

Population age structure and growth in four syntopic amphibian species inhabiting a large river floodplain

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Abstract: River floodplains are disturbance-dominated landscapes where floods are major regulators of both aquatic and nearby terrestrial communities. Amphibians are common inhabitants of floodplains and their life cycle depends on both aquatic and terrestrial habitats. We focused on how different syntopic species of amphibians reacted to the environmental conditions of a large river floodplain. We examined life-history traits such as population age structure and growth in small- and large-bodied species of anurans and urodeles in the lower Danube River floodplain in Romania. Two newt species, *Triturus vulgaris* (small-bodied) and *Triturus dobrogicus* (large-bodied), and two anuran taxa, *Bombina bombina* (small-bodied) and the *Rana esculenta* complex (large-bodied), were included in the study. The ages of individuals estimated by skeletochronology varied from 3 to 5–6 years for *T. vulgaris* and from 2–3 to 4–5 years for *T. dobrogicus*. In the anurans, ages varied from 2 to 5 years in *B. bombina* and from 4 to 10 years in the *R. esculenta* complex. The numbers of breeding opportunities (i.e., the number of years the adults reproduce) are similar in both newt species (3), while growth rates and age at maturity differ between the large- and small-bodied species. In anurans, the number of breeding opportunities for the smallest species, *B. bombina* (4), is associated with a high growth rate and earlier maturation. In the larger *R. esculenta* complex, the higher number of breeding opportunities (7) is associated with a low growth rate and delayed maturation. The study of age distribution and associated parameters provides useful information on population life history. We discuss how age structure and growth of amphibian populations in large river floodplains can be used as indicators of environmental conditions.

Résumé : Les plaines inondables des rivières sont des paysages fortement changeants, où les crues jouent un rôle important dans l'établissement des communautés aquatiques et des communautés terrestres adjacentes. Les amphibiens sont des habitants communs de ces plaines inondables et leur cycle biologique nécessite à la fois des habitats aquatiques et des habitats terrestres. Nous nous sommes intéressés à savoir comment les différentes espèces syntopiques d'amphibiens réagissent aux conditions environnementales d'une vallée inondable d'un grand fleuve. Nous avons étudié des caractéristiques du cycle biologique, comme la structure d'âge et la croissance, chez des espèces d'anoures et d'urodèles de petite et de grande taille dans la basse vallée du Danube (Roumanie) : deux espèces de tritons, *Triturus vulgaris* (espèce de petite taille) et *Triturus dobrogicus* (grande taille), et deux espèces d'anoures, *Bombina bombina* (espèce de petite taille) et *Rana* sp. du complexe *esculenta* (grande taille). L'âge des individus — estimé par squeletochronologie — varie chez les tritons, de 3 à 5–6 ans chez *T. vulgaris* et de 2–3 à 4–5 ans chez *T. dobrogicus*. Chez les anoures, les âges varient de 2 à 5 ans chez *B. bombina* et de 4 à 10 ans chez *Rana* sp. du complexe *esculenta*. Le nombre d'occasions de reproduction (i.e. 3 fois) est similaire chez les deux espèces de tritons, alors que la croissance et l'âge à la maturité diffèrent entre la grande et la petite espèce. Chez les anoures, le nombre d'occasions de reproduction de la plus petite espèce, *B. bombina*, (i.e. 4 fois) est lié à un taux de croissance fort et une maturation sexuelle précoce. À l'inverse, chez les grandes grenouilles vertes, *Rana* sp. du complexe *esculenta*, le nombre d'occasions de reproduction plus élevé (i.e. 7 fois) est en relation avec un taux de croissance plus faible et une maturation retardée. L'étude de la structure d'âge et des paramètres associés fournit des informations utiles sur le fonctionnement des populations. Nous discutons comment les données sur la structure d'âge et la croissance tirées d'échantillons de populations d'amphibiens des plaines inondables des grands fleuves peuvent servir d'indicateurs des conditions environnementales.

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Introduction

River floodplains are disturbance-dominated landscapes characterized by high levels of habitat diversity and the presence of biota adapted to exploit the spatial and temporal heterogeneity (Junk et al. 1989; Ward et al. 1999). Floods are considered to be the major regulator of both aquatic (Jowett and Richardson 1994) and nearby terrestrial communities (Bosman et al. 1997). Fluvial dynamics play a major role in maintaining a diversity of lentic, lotic, and semi-aquatic habitat types, each represented by a diversity of successional stages (Ward et al. 1999). Amphibians are frequent inhabitants of floodplains. Their life cycle depends on both aquatic and terrestrial habitats, and amphibian species richness in floodplains can vary according to levels of disturbance induced by flood events (Pechmann et al. 1989; Morand and Joly 1995).

This study of the amphibian communities inhabiting a natural island in the lower Danube River floodplain was done between 1994 and 1997 as part of an intensive research program on the role and function of floodplains (Cogălniceanu et al. 1997). Biological and ecological processes on the island are determined by periodic floods on the Danube River (Botnariuc 1967) that can submerge most of it and pose a threat to amphibian survival. Most of the animals survive during this interval by aggregating in the higher parts of islands or seeking refuge on floating debris or old willow trees. During this period amphibians feed less frequently, with a subsequent decrease in body condition (Cogălniceanu 1997) (e.g., water frogs) and reproductive output (Cogălniceanu 1999) (e.g., the smooth newt, *Triturus vulgaris*).

Amphibians are valuable biological models because their reproductive biology (i.e., aggregations of reproductive individuals in breeding areas) allows access to a large part of the population. In floodplain environments the availability and accessibility of suitable breeding places are controlled by the water level. This results in fragmentation of the breeding population in several breeding sites that are often unpredictable and vary in location from one breeding season to another. This results in an uneven spatial distribution that makes it difficult to sample the population effectively.

The age structure of a population is an integrative demographic parameter (Stearns and Koella 1986). Skeletochronology, i.e., recording the periods of arrested growth in long bones like the phalanges (Castanet and Smirina 1990), allows the age structure of amphibian populations to be estimated in natural conditions. Several studies have been conducted at the community level (Gibbons and McCarthy 1983; Miaud 1991; Gokhelašvili and Tarkhnišvili 1994; Guarino et al. 1995; Sullivan and Fernandez 1999), but few have attempted to explain the differences in age structure between the syntopic species investigated. While age at maturity can be partly genetically controlled (Berven 1982; Bernardo 1993), age at maturity and longevity of amphibians are mainly environmentally influenced and age structure may serve as an indicator of environmental variation along climatic (Bernardo 1993; reviews in Miaud et al. 1999, 2000) or pollution (Smirina 1994) gradients.

The aim of this paper is to estimate age structure and growth in four syntopic amphibian species (two anurans and two urodeles) of small and large body size inhabiting an island in

the lower Danube River floodplain. We compare the results with those obtained from populations exposed to other environments and discuss on how age structure and growth can be used to describe the life history of amphibian populations in complex disturbance-dominated ecological systems.

Methods

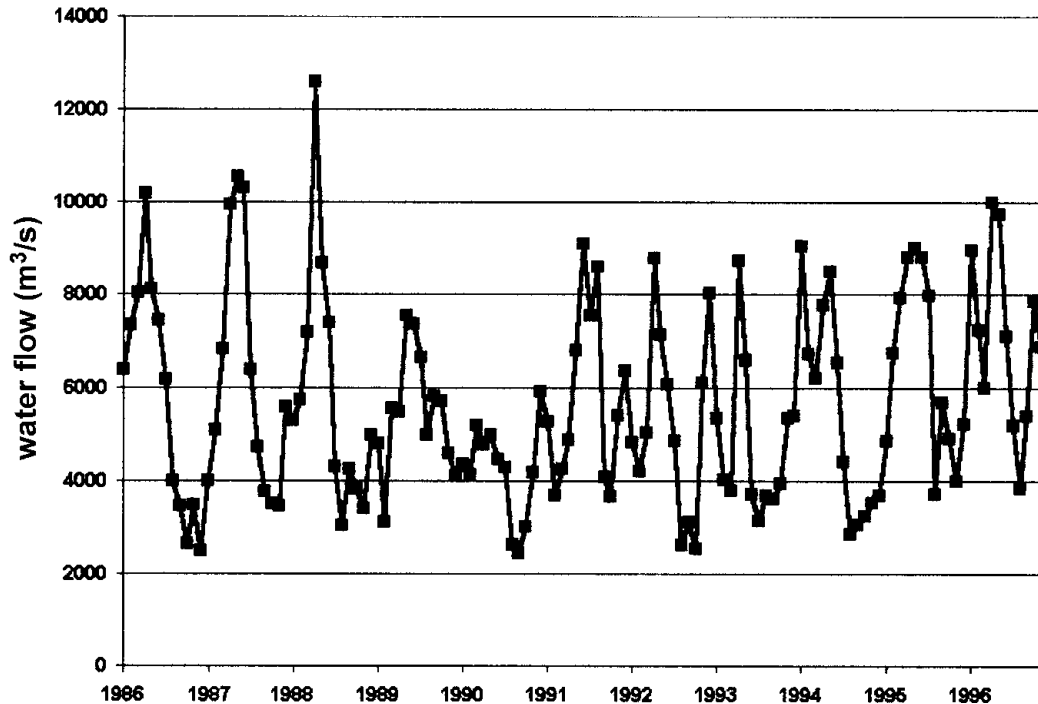
Study area

The study site, Insula Mică a Brăilei, is an island situated in the lower Danube River floodplain south of the town of Brăila, Romania. With an area of 17.58 km² it is one of the largest wetlands left upstream of the Danube River delta, which is still under a natural inundation regime. The area is protected at the national level and was established as a site under the Ramsar Convention on Wetlands in 2001 in recognition of its importance. It is flat in relief, with an average elevation of 4.5 m and a maximum elevation of 8.2 m. Besides the network of river branches and channels that surrounds a number of islands, there are several large shallow lakes in the inner parts. Amphibians were sampled from two similar sites, Fundu Mare (45°10'N, 27°49'E) and Ostrovu Popa (44°47'N, 27°49'E). A detailed description of the sampling methodology is given in Cogălniceanu et al. (2001). The vegetation cover is dense, ranging from cattails (*Typha* sp.) and reeds (*Phragmites* sp.) in the marshy parts bordering the lakes and channels to natural old willow forests and willow (*Salix* sp.) and poplar (*Populus* sp.) plantations. Clearcuts and pastures add to the heterogeneity of the landscape. The landscape is in constant change, depending on the water level. In late spring the island can be almost entirely covered by water and in late summer and autumn the inner lakes and channels can be entirely dry. There are at least two major flood events each year, in spring and in autumn, sometimes lasting 3 months (Fig. 1). Apart from the naturally occurring changes in water level there are unpredictable changes due to variable rates of hydroelectric-power exploitation in reservoirs along the main river and its tributaries. Changes in water level are rapid, since most of the floodplain upstream was dammed and drained and its buffering capacity lost. A much larger island nearby, Insula Mare a Brăilei, was completely dyked and drained in the early 1960s, adding new pressure on the remaining wetlands by increasing the inundation level.

Choice of species

Two species of newts inhabit the islands and both were included in this study: *T. vulgaris* (small-bodied) and the Danube crested newt, *Triturus dobrogicus* (large-bodied). The latter has a limited range, inhabiting only the Danube River floodplain and its main tributaries, and is threatened by habitat destruction and pollution (Arntzen et al. 1997). Of the five species of anurans inhabiting the islands, we focused on one of the two small-bodied species, the fire-bellied toad, *Bombina bombina*. The other small-bodied species (the tree frog *Hyla arborea*) was not considered because it is affected differently by changes in water level, since it stays mostly above ground on vegetation. Of the large-bodied anuran species we focused on water frogs (the *Rana esculenta* complex), since the common toad, *Bufo bufo*, is very rare and

Fig. 1. Mean monthly water flow in the Danube River at Brăila during the decade 1986–1996 (data from Brăila Hydrological Station).



apparently not very successful in coping with inundation (Bosman et al. 1996). The spadefoot toad, *Pelobates fuscus*, because it is of intermediate size and predominantly terrestrial, was not considered either. The *R. esculenta* complex is composed of two parental species (*Rana ridibunda* and *Rana lessonae*) and one hybridogenetic, hemiclinal species (*R. esculenta*). We preferred to pool the two taxa inhabiting the island (*R. ridibunda* and *R. esculenta*) because they are very difficult to distinguish in the field on the basis of morphology only (Pagano and Joly 1998). We assumed that the dynamic changes in habitat availability and quality do not allow for proper segregation and differential development of the two species.

Each of the investigated species has different habitat requirements, and in the *R. esculenta* complex this is so for age classes also. Newts live a more secretive life, hiding under logs and other debris; water frogs are found mostly along the banks of rivers or the borders of lakes, and *B. bombina* are found in the shallow water bordering interior lakes and marshes. Availability and accessibility of food and habitat resources are restricted during certain periods when water levels are high, but this does not seem to be a limiting factor (Cogălniceanu et al. 2001).

Sampling

Amphibians of the lower Danube River floodplain were sampled for various purposes, such as food-content, chemical, and fecundity analyses (Cogălniceanu et al. 1997, 1998, 2001). Individuals used in the present skeletochronological study were captured between October 1994 and August 1996. Adults were sexed using external secondary sexual characters or, when sacrificed, the presence and (or) development of gonads. Mark–recapture methods cannot be used in this area, since animals are continuously on the move because of changes in habitat quality and availability. There

are no distinct populations, only areas with temporary higher concentrations of individuals because of favourable local conditions. A precise description of field conditions is provided in Cogălniceanu et al. (1998).

Body length (snout–vent length, SVL) was measured with dial callipers with a precision of 0.5 mm. The left front limb in sacrificed animals (*B. bombina* and *T. vulgaris*) or the toe of the left hind limb (*T. dobrogicus* and *R. esculenta* complex) was sectioned and stored in 80% alcohol until analysis.

Skeletochronological analysis

The skeletochronological analysis followed previous procedures (Castanet and Smirina 1990; Miaud et al. 1993). Muscle and skin were removed and the bone was decalcified in 3% nitric acid for 1–4 h according to size, and washed in running tap water for 12 h. Cross sections (12–16 μm) of the diaphyseal region of the bone were obtained using a freezing microtome, stained with Ehrlich's haematoxylin, and analysed with a light microscope. A total of 173 bones were used (19 from *T. vulgaris*; 51 from *T. dobrogicus*; 42 from *B. bombina*; 61 from the *R. esculenta* complex), 16 of which did not allow age to be estimated with certainty and were not included in the analysis (6.5% of the samples from *T. dobrogicus* and 10% from the other species).

Data analysis

The normality of age and body-size distributions was verified with a Kolmogorov–Smirnov *D* test (Siegel 1956). Age and SVL were normally distributed in *T. dobrogicus*, *B. bombina*, the *R. esculenta* complex (females), and *T. vulgaris* (females) (Kolmogorov–Smirnov *D* test, all $p < 0.05$), allowing a comparison of means using parametric tests (*t* test). A Mann–Whitney *U* test was used for the *R. esculenta* complex (juveniles and males). The small sample of male *T. vulgaris* did not allow statistical comparisons.

Table 1. Population age structure (assessed by skeletochronology) and body lengths for four syntopic amphibian species from the lower Danube River floodplain.

	Age (years)						Body length (mm)					
	<i>N</i>	Mean	Min.	Max. ^a	SD	CV (%)	<i>N</i>	Mean	Min.	Max. ^a	SD	CV (%)
<i>Triturus vulgaris</i>												
Males	3	—	3	5	—	—	4	—	30.0	36.9	—	—
Females	14	4.1	3	6	1.2	29.7	17	34.7	30.9	39.8	2.09	6.1
<i>Triturus dobrogicus</i>												
Juveniles	11	1.7	1	3	0.79	45.4	10	46.3	38.1	61.8	6.71	14.5
Males	16	3.2	2	4	0.75	23.5	16	65.0	41.2	78.1	8.80	13.5
Females	21	3.5	3	5	0.68	19.5	21	68.9	62.0	84.8	6.60	9.6
<i>Bombina bombina</i>												
Males	13	3.4	2	5	0.93	27.6	13	36.6	30.3	40.0	2.95	8.1
Females	20	3.4	2	5	1.04	31.2	20	36.8	30.5	41.0	2.96	8.0
<i>Rana esculenta</i> complex												
Juveniles	9	2 ^b	0	4	—	—	9	46.9 ^b	32.1	67.8	—	—
Males	7	5 ^b	4	10	—	—	7	81.5 ^b	64.2	89.0	—	—
Females	29	6.7	4	10	1.89	28.28	29	95.6	66.6	118.8	16.29	17.1

^aLongevity.
^bMedian.

Table 2. Growth in four syntopic amphibian species from the lower Danube River floodplain.

	<i>N</i>	SVL _{max.} ± CI	<i>K</i> ± CI	<i>R</i>	Variance (%)
<i>Triturus vulgaris</i>					
Females	14	36 ± 0.4	0.73 ± 0.06	0.54	29.09
<i>Triturus dobrogicus</i>					
Males	16	94 ± 2.7	0.27 ± 0.02	0.78	60.31
Females	21	107 ± 3.3	0.20 ± 0.01	0.82	67.36
<i>Bombina bombina</i>					
Males	13	40 ± 1.1	0.95 ± 0.23	0.67	37.45
Females	20	39 ± 0.62	1.02 ± 0.13	0.53	27.54
<i>Rana esculenta</i> complex					
Males	16 ^a	95 ± 3.9	0.22 ± 0.02	0.90	81.43
Females	29 ^a	108 ± 3.7	0.28 ± 0.03	0.76	58.32

Note: SVL_{max.}, maximum body length; *K*, growth coefficient; CI, confidence interval; *R*, correlation coefficient.

^aEquation fitted with nine juveniles added to adults.

We considered growth to be an incremental change in size (Busacker et al. 1990). Growth was estimated according to von Bertalanffy's (1938) equation, previously used in several studies of amphibians (e.g., Hemelaar 1988; Arntzen 2000; Miaud et al. 2001). The starting point of the growth curve was at metamorphosis; growth during the aquatic larval stage was not considered. To estimate the mean SVL at metamorphosis we used field data from metamorphs caught at the end of summer and also verified our data with values from the literature for *B. bombina* (15 mm; Rafińska 1991) and *T. vulgaris* (16 mm; Bell 1977). In *T. dobrogicus* and the *R. esculenta* complex, SVL of metamorphs was also estimated from the age/SVL linear regression for juveniles (*T. dobrogicus*: SVL at metamorphosis = 35 ± 4.1 mm (mean ± SE), $R^2 = 0.51$, $F = 8.4$, $p = 0.019$, $N = 10$; *Rana esculenta* complex: SVL at metamorphosis = 32 ± 3.6 mm, $R^2 = 0.77$, $F = 22.9$, $p = 0.001$, $N = 9$).

The growth coefficient, *K*, the rate at which maximum body length (SVL_{max.}) is approached, defines the shape of the curve. The parameters SVL_{max.} and *K* and their asymptotic confidence intervals were estimated by nonlinear least-

squares regression. Two estimated SVL_{max.} and *K* values were considered to be significantly different at the 0.95 level when their confidence intervals did not overlap (El Mounden et al. 1999; Miaud et al. 2001). All tests were performed with the Statistica 5.0/W software package (Statsoft Inc. 1996).

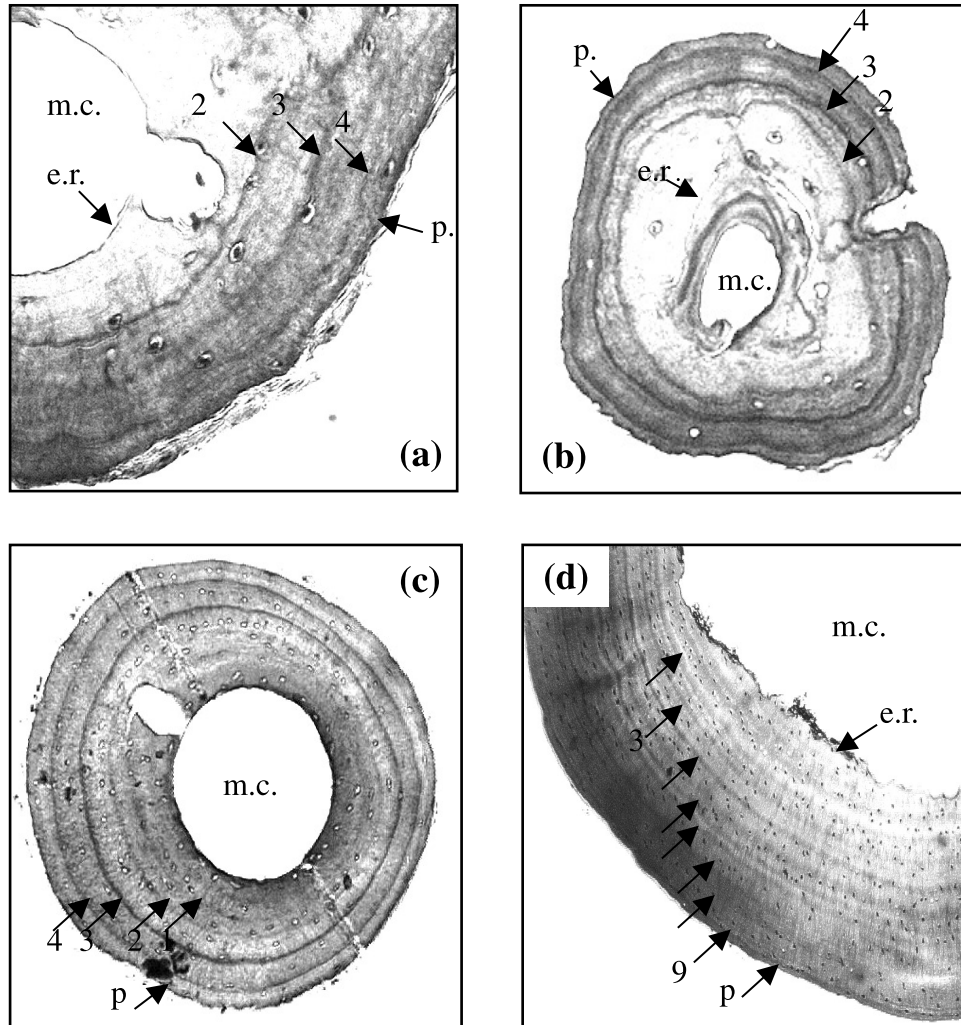
Results

Age structure and body size

Mean age and body length, minimum age and length (i.e. at maturity), maximum age recorded (i.e., longevity), and growth characteristics are presented in Tables 1 and 2. The cross sections of phalanges of each amphibian species investigated are shown in Fig. 2 and age structure in Fig. 3.

In the two newt species, the youngest age at maturity in adult *T. vulgaris* was 3 years for both sexes, while male *T. dobrogicus* matured 1 year earlier than females (at 2 vs. 3 years of age). The mean age and age distribution for male and female *T. dobrogicus* did not differ significantly (*t* test, $t = 1.22$, $df = 35$, $p = 0.23$; Kolmogorov–Smirnov *D* test,

Fig. 2. Cross sections of the bones of four syntopic amphibian species in the lower Danube River floodplain. (a) Cross section of the humerus of a 5-year-old smooth newt, *Triturus vulgaris*. The inner line of arrested growth (LAG) is eroded. (b) Cross section of the phalanx of a 5-year-old Danube crested newt, *Triturus dobrogicus*. The first LAG has been eroded by endosteal resorption. Three LAGs are stained in the periosteal bone. Note that one LAG is also present in the endosteal bone, between the marrow cavity and the endosteal line of resorption. (c) Cross section of the phalanx of a 5-year-old fire-bellied toad, *Bombina bombina*. There is no endosteal resorption. Four LAGs are present. (d) Cross section of the phalanx of a 10-year-old female water frog (*Rana esculenta* complex). The two inner LAGs have been eroded by endosteal resorption. The numbers denote LAGs; *e.r.*, endosteal resorption; *m.c.*, marrow cavity; *p.*, periphery.



$D_{\max} = 0.18$, $p > 0.10$, $N_1 = 16$, $N_2 = 21$). Longevity ranged between 5 and 6 years in *T. vulgaris* and between 4 and 5 years in *T. dobrogicus* (Table 1, Fig. 3).

In the two frog species, the sexes matured at similar ages, 2 years in *B. bombina* and 4 years in the *R. esculenta* complex. The mean age and distribution did not differ significantly between the sexes in *B. bombina* (t test, $t = 0.02$, $df = 31$, $p = 0.98$; Kolmogorov–Smirnov D test, $D_{\max} = 0.11$, $p > 0.10$, $N_1 = 13$, $N_2 = 20$) and the *R. esculenta* complex (Mann–Whitney U test, $U = 75.5$, $p = 0.29$, $N_1 = 7$, $N_2 = 29$; Kolmogorov–Smirnov D test, $D_{\max} = 0.33$, $p > 0.10$). Longevity varied from 5 years in *B. bombina* to 10 years in the *R. esculenta* complex (Table 1, Fig. 3).

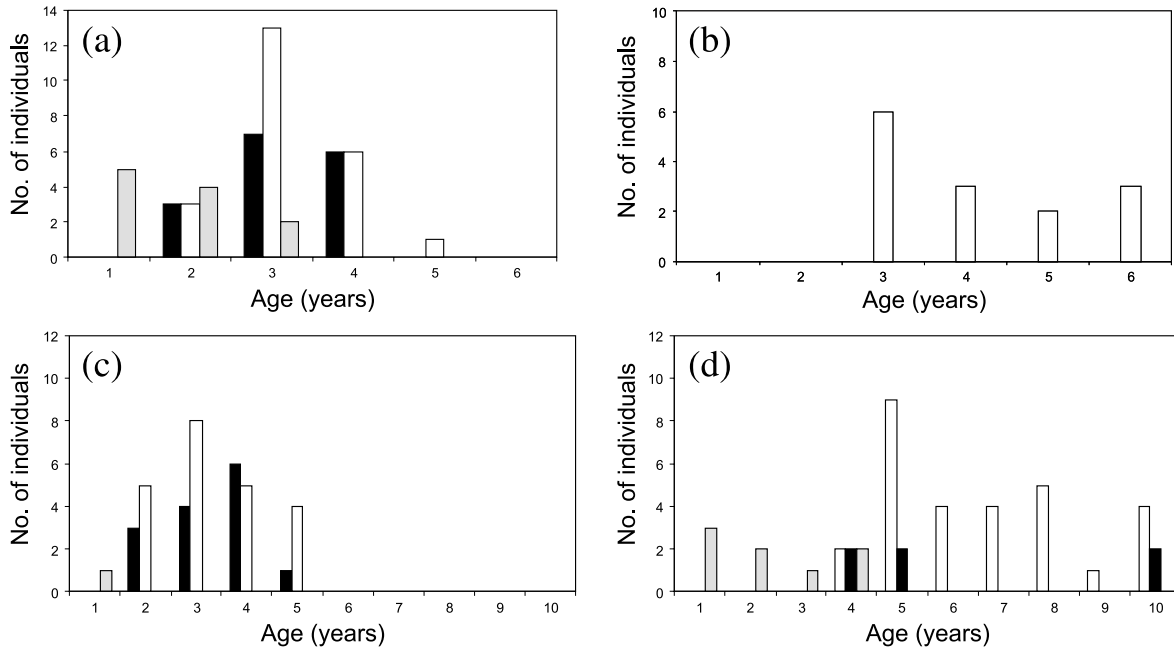
Of the newt species, the sexes had similar mean SVLs in *T. dobrogicus* (t test, $t = 1.52$, $df = 35$, $p = 0.15$) (Table 1). In the frogs, the sexes had similar SVLs in *B. bombina*

(t test, $t = 0.10$, $df = 31$, $p = 0.92$), while females of the *R. esculenta* complex were significantly larger than males (Mann–Whitney U test, $U = 33.5$, $p = 0.006$, $N_1 = 7$, $N_2 = 29$; Table 1).

Growth

Von Bertalanffy's growth model fits the relation between age and SVL relatively well in all species (Table 2; coefficients of correlation from 0.53 to 0.90). Parameters of the growth curve differed significantly between the sexes in *T. dobrogicus*: SVL_{\max} was higher in females, while K was higher in males (Table 2, Fig. 4a). In the anurans, the growth curves for male and female *B. bombina* did not differ significantly. In the *R. esculenta* complex, both SVL_{\max} and K were significantly higher in females than in males (Table 2, Fig. 4b).

Fig. 3. Population age structure for four syntopic amphibian species from the lower Danube River floodplain assessed by skeletochronology. (a) *Triturus dobrogicus*. (b) *Triturus vulgaris*. (c) *Bombina bombina*. (d) *Rana esculenta* complex. Solid bars denote males, open bars denote females, and shaded bars denote juveniles.



Comparison between large- and small-bodied species

The two newt species differed strongly in body length: SVL at metamorphosis in *T. dobrogicus* was the same as SVL at maturity in *T. vulgaris*. However, the larger *T. dobrogicus* matured earlier than the smaller *T. vulgaris* (Table 1), while the oldest individuals were found in *T. vulgaris*. The growth coefficient for *T. vulgaris* was clearly higher than that for the larger *T. dobrogicus* (Table 2), but the age distributions did not differ significantly between these species (Kolmogorov–Smirnov *D* test, $D_{max.} = 0.30$, $p > 0.10$, $N_1 = 17$, $N_2 = 37$). While the smaller species grew faster and the larger species matured earlier, their annual breeding opportunities were similar (i.e., the average life-span of adults, since all species are annual breeders).

The larger frog species (*R. esculenta* complex) matured later than *B. bombina* (Table 1). The growth coefficient of *B. bombina* was also higher than that of the *R. esculenta* complex (Table 2). Longevity was greater in the larger than in the smaller species (the age distributions differed significantly between the species; Kolmogorov–Smirnov *D* test, $D_{max.} = 0.75$, $p < 0.01$, $N_1 = 33$, $N_2 = 36$). In the small *B. bombina*, the lower annual breeding opportunities are coupled with faster growth and earlier maturation. In the *R. esculenta* complex frogs, the higher annual breeding opportunities are coupled with slower growth and delayed maturation.

Discussion

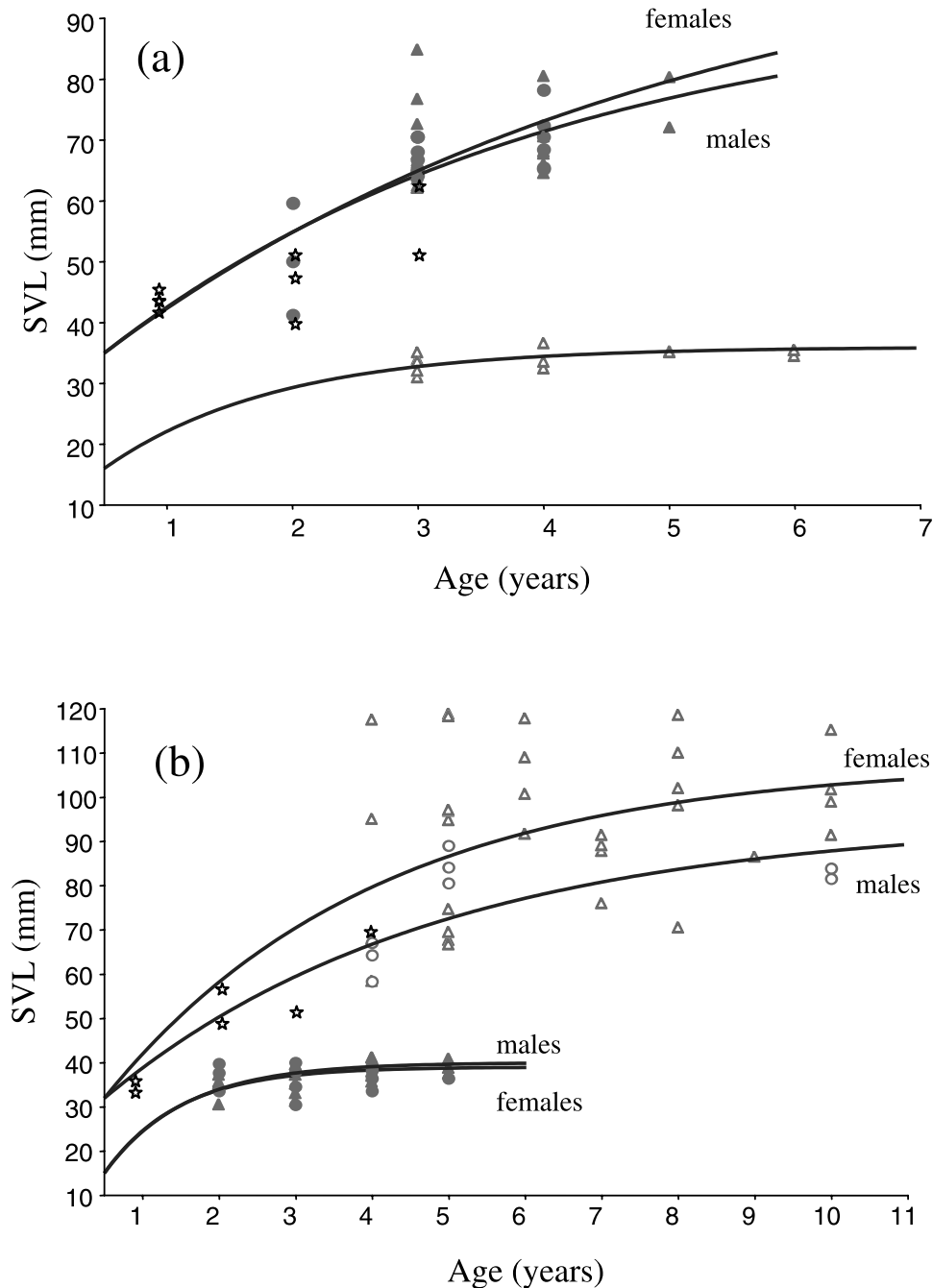
The effects of floods on amphibian communities can be separated into direct and indirect effects with either positive or negative consequences. The flood waves that occur at the beginning of a flood event can, by causing a drifting effect, be unfavourable to each stage of the amphibian life cycle (egg, tadpole, juvenile, and adult). In floodplains interrupted

by forests, where the current is lower, the danger of being caused to drift appears to be only moderate (Marián 1977). Flood events also allow predators of amphibians, such as fish, to colonize breeding ponds normally not connected with the river. The highest amphibian species richness in the Rhône River floodplain was observed in temporary fishless sites that were protected from disturbance by floods (Joly and Morand 1994; Morand and Joly 1995). On the other hand, seasonal floods leave behind numerous water bodies that are favourable to amphibians (i.e., the highly nutrient-enriched flood water ensures optimum growth of phytoplankton and amphibian larvae). Amphibians deposit their eggs in spring as either a single large clutch (*R. esculenta* complex), several small clutches (*B. bombina*), or individually deposited eggs (newts). The exact timing depends not so much on environmental temperature but mainly on water level. The more mobile water frogs deposit their eggs quite early in inner lakes and ponds, where the dense vegetation cover offers protection against strong currents when water levels are high. *Bombina bombina* and the newt species tend to start depositing eggs later, in the shallow water bodies left behind by floods.

Age structure in a floodplain amphibian community

Estimated age structure and SVLs of the studied species of newts reported from populations experiencing various environmental conditions are shown in Table 3. In the smaller newt, *T. vulgaris*, age at maturity varies between 2 and 5 years and longevity between 5 and 10 years (Table 3). Nobili and Accordi (1997) compared populations from permanent and temporary ponds and showed that age at maturity was younger and longevity tended to decrease in the most unpredictable environment, temporary ponds. This lower longevity was also observed in *T. vulgaris* in the lower Danube River floodplain. Ellinger and Jehle (1997) conducted a 9-year

Fig. 4. Growth curves for four syntopic amphibian species from the lower Danube River floodplain. (a) Growth curves fitted to von Bertalanffy's model for newts. The upper curves show *T. dobrogicus* (●, males; ▲, females; ☆, juveniles) and the lower curve shows female *T. vulgaris* (△). (b) Growth curves fitted to von Bertalanffy's model for frogs. The upper curves show the *Rana esculenta* complex (○, males; △, females; ☆, juveniles) and the lower curves show *B. bombina* (●, males; ▲, females). Growth parameters (the growth coefficient, K , and asymptotic maximum size, SVL_{max}) for both sexes and all species are presented in Table 2.



capture–mark–recapture study on *T. dobrogicus* on an upstream island in the Danube River near Vienna. The estimated mean ages of males and females (2.9 and 3.1 years, respectively) are similar to those observed in the lower Danube River floodplain. Their estimated longevity of 9 years is much higher than that observed in the lower Danube River, suggesting that the disturbance caused by floods induces

higher mortality, or dispersal, not observed upstream, where most of the river is no longer free-flowing (Schiemer et al. 1999). Considering the width of the Danube River arms, the speed of the current, and the high risk of fish predation, we estimate that dispersal in this case involves a high risk of mortality. Other taxonomically related large-bodied newts (e.g., *Triturus cristatus*, *Triturus carnifex*, and *Triturus*

Table 3. Age structure of different newt populations in Europe assessed by skeletochronology.

Species and location	Sex	N	Age at maturity (years)	Mean age (years)	Max. age (years)	SVL (mm)			Reference
						Avg.	At maturity	Max.	
<i>Triturus vulgaris</i>									
Norway	Male	26	3	—	6	—	—	—	Dolmen 1982
Yugoslavia	Male	18	4	7.1	9	41.2	37	44.5	Kalezic et al. 1996
	Female	19	5	6.9	9	43.2	38.5	47.2	
England	Male	26	2	3.5	6	45.5	40	51	Verrell and Francillon 1986
	Female	24	3	3.6	5	45.1	32	51	
Sweden	Male	124	3	—	10	—	37.5	49	Hagström 1977
	Female	96	3	—	8	—	39.7	48	
Ireland	Male	—	3	4.2	7	—	—	—	Marnell 1998
	Female	—	3	4.6	7	—	—	—	
Italy (temporary pond)	Male	11	2	—	5	35	36	38	Nobili and Accordi 1997
	Female	16	2	—	5	36	36	38	
Italy (permanent pond)	Male	9	3	—	6	40	39	43	
	Female	11	3	—	5	42	40.5	46	
<i>Triturus cristatus</i> superspecies									
<i>Triturus carnifex</i>									
Yugoslavia	Male	32	3.6	8.8	14	75.1	63.8	87.5	Cvetkovic et al. 1996
	Female	34	3.8	8.3	13	76.25	62.4	88.9	
Italy	Male	15	2	4.6	9	58.2	—	—	Pagano et al. 1990
	Female	16	2	4.4	11	60.8	—	—	
Montenegro	Male	29	4	—	11	—	67.1	—	Kalezic et al. 1994
	Female	20	—	—	—	—	65.6	—	
<i>Triturus marmoratus</i>									
Portugal (lowland)	Male	34	5	—	10	62.2	—	—	Caetano et al. 1985
	Female	30	4	—	10	71.8	—	—	
Portugal (highland)	Male	52	6	—	14	64.1	—	—	
	Female	67	6	—	14	70.4	—	—	
France	Male	32	4	—	14	62.4	—	75	Francillon-Veillot et al. 1990
	Female	37	4	—	13	68.0	—	80	
<i>Triturus cristatus</i>									
France	Male	49	2–3	—	14	62.5	—	80	Francillon-Veillot et al. 1990
	Female	39	2–3	—	8	69.7	—	80	
Norway	Male	47	4	—	16	—	—	—	Dolmen 1982
Sweden	Male	42	3	—	16	66.6	61.5	77	Hagström 1977
	Female	43	3	—	13	70.8	67.3	85	
France	Male	187	2	—	17	68.9	64.9	79	Miaud et al. 1993
	Female	152	2	—	16	72.6	63.6	88	
<i>Triturus dobrogicus</i>									
Austria	Male	520	—	—	—	695	38 ^b	83	Jehle et al. 1995
	Female	477	—	—	—	755	45 ^b	94	
Austria	Male	—	—	2.9 ^a	9 ^a	—	—	—	Ellinger and Jehle 1997
	Female	—	—	3.1 ^a	9 ^a	—	—	—	

^aAge estimated from capture–mark–recapture of individuals.

^bMinimum size recorded in adults.

marmoratus; Table 3) living in permanent habitats (i.e., breeding in ponds or lakes) also exhibit higher longevity (from 8 to 17 years old).

These comparisons are yet more difficult to make between *B. bombina* and the *Rana esculenta* complex because fewer studies are available. In the small-bodied toads of the genus *Bombina*, longevity can reach 11 years in *B. bombina* in Russia (Ananjeva and Borokin 1979; in Smirina 1994), 12 years in Denmark (Briggs 1996), 12 years in *Bombina variegata* (a parapatric western species) in Germany (estimated from successive recaptures; Sy and Grosse 1998), and more than 20 years in Poland (Płytycz and Bigaj 1993). The oldest

B. bombina observed in the lower Danube River floodplain was only 5 years of age. On the other hand, in water frogs, the maximum ages recorded, 12 years in *R. ridibunda* (Aleksandrovskaia and Kotova 1986) and 10 years in the *R. esculenta* complex (Shaldybin 1976, cited in Smirina, 1994), are similar to the longevity observed in both sexes of water frogs in this study.

The lower observed longevity of both small and large newts and the small toad in the Danube River floodplain corroborates the decrease in body condition (Cogălniceanu 1997) and reproductive success (Cogălniceanu 1999). The floodplain environment seems to be unfavourable for

Triturus and *Bombina* species, probably because of their lower migratory capacity in terms of both distance travelled and speed (e.g., Jehle and Arntzen 2000). On the other hand, the longevity of water frogs is similar to that of other populations, and Gubanyi and Creemers (1994) state that migration of water frogs in floodplains is considerable and is induced by rapid changes in water level.

The increased mortality risk observed in floodplains could contribute to the observed differences in species assemblages between floodplains and surrounding river terraces (Joly and Morand 1994).

Growth in a floodplain amphibian community

The mean SVL of *T. vulgaris* in the lower Danube River floodplain was smaller than the SVLs of other European populations (Table 3), but was similar to that observed in a population in a temporary pond in Italy (Nobili and Accordi 1997). In the large newt, *T. dobrogicus*, the mean SVL of both sexes was smaller than that of adults from upstream, near Vienna (Table 3). Females of the small toad *B. bombina* in Poland had a mean SVL of 47.1 mm (Rafińska 1991), i.e., larger than the mean of 35.2 mm in our study. The maximum SVL of 50 mm reported from populations in Denmark (Fog 1996) is also larger than values reported from populations on the floodplain. In water frogs, the mean SVL was similar to that observed in populations in Russia (Ananjeva and Borkin 1979, cited in Smirina 1994).

The mean SVLs of both species of newts do not reach the mean SVL observed in other European populations. This shorter body length may be explained by the observed lower longevity (i.e., growth opportunity), indicating that the floodplain environment does not seem to positively influence newt growth.

Conclusion

As amphibians are perennial species with indeterminate growth (i.e., growth does not cease at maturity), they must optimize not only their age and body length at sexual maturity, but also the trade-off between growth and reproduction in the years following maturation (Kozłowski and Uchmanski 1987). Their occurrence along environmental gradients can serve to test some predictions of life-history theories (e.g., the effects of variability in timing of growth and reproduction and its dependence on annual survival in different environments). A comparison of the lower longevity and shorter body length observed in the newts and *B. bombina* in the present study with those of other populations could indicate such a gradient from disturbed floodplains to more predictable surrounding habitats. Fully testing these hypotheses will require that larger samples be obtained along replicated gradients.

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