

Age structure and size of the syntopic populations of *Triturus carnifex* (LAURENTI, 1768), *Triturus vulgaris* (LINNAEUS, 1758) and *Triturus alpestris* (LAURENTI, 1768) in the lake Ameisensee (1,282 m a.s.l.)

(Amphibia: Caudata: Salamandridae)

Altersstruktur und Größe der syntopen Populationen von *Triturus carnifex* (LAURENTI, 1768), *Triturus vulgaris* (LINNAEUS, 1758) und *Triturus alpestris* (LAURENTI, 1768) im Ameisensee (1282 m Seehöhe)

(Amphibia: Caudata: Salamandridae)

ANDREAS MALETZKY & JULIA PESTA & ROBERT SCHABETSBERGER
& ROBERT JEHLE & MARC SZTATECSNY & ALFRED GOLDSCHMID

KURZFASSUNG

Der im Salzburger Tennengau liegende Ameisensee (1282 m Seehöhe) stellt durch seinen hohen Individuenreichtum ein wichtiges Reproduktionsgewässer für sechs lokal gefährdete Amphibienarten (*Triturus carnifex*, *T. vulgaris*, *T. alpestris*, *Rana temporaria*, *Bufo bufo* und *Bombina variegata*) dar.

Die mit Hilfe der Fang-Wiederfang-Methode geschätzten Populationsgrößen betragen 805 (2000) und 327 (2001) für *T. carnifex*, 2362 (2000) und 1637 (2001) für *T. vulgaris*, sowie 1090 (2000) und 7027 (2001) für *T. alpestris*. Dies sind die größten für Österreich dokumentierten Alpenkammolch- und Teichmolchpopulationen in einer Seehöhe von über 1100 m.

Das Alter von 21 *T. carnifex*, 18 *T. vulgaris* und 19 *T. alpestris* wurde anhand skelettochronologischer Befunde ermittelt. Das durchschnittliche Alter betrug 8 Jahre (Median) für *T. carnifex* und *T. alpestris*, sowie 7,5 Jahre (Median) für *T. vulgaris*. Das Höchstalter lag bei 16 Jahren (*T. carnifex*), 11 Jahren (*T. vulgaris*) und 10 Jahren (*T. alpestris*). Es wurden keine signifikanten Unterschiede in der Altersstruktur der Populationen der drei Molcharten festgestellt.

ABSTRACT

The lake "Ameisensee" (1,282 m a.s.l.) is situated in the Northern Calcareous Alps of Austria, and represents an important breeding site for six species of locally endangered amphibians (*Triturus carnifex*, *T. vulgaris*, *T. alpestris*, *Rana temporaria*, *Bufo bufo* and *Bombina variegata*).

Estimated population sizes by means of the capture-mark-recapture method were 805 (2000) and 327 (2001) in *T. carnifex*, 2362 (2000) and 1637 (2001) in *T. vulgaris*, 1090 (2000) and 7027 in *T. alpestris*, respectively. These are the largest known populations of *T. carnifex* and *T. vulgaris* from above 1100 m altitude in Austria.

The age of 21 *T. carnifex*, 18 *T. vulgaris* and 19 *T. alpestris* was assessed using skeletochronological techniques. The median age was 8 years in *T. carnifex* and *T. alpestris*, and 7.5 years in *T. vulgaris*. Maximum longevities were 16 years (*T. carnifex*), 11 years (*T. vulgaris*) and 10 years (*T. alpestris*). Concerning the age structure there were no significant differences observed between the populations of the three newt species studied.

KEY WORDS

Amphibia: Caudata: Salamandridae: *Triturus alpestris*, *Triturus carnifex*, *Triturus vulgaris*; age, high altitude population, population size, skeletochronology, population ecology, Austria

INTRODUCTION

Large syntopic high altitude populations of Italian Crested Newts, Smooth Newts and Alpine Newts - *Triturus carnifex* (LAURENTI, 1768), *T. vulgaris* (LINNAEUS,

1758), *T. alpestris* (LAURENTI, 1768) - are rarely found in Austria where all three species show a wide vertical distribution with maxima higher than 1,400 m a.s.l..

Triturus carnifex and *T. vulgaris* are most abundant between 200 m and 600 m a.s.l., while *T. alpestris* is dominant above 800 m (CABELA et al. 2001).

Lower temperatures and shorter activity seasons in mountain areas lead to slow metabolism producing decreased growth and delayed age of maturation (JØRGENSEN 1992). Age at first reproduction and longevity increase with altitude and latitude of the breeding site (e.g., DOLMEN 1983; CAETANO & CASTANET 1993; SMIRINA 1994). Larger bodied newts achieve higher individual ages than smaller bodied newts (GRIFFITHS 1996). While there are several studies on the age structure of *T. alpestris* from different altitudes (MIAUD et al. 2000; PERRET et al. 2003), little is known about the two other

newt species (but see COGALNICEANU & MIAUD 2003), particularly at higher elevation.

This study is part of a research project on the conservation of high altitude newt populations. SCHABETSBERGER et al. (2004) studied post-breeding migrations of Italian Crested Newts, focussing on terrestrial habitats and their protection. A potential threat to the aquatic habitat may arise from a change in the dynamics of the water level, for example due to climate change which could lead to an increasing number of seasons with reproductive failures. Population size and age structure represent two main parameters to monitor the abovementioned adverse effects.

STUDY SITE AND METHODS

Study site

The lake "Ameisensee" (0.5 ha maximum extension, 4.1 m maximum depth) is situated south-east of the city of Salzburg (Austria) in the foothills of the Gosaukamm limestone massif, at 1,282 m a.s.l. It is surrounded by an old growth spruce forest and alpine pastures used for extensive cattle grazing during summer. Slopes of the Dachstein-West ski-resort border the area 0.5 km further east.

In spring (April-May), the lake basin fills with melting water which enters through creeks in the South and South-west and numerous small inflows from an adjacent mossy meadow, flooding parts of the latter. During summer the water level drops, however rises again after extended periods of rainfall. The lake dried out completely in early November 2000 and early August 2001, respectively.

Six amphibian species (*Triturus carnifex*, *T. vulgaris*, *T. alpestris*, *Rana temporaria*, *Bufo bufo* and *Bombina variegata*) use the lake for reproduction. The closest breeding sites of *T. carnifex* and *T. vulgaris* are known from a distance of more than 20 km from the lake, whereas *T. alpestris* is present in the surrounding area (CABELA et al. 2001). In absence of submersed macro-

phytes and algae, the flooded meadow and fallen timber provide egg deposition sites for newts.

Methods

Population size of each newt species was estimated in two consecutive years (2000, 2001), using the Petersen capture-mark-recapture method (in KREBS 1989). Newts were caught with dip nets, anaesthetised with MS 222® (Sigma-Aldrich®, Vienna) and marked ventrally by tattooing with Alcian-blue (JOLY & MIAUD 1990).

Skeletochronology is the most reliable method for age determination in newts (CASTANET & SMIRINA 1990). We assessed the age of 21 Italian Crested Newts (10 females, 11 males), 18 Smooth Newts (9 females, 9 males), and 19 Alpine Newts (9 females, 10 males) caught in 2001. Snout-vent-length (to the nearest 1 mm) was measured with vernier callipers. The fourth toe of the right hindlimb was clipped with scissors during anaesthesia and fixed in 10% formaldehyde. Individual ages were assessed by counting the Lines of Arrested Growth (LAGs) in histological cross-sections of the diaphyseal regions of phalanges (see SCHABETSBERGER et al. 2000 for details).

Table 1: Number of newts caught at Captures 1 and 2, number of marked Recaptures at Capture 2, and estimated Number of individuals (95% confidence intervals in parentheses) in the study seasons 2000 and 2001.

Tab. 1: Anzahl der in den Untersuchungsjahren 2000 und 2001 am ersten (Capture 1) und zweiten (Capture 2) Untersuchungstag gefangenen, sowie der am zweiten Untersuchungstag wiedergefangenen markierten (Recaptures) Molche, Schätzwerte der Individuenzahlen (Number of individuals) und die 95%-Konfidenzgrenzen (in Klammern).

	2000			2001		
	Capture 1 11.07.	Capture 2 12.07.	Recaptures 12.07.	Capture 1 19.06.	Capture 2 21.06.	Recaptures 21.06.
<i>T. carnifex</i>	Number of individuals = 805 (353-1772)			Number of individuals = 327 (165-634)		
Females/Weibchen	37	-	-	34	21	3
Males/Männchen	24	-	-	21	19	3
Total	61	51	3	55	40	6
<i>T. vulgaris</i>	Number of individuals = 2362 (1037-5197)			Number of individuals = 1637 (772-3461)		
Females/Weibchen	58	70	-	63	42	2
Males/Männchen	31	34	-	53	27	2
Total	89	104	3	116	69	4
<i>T. alpestris</i>	Number of individuals = 1090 (552-2112)			Number of individuals = 7027 (4206-13340)		
Females/Weibchen	23	33	-	173	189	9
Males/Männchen	68	49	-	99	119	2
Total	91	82	6	272	308	11

RESULTS

In *T. carnifex* the estimated population size was 805 individuals in 2000, and 327 individuals in 2001. *Triturus vulgaris* (2362 individuals) was more abundant than *T. alpestris* (1090 individuals) in 2000, whereas the opposite was found in 2001 (1637 *T. vulgaris* vs. 7027 *T. alpestris*) (table 1).

The age of *T. carnifex* (figs. 1 and 2a) was 6-14 (median = 9, mode = 9, arithmetic mean = 9.3) years in females and 6-16 (med. = 8, mode = 8, arithmetic mean = 8.7) in males. *Triturus vulgaris* (fig. 2b) females were 5-9 (med. = 7, mode = 6, arith-

metic mean = 6.9) years old, males 4-11 (med. = 8, mode = 9/10, arithmetic mean = 8.2). The age of *T. alpestris* (fig. 2c) ranged from 7-10 years (med. = 8, mode = 8, arithmetic mean = 8.2) in females, and from 6-10 (med. = 8, mode = 10, arithmetic mean = 8.3) in males. We did not detect significant differences in age frequency distributions between males and females within any species (Kolmogorov-Smirnov Test, $p > 0.638$), or between the three species (sexes pooled, Kolmogorov-Smirnov Test, $p > 0.537$).

Table 2: Snout-vent-lengths of *Triturus carnifex*, *T. vulgaris*, and *T. alpestris* at the high altitude study site Ameisensee (Salzburg, Austria).

Tab. 2: Kopf-Rumpf-Längen von *Triturus carnifex*, *T. vulgaris* und *T. alpestris* vom hochgelegenen Untersuchungsgewässer Ameisensee (Salzburg, Österreich).

	n	Minimum (mm)	Maximum (mm)	Mean ± Standard deviation (mm) Mittelwert ± Standardabweichung (mm)
<i>T. carnifex</i>				
Females/Weibchen	9	76	88	83 ± 3.9
Males/Männchen	12	70	82	75 ± 3.6
<i>T. vulgaris</i>				
Females/Weibchen	9	41	52	47 ± 3.8
Males/Männchen	9	43	49	46 ± 1.8
<i>T. alpestris</i>				
Females/Weibchen	9	48	57	53 ± 3.0
Males/Männchen	10	38	46	43 ± 2.2

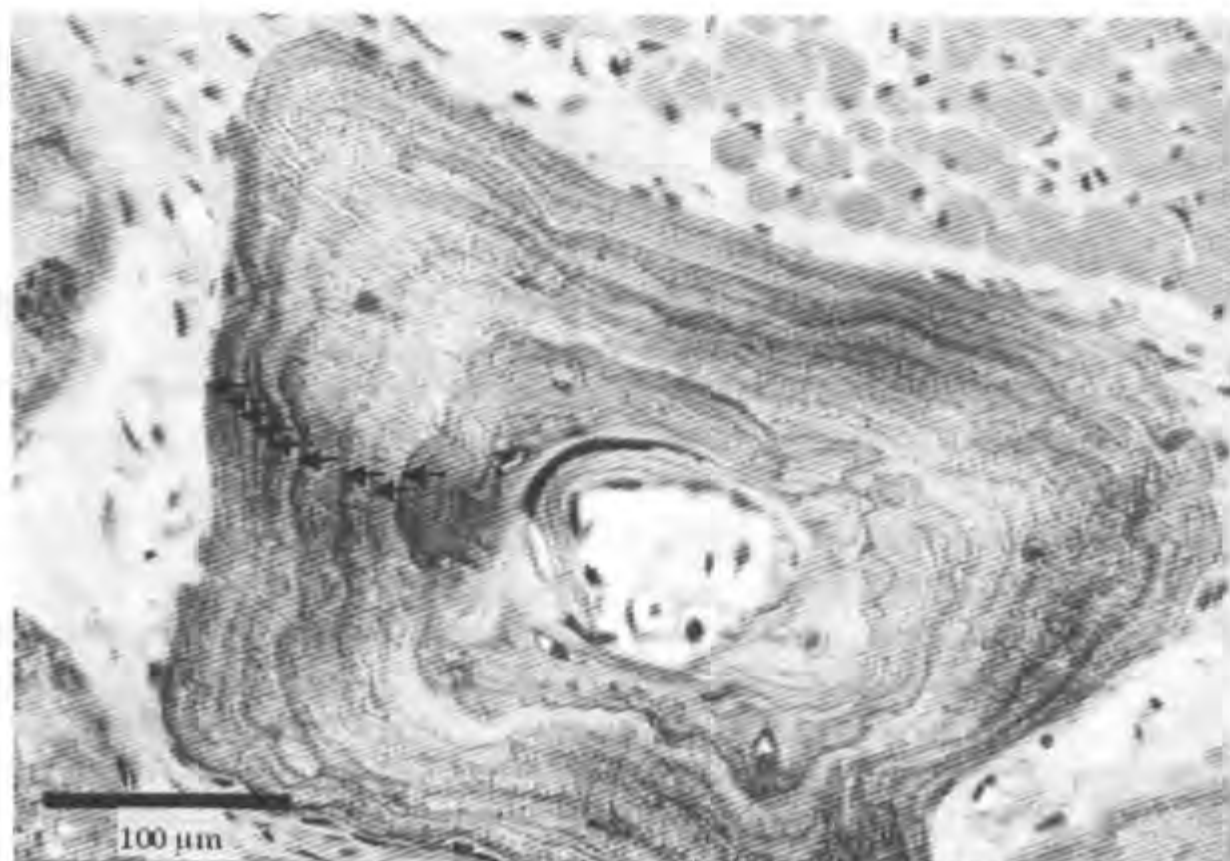


Fig. 1: Diaphyseal cross-section of the proximal phalanx of the fourth toe in a 9-year-old male *Triturus carnifex*. Black arrows indicate Lines of Arrested Growth.

Abb. 1: Querschnitt durch die Diaphysenregion eines proximalen Zehngliedes bei einem 9 Jahre alten männlichen *Triturus carnifex*. Schwarze Pfeile bezeichnen Wachstumspausen.

Females were significantly larger than males in *T. carnifex* (t -test: $p < 0.001$, $t = 4.55$, $df = 19$) and *T. alpestris* (t -test: $p < 0.001$, $t = 8.37$, $df = 17$), but not in *T. vulgaris* (t -test: $p < 0.486$, $t = 0.71$, $df = 16$, table 2). The expected positive correlation between size and age was significant only in male *T. alpestris* (linear regression: $r^2 =$

0.549 , $p = 0.014$). This correlation was not significant in the males of *T. carnifex* ($r^2 = 0.037$, $p = 0.574$) and *T. vulgaris* ($r^2 = 0.162$, $p = 0.283$) as well as in the females of all three species, (*T. carnifex*: $r^2 = 0.004$, $p = 0.875$; *T. vulgaris*: $r^2 = 0.361$, $p = 0.087$; *T. alpestris*: $r^2 = 0.007$, $p = 0.831$).

DISCUSSION

Population size

The population at Ameisensee is the largest one of *T. carnifex* recorded from above 1,000 m altitude in Austria (A. CABELLA, pers. comm.). While populations comprising several hundred adults are common in the southern part of the distribution range (e.g., GIACOMA et al. 1988; KLETECKI 1995), they appear to be rare in the Alps, especially at high altitudes (K. GROSSENBACHER, pers. comm.). From southern Bavaria (Germany) an allochthonous *T. carnifex* population with several hundred individuals was

described recently (FRANZEN et al. 2002). For the closely related species *T. cristatus* (LAURENTI, 1768), population size estimates from capture-mark-recapture studies ranged from 20 to 1,400 newts (average approximately 300 individuals; 20 surveyed populations THIESMEIER & KUPFER 2000). Only 1% of 496 populations surveyed in Westphalia and Rhineland-Palatinate (Germany) comprised more than 100 individuals (THIESMEIER & KUPFER 2000).

We detected differences in our estimates of population sizes between years. Since long-term-studies of population dy-

namics in Crested Newts (e.g., *T. cristatus*: GLANDT 1982; ARNTZEN & TEUNIS 1993 - *T. dobrogicus*: ELLINGER & JEHL 1997) showed considerable fluctuations in population size, further investigations are needed to discriminate between short term fluctuations and long term trends in population dynamics. Due to the low number of recaptures the variation between estimates in this case may be viewed as a methodical issue and not as evidence for fluctuations in population size. A possible explanation for the little number of recaptures could be "trap shyness", meaning the animals captured once behaving shy and less active and are therefore hard to recapture when there is only little time between two sampling sessions.

The Ameisensee population of *T. vulgaris* is outstandingly large when compared to what is known from mountainous regions in Central Europe (K. GROSSENBACHER pers. comm.). In Austria, only one more site above 1,000 m is on record (Weißpriach, Lungau, province of Salzburg, 1,100 m a.s.l.) which holds comparable numbers. Here, between 1995 and 2003, an annual average of 2,198 migrating Smooth Newts breeding in several ponds has been counted at a drift fence 1.5 km long (M. KYEK, pers. comm.). *Triturus vulgaris* populations can reach sizes of more than 1,000 individuals elsewhere in Europe (e.g., BELL 1977; JAHN 1995; STENSIÖ 1998). However, due to destruction of aquatic and terrestrial habitats, such sites have become increasingly rare (NÖLLERT & NÖLLERT 1992). In a study on two Croatian newt communities in which *Triturus vulgaris meridionalis* (BOULENGER, 1882) co-occurs with *T. carnifex* and *T. alpestris*, the Smooth Newt was the rarest species in the ponds surveyed, with proportions of 5.4% and 13.3%, respectively (KLETECKI 1995).

At high altitudes, *T. alpestris* is usually the dominant newt species and can reach population sizes of over 20,000 individuals in a lake of 0.75 ha (DENOËL & SCHABETSBERGER 2003). At Ameisensee it is by far the most abundant species. In the first study season (2000) the population size was probably underestimated due to the late survey date, when a large part of the Alpine Newts had presumably already left the lake.

Age structure

In disagreement with the common concept of larger newt species attaining higher ages (GRIFFITHS 1996), we did not observe significant differences between the three species in this respect. Individuals of the large bodied species *T. carnifex* reached the highest maximum (14-16 years) and median (9 years) ages and were the oldest (6 years) to arrive at sexual maturity though. The majority of newts had attained ages between 7 and 9 years in all three species, while sexual maturity (= age of the youngest adults present in the water) was generally reached at 4-6 years. However, the considerable intraspecific variation, calls for the analysis of a larger sample in order to obtain significant results.

The Italian Crested Newts at Ameisensee attained slightly higher ages than specimens from a lowland population (400 m a.s.l.) of *T. carnifex macedonicus* (KARAMAN, 1922) in Montenegro, where males were found to be 5-14 years old (mode = 8 years) and females 5-13 (mode = 6 years) (CVETKOVIC et al. 1996). Longevities in the Ameisensee population were similar to those in populations of Crested Newts (*T. cristatus*) in Scandinavia (HAGSTRÖM 1977; DOLMEN 1982). In lowland areas, Crested Newts reach a maximum age of up to 17 years as well, but generally mature already at an age of 1-2 years. Moreover, the median age (3-5 years) is lower than in our study (FRANCILLON-VIEILLOT et al. 1990; MIAUD et al. 1993; COGALNICEANU & MIAUD 2003).

There is only little comparable information on high altitude populations of *T. vulgaris*. Smooth Newts from Serbia and Montenegro (990 m a.s.l.) showed an age distribution similar to that found in our study (range: 4-9 years, arithmetic mean: 7 years, KALEZIC et al. 1996). The aforementioned study also showed a significantly shorter longevity in the Smooth Newt compared to the Alpine Newt. Lowland populations of *T. vulgaris* in Scandinavia (range: 3-10 years, arithmetic mean: 5.07 years, HAGSTRÖM 1977; range 2-6 years, arithmetic mean: 4.38 years, DOLMEN 1982) and Ireland (range: 3-7 years, arithmetic mean: 4.38 years, MARNELL 1998) are generally more short-lived.

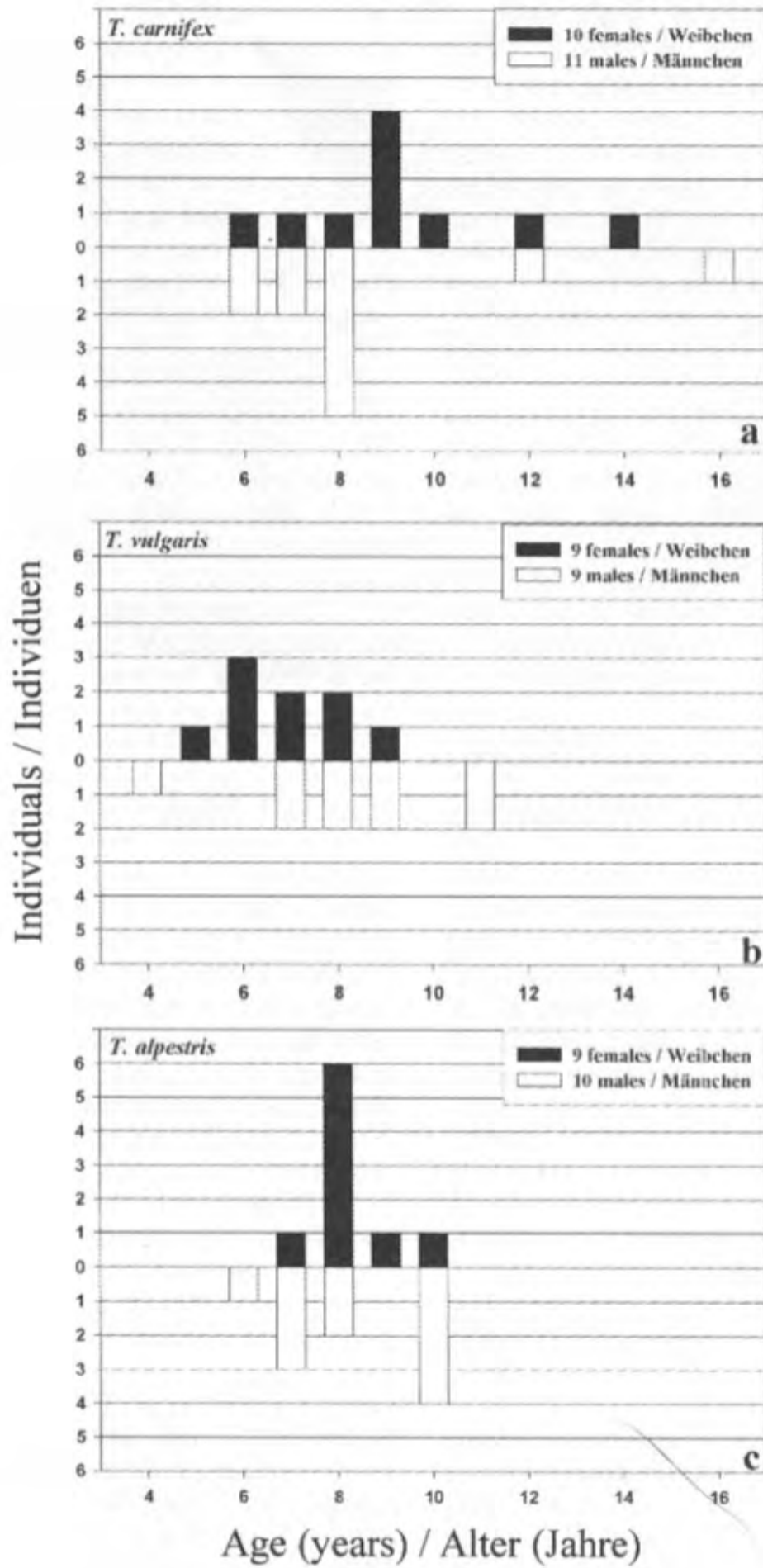


Fig. 2: Distribution of age classes in the newts of the lake Ameisensee. a - *Triturus carnifex*, b - *T. vulgaris*, c - *T. alpestris*.

Abb. 2: Verteilung der Altersklassen bei den Molchen im Ameisensee. a - *Triturus carnifex*, b - *T. vulgaris*, c - *T. alpestris*.

Among the European newt species *T. alpestris* inhabits the widest altitudinal range. In Austria, this species occurs between 200 m and 2,400 m a.s.l. (CABELA et al. 2001). Individuals of high altitude populations attain maturity at the age of 10-11 years and maximum ages exceeding 20 years (MIAUD et al. 2000; SCHABETSBERGER

et al. 2001), whereas individuals of lowland populations can reach sexual maturity at the age of 1-2 years and live up to only 6 years (JOLY & GROLET 1996). Our data (maturity reached at the age of 4-5 years, longevity about 10 years) obtained from a site at 1,282 m altitude fit well into these findings.

CONSERVATION

The water body proper of the lake Ameisensee is already protected from any kind of modifications by regional regulations. Based on amphibian radio tracking data SCHABETSBERGER et al. (2004) recently suggested the establishment of a terrestrial reserve, and the launch of a monitoring programme at the lake as a further measure assuring long term conservation. The fact that the lake Ameisensee dries out each year is one of the main reasons for its richness in amphibians, rendering the introduction of fishes impossible. In the last years howev-

er, we observed that, possibly due to dry and hot summers, the lake can dry out too early for the larvae to complete their development. This led to a complete reproduction failure in two of the past four years. The large population sizes and the observed longevities suggest no immediate threat. However, future climate change could lead to extended periods without juvenile recruitment and a decline or extinction of the newt populations. We therefore strongly recommend to launch a monitoring programme to ensure their long-term conservation.

ACKNOWLEDGEMENTS

We would like to thank the Department of Conservation of the Provincial Government of Salzburg, the Austrian Academy of Sciences, the University of Salzburg and the "Stiftungs- und Förderungsgesellschaft der Paris-Lodron Universität Salzburg" for funding this study. W. HÖDL (Vienna) and H. LANGER (Salzburg) provided logistic help and discussions. F.

HOCHRAINER and A. ENGEL from the Department of Forestry (Abtenau), and E. STÜBER and M. KYEK from the "Haus der Natur" (Salzburg) supported the investigations. L. POPE provided valuable language comments. Permits were acquired from the Provincial Government of Salzburg (3/253-810/13-2000, 3/253-810/22-2001).

REFERENCES

- ARNTZEN, J. W. & TEUNIS, S. F. M. (1993): A six year study on the population dynamics of the crested newt (*Triturus cristatus*) following the colonisation of a newly created pond.- *Herpetol. J.*, London; 3: 99-111.
- BELL, G. (1977): The life of the smooth newt (*Triturus vulgaris*) after metamorphosis.- *Ecological Monogr.*, Washington; 47: 279-299.
- CABELA, A. & GRILLITSCH, H. & TIEDEMANN, F. (2001): Atlas zur Verbreitung und Ökologie der Amphibien und Reptilien in Österreich; Umweltbundesamt, Wien, Austria, 880 pp.
- CAETANO, M. H. & CASTANET, J. (1993): Variability and microevolutionary patterns in *Triturus marmoratus* from Portugal: age, size, longevity and individual growth.- *Amphibia-Reptilia*, Leiden; 14: 117-129.
- CASTANET, J. & SMIRINA, E. M. (1990): Introduction to the skeletochronological method in amphibians and reptiles.- *Ann. Sci. Nat. Zool.*, Paris; 13: 191-196.
- COGALNICLANU, D. & MIAUD, C. (2003): Population age structure and growth in four syntopic amphibian species inhabiting a large river floodplain.- *Canadian J. Zool.*, Toronto; 81: 1096-1106.
- CVETKOVIC, D. & KALEZIC, M. L. & DJOROVIC, A. & DZUKIC, G. (1996): The crested newt (*Triturus carnifex*) in the Submediterranean: reproductive biology, body size, and age.- *Italian J. Zool.*, Roma; 63: 107-111.
- DENOËL, M. & SCHABETSBERGER, R. (2003): Resource partitioning in two heterochronic populations of Greek alpine newts, *Triturus alpestris veluchiensis*.- *Acta Oecologica*, Paris; 24: 55-64.
- DOLMEN, D. (1982): Skeletal growth marks and testis lobulation as criteria for age in *Triturus* spp. (Amphibia) in central Norway.- *Acta Zool.*, Stockholm; 63: 73-80.
- DOLMEN, D. (1983): Growth and size of *Triturus vulgaris* and *T. cristatus* (Amphibia) in different parts of Norway.- *Holarctic Ecology*, Copenhagen; 6: 356-371.

- ELLINGER, N. & JEHLE, R. (1997): Struktur und Dynamik einer Donaukammolch-Population (*Triturus dobrogicus*, KIRITZESCU, 1903) am Endelteich bei Wien: ein Überblick über neun Untersuchungsjahre; pp. 133-150. In: HÖDL, W. & JEHLE, R. & GOLLMANN, G. (Eds.): Populationsbiologie von Amphibien. Eine Langzeitstudie auf der Wiener Donauinsel.- Stapfia, Linz; 51.
- FRANCILLON-VIEILLÔT, H. & ARNTZEN, J. W. & GERAUDIE, J. (1990): Age, growth and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): A skeletochronological comparison.- *J. Herpetol.*, St. Louis; 24: 13-22.
- FRANZEN, M. & GRUBER, H.-J. & HECKES, U. (2002): Eine allochthone *Triturus carnifex*-Population in Südbayern (Deutschland).- *Salamandra*, Rheinbach; 38: 149-154.
- GIACOMA, C. & PICARIELLO, O. & PUNTILLO, O. & ROSSI, F. & TRIPEPI, S. (1988): The distribution and habitats of the newt (*Triturus*, Amphibia) in Calabria (Southern Italy).- *Monit. Zool. Italiano*, Firenze; (N. S.) 22: 449-464.
- GLANDT, D. (1982): Abundanzmessungen an mitteleuropäischen *Triturus*-Populationen (Amphibia, Salamandridae).- *Amphibia-Reptilia*, Leiden; 3: 317-326.
- GRIFFITHS, R. A. (1996): Newts and salamanders of Europe; London (Poyser Ltd.), pp. 188.
- HAGSTRÖM, T. (1977): Growth studies and ageing methods for adult *Triturus vulgaris* L. and *Triturus cristatus* LAUR. (Urodela, Salamandridae).- *Zoologica Scripta*, Oxford; 6: 61-68.
- JAHN, P. (1995): Untersuchungen zur Populationsökologie von *Triturus cristatus* (LAURENTI, 1768) und *T. vulgaris* (LINNAEUS, 1758) am Friedeholzer Schlatt.- Thesis, University of Bremen, unpubl., pp. 91.
- JOLY, P. & GROLET, O. (1996): Colonization dynamics of new ponds, and the age structure of colonizing alpine newts, *Triturus alpestris*.- *Acta Oecologica*, Paris; 17: 599-608.
- JOLY, P. & MIAUD, C. (1990): Tattooing as an individual marking technique in urodeles.- *Alytes*, Paris; 8: 11-16.
- JØRGENSEN, C. B. (1992): Growth and reproduction; pp. 439-467. In: FEDER, M. E. & BURGGREN, W. W. (Eds.): Environmental physiology of the amphibians. Chicago & London (Univ. Chicago Press).
- KALEZIC, M. L. & CVETKOVIC, D. & DJOROVIC, A. & DZUKIC, G. (1996): Alternative life-history pathways: paedomorphosis and adult fitness in European newts (*Triturus vulgaris* and *T. alpestris*).- *J. Zool. Syst. Evol. Res.*, Berlin; 34: 1-7.
- KALEZIC, M. L. & DJOROVIC, A. (1998): Life history-dependent sexual size dimorphism in the crested newt, *Triturus carnifex* (Caudata).- *Folia Zool.*, Brno; 47: 317-319.
- KLETECKI, E. (1995): Population density, space arrangement and sex ratio for sympatric populations of the three species of newts in two puddles in Zumberak, Croatia. pp. 141-153. In: LLORENTE, G.A. & MONTORI, A. & SANTOS, X. & CARRETERO, M. A. (Eds.): *Scientia Herpetologica*. Barcelona (Asociacion Herpetologica Española).
- KREBS, C. J. (1989): *Ecological methodology*. New York (Harper & Row), pp. 654.
- MARNELL, F. (1998): A skeletochronological investigation of the population biology of smooth newts *Triturus vulgaris* L. at a pond in Dublin, Ireland.- *Biology and Environment: Proc. Royal Irish Acad.*, Dublin; (B) 98: 31-36.
- MIAUD, C. & GUYETANT, R. & FABER, H. (2000): Age, size, and growth of the alpine newt, *Triturus alpestris* (Urodela: Amphibia), at high altitude and a review of life-history trait variation throughout its range.- *Herpetologica*, Emporia; 56: 135-144.
- MIAUD, C. & JOLY, P. & CASTANET, J. (1993): Variation in age structures in a subdivided population of *Triturus cristatus*.- *Canadian J. Zool.*, Toronto; 71: 1874-1879.
- NÖLLERT, A. & NÖLLERT, C. (1992): *Die Amphibien Europas: Bestimmung, Gefährdung, Schutz*.- Stuttgart (Franckh-Kosmos), pp. 382.
- PERRET, N. & PRADEL, R. & MIAUD, C. & GROLET, O. & JOLY, P. (2003): Transience, survival and dispersal rates in patchy newt populations.- *J. Animal Ecol.*, London; 72: 567-575.
- SCHABETSBERGER, R. & JEHLE, R. & MALETZKY, A. & PESTA, J. & SZTATECSNY, M. (2004): Delineation of terrestrial reserves for amphibians: post-breeding migrations of Italian crested newts (*Triturus c. carnifex*) at high altitude.- *Biol. Conserv.*, Oxford; 117: 95-104.
- SCHABETSBERGER, R. & JERSABEK, C. D. & GOLDSCHMID, A. (2001): Sex reversal cannot explain female-biased sex ratios in high altitude populations of the alpine newt *Triturus alpestris*.- *Biota, Race*; 2 (1): 75-87.
- SCHABETSBERGER, R. & LANGER, H. & JERSABEK, C. D. & GOLDSCHMID, A. (2000): On age structure and longevity in two populations of *Bufo bufo* (LINNAEUS, 1758), at high altitude breeding sites in Austria.- *Herpetozoa*, Wien; 13: 187-191.
- SMIRINA, E. M. (1994): Age determination and longevity in Amphibians.- *Gerontology*, Moscow; 40: 133-146.
- STENSJÖ, J.-O. (1998): Population genetics of the common newt (*Triturus vulgaris*) and the crested newt (*Triturus cristatus*), with implications for conservation.- PhD Thesis, University of Uppsala, pp. 22.
- THIESMEIER, B. & KUPFER, A. (2000): *Der Kammolch: Ein Wasserdrache in Gefahr*. Bochum (Laurenti-Verlag), 158 pp.

DATE OF SUBMISSION: September 26, 2003

Corresponding editor: Heinz Grillitsch

AUTHORS: Andreas MALETZKY, Institute of Zoology, University of Salzburg, Hellbrunnerstraße 43, A-5020 Salzburg, Austria < andreas.maletzky@sbg.ac.at >; Julia PESTA, Robert SCHABETSBERGER, Institute of Zoology, University of Salzburg, Hellbrunnerstraße 43, A-5020 Salzburg, Austria; Robert JEHLE, Institute of Zoology, University of Vienna, Althanstraße 14, A-1090 Vienna, Austria & Department of Animal and Plant Sciences, University of Sheffield, Western Bank, S10 2TN Sheffield, UK < R.Jehle@sheffield.ac.uk >; Marc SZTATECSNY, Institute of Zoology, University of Vienna, Althanstraße 14, A-1090 Vienna < marc.szatecsny@univie.ac.at >; Alfred GOLDSCHMID, Institute of Zoology, University of Salzburg, Hellbrunnerstraße 43, A-5020 Salzburg, Austria