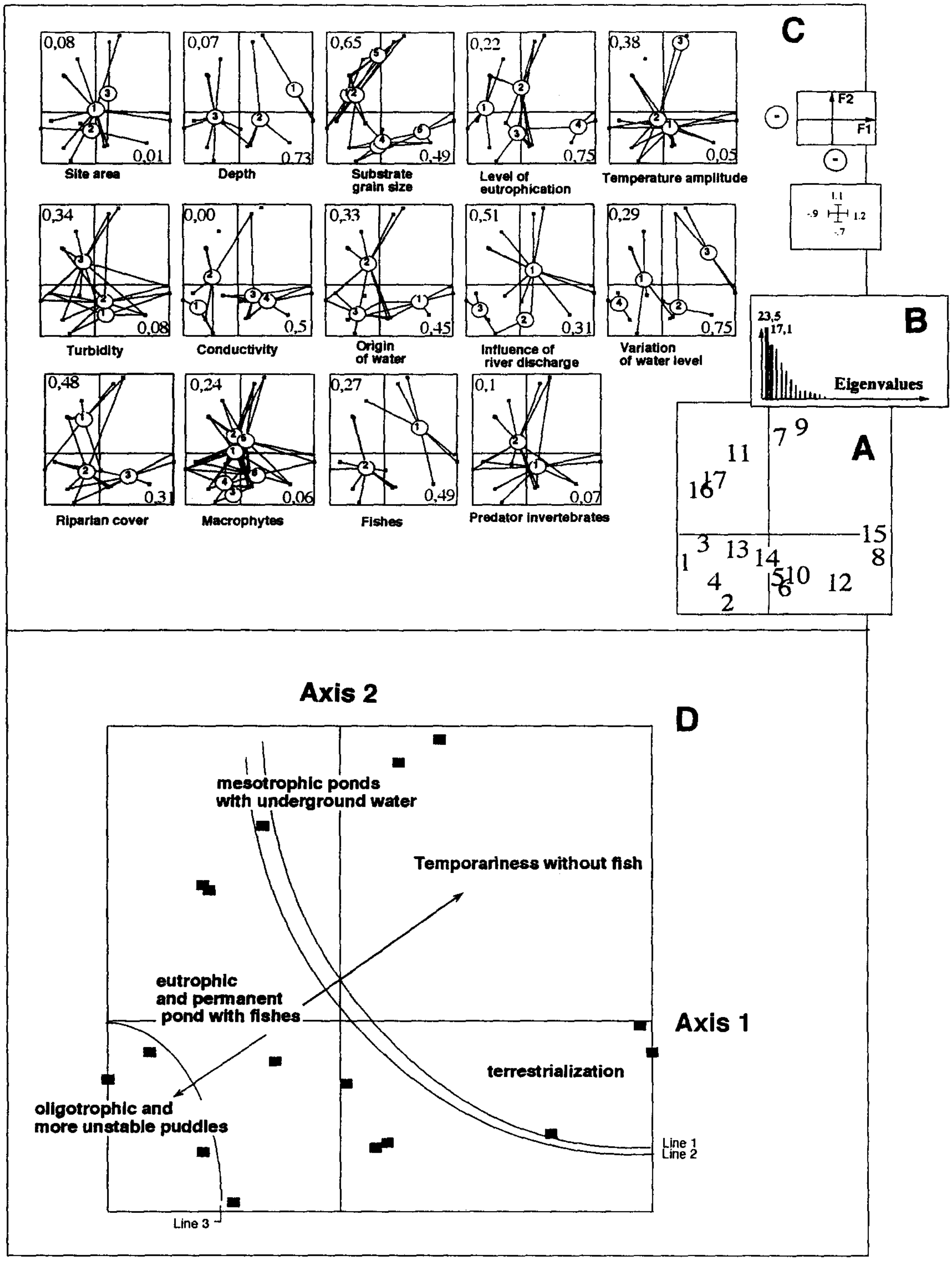

Fig. 2. A. F1–F2 factorial maps of the correspondence analysis. Projection of the mean coordinates of each site. B. Eigenvalues. C. Projection of the modalities of each variable. The lines link the position of each site (small squares) to the modality (ies) that are characteristic for that site. The numbers on the axes indicate the correlation (*r*-value) of a variable with each axis. See Appendix 2 for modality values. D. Interpretation of the factorial map. Black squares: sites. Water is temporary in sites above of line 1. Sites above line 2 are fishless. Instability is very high in sites on the left of line 3.

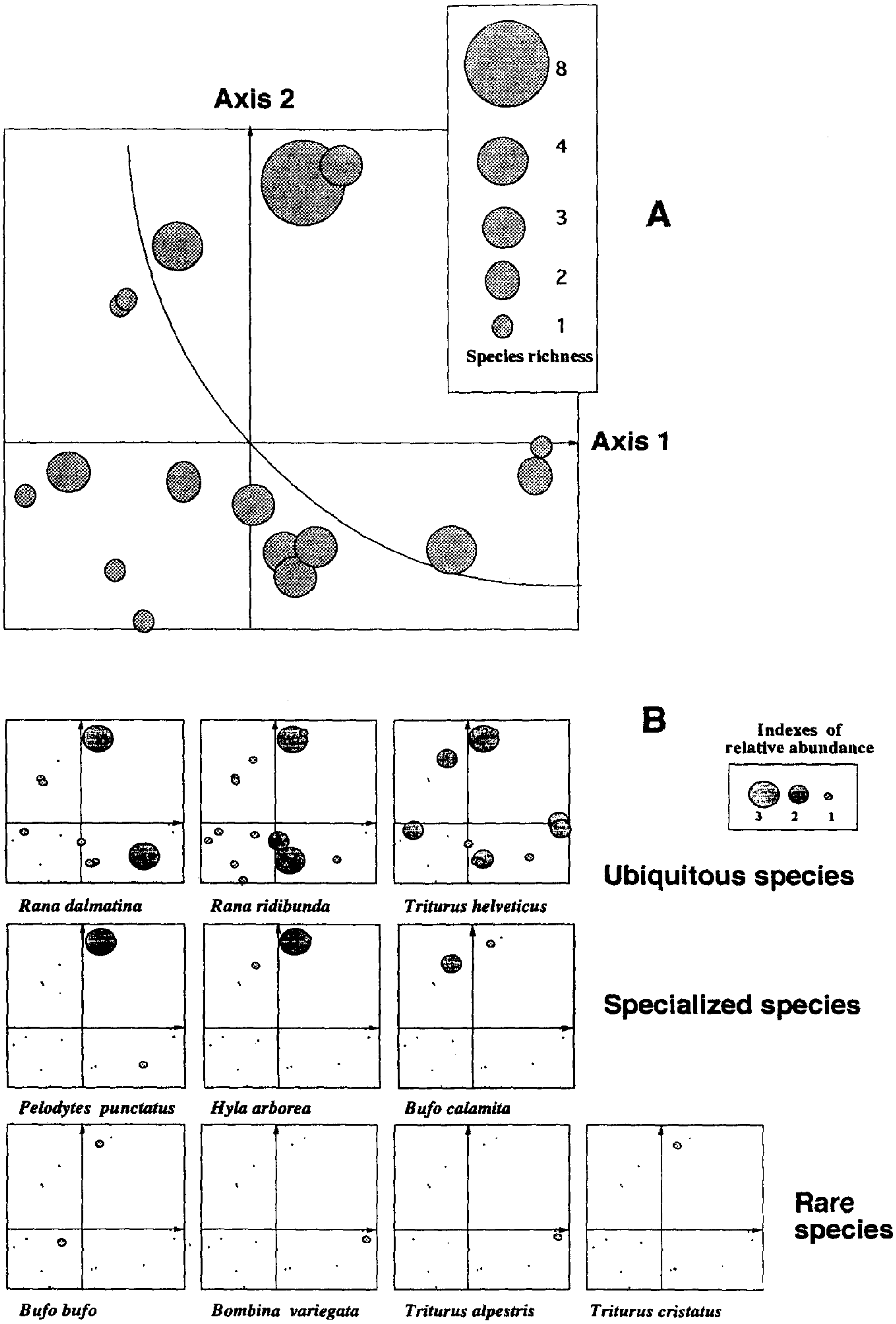

Fig. 3. A. Projection of species richness on F1–F2 factorial map of the correspondence analysis. The size of each circle indicates species richness of the amphibian community in each site, (see Appendix 1). B. Projection of the relative abundance of each species on F1–F2 factorials map of the correspondence analysis. The size of each circle indicates the relative abundance of the species in each site. See Appendix 1 for the values of relative abundance.

by using a unique technique. In order to homogenize the estimation of abundance for all the species, we applied different techniques (visual detection, fishing using two types of dip-net, listening for calling, clutch counting). Sampling was regularly distributed throughout the breeding season in 1992. Relative abundance in each aquatic site was coded according to a four-level geometric scale (see Appendix 1).

Environmental variables

In each site we measured 14 variables which described (1) mesological (site area, depth), (2) physico-chemical characteristics (substrate grain size, level of eutrophication, range of temperature variation, turbidity, conductivity), (3) hydrological (origin of water, influence of river discharge, variation of water level), (4) biotic variables (riparian cover, macrophytes, occurrence of both fish and invertebrate predators).

Biological traits

Biological variables were documented from both literature data and personal observations. These variables concerned life history traits (fecundity and relative egg size), spatial-temporal pattern of reproduction (reproductive period, reproductive display). The amphibians studied were all the species potentially present in the region on the basis of biogeographic data (Castanet & Guyetant, 1989; Joly, 1992).

Data processing

In order to establish a fuzzy coded matrix, the range of variation of each environmental variable was divided between several modalities. For each site, the affinity of the measures with each modality was estimated using a four-level scale. The resulting data set constituted an incomplete disjunctive matrix (see Appendix 2). This matrix was analyzed by a correspondence analysis adapted for fuzzy coding (ADE package, version 3.4, Chessel & Doledec, 1992).

Results and discussion

Environmental variables

The first two axes of the analysis accounted for 40% of total variance. In order to explain the ecological significance of the factorial map of the sites, each variable was projected on this map (Fig. 2A). The first factor (explaining 23,5% of the variance; Fig. 2B) was mainly correlated with depth ($r = 0.73$), level of eutrophication ($r = 0.75$), substrate grain size ($r = 0.49$) (Fig. 2C), variation of water level ($r = 0.76$), and occurrence of fish ($r = 0.50$). The second factor (explaining 17,1% of the variance; Fig. 2B) was correlated with the substrate grain size ($r = 0.65$), temperature variation ($r = 0.40$), influence of the riparian cover ($r = 0.48$), and influence of river discharge ($r = 0.51$) (Fig. 2C).

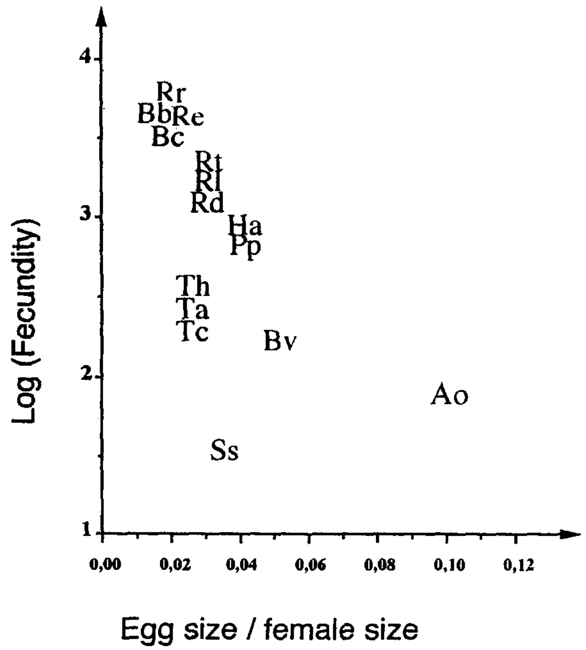

Fig. 4. Relationship between fecundity (Y-axis, in log) and ratio egg size to female size (X-axis). Abbreviations: Anurans: Ao: *Alytes obstetricans*; Bv: *Bombina variegata*; Pp: *Pelodytes punctatus*; Ha: *Hyla arborea*; Bc: *Bufo calamita*; Bb: *Bufo bufo*; Rd: *Rana dalmatina*; Rt: *Rana temporaria*; Rl: *Rana lessonae*; Re: *Rana esculenta*; Rr: *Rana ridibunda*; Th: *Triturus helveticus*; Ta: *Triturus alpestris*; Tc: *Triturus cristatus*; Ss: *Salamandra salamandra*.

On the factorial map, the sites distributed according to two series. The sites of the first series distributed regularly along the first axis, but they all showed negative values on the second axis. Scattering along the first axis signified both a eutrophication gradient and terrestrialization. The negative value on the second axis meant low temperature variation and presence of riparian cover. In contrast, all sites of the second series showed intermediate values on the first axis and positive values on the second axis. These characteristics indicated an intermediate level of eutrophication, high temperature variation and the absence of riparian cover.

Searching for explanations, lines separating (1) temporary waters, (2) sites without fish, and (3) high astatic sites made it possible to define five groups of sites (Fig. 2D). In the first series, sites J1 to J4 were assembled on the basis of both oligotrophic state and high disturbance level. A second group is composed of sites J5, J6, J10, J13 and J14. These sites were deep, eutrophic, and permanent. Disturbance level was from low to intermediate. Sites J8, J12 and J15 were shallow temporary sites located on the border of the floodplain. They were forested and highly terrestrialized. In the second series, the sites were characterized by the near absence of riparian cover allowing high access of light and high temperature variation. The alluvial substrate (pebbles) was overlain by a thin layer of fine sediment. Such a mesotrophic state is maintained by the underground origin of the water (Rostan *et al.*, 1987). In this series, sites J7 and J9 were temporary ponds with shallow water, while a second group (J11, J16, and J17) were deep permanent ponds.

In conclusion, the main factors influencing the aquatic sites of the floodplain were (1) the disturbance induced by floods which determined, at least partly, a eutrophication gradient; (2) the origin of the water, as underground water limits eutrophication; (3) the temporariness of water filling, which was correlated with the absence of fish.

Habitat use and species distribution

Ten taxa (7 anurans and 3 urodeles) belonging to 6 families, were sampled in the floodplain. Overall species richness was relatively high with respect to the small area of the sector studied and to the fact that the whole region counts 14 amphibian species (Castanet & Guyetant, 1989). The species missing in the floodplain were *Salamandra salamandra*, *Alytes obstetricans*, *Rana temporaria*, and *Rana lessonae*.

Richness (Fig. 3A) and abundance (Fig. 3B) varied greatly among reproductive sites. Richness was very low (never >3 species) in both the most unstable sites located near the active channel and in the permanent sites inhabited by fishes.

In the first habitat type, low richness was explained by both extremely short water retention and mechanical stress caused by flood events. In the second habitat type, fish predation and probably competition were assumed to prevent the occurrence of certain species of amphibians such as *Triturus cristatus* (Beebee, 1985; Dolmen, 1988; Grossenbacher, 1988; Pavignano, 1989; Oldham & Swan, 1991).

The highest richness was observed in temporary fishless sites which were protected from disturbance by floods. In order to explain the extreme richness of site J7 (8 species) we may consider the large area of this site which determined a high spatial heterogeneity, and the underground origin of the water which maintained a low level of eutrophication. We assumed that the intermediate level of perturbation was sufficient to prevent the development of structured communities of predators. However, such an intermediate perturbation level was assumed to allow sufficient spatial heterogeneity for the coexistence of different amphibian species by making niche partitioning possible.

Three groups of species can be distinguished according to abundance (Fig. 3B): (1) ubiquitous species (*Rana ridibunda*, *R. dalmatina* and *Triturus helveticus*), which were observed in nearly all the sites and (2) species characteristic of sites of intermediate spatial-temporal variability (*Hyla arborea*, *Bufo calamita* and *Pelodytes punctatus*). The opening of the environment of these sites allows high access of light, which is favourable for thermophilic species such as *Hyla arborea* (Tester, 1991) and (3) rare species (*Triturus cristatus*, *T. alpestris*, *Bufo bufo* and *Bombina variegata*).

In conclusion there is no real gradient from the central channel to the farthest annexes of the Upper Rhone river, but distribution pattern exist in relation to habitat unpredictability and interspecific constraint. One of the most important problems is to determine how such a distribution pattern can be related to amphibian life history traits.

Habitat use and biological traits

According to several authors the reproduction strategy of many amphibians has evolved toward the reduction of the length of the larval period by increasing egg size and developing parental care (Duellman & Trueb, 1985). This tendency is assumed to respond to the selective pressure induced by high predation on amphibian larvae in most aquatic sites (Trivers, 1972; Lamotte & Lescure, 1977).

In the region surrounding the Rhone floodplain, two species exhibit parental care. The first is the fire salamander (*Salamandra salamandra*) the eggs of which hatch inside the oviducts. The second is the midwife toad (*Alytes obstetricans*), in which males carried the

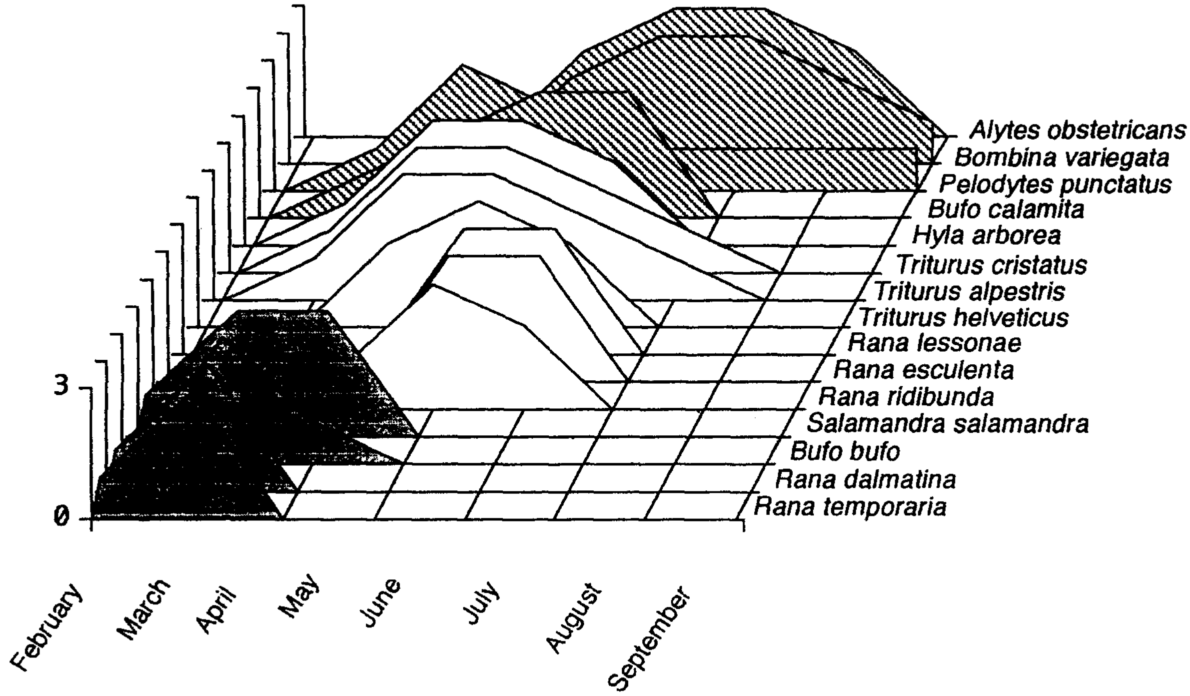

Fig. 5. Temporal pattern of reproduction of each amphibian species. The highest value (3) denotes a high average probability of reproduction. Black pattern: explosive breeders; open pattern: synchronous but not explosive breeders; dotted pattern: staggered breeders.

eggs during the whole embryonic period. It is noticeable that these two species were absent from the sites studied. They were not found elsewhere in the floodplain. A possible cause of the absence of these species in the floodplain is that their adults have lost the ability of survive disturbance such as long submersions. Such a hypothesis remains to be tested.

Specialized species (*H. arborea*, *P. punctatus*, *B. calamita*) seem to avoid fish by spawning in temporary waters. Fish avoidance involves taking the risk of mortality due to site drying. An adaptive trait may be to reduce development length by increasing egg size (Woodward, 1982). This trend was actually observed in all these species except *B. calamita* (Fig. 4). However, the development of the tadpole of *B. calamita* is also short because of a reduction of the size at metamorphosis (Knopffler, 1962; Beebee, 1985; Bregulla, 1988). Another adaptive trait to instability of water level leads to a higher temporal flexibility in these specialized species as shown in Fig. 5. Such a flexibility makes a rapid response possible when conditions become favourable for reproduction (Diaz-Paniagua, 1988).

Ubiquitous species are faced either with predation or with dessiccation risk. In these species (*R. ridibunda*, *R. dalmatina*), egg size is small and fecundity is high. The temporal pattern of reproduction appears to be less flexible than in more specialized species (Fig. 5). This result disagrees with the ecological theory assuming that colonization abilities are balanced with the ability for resistance to predation and competition.

The absence or the low abundance of species such as *Rana temporaria*, *R. lessonae*, *Bufo bufo*, and *Triturus alpestris*, which are abundant in the region surrounding the floodplain, can be explained through competition processes and/or probably important biological traits that are not as yet included in this study. Amphibiotic amphibians probably experience selective pressure during their terrestrial phase, which was not investigated in this study. Other species traits than those studied in this paper are assumed to play an important role in amphibian population dynamics.

For example, reproductive success may depend on the range of size variation at metamorphosis and on the range of the length of development in relation to habitat stability. Unpredictability of favourable sites may be compensated for by calling power. By increasing the number of life-history traits investigated and the number of sites studied (taking into account variation of terrestrial environment), we should improve the accurancy of our understanding of the interactions between environmental variability and amphibian community structure in a floodplain landscape.

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Appendix 1

Coding of species richness and relative abundance in seventeen locations.

	Bv	Pp	Ha	Bc	Bb	Rd	Rr	Th	Ta	Tc	Species richness
1	–	–	–	–	–	–	1	–	–	–	1
2	–	–	–	–	–	–	1	–	–	–	1
3	–	–	–	–	–	1	1	2	–	–	3
4	–	–	–	–	–	–	1	–	–	–	1
5	–	–	–	–	–	1	1	1	–	–	3
6	–	–	–	–	–	1	1	2	–	–	3
7	–	3	3	1	1	3	3	3	–	1	8
8	1	–	–	–	–	–	–	2	1	–	3
9	–	–	1	–	–	–	1	1	–	–	3
10	–	–	–	–	–	1	3	1	–	–	3
11	–	–	1	2	–	–	1	2	–	–	4
12	–	1	–	–	–	3	1	1	–	–	4
13	–	–	–	–	1	–	1	–	–	–	2
14	–	–	–	–	–	1	2	1	–	–	3
15	–	–	–	–	–	–	–	2	–	–	1
16	–	–	–	–	–	1	1	–	–	–	2
17	–	–	–	–	–	1	1	–	–	–	2

Appendix 2

Variables	Modalities	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Site area (m)	<500	–	3	3	3	3	3	–	3	3	–	3	–	–	–	3	3	3
	500–2000	3	–	–	–	–	–	–	–	–	–	–	3	3	3	–	–	–
	>2000 m	–	–	–	–	–	–	3	–	–	3	–	–	–	–	–	–	–
Depth (cm)	20–50	–	–	–	–	–	–	–	3	3	–	–	–	–	–	3	–	–
	50–100	–	–	–	–	3	3	3	–	–	–	–	3	–	–	–	–	–
	>100 cm	3	3	3	3	–	–	–	–	–	3	3	–	3	3	–	3	3
Substrate grain size	Gravel/pebble/blocks	3	–	2	–	–	–	1	–	–	–	1	–	2	–	–	3	2
	Silty sand	2	–	3	1	–	–	1	–	1	–	–	–	2	–	–	2	3
	Silty mud	–	–	–	2	1	1	–	–	–	–	–	1	–	–	–	–	–
	Mud/peat	–	3	–	–	3	3	–	–	–	–	–	2	3	3	–	–	–
	Silted gravel	–	–	1	–	–	–	3	–	2	–	3	–	–	–	–	1	1
	Organic mud/leaves	–	1	–	1	–	–	–	3	–	3	–	3	–	–	3	–	–
Level of eutrophication	Oligotrophic	3	–	3	3	–	–	–	–	–	–	3	–	–	–	–	1	1
	Mesotrophic	–	–	–	–	3	3	3	–	3	–	–	–	1	–	–	2	2
	Eutrophic (aquatic)	–	3	–	–	1	1	2	–	–	3	–	–3	3	–	–	–	–
	Eutrophic (terrestrialization)	–	–	–	–	–	–	–	3	–	–	–	3	–	2	3	–	–
Range of temperature variation	5–10	1	1	3	1	3	3	–	2	–	1	–	1	1	1	3	1	1
	10–15	3	3	–	3	–	–	1	2	1	3	–	3	3	3	–	3	3
	15–20°	–	–	–	–	–	–	3	–	3	–	–	–	–	–	–	–	–
Turbidity	High	–	3	1	–	1	1	–	2	–	1	–	1	–	–	–	–	–
	Moderate	2	1	1	3	3	3	1	2	–	3	–	3	–	1	3	1	1
	Low	3	–	3	1	–	–	3	–	3	–	3	1	3	2	1	3	3
Conductivity	<300	3	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
	300 400	–	2	2	2	–	–	2	–	–	–	–	–	–	–	–	3	3
	400 500	–	–	–	–	2	2	2	–	–	–	–	3	2	2	1	–	–
	>500 US	–	–	–	–	2	2	–	3	–	3	–	–	1	1	3	–	–
Origin of water	Rain water	–	–	–	1	–	–	–	3	–	3	–	3	–	3	3	–	–
	Groundwater	2	2	3	–	3	3	3	–	3	–	3	–	–	1	–	3	3
	Others	3	3	1	3	1	1	–	–	–	1	–	–	–	1	–	–	–
Influence of river discharge	None	–	–	–	–	–	–	3	3	3	3	3	3	3	3	3	3	3
	Slight	–	1	–	–	3	3	–	–	–	–	–	–	–	–	–	–	–
	Strong	3	3	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–
Variation of water level	Permanent pond	–	3	–	–	–	–	–	–	–	3	3	–	3	–	–	3	3
	Partially dried in summer	–	–	–	–	3	3	1	–	–	–	–	3	–	3	–	–	–
	Totally dried up in summer	–	–	–	–	–	–	3	3	3	–	–	–	–	–	3	–	–
	Highly astatic biotope	3	–	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–
Riparian cover	Nul	3	–	–	–	–	–	3	–	3	–	3	–	–	3	–	3	3
	Riparian	–	3	3	1	3	1	–	–	1	3	–	–	3	1	–	–	1
	>50% of the water surface	–	1	1	3	2	3	–	3	–	1	–	3	–	–	3	–	–
Macrophytes	Free water	3	–	2	1	–	–	1	–	–	–	–	3	1	1	2	3	1
	Submersed plants	–	–	–	–	2	2	1	–	1	–	3	–	2	1	–	1	3
	Aquatic floating plants	–	2	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–
	Plants with floating leaves	1	3	–	–	1	–	–	–	–	2	–	–	2	1	–	–	–
	Amphibious plants	1	–	2	3	1	1	3	3	3	1	2	1	1	3	2	1	3
	Logges debris	1	–	1	1	1	1	–	3	–	1	–	3	1	–	–	–	–
Fishes	Absent	–	–	–	–	–	–	3	3	3	–	3	3	–	–	3	–	–
	Present	3	3	3	3	3	3	–	–	–	3	–	–	3	3	–	3	3
Invertebrate predators	Absent	2	3	2	3	–	–	–	3	3	3	–	3	2	–	3	–	–
	Present	1	–	3	–	3	3	3	–	1	1	3	1	1	3	–	3	3