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New data on paedomorphism in Italian populations of the Alpine Newt, *Triturus alpestris* (LAURENTI, 1768) (Caudata: Salamandridae)

Neue Angaben zur Pädomorphose italienischer Populationen des Alpenmolches, *Triturus alpestris* (LAURENTI, 1768) (Caudata: Salamandridae)

FRANCO ANDREONE & BRUNO DORE

KURZFASSUNG: Neue Angaben zur Häufigkeit des Vorkommens von Pädomorphose (Neotenie s. l.) bei den drei italienischen Bergmolch-Unterarten *Triturus alpestris alpestris* (LAURENTI, 1768), *T. a. apuanus* (BONAPARTE, 1839) und *T. a. inexpectatus* (DUBOIS & BREUIL, 1983) werden vorgelegt. Pädomorphotische Individuen (gelegentlich geschlechtsreif: pädogenetisch) wurden insbesondere in stabilen, permanenten Gewässern beobachtet. Möglicherweise läßt sich Pädomorphose bei diesen Molchen als eine Tendenz auffassen, die Dauer des aquatischen Aufenthaltes in permanenten Wasserkörpern zu verlängern und damit die Vorteile zu nutzen, die diese hinsichtlich Gleichförmigkeit und Stabilität gegenüber dem Landhabitat bieten.

ABSTRACT: New information on the occurrence of paedomorphism (neoteny s. l.) is reported for populations of the Italian subspecies of the Alpine newt, *Triturus alpestris alpestris* (LAURENTI, 1768), *T. a. apuanus* (BONAPARTE, 1839), and *T. a. inexpectatus* (DUBOIS & BREUIL, 1983). Paedomorphic specimens (sometimes sexually mature: paedogenetic) were observed in *T. a. apuanus*, and *T. a. inexpectatus* only and found mainly in permanent and stable breeding sites. It is suggested, that in this newt species paedomorphism could be intended as a tendency to prolong the duration of stay in permanent aquatic habitats and thus utilize the advantages of this environment which is more homogenous and stable than the terrestrial one.

KEYWORDS: *Triturus alpestris alpestris*, *T. a. apuanus*, *T. a. inexpectatus*, paedomorphism, neoteny, biology, Italy

INTRODUCTION

Cases of paedomorphism or paedomorphosis (neoteny sensu lato, involving retardation of development of one or more somatic and/or sexual characters; DUBOIS 1985) are known from several urodelan species. Among European species this phenomenon is frequently displayed by the Alpine Newt, *Triturus alpestris* (LAURENTI, 1768). Observations on Italian paedomorphic *Triturus* populations were summarized by DOLCE & STOCH (1984), ANDREONE

& SINDACO (1987), MAZZOTTI (1988), and BERNINI & MEZZADRI (1989).

On the occasion of a research on the morphological and reproductive variability of Alpine Newts (ANDREONE 1990) a number of populations of the three Italian subspecies, *T. a. alpestris* (LAURENTI, 1768), *T. a. apuanus* (BONAPARTE, 1839), and *T. a. inexpectatus* (DUBOIS & BREUIL, 1983) were examined. This paper reports on the cases of paedomorphism observed, and provides with some general considerations concerning its possible objective.

MATERIALS AND METHODS

Six breeding sites of *T. a. alpestris*, seventeen of *T. a. apuanus*, and three of *T. a. inexpectatus*, all of them described in detail by ANDREONE (1990), were inspected. They are defined "permanent" (P) if water had been present at least for longer periods, or "temporary" (T) if they had been dried up and refilled more or less frequently (table 1).

The term "paedomorphic" refers to gilled individuals with a size longer than that of pre-metamorphic larvae. It often was difficult to decide from external features whether these animals were sexually mature and, thus, paedogenetic (neotenous sensu stricto, according to DUBOIS' (1985) definition), or whether they were sexually immature giant larvae. This came particularly true for females, whose secondary sexual characters generally are not that much pronounced as in adult males with their prominent cloaca, extended crests and bright blue lateral stripes present.

Larvae found in winter or early spring are defined "overwintered", as they must have hatched from eggs laid in the preceding summer or autumn (ANDREONE & DORE in press).

Since classification of paedomorphic individuals according to FUHN (1963) and DUBOIS (1979), in our opinion, frequently turns out to be subjective, only an unspecified indication of the relative frequency of paedomorphic individuals collected in each single population is given in table 1.

Paedomorphism in Italian Alpine Newts

Table 1: Summarizing table on the breeding sites of *Triturus alpestris* inspected. SSP = subspecies (*al* - *T. a. alpestris*, *ap* - *T. a. apuanus*, *in* - *T. a. inexpectatus*); Locality, Province, Altitude (in meters above sea level); Char = site character (T = temporary, P = permanent); OL = presence of overwintering larvae; A = isolated paedomorphic specimens ($n < 10\%$ of population, larvae excluded); B = mean density of paedomorphic specimens ($10\% < n < 50\%$); C = high density of paedomorphic specimens ($n > 50\%$); References (bibliography dealing with this very breeding site).

Tab. 1: Tabellarische Zusammenfassung der untersuchten *Triturus alpestris* Laichplätze. SSP = Unterart (*al* - *T. a. alpestris*, *ap* - *T. a. apuanus*, *in* - *T. a. inexpectatus*); Locality = Fundort; Province = Region; Altitude = Höhenlage (in Metern über dem Meer); Char = Gewässertyp (T - temporär, P - permanent); OL = Vorkommen überwinternder Larven; A = vereinzelt pädomorphen Exemplare ($n < 10\%$ der Population, Larven nicht berücksichtigt); B = pädomorphen Exemplare in mittlerer Dichte ($10\% < n < 50\%$); C = pädomorphen Exemplare in hoher Dichte ($n > 50\%$); References = Literatur zum jeweiligen Fundort.

SSP	Locality	Province	Altitude	Char	OL	A	B	C	References
<i>al</i>	Lago di Arpy	Aosta	2066	T					ANDREONE & al. (in press)
<i>al</i>	Lago Nero	Novara	1974	P	*				ANDREONE & al. (in press)
<i>al</i>	Pozza Morta	Vicenza	1450	T					ANDREONE (1990)
<i>al</i>	Passo della Pura	Udine	1425	T					ANDREONE (1990)
<i>al</i>	Rodoro	Udine	1950	T					ANDREONE (1990)
<i>al</i>	Alpe del Gallo	Sondrio	2060	T					ANDREONE (1990)
<i>ap</i>	Revigliasco	Turin	360	P	*	*			ANDREONE & SINDACO (1987)
<i>ap</i>	Parco della Maddalena	Turin	700	T					ANDREONE & SINDACO (1987)
<i>ap</i>	Montezemolo	Cuneo	793	P	*	*			ANDREONE (1990)
<i>ap</i>	Murazzano	Cuneo	739	P	*	*			ANDREONE (1990)
<i>ap</i>	Bossolasco	Cuneo	757	P	*				ANDREONE (1990)
<i>ap</i>	Cástino	Cuneo	540	P	*				ANDREONE (1990)
<i>ap</i>	Massimino	Savona	527	P	*				ANDREONE (1990)
<i>ap</i>	Rossiglione	Genoa	600	P					ANDREONE & al. (in press)
<i>ap</i>	Santa Giulia	Genoa	230	P	*	*			ANDREONE (1990)
<i>ap</i>	Diga di Val Noci	Genoa	500	P	*	*			ANDREONE (1990)
<i>ap</i>	Negruzzo	Pavia	1400	T					ANDREONE & al. (in press)
<i>ap</i>	Val di Nure	Piacenza	1350	P		*			ANDREONE (1990)
<i>ap</i>	Vergato	Bologna	590	T					ANDREONE (1990)
<i>ap</i>	Pratieghi	Arezzo	1079	P	*	*			MAZZOTTI (1988)
<i>ap</i>	Lago della Bega	Lucca	960	T					FERRACIN & al. (1980)
<i>ap</i>	Camporgiano	Lucca	540	T					FERRACIN & al. (1980)
<i>ap</i>	Monti della Laga	Rieti	1496	P	*	*			CAPULA & BAGNOLI (1982)
<i>in</i>	"fosso Armando"	Cosenza	1100	T					ANDREONE (1990)
<i>in</i>	Lago Laghicello	Cosenza	1130	P		*			DUBOIS & BREUIL (1983)
<i>in</i>	Lago dei due uomini	Cosenza	1080	P					DUBOIS & BREUIL (1983)

RESULTS

The results are synoptically arranged in table 1, which presents

- subspecies observed,
- toponyms or currently used names of the sites, including province and altitude,
- their hydrodynamic characters (if temporary or permanent),
- the presence of overwintering larvae,
- the frequency of paedomorphic individuals,
- bibliography referring to this.

Paedomorphic individuals were found in 47% of *T. a. apuanus* populations, and in 33% of *T. a. inexpectatus* populations. No paedomorphic specimens were observed in localities where *T. a. alpestris* occurs.

Overwintering larvae were found in 59% of *T. a. apuanus* populations, and in 17% of *T. a. alpestris* populations. No overwintering larvae were observed in *T. a. inexpectatus* sites.

As can be seen in table 1, paedomorphic newts exclusively inhabit permanent or rarely desiccating water bodies, while in temporary breeding sites only metamorphosed adults and ordinary larvae were found. Of course there are also permanent water bodies where only adults and larvae were observed (e. g. Rossiglione, Massimino).

DISCUSSION

The data presented indicate that the percentage of larval, paedomorphic, and metamorphosed individuals varies markedly within different populations of the Alpine Newt.

We actually neither know, if a certain composition is typical for a certain population, nor if the relative frequency of paedomorphic individuals within a population is subject to variation. A moderate long term study, focused on a single population, should be carried out for better understanding of the life history of these animals, and of the paedomorphic ones in particular. Moreover, since the type of paedomorphism is hardly determinable from externally, appropriate techniques (i. e. histological and physiological ana-

lyses) must be elaborated and applied, as suggested in preliminary studies (LODI & al. 1990).

Probably adaptive responses in newts show high plasticity, according to the scheme proposed by VERRELL (1985) and ANDREONE & al (in prep.). Paedomorphic individuals may metamorphose and so become "aquatic efts" (metamorphosed juveniles), or, if metamorphosis occurs at the paedogenetic stage, immediately transform into sexually mature adults.

As previously shown, paedomorphic individuals seem to be present almost exclusively in permanent waters, and lacking the temporary ones. But this statement should not be interpreted in an absolute way, as it considers the short term and moderately long term evolution of the water body.

As an example we refer to the case of the *T. a. apuanus* population of Monti della Laga, where the percentage of paedomorphic individuals was about 80, according to CAPULA & BAGNOLI (1982). At our first visit in summer 1987 only paedomorphic specimens were found, while in summer 1989 just a few metamorphosed animals were observed. One could hypothesize, that, after environmental changes (e. g. desiccation), the paedomorphic individuals might have metamorphosed and left the pond or died. In another case concerning the Lago della Bega population, FERRACIN & al. (1980) reported on a high number of neotenic specimens, but in 1989 we only found metamorphosed newts. Anyway, it should be stressed that FERRACIN & al. (1980) made their observations in the permanent main pond, while our observations referred to the small temporary lateral pools. The absence of newts in the main pond at the time of our visit might be due to the introduction of fishes (FERRACIN pers. comm.).

Disagreeing with considerations of DOLCE & STOCH (1984) it should be stressed, that the depth of the water does not seem to be determinant for the formation of paedomorphic newts. In fact, in the ponds of Montezemolo and Pratieghi, although of limited surface area and depth (about 1 m), a relatively high frequency of paedomorphic individuals has been observed, while, on the contrary, in the deeper (about 3 m) Lago negro only metamorphosed newts and larvae were found.

In populations with a relatively high percentage of paedomorphic individuals (categories B and C) at least part of them seems to be paedogenetic and

reproductive, since the males exhibit their breeding habitus (including well developed crests), and display the classic courtship behaviour (ANDREONE & al. 1990; BOVERO 1991).

Analysis of the gonads revealed the complete spermatogenic cycle (ANDREONE & al. 1991), while the presence of overwintered larvae in permanent breeding sites of *T. a. alpestris* (e. g. Lago Nero) confirms the reproductive cycle to be biennial in high altitude populations with a short period of summer activity (GUYETANT 1986). On the other hand, overwintered larvae from mean altitude populations of *T. a. apuanus* witness autumnal egg deposition (ANDREONE & DORE in press).

Although paedomorphism may be based on genetic, pathological and/or environmental causes (BREUIL 1986), we want to hypothesize that there is another aspect worth to be taken into consideration: the tendency of the Alpine Newt to extend the permanence of residence in the aquatic habitat, which is more stable than the terrestrial one (WILBUR & COLLINS 1973). In fact, this would allow to shorten the inactive periods of summer and winter latency; according to preliminary observations (ANDREONE & al. 1991) paedomorphic newts attain sexual maturity in a shorter period of time than metamorphosed ones.

We therefore propose that differences in the incidence of paedomorphism should be seen in the scope of the remarkable biological (morphological, genetic, reproductive) variability of this newt species, thus reflecting its considerable adaptive plasticity (ANDREONE 1990).

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AUTHORS: Dr. Franco ANDREONE, Museo regionale di Scienze naturali, Section of Zoology, via G. Giolitti 36, I-10123 Torino, Italy. Prof. Dr. Bruno DORE, Dipartimento di Biologia Animale, Università di Torino, via A. Albertina 17, I-10123 Torino, Italy.

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Autor(en)/Author(s): Andreone Franco, Dore Bruno

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