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ABSTRACT.—Amphibians are in decline in many parts of the world. Understanding the population dynamics of amphibian species is an important prerequisite for developing effective conservation strategies. We used capture–mark–recapture and skeletochronological techniques to investigate population size, body size, and age structure of metamorphic and pedomorphic forms of *Ommatotriton ophryticus* between 2006 and 2009 in the northwestern Black Sea region of Turkey. Our findings showed that time-specific survival rate, constant capture probability, no temporary emigration, and time-specific population size were the most appropriate models for this population. According to the best model (*Model 6*), population size of metamorphic forms of *O. ophryticus* was estimated as 517 (95% confidence interval [CI] = 338–851) adults in 2006, 338 (95% CI = 282−421) adults in 2008, and 527 (95% CI = 443–646) adults in 2009. Average annual capture probability was estimated at 0.21, although average survival rate across years was 0.35. The mean body size and age structure of the pedomorphs and metamorphs was significantly different for both sexes. Also, body size of both forms of *O. ophryticus* showed positive significant correlations with age. In addition to this, both forms shared a common allometric slope of the snout–vent lengths vs. age, and older individuals had larger bodies. Moreover, age at first reproduction and longevity exhibited great differences between forms whereas the median age was 4 yr for each newt category, except for metamorphosed males, in which it was 5 yr. These results indicate that pedomorphs in this population show retardation of the somatic development and an earlier maturation.

The Northern Banded Newt *Ommatotriton ophryticus* (Berthold, 1846) ranges from western Caucasus in southern Russia and Georgia, through northwestern Armenia and northern Turkey, west to the Bosphorus Strait. *Ommatotriton ophryticus* has been recorded at near sea level (along the coast of the Black Sea) to around 2,750 m a.s.l. (in the Kaçkar Mountains in Turkey). It is found in coniferous, mixed, and deciduous forests up to subalpine meadows. Reproduction of this species occurs generally in shallow, still, or slowly flowing waters. Reproduction may occur in brackish waters found in lakes, ponds, large puddles, or even drainage canals and in open areas near or within forests (Özeti and Yılmaz, 1994; Baran and Atatür, 1998). The Northern Banded Newt has been listed as near threatened (NT) in the Red List category (IUCN, 2010) in view of the rapid declines in Caucasus populations, and particularly in Turkish populations.

Pedomorphic forms of *O. ophryticus* were described in 2008 by Kaya et al. (2008) near Karasu in the vicinity of Sakarya, Turkey. The retention of ancestral juvenile characteristics by adult stages of descendants is called pedomorphosis (Gould, 1977; Alberch et al., 1979). In many caudates, including European newts (especially in *Mesotriton* sp., *Lissotriton* spp.) there are populations with alternative life-history pathways: metamorphosis vs. pedomorphosis (e.g., Duellman and Trueb, 1994). Most larvae transform into immature individuals that remain more or less terrestrial before reaching sexual maturity; however, some larvae attain sexual maturity with larval morphology. Such a discrete life-history polymorphism has both genetic and environmental components, and is usually viewed as an adaptation to contrasted environments in time and space (e.g., Denoël et al., 2005).

Several methods are available for determining the age of individual amphibians. One can use the relationship between age and the size frequency distributions of individuals by conducting a capture–mark–recapture (CMR) study or initiating skeletochronology studies. CMR data can provide fundamental insights into the ecology of species while allowing the estimation of demographic parameters such as capture probability, survival rate, and population size as well as categorization of the population by age class. Skeletochronology is an excellent tool in evaluating the pattern of age and bone structure in wild amphibians, especially if there are pedomorphic forms occurring in a population. When available, age-dependent estimates can be obtained for parameters such as survival, mortality, growth, and reproductive traits (e.g., age of sexual maturity and fecundity).

Here we aimed to describe the population and age structure of pedomorphic and metamorphic forms of the Northern Banded Newt that are living syntopically in a wild population. A 4-yr study was conducted on two separate but nearby irrigation pools. We also aimed to determine the cause of pedomorphosis in the Northern Banded Newt. In addition, we constructed the most appropriate biological model based on the information criteria for these populations. We estimate the population size, survival rates, and capture probabilities and discuss the demographic structure of the populations.

MATERIALS AND METHODS

The study site is approximately 513 m^2 and contains two separate irrigation pools that are connected by large pipes, in the vicinity of Sakarya, Turkey. The pedomorphic individuals of *O. ophryticus* were first described in these pools (Kaya et al., 2008). *Lissotriton vulgaris*, *Triturus karelinii*, *Hyla arborea*, *Pelophylax ridibundus*, *Mauremys caspica*, and *Natrix tessellata* co-occur in this locality with the Northern Banded Newt.

This survey was conducted between late February and early March 2006–2009. These months were reported previously as the breeding season of *O. ophryticus* (Andren, 1997; Kutrup et al., 2005). There were three sampling sessions in 2006 and two each year thereafter. Three researchers conducted the sampling sessions, which lasted 5 h each. *Ommatotriton ophryticus* were captured with the use of a dip net. They were kept in a plastic container until they were photographed, and then were released back to the same pool. Digital photographic identification was

used to record and map the patterning on the body parts of individuals captured in this study. This technique is used for recognizing individuals from the natural body patterns in amphibians (Hagstrom, 1973; Loafman, 1991; Doody, 1995). Photographs were taken in the field with the use of Nikon D70 and Nikon Coolpix 4600 digital cameras. The lateral part of the tail and lateral body bands were found to be suitable to distinguish individual *O. ophryticus*. A small aquarium ($2.5 \times 20 \times 15$ cm) was used for photographing *O. ophryticus*. More than one photograph was taken for each newt; the best image for recognizing each individual was selected from the monitor. All newts were photographed from a fixed distance of 15 cm. All images were transferred to a computer and classified in different folders. Images of all individuals in folders were matched visually and the images of the same individuals from different folders were recorded with the use of Microsoft Office Picture Manager.

We assumed for the CMR models that 1) populations are closed within years and are open year after year, 2) marks are not lost over the sampling period because no marks are applied (recognition via photographs), 3) there is equal catchability of each individual in every sample session and catchability does not vary within individuals. Also, it was assumed that marked and unmarked animals mix completely within pools between sampling sessions because of the short intervals between the sampling sessions.

We used Pollock's (1982) robust design to estimate population size and parameters for metamorphs. It allows estimating capture probabilities (P), recapture probabilities (c), and population size (N) within primary sessions. Primary sessions are separated by longer time intervals (i.e., years). It also considers that the population is open between primary sessions, allowing immigration, emigration, birth, and death. It thus also permits us to estimate annual survival (Φ) as well as temporary emigration (γ). Under Pollock's robust design, primary sessions contain secondary sessions that are separated by a short time interval, and it is assumed that the population is effectively closed during a given primary session (i.e., no births, deaths, immigration, or emigration).

We constructed eight models to test our hypotheses, which represent alternate biological hypotheses. We assumed population size $N(t)$ is year specific and capture and recapture probabilities are equal in all eight models.

Our constructed models are summarized as follows:

Models 1 and *2*. Constant temporary emigration [$\gamma(\cdot)$], constant and equal capture and recapture probabilities [$p(\cdot) = c(\cdot)$], and survival rate constant [$\Phi(\cdot)$] *(Model 1)* or year specific [$\Phi(t)$] *(Model 2)*. Our two models read as $\Phi(\cdot) \gamma(\cdot) p(\cdot) = c(\cdot) N(t)$ and $\Phi(t) \gamma(\cdot) p(\cdot) = c(\cdot) N(t)$, respectively.

Models 3 and *4*. Temporary emigration was constant [$\gamma(\cdot)$], capture and recapture probabilities were year-specific and equal [$p(t)=c(t)$] and survival rate is constant [$\Phi(\cdot)$] *(Model 3)* or year specific [$\Phi(t)$] *(Model 4)*. Models 3 and 4 read as $\Phi(\cdot) \gamma(\cdot) p(t) = c(t) N(t)$ and $\Phi(t) \gamma(\cdot) p(t) = c(t) N(t)$, respectively.

Models 5 and *6*. Temporary emigration absent [$\gamma(\cdot)=0$], constant and equal capture and recapture probabilities [$p(\cdot)=c(\cdot)$], and survival rate is constant [$\Phi(\cdot)$] *(Model 5)* or year specific [$\Phi(t)$] *(Model 6)*. Models 5 and 6 read as $\Phi(\cdot) \gamma(\cdot) = 0, p(\cdot) = c(\cdot) N(\cdot)$, and $\Phi(t) \gamma(\cdot)=0, p(\cdot)=c(\cdot) N(t)$, respectively.

Models 7 and *8*. Temporary emigration was absent [$\gamma(\cdot)=0$], capture and recapture probabilities were year specific and equal [$p(t)=c(t)$] and survival rate is constant $\Phi(\cdot)$ *(Model 7)* or year specific $\Phi(t)$ *(Model 8)*. Models 7 and 8 read as $\Phi(\cdot) \gamma(\cdot) = 0, p(t) = c(t) N(t)$ and $\Phi(t) \gamma(\cdot) = 0, p(t) = c(t) N(t)$, respectively.

We fitted our eight models to the data presented in Table 1 and estimated parameters with the use of program MARK v. 4.3 (White and Burnham, 1999; Cooch and White, 2004). We based model selection on Akaike's Information Criterion corrected for small sample size (Burnham and Anderson, 2002). To provide further information regarding model selection, we calculated mean Akaike weights w for each model across all years. We assessed the relative importance of each parameter by summing mean Akaike weights across all models. Goodness-of-fit tests are not currently possible for the robust design in program MARK. We therefore tried to fit our most general model [*Model 4*: $\Phi(t) \gamma (\cdot) p(t)=c(t) N(t)$] to each of our data sets with the use of program RDSURVIV (Kendall and Hines, 1999). However, we failed to obtain a goodness-of-fit statistic for our global model (*Model 4*) because of small sample size.

Pedomorphic individuals were collected from the study site during sampling sessions in 2006–2009 for skeletochronological studies. All captured pedomorphic individuals were transported alive to our laboratory in covered plastic boxes, and then skeletochronological procedures were performed. To compare between forms, metamorphic individuals were selected randomly from the second sampling session of the 2009 primary session of the CMR data. The same individuals were not used more than once in the age structure analyses. Snout–vent lengths (SVL) of both forms were also measured with digital calipers with an accuracy of 0.02 mm, to compare SVL and age. The external gills can be a misleading character for assessing the maturity on pedomorphic and metamorphic individuals. We assumed that if the individual lays eggs (female) or if it has courtship behavior (male), it has reached sexual maturity.

For skeletochronological studies, we cut the longest digit from the hind foot (or sometimes femur of museum specimens) and fixed it in 70% ethanol. Ages of the specimens were estimated by these bone samples. The procedure for skeletochronology followed previous descriptions (e.g., Castanet and Smirina, 1990; Smirina, 1994). The bones of each animal were cleaned of surrounding tissues, washed in running water for 12 h, decalcified for 3–5 h in 3% nitric acid, then placed in distilled water overnight. The bones were dehydrated with the use of a graded ethanol series and then cleared in xylene before being embedded in paraffin. with the use of a rotary microtome, we obtained 16-μm cross sections from the central region of the diaphysis, stained them with H&E, and made our observations with the use of a binocular microscope.

Because of the small sample size, although we performed our study for 4 yr, we pooled the skeletochronological data to compare metamorph and pedomorph age structures. As age structures did not show normal distributions as shown in Kolmogorov-Smirnov tests, all $P < 0.05$, metamorphic and pedomorphic forms were compared with the use of the Mann-Whitney U-test, and distributions of body sizes were compared with the Student's t-test with the use of Statgraphics v. 5.0. The ages were regressed to SVL in standardized major axis (SMA) analysis. SMA analysis provided a better estimate of the line summarizing the relationship between the two variables (i.e., the main axis along which two variables are correlated) relative to ordinary linear regression because the residual variance in both x and y dimensions are minimized. The analysis also determined the differences between the slopes obtained for each

TABLE 1. Sampling dates and summary of the capture history over 3 years. *N* is the number of metamorphic individuals captured and released on each captured session. Every subsequent cell number represents the number of recaptured individuals for each recapture session.

		Recapture session					
	N	21 March 2006	22 March 2006	23 March 2006	19 April 2008	20 April 2008	24 April 2009
Capture session							
21 March 2006	36						
22 March 2006	47	3					
23 March 2006	62	6	5				
19 April 2008	84	1	3	1			
20 April 2008	100	4	3	4	27		
24 April 2009	146	0	0	1	7	6	
25 April 2009	128	0	0	0	3	3	34

species or for each mother tree, so that a significant *P* value indicated differences between the slopes of the groups studied. We used the statistics package SMART (v. 2.0, Falster et al., 2006) for analysis.

RESULTS

Capture histories were generated from field surveys during the breeding seasons of 2006, 2008, and 2009 (Table 1). Although we captured 146 individuals in 2007, we were unable to estimate parameters for that breeding season because of excessive differences in the number of captured individuals and a lack of recaptures, making CMR analysis impossible. According to capture histories female:male ratios were 1.3:1 for this population. A very small number of pedomorphic individuals were captured (2.8%) during sampling periods; thus, they were excluded from the population size estimates.

Model selection indicated that the models assuming time-specific survival rate, constant capture probability, and no temporary emigration best explained our data (Table 2). This model suggests that individuals of *O. ophryticus* do not skip the breeding seasons, survival rates varied between primary sessions, and capture probabilities were constant. Population size estimations were successfully obtained for metamorphs. According to the best model (*Model 6*), population size was estimated as 517 ± 124.8 (95% confidence interval [CI] = 338–851) adults in the 2006 breeding season and 338 ± 35.0 (95% CI = 282–421) and 527 ± 51.2 (95% CI = 443–646) adults in the 2008 and 2009 breeding seasons, respectively. In addition, 325 adults in 2006, 306 adults in 2008 and 482 adults in 2009 were estimated from model averaging. Given that the study site had approximately the same water volume during each breeding season, results suggest a density of 0.5 (range = 0.3–0.6) newt per cubic meter. Annual capture probability was estimated on average to be 0.21. This result indicated that in most cases, we

recaptured less than one-quarter of the breeding individuals each year. Annual survival rate across years was on average 0.35. Survival rates were estimated as 0.18 ± 0.085 (95% CI = 0.06–0.40) between the 2006 and 2008 breeding seasons, and 0.51 ± 0.267 (95% CI = 0.12–0.90) between the 2008 and 2009 breeding seasons.

The mean SVL of the pedomorphs and metamorphs were significantly different for both sexes, as shown in Table 3. Metamorphic males were on average 34% larger than pedomorphic males, and metamorphic females were on average 24% larger than pedomorphic females.

A total of 21 pedomorphic (12 females, 9 males) and 23 metamorphic (10 females, 13 males) individuals exhibited lines of arrested growth in the bone cross sections (Fig. 1). Age structures differed significantly between pedomorphs and metamorphs in both sexes (Table 3). Pedomorphs mature earlier than metamorphs in both sexes of *O. ophryticus*. Age at first reproduction was estimated as 2 yr old for pedomorphic males and 3 yr old for metamorphic males, and it was 2 yr old in both morphs of females (Fig. 2). Longevity of males was 4 yr in pedomorphs and 8 yr in metamorphs, and in females it was 5 yr in pedomorphs and 6 yr in metamorphs (Fig. 2). The median age was 4 yr for each newt category, except for metamorphosed males, in which it was 5 yr.

On the other hand, in females, SVL and age were positively correlated for both pedomorphs (Pearson's correlation, $r^2 = 0.5$; $n = 12$; $P < 0.05$) and metamorphs ($r^2 = 0.6$; $n = 10$; $P < 0.01$). In the same way, in males, SVL and age were positively correlated in both forms ($r^2 = 0.6$; $n = 9$; $P < 0.05$ and $r^2 = 0.4$; $n = 13$; $P < 0.05$, respectively). SMA analysis showed that both forms shared a common allometric slope of the SVL vs. age. Pairwise combinations of SVL and age showed significant differences across a gradient of elevation (Table 4). Consequently, our results indicate that older individuals have mostly larger body size in both forms.

TABLE 2. Candidate model selection for population size estimation of metamorphic forms. Population sizes [*N(t)*] are always year specific and capture and recapture probabilities are always equal. *K* is the number of parameters and *w* is Akaike weight of the models.

Model number	Model name	AIC$_c$	ΔAIC	*K*	*w*
6	$\Phi(t)\gamma(\cdot) = 0, p(\cdot) = c(\cdot)N(t)$	−3,107.1689	0.0000	6	0.54992
1	$\Phi(\cdot)\gamma(\cdot)p(\cdot) = c(\cdot)N(t)$	−3,105.1219	2.0470	7	0.19761
5	$\Phi(\cdot)\gamma(\cdot) = 0, p(\cdot) = c(\cdot)N(t)$	−3,104.8669	2.3020	7	0.17395
2	$\Phi(t)\gamma(\cdot)p(\cdot) = c(\cdot)N(t)$	−3,103.2760	3.8929	8	0.07852
7	$\Phi(\cdot)\gamma(\cdot) = 0, p(t) = c(t)N(t)$	−2,971.1735	135.9954	7	0.00000
8	$\Phi(t)\gamma(\cdot) = 0, p(t) = c(t)N(t)$	−2,969.2472	137.9217	8	0.00000
3	$\Phi(\cdot)\gamma(\cdot)p(t) = c(t)N(t)$	−2,969.1605	138.0084	8	0.00000
4	$\Phi(t)\gamma(\cdot)p(t) = c(t)N(t)$	−2,967.2514	139.9175	9	0.00000

TABLE 3. Results of the descriptive statistics, Student's *t*-test and Mann-Whitney *U*-test: (A) Body size structure of pedomorphs and metamorphs. (B) Age structures of pedomorphs and metamorphs.

Sex	Organism	*n*	Min–Max (mm)	Mean	SE	*t*	*P* value
(A)							
SVL							
Female	Pedomorph	12	54.18–75.02	62.86	1.525	7.45	0.000*
	Metamorph	10	71.52–93.24	86.06	2.594		
Male	Pedomorph	9	47.12–69.42	59.33	2.318	10.24	0.000*
	Metamorph	13	71.52–112.28	90.79	3.217		
(B)							
Age							
Female	Pedomorph	12	2–5	3.00	0.277	15.50	0.001*
	Metamorph	10	2–6	4.90	0.348		
Male	Pedomorph	9	2–4	3.11	0.200	12.00	0.001*
	Metamorph	13	3–8	4.92	0.366		

* *P* < 0.01.

DISCUSSION

Decline and loss of amphibian populations are increasingly becoming an international concern (Heyer et al., 1988; Barinaga, 1990; Blaustein and Wake, 1990; Wyman, 1990; Alford and Richards, 1999). Estimates of population size are fundamental tools for conservation biologists and give helpful knowledge to the development of effective conservation actions of threatened species (Kaya et al., 2010). Understanding population dynamics and estimating demographic parameters are the central issues in amphibian conservation biology (Marsh and Trenham, 2001). Without such basic information, we are unlikely to understand and reverse amphibian declines (Schmidt et al., 2002; Stuart et al., 2004).

Model selection for the population estimate showed year-specific variation in survival rates (Table 2). Almost 35% of individuals survived annually. When the survival rates were examined in detail, the survival rate for 2006–2008 was smaller than for 2008–2009. This difference is has two possible causes: Survival rate of 2006–2008 (2-yr interval) had a longer time interval than the survival rate of 2008–2009 (1-yr interval), and the changes in the population size over the years. Capture probability was constant during primary sessions in the best model for the population estimate (*Model 6*). This means that capture, handling, and marking animals multiple times has no effect on behavior or on an individual's subsequent chance of capture (i.e., trap happiness or trap shyness). Approximately 20% of the population was captured each year. Although some species can skip a breeding season (Schmidt et al., 2002), there was no evidence of skipped breeding in our data.

Population size of *Triturus* species can vary noticeably in different regions, and by climatic conditions and landscape structures (Griffiths, 1984; Arntzen and Teunis, 1993; Tarkhnishvili and Gokhelashvili, 1999; Kupfer and Kneitz, 2000; Arntzen, 2003). The number of individuals in the Caucasian population of *O. ophryticus* varies between several hundred and several thousand (Tarkhnishvili and Gokhelashvili, 1999). Similarly, we estimated population size of *O. ophryticus* as 517 adults in the 2006, 338 adults in the 2008, and 527 adults in the 2009 breeding seasons in these pools, but the occurrence of pedomorphs seemed to be very low (less than 3%). The decrease in the population size of 2008 could be due to unfavorable weather conditions, as well as being one of the main reasons for the presence of pedomorphosis.

Body size can vary between pedomorphs and metamorphs in different populations and across the range of the species. For example, pedomorphic smooth newts were significantly smaller than metamorphs (Kalezić et al., 1996). However, Denoël et al. (2009) investigated three populations of smooth newt and found a diversified pattern in smooth newts, and that metamorphs were larger than pedomorphs in both sexes in one population, but smaller than pedomorphs in another. In the third population, metamorphs were smaller than pedomorphs in females and larger than pedomorphs in males. In alpine newts, pedomorphic females were significantly smaller than metamorphs, whereas pedomorphic males were not larger than metamorphs (Kalezić et al., 1996). In the palmate newt, metamorphs were larger than pedomorphs in two populations, but in one population, males of both morphs were approximately the same size (Denoël et al., 2009). In our study, the body size of pedomorphs was significantly smaller than metamorphs for both sexes of the northern banded newt.

Skeletochronology is now used widely to determine age in amphibians (e.g., Castanet and Smirina, 1990; Castanet et al., 1993; Üzüm and Olgun, 2009; Üzüm et al., 2011). The resting lines, or lines of arrested growth (LAGs), laid down in the long bones during periods of unfavorable growing conditions (e.g., winter), allow accurate calculations of the number of years that the bone has been growing (age). The maximum life span for *O. ophryticus* was calculated as 8–21 yr in different parts of its range (Kuzmin, 1999; Tarkhnishvili and Gokhelashvili, 1999). Kutrup et al. (2005) compared the age structure of *O. ophryticus* in lowland (300 m a.s.l.) and highland (1,300 m a.s.l.) populations. They found the oldest *O. ophryticus* individual as 10 yr old in a lowland population and 16 yr old in a highland population, and the minimum maturing age as 2–3 yr old in a lowland populations and 4 yr old in a highland population. In this context, our results resembled the lowland population and we estimated the maximum life span of metamorphic *O. ophryticus* as 8 yr old. The age of first reproduction for individuals at our sample sites was estimated as 2 yr old. Comparing allometries in both forms, we found that age and SVL share a common allometry, which most likely indicates that both forms show similar growth rates.

Pedomorphosis consists of two heterochronic processes: neoteny and progenesis. Both of these are related to retardation of somatic development; however, they are separated by the age of sexual maturity. The first reproduction age in neotenic individuals is close to that of metamorphic individuals; however, progenetic individuals show an earlier reproduction age than metamorphs. In newts and salamanders, pedomorphosis is usually considered to result in neoteny (Gould, 1977; Gilbert, 1994; Kalezić et al., 1996; Raff, 1996; Ridley, 1996). Some
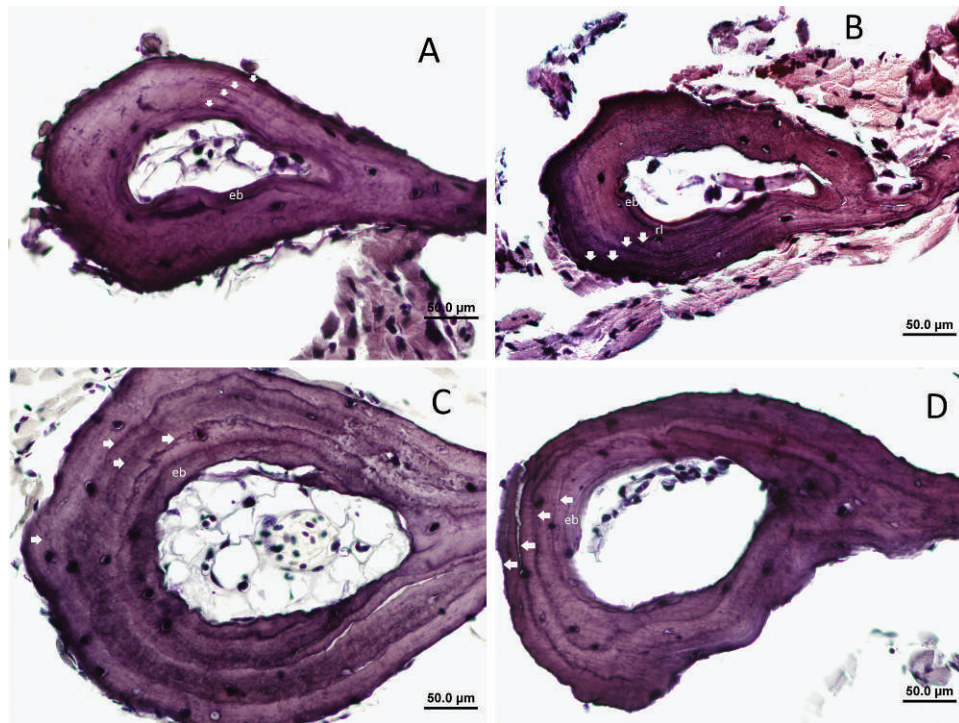
FIG. 1.   Phalangeal cross sections of *Ommatotriton ophryticus*. (A) Pedomorphic male, 30.14 mm in snout–vent length (SVL), showing four lines of arrested growth (LAGs). (B) Pedomorphic female, 31.36 mm in SVL, showing four LAGs. (C) Metamorphic male, 46.06 mm in SVL, showing four LAGs. (D) Metamorphic female, 43.02 mm in SVL, showing four LAGs. eb, endosteal bone; rl, reversal line.

authors provided evidence of progenesis in newts and salamanders by skeletochronological studies (Ryan and Semlitsch, 1998; Denoël and Jolly, 2000). In our study, the age structure and mean body size of metamorphic and pedomorphic forms differed widely (Table 3 and Fig. 2). In this population pedomorphosis resulted in earlier maturation.

Environmental conditions causing pedomorphosis are multifactorial, vary among species, and are often related to unsuitable terrestrial conditions, such that an aquatic lifestyle is more beneficial. Possible causes of pedomorphosis in natural conditions are: The abiotic (temperature, salinity, dissolved oxygen, deficiency of iodine) and biotic factors (food availabil-
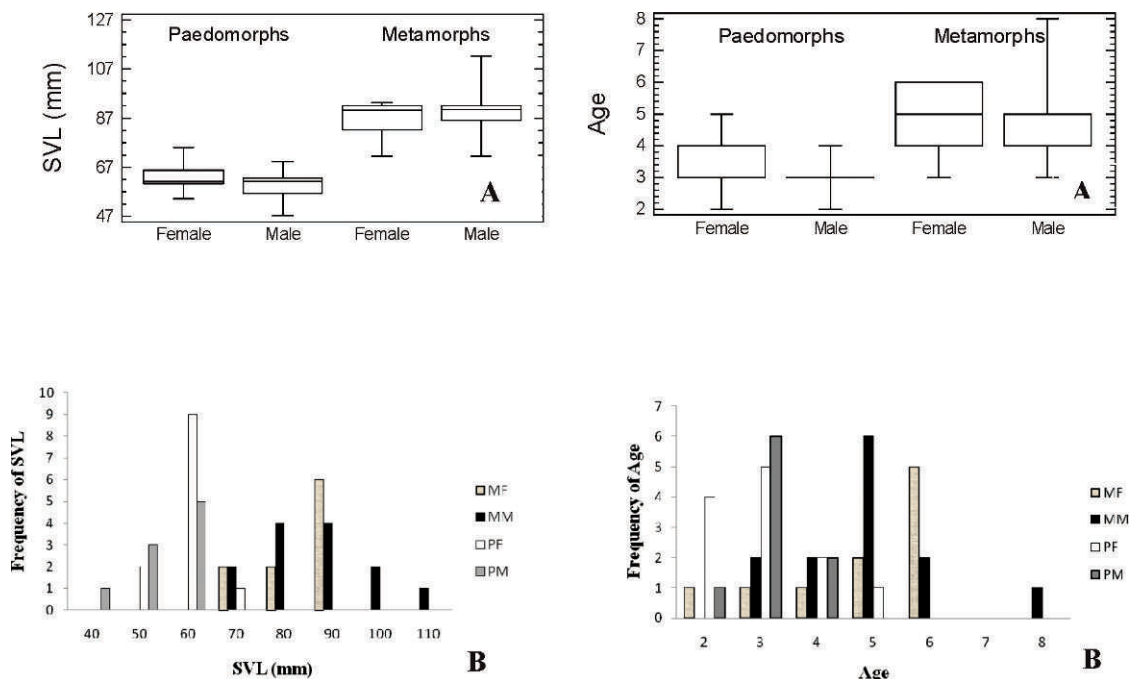

FIG. 2.   Body size and age structures of metamorphs and pedomorphs. (A) Distribution of SVL and age between sexes in both forms (whisker = standard deviation; box = standard error; median line = mean), and (B) frequency of snout–vent length and age in both forms (MF = metamorphic female; MM = metamorphic male; PF = pedomorphic female; PM = pedomorphic male).

TABLE 4. Results of standardized major axis (SMA) regression analysis for all pairwise combinations of snout–vent length (SVL) and age. P = pedomorphs, M = metamorphs.

Trait pair (X and Y)	Forms	n	r^2	p	Slope	Intercept	Slope homogeneity (p)	Shift in elevation (p)	Shift along slope (p)
SVL and age	P	21	0.392	0.001	0.4645	1.630	0.774	0.000	0.000
	M	23	0.371	0.003	0.4298	1.574			

ity, crowding of conspecifics, starvation of larvae) of aquatic environments, genetic factors, and disruption of normal hormonal activities (Doetsch, 1949; Tihen, 1958; Dely, 1967; Sprules, 1974; Harris, 1987; Voss, 1995). Denoël and Joly (2000) indicated that ecological conditions such as shallow water, absence of fish, and low elevation are favorable for progenesis. Ecological conditions at our sites are similar to these conditions with the exception of water depth. In addition, the large decrease in proportion of pedomorphs could be explained by the high density of newts in a population (Semlitsch, 1987; Denoël and Joly, 2000). The average density of northern banded newts is very low in this habitat (0.5 newts per cubic meter). The decreasing proportion of pedomorphs may be affected by the presence of the other amphibian species (*L. vulgaris*, *T. karelinii*, *H. arborea*, and *P. ridibundus*), leading to interspecific competition and food scarcity in the limited aquatic habitats.

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