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OBSERVATIONS OF PAEDOMORPHIC NEWTS (*Triturus vulgaris*) FROM THE FORMER SOVIET UNION

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The reliable data on paedomorphosis in two subspecies of the common newt *Triturus vulgaris lantzi* (Abkhazia, western Caucasus) and *T. v. vulgaris* (the vicinity of St. Petersburg) are given for the first time for the former Soviet Union. Data on the appearance, occurrence, development and distribution of paedomorphic larvae are given based on field and laboratory observations beginning in 1986. The life cycles of paedomorphic and metamorphosed newts are discussed.

Key words: Paedomorphosis, *Triturus vulgaris lantzi*, *Triturus vulgaris vulgaris*, Abkhazia (western Caucasus), St. Petersburg region (Russia).

INTRODUCTION

Paedomorphosis is widespread among the urodeles and very common in European newts of the genus *Triturus.* Many records exist for both occasional individuals and for the populations containing a large fraction of paedomorphic animals. Such populations were found in only four species:

1. *Triturus alpestris* from former Yugoslavia, Greece and Italy (Radovanović, 1951, 1961; Breuil and Thuot, 1983; Henle, 1983; Džukić and Kalezić, 1984; Breuil and Parent, 1987; Andreone and Sindaco, 1987; Kalezić et al., 1989, 1990; Breuil, 1992).

2. *Triturus helveticus* from the Netherlands and France (van Gelder, 1973; Gabrion et al., 1977).

3. *Triturus vulgaris* from Germany, Romania, Hungary, Sweden, England, and former Yugoslavia (Hartwig and Rotmann, 1940; Fuhn, 1963; Dely, 1967; Dolmen, 1978; Banks, 1985; Kalezić and Džukić, 1986; Kalezić et al., 1990).

4. *Triturus carnifex* from Yugoslavia (Kalezić et al., 1994).

In old European (including Russian) literature this phenomenon was designated by the term "*neoteny*," whereas in the current literature the term "*paedomorphosis*" is mostly used. The former was introduced by Kollmann (1884) with reference to the green frogs, European newts, and axolotl. However, as it was later discovered, this phenomenon is much more complicated, and cases related to the delay of somatic development or acceleration of sexual development were distinguished. Several classifications were proposed; however, some authors used the same terms for denoting different phenomena (see, for instance, Gould, 1977; Pierce and Smith, 1979; Dubois, 1987).

If larvae differ from the normal individuals in size and coloration and there are no data about their reproduction, e.g., large larva found in autumn, then following Andreone et al. (1993) we designate them *paedomorphic* in the broad sense. If we know that paedomorphic individuals do reproduce, we call them *paedogenetic* (paedogenetic sensu Dubois, paedomorphic sensu Gould, and neotenic s. l. sensu Pierce and Smith). Therefore we regard paedogenesis as a particular case of paedomorphosis.

The reliable records of paedomorphic newts from the former Soviet Union have not existed. In this paper we give the data on paedomorphosis (paedogenesis) in two subspecies of *T. vulgaris* that were obtained during the field and laboratory observations for several years.

MATERIAL AND METHODS

Newts in water were caught using the hand-netting; on land, newts were found under stones, logs, and other objects close to water.

Some of the individuals were preserved in formaldehyde (paedomorphic and metamorphosed *T. vul-*

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garis lantzi, see Table 1) or in 70% alcohol, respectively. They were deposited in collections of the Department of Herpetology, Zoological Institute, Russian Academy of Sciences (ZISP 5780 – 5781) and the Museum of Nature, Kharkov State University, Kharkov (Nos. G-812 and G-813). Morphometric measurements (Table 1) were made using the vernier callipers with a precision of 0.1 mm. Lengths of the body and the tail were measured from the anterior margin of the cloacal slit.

Other individuals were delivered to the laboratories in Kharkov and St. Petersburg for observation starting in 1986. The newts were kept at room temperature (18 – 24°C) in rectangular glass aquaria (40 – 60 liter) with ground and vegetation (in St. Petersburg) or without them (in Kharkov). Tap water was settled for two days before use. After metamorphosis, newts lived in humid terraria. Some individuals reached maturity and did reproduced. Observations on these individuals are continuing.

TABLE 1. Sizes (mm) in Paedomorphic and Metamorphosed Individuals of *Triturus vulgaris lantzi*

Character	*N*	Range	Mean ± standard error
Paedomorphic males			
Total length	5	48.3 – 59.0	54.7 ± 1.9
Body length	8	22.3 – 26.5	24.6 ± 0.5
Tail length	5	26.0 – 33.0	29.7 ± 1.4
Paedomorphic females[*1]			
Total length	21	40.1 – 74.5	56.6 ± 2.3
Body length	36	14.6 – 37.7	25.6 ± 0.9
Tail length	21	19.7 – 40.2	29.4 ± 1.3
Metamorphosed juveniles			
Total length	2	27.0 – 28.0	–
Body length	2	14.2 – 14.5	–
Tail length	2	12.5 – 13.8	–
Adult metamorphosed males[2]			
Total length	6	75.5 – 84.5	79.8 ± 1.6
Body length	6	36.7 – 40.5	38.5 ± 0.5
Tail length	6	38.0 – 45.0	41.3 ± 1.2
Adult metamorphosed females[*2]			
Total length	4	73.2 – 80.3	78.2 ± 1.7
Body length	9	38.2 – 43.0	41.0 ± 0.5
Tail length	4	35.0 ± 39.8	38.2 ± 1.1

[1] The sample seems to be heterogeneous because it is very difficult to distinguish between paedomorphic females and immature paedomorphic newts; all paedomorphic specimens (including males) were collected April 3, 1987.

[2] Adult normal newts were collected in the Mountain Achishkho, Caucasian Biosphere Reserve, Russia (ZISP 3523, B. S. Tuniyev).

RESULTS

1. *Triturus vulgaris lantzi*

1.1. Field Observations

For the first time in the Soviet Union paedomorphic newts were recorded in Georgia, western Caucasus (Rudyk, 1989). On April 9, 1986, a small artificial water-body inhabited by *T. vittatus ophryticus* and *T. vulgaris lantzi* was found in the vicinity of Lidzava village on the Pitsunda Peninsula (Abkhazia) in the canyon of the Tsanigvarta River at an altitude of approximately 10 m above sea level (Fig. 1). *T. vulgaris lantzi* was represented by normal and paedomorphic individuals. Among 84 specimens of *T. vulgaris lantzi*, along with normal 34 newts (13 females and 21 males), 50 paedomorphic specimens, including 48 females and 2 males, were collected. Newts of both species, including paedomorphic *T. vulgaris lantzi*, demonstrated breeding behavior. Most frequently pairs of a normal male and a paedomorphic (paedogenetic) female of *T. vulgaris lantzi* occurred. The detailed investigations of the region showed in other water-bodies only normal individuals of three species (indicated above plus *T. karelinii*).

Water-body No. 1 with paedomorphic newts represented a pit with an area of approximately 150 m^2 with vertical clayey gravel walls and bottom covered with filamentous algae *Cladophora* sp. The depth of the pit was equal to 1.5 m, that of water in it 1.3 m, water temperature was 17.6°C at the surface, and 15.2°C near the bottom. Hardness of water was 2.8 mg eq./liter; pH 7.9. Water transparency permitted a view of all inhabitants of water-body. Apart from the two species of newts indicated above, three common anuran species were also found, i.e., *Rana ridibunda*, *Rana macrocnemis*, and *Hyla arborea*, represented by adult and larval stages, and also large larvae of dragonflies. No fish were found, although normally water-bodies of this region are inhabited with mosquito fish (*Gambusia affinis*); it was introduced in Abkhazia, including the Pitsunda Peninsula, as long ago as 1928 and 1930 for malaria control (Khosatzky, 1944). According to the local inhabitants, the water-body was excavated a year before our first visit, apparently in spring 1985.

Paedomorphic males of *T. vulgaris lantzi* (Fig. 2) were much smaller than metamorphosed males (Table 1). They had well-developed gills of a reddish-rust color. A smooth high dorsal-caudal fin fold,

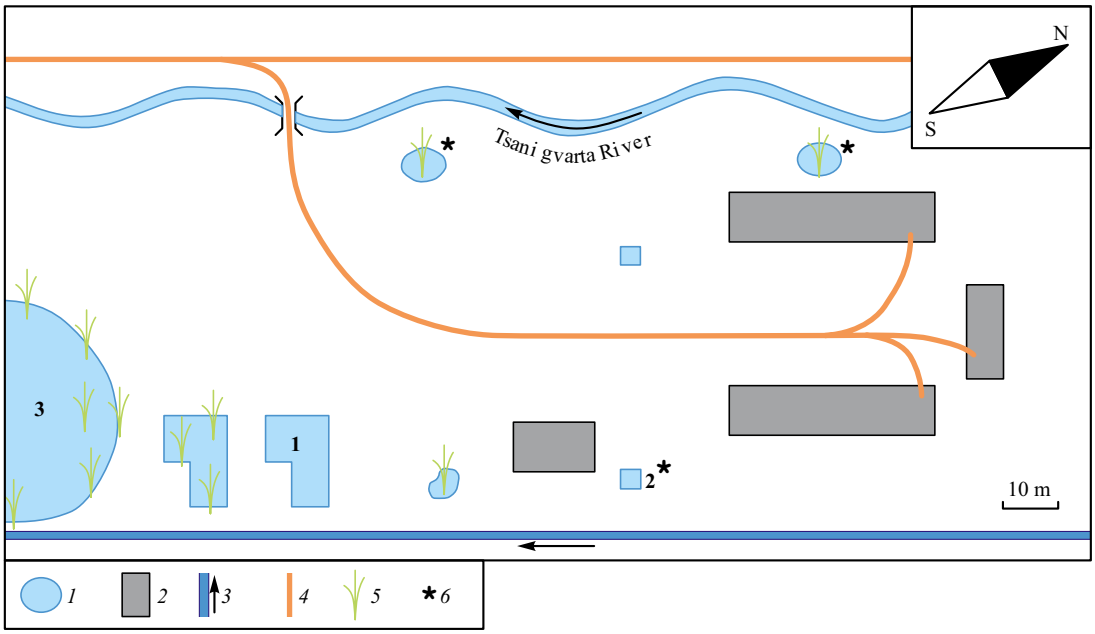

Fig. 1. Location of water-bodies studied in the vicinity of Lidzava village, Abkhazia, western Caucasus. *1*) Water-bodies (Nos. **1 – 3** with paedomorphic larvae), *2*) poultry farm buildings, *3*) open water-pipe, *4*) ground roads, *5*) swamp vegetation, *6*) water-bodies with introduced paedomorphic larvae.

without notches, originated immediately behind the head and had its maximum height at the tail base. The fold itself, the back sides, the upper part of the head, and the tail were covered with small and medium-size black spots against a light brown background. The lower part of the sides, the anterior part of the head, and the belly were covered with black spots against a white background. There were small indistinct spots on the white throat. The pale white-blue band on the lower caudal fin fold was hardly visible. The paws were thin and long, the toe fringes were less developed than those in normal males. The dark-colored swollen cloaca was well-developed.

Paedomorphic females resembling paedomorphic males, differed from them by a less developed fin fold, lack of the folds on the toes, and by the shape of cloaca. The coloration of females was lighter than that of males. The dorsal side was pale-yellowish clayey, without any pattern, except a few individuals. The ventral side was white. In older females dark spots appeared on the abdomen and later on the throat. The total length of the largest paedomorphic female reached 74.5 mm (Table 1).

During the next visit of the same year from August 29 to September 2, 1986, we found only one paedomorphic female of a very large size (about 70 mm) without any signs of metamorphosis. We can place it into the generation of 1985. A great number of larvae of a normal size were also found in the water-body both without any obvious characters of metamorphosis and in its various stages. That season in Pitsunda was characterized by a strong drought rare for that region. Most of the water-bodies ran dry, but this water-body and the neighboring one retained the previous level of water which flowed from the Tsanigvarta River and the drainage canal located near the water-body.

On April 3, 1987 in the water-body No. 1, a large number of paedomorphic individuals were found, the females being obviously predominant (about 10% males). The adult metamorphosed males were absent. Therefore all neighboring water-bodies were studied in search for newts. The only metamorphosed adult male was found in the neighboring ravine. The disappearance of terrestrial individuals is most probably related to the drought of the preceding year. We caught about 50 newts for collections and laboratory studies. Also, 36 animals were moved to three water-bodies (2 males and 10 females in each) located in the area of a poultry farm (Fig. 1). Two water-bodies were small swamps with an area of about 10 m^2 and a depth of not more than 1 m, with abundant vegeta-

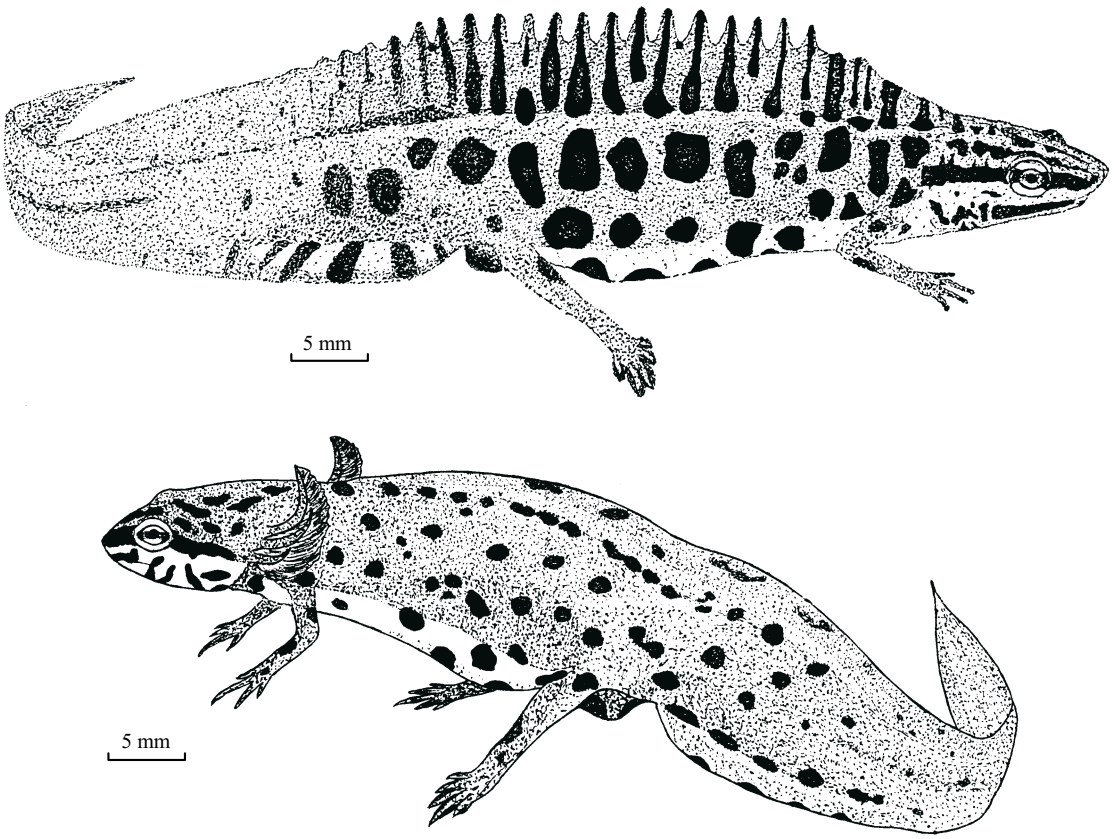

Fig. 2. Metamorphosed (above) and paedomorphic (below) males of *Triturus vulgaris lantzi.*

tion, without fish, and the third (No. 2) represented a new concrete pool with an area of 10 m^2 and depth 1.8 m (depth of water 1.5 m), without vegetation.

By the summer of the next year (June 24, 1988) walls of water-body No. 1 were washed and it became a half-drained pool with a depth of 0.4 m, at times connected with the swamp (water-body No. 3) located somewhat lower. The entire water-body No. 1 was covered with swamp vegetation (*Typha* sp., etc.). Only one large paedomorphic female and 14 normal larvae were found in it. Paedomorphic specimens were found only in water-body No. 2 of the three water-bodies where they were released in the previous spring. By that time the walls of water-body No. 2 were covered with filamentous algae and the animal plankton became visible in water. Approximately 30 – 40 paedomorphic specimens and numerous small larvae of *T. vulgaris lantzi* and also one adult male of *T. vittatus ophryticus* inhabited this water-body. The paedomorphic individuals were in the different stages of metamorphosis. For the first time after the drought of 1986, we noticed the appearance of adult metamorphosed common newts in that area in a number of neighboring water-bodies.

On May 3 – 4, 1989, paedomorphic specimens were also found only in water-body No. 2. The 93 newts caught included 68 paedomorphic females, 10 paedomorphic, and 10 metamorphosed males, and 5 metamorphosed females.

On August 10, 1990, again, in water-body No. 2, 22 apparently paedomorphic larvae were recorded. They differed from the normal ones by their larger size and brighter coloration. There were neither mature newts (paedomorphic and normal), nor normal larvae in the water-body, although they were abundant in neighboring water-bodies.

On March 7, 1992, no paedomorphic individuals were found in water-body No. 2. Only one normal male of *T. vulgaris lantzi* and one male and two females of *T. vittatus ophryticus* were recorded. Paedomorphic specimens were found in water-body No. 3. It is a swamp with an area of 2000 m^2 located slightly

lower than water body No. 1. Fourteen paedomorphic newts were caught. One normal male *T. vulgaris lantzi* was also caught. Two years before (August 10, 1990) only normal larvae of *T. vulgaris lantzi* and *T. vittatus ophryticus* were found in the different stages of metamorphosis.

1.2. Laboratory Observations

According to our observations conducted in Kharkov and St. Petersburg, nearly all paedomorphic larvae ($n = 40$) caught in spring reproduced, demonstrating sexual behavior of metamorphosed newts. Therefore, these paedomorphic larvae can be termed paedogenetic. When reproduction was completed they began to metamorphose, except one female which metamorphosed in the second year. Having completed metamorphosis, newts lost marked secondary sexual characters and acquired coloration of terrestrial juveniles, i.e., the normal newts of the same age. The majority of animals became terrestrial. However, some individuals stayed in water after metamorphosis, which results in the other variant of the life cycle.

The former paedogenetic individuals that got terrestrial began breeding only at the age of 3 years having reached the size of mature normal newts. Therefore, 2 years passed between the first reproduction in the paedomorphic stage, i.e., after the first winter, and the second reproduction after metamorphosis (see Fig. 3). If the newts stayed in water after metamorphosis they could reproduce both in autumn and next spring; however, small individuals begin breeding one more year later. Therefore, manifestations of the life cycle in laboratory conditions are more labile than in nature.

We observed a different situation during maintenance of immature paedomorphic individuals caught in autumn. On September 2, 1986, 19 largest larvae without any features of metamorphosis were caught in water-body No. 1. However, specimens placed in an aquarium (Kharkov) metamorphosed in one month from September 14 up to October 2. Their body length was between 15 – 25 mm, 19.4 ± 0.7 mm, on average. In 1990, the immature paedomorphic individuals caught in August in water-body No. 2 metamorphosed in the laboratory in St. Petersburg within a month after they were caught. In both cases these larvae metamorphosed without attaining maturity much earlier, compared to paedogenetic specimens. This may be related to high sensitivity of larvae in this stage to the impact of stress, i.e., transportation, change in the habitat, because stress may trigger metamorphosis. This supposition is based on our observations on normal larvae of different newt species.

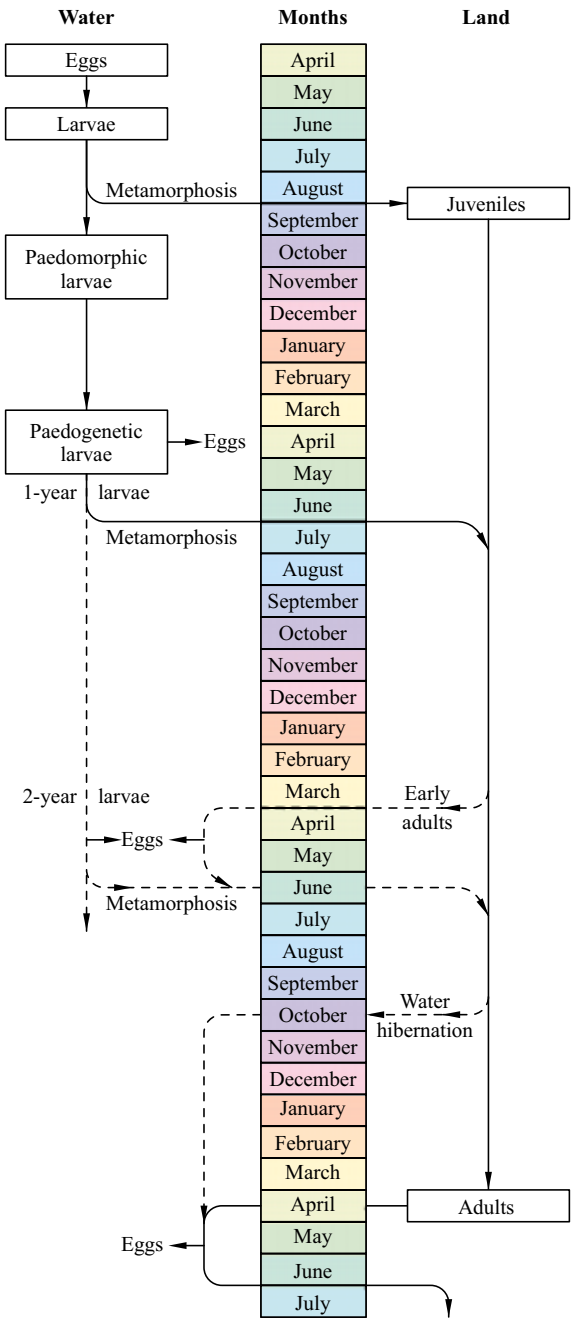

Fig. 3. Life cycles in metamorphosed and paedomorphic individuals of *Triturus vulgaris lantzi*. The continuous line refers to the basic life cycle, the dashed line follows additional and possible cases.

TABLE 2. Some Features of Paedogenetic and Metamorphosed Newts of *Triturus vulgaris lantzi* and Its Progeny in Captivity (April 1986)

	Features	Paedogenetic (2 ♂♂ + 4 ♀♀)	Metamorphosed (2 ♂♂ + 2 ♀♀)
1.	Average number of eggs per female	85.25	79.00
2.	Portion of normally developed embryos	19.9% (out of 137)	10.9% (out of 82)
3.	Average number of larvae attending metamorphosis per female	6.8	3.5
4.	Last spawn	June 23	June 11
5.	Migration of the parents on land after reproduction	June 21 (♂) – 27 (♀)*	June 4 – 24
6.	Start of migration of the progeny F_1 on land after metamorphosis	May 22	June 24

* Four other newts (1 ♂ + 3 ♀♀) remained in water.

According to our observations, 1-year-old paedogenetic females have nearly the same fecundity (Table 2) as metamorphosed females of the same size. The survival ability of progeny of paedogenetic females was much higher than that of metamorphosed females (Table 2).

2. *Triturus vulgaris vulgaris*

2.1. Field Observations

Paedomorphic individuals of the common newt were found together with normal larvae in a water-body on the outskirts of the town of Gatchina 46 km south of St. Petersburg on August 3, 1993. The adult metamorphosed newts had already left water-bodies. The water-body is in fact an isolated part of the municipal system of concrete wells connected by an underground concrete tube of about 40 cm in diameter at a depth of 30 – 50 cm. The system was not in use for the last 4 or 5 years.

Paedomorphic larvae were found in two concrete wells (18 animals of No. 1 and 2 of No. 2) separated from each other by a distance of approximately 30 m (Fig. 4). The diameter of the wells is 2.1 m. Water depth normally did not exceed 65 cm. The bottom was covered with a layer of mud of about 10 cm. During heavy rains water depth may increase more than twice. In such cases water level exceeds the depths of wells and newts can get into neighboring pools that do not get dry. However, when rains are over, water levels drop quickly and newts cannot return into the wells. According to our observations, the neighboring pools are a kind of a trap for the newts because the latter disappear in them rather rapidly. They possibly metamorphose or most likely die. In August, water temperature in the well was 17.5°C, at the end of November 4.5°C, and in December about 0°C, and one of them, i.e., No. 1, like pools in that area, was frozen to the bottom.

In summer, the walls and bottom of well No. 1 and pools were covered with dense accumulations of filamentous algae Rhizoclonium sp. Well No. 2 was devoid of vegetation, as it is covered from above and light does not penetrate it. Apart from newts *Rana temporaria* (the immature frog), large larvae of dragonflies, beetles, and their larvae (*Dytiscus marginalis*) were also found in the wells. The crested newt (*T. cristatus*) does not occur in that locality.

A total of 20 paedomorphic individuals were caught in the wells from August until October. The normal larvae completed metamorphosis by August 6 and did not occur again. The last occurrence of paedomorphic larvae was on October 6, 1993. Terrestrial newts were also not recorded after this date.

In March – June 1994, newts, both paedomorphic and metamorphosed, were not found in the above-mentioned water-bodies, although they were recorded in other water-bodies. Three newts, one male and two females, from a neighboring water-body were introduced into well No. 1 (June 13, 1994). In July, normal larvae were recorded here which completed metamorphosis between August 31 and September 15, 1994. No paedomorphic larvae were found.

However, 6 paedomorphic and 66 normal larvae occurred around well No. 2 between August 25 and September 15. Paedomorphic larvae preferred to concentrate in the deepest part (ca. 1 m) of water body; the normal ones occurred peripherally. The average total length (body + tail) of 14 normal larvae was equal to 30.3 ± 1.2 mm, that of 5 paedomorphic ones was 44.6 ± 1.6 mm. Normal larvae metamorphosed reaching 33 – 35 mm in total length.

One paedomorphic larva (the total length was 45 mm) was caught in well No. 3 (Fig. 4) with 31

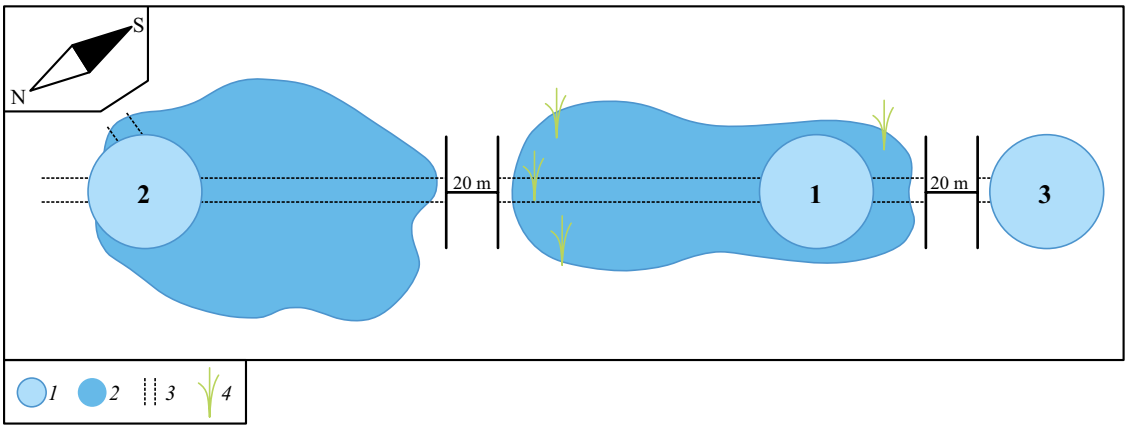

Fig. 4. Scheme of water-bodies in the town of Gatchina, near St. Petersburg. *1*) Concrete wells, *2*) permanent shallow water-bodies, *3*) underground tubes, and *4*) swamp vegetation.

normal larvae. The latter were smaller (the average total length was 25.3 ± 1.3 mm, $n = 12$) and metamorphosed very late (September 30). Well No. 3 was devoid of any vegetation; its water depth was about 30 – 40 cm.

Paedomorphic specimens ($n = 14$) had a total length from 40 to 60 mm; more than a half of the length is falling on the tail. The well-developed gills were red-brown. A rather low fin fold was semitranslucent, with light-brown and small black spots near the upper margin. The back and the upper part of the head were grayish dark-brown with a light stripe at the base of the fin. Some specimens had dark spots on the back and sides. The narrow black stripes stretch from the nostrils to the eyes. They formed a sharp boundary between the broad gray stripe on the sides and the white color of the belly. In the largest individuals the throat and the belly were not purely white, but had numerous indistinct gray spots which become darker with maturation. The lower caudal fin fold was light-brown without spots. The fore- and hindlimbs were long and thin, dark from above, white from below. The shape of the head was larval with a convex forehead. The end of the tail was sharpened, but did not form a thread.

Both paedomorphic and normal larvae were not registered during 1995, although metamorphosed newts were observed at the breeding time. It seems to be associated with an introduction of the fish *Pungitius pungitius* which inhabited this water-body this year.

2.2. Laboratory Observations

For the laboratory observations, 7 paedomorphic specimens were captured in the summer of 1993 and 6 in the autumn of 1994. After one month of a normal life in an aquarium, only 2 newts of 1994 began metamorphosis. These newts got terrestrial, having reached the total length of 52.5 mm (tail length 26.9 mm), and 53.5 mm (tail length 27 mm) with the rudimentary gills and fins. Their skin became velvet, and the outer appearance and coloration resembled that of the typical immature individuals. Both newts differed from the norm, due to retention of the rudimentary gills and visibly swollen thyroid glands. During this one-month period of terrestrial life, the newts did not eat and died of starvation.

The remaining (11) paedomorphic newts normally fed and quickly grew. However, having reached the total length of 60 – 70 mm within a 2 – 3-month period, 6 individuals grew much slower and became thinner, although the remaining newts fed normally. In these 6 newts, the gill and fin size markedly decreased; however, the skin structure did not change and newts showed no signs of leaving water. The dorsal coloration of these newts was relatively dark; on the belly appeared first unclear and then distinct small black spots, sometimes fusing into a long stripe. Five out of six newts died, having lived in captivity about one year. All newts had reddish swellings on the throat and one swelling on the chin.

The remaining newts grew well and their total length reached 80 – 90 mm. In October 1993, one female laid about 20 unfertilized eggs. No records exist

Fig. 5. A paedomorphic male from Gatchina, St. Petersburg region (December 1995).

for the other newts. After hibernation, which finished in February, paedomorphic newts did not breed; however, 1 individual in late April appeared to be male (Fig. 5). The total length of this newt was 85 mm (the tail length was 44 mm). It had well developed dark-brown gills and the dorsocaudal fin of a larval type; this fin was higher than in other paedomorphic newts. The dorsal coloration was grayish-brown with scarce unclear black spots. Below on the belly were large round black spots in a white background. The lower part of the tail had a pale-blue stripe, below which were large black spots. The hind legs were not webbed. The cloacal lips were dark and swollen. The male demonstrated normal sexual behavior and mated with a normal metamorphosed female provided to it. This female gave offspring (15 larvae), which normally metamorphosed. After breeding, the male became less brighter in coloration and the size of the cloacal lips became smaller.

Among these five newts, two specimens died for unknown reasons, being externally normal. After hibernation, one female had a swollen belly and died. The gills of newts were infected with fungi; however, newts rapidly recovered.

Our observations on the living newts continue.

DISCUSSION

The life cycle in newts begins in water where eggs develop into larvae which, having reached a certain size after metamorphosis, get terrestrial. Juveniles continue to live on land until maturation, which in *T. vulgaris lantzi* apparently begins in the third or fourth year, i.e., after 2 – 3 winters (Gorovaya and Tertyshnikov, 1983; our data). In adults the annual cycle normally consists of two phases: an aquatic, i.e., the breeding period, and a terrestrial, i.e., the remaining period. According to our observations, some adults of *T. vulgaris lantzi* can also hibernate in water.

If the population contains paedomorphic individuals the life cycle becomes more complicated owing to paedomorphic stage (Fig. 3). Paedomorphic larvae unlike normal ones remain in water during winter and, for *T. vulgaris lantzi*, reproduce the next spring in the second year of life. This fast maturation, i.e., immediately after the first winter, is apparently related to the absence of the stage of passive wintering typical of other populations. In autumn and winter larvae actively feed and as a consequence increase in size during that period nearly twofold (Table 1). After reproduction nearly all paedogenetic larvae metamorphose and leave water in June – July, which is confirmed by our field and laboratory observations. Former paedogenetic larvae, according to our laboratory observations, after the first reproduction and metamorphosis lived like metamorphosed juvenile newts. They began to reproduce again only two winters later. Probably, in natural conditions some individuals may reproduce also a year earlier (see Fig. 3).

In rare cases paedogenetic larvae can apparently metamorphose at the age of 2 years, having attained a large size. These large larvae can possibly reproduce without metamorphosis more than once.

The life cycle of paedomorphic newts *T. v. vulgaris* from Gatchina markedly differed from the above description. Gatchina newts, apparently, cannot normally metamorphose. This seems to be associated with the severely disturbed function of the thyroid gland. In addition, we were unable to find any paedomorphic specimens after hibernation. This allows us to suggest that during the years of observation, paedomorphic newts did not reach maturation, and did not breed. Therefore, we could consider the appearance of paedomorphic specimens in 1994 to be a result of breeding of metamorphosed newts. In order to examine whether newts from the other water-bodies could provide paedomorphic offspring, we introduced metamorphosed newts from neighboring water body into water body where paedomorphic newts had lived. However, the introduced newts did not provide such an offspring. Therefore, we are inclined to consider the appearance of paedomorphic newts to be a

result of the mutation process taking place only among the newts in a given water body.

The sex ratio in the studied populations of *T. vulgaris lantzi* and possibly *T. v. vulgaris* was shifted towards females (see "Field observations"). The same disproportion was noted (Hartwig and Rotmann, 1940; van Gelder, 1973; Džukić and Kalezić, 1984; Kalezić and Džukić, 1986; Kalezić et al., 1989, 1990). Only in rare instances the number of males was equal or slightly larger than that of females (Radovanović, 1951; Fuhn, 1963; Breuil and Parent, 1987). There may be a genetic explanation for the disproportion in sexes if we assume that paedomorphosis is controlled by a gene (genes) located in sex chromosomes. This hypothesis should be verified by thorough laboratory studies.

Many authors usually give data on the ratio of normal and paedomorphic newts within a population. However, this ratio may vary and depend on the season and climatic conditions (Tucić et al., 1985; Kalezić et al., 1990; Andreone and Dore, 1991; our data). As is known, metamorphosed newts occur in water-bodies in the breeding period, and sometimes during winter. During drought water-bodies with paedomorphic larvae may dry; they either die or metamorphose (Andreone and Dore, 1991). In Abkhazia, during the drought of 1986, newts on land disappeared, whereas paedomorphic individuals survived.

Some paedomorphic individuals change with maturation: the fin fold and the size of the gills decrease up to a complete reduction, there are changes in body proportions, coloration, and skin structure (Gabrion and Sentein, 1976; Andreone et al., 1993; our data). Based on these and other data (Smirina and Sofianidou, 1985) we can conclude that even after acquiring features of metamorphosis, paedomorphic individuals can remain in a partly metamorphosed state for a long time, and some, perhaps, for the whole life.

Water-bodies inhabited by paedomorphic individuals are rather diverse (from deep mountain lakes to shallow temporary water-bodies in plains, e.g., Gislén and Kauri, 1959; Fuhn, 1963; Džukić and Kalezić, 1984; Breuil, 1992; our data). However all water-bodies, where paedomorphic newts would be a permanent part of the population, should have the following features in common: they do not freeze to the bottom in winter, retaining a sufficient amount of oxygen; they contain no fish or other numerous predators. Moreover, these water-bodies contain abundant food, for both larvae and adult paedomorphic individuals. Paedomorphic specimens often inhabit artificial water-bodies with vertical walls (Smith, 1954; Andreone et al., 1993; our data).

What are the advantages of the population containing paedomorphic individuals? Normally, the newts of the genus *Triturus* mainly inhabit temporary or frozen water-bodies where their main competitors and enemies (primarily fishes) are absent. In such cases, paedomorphic individuals cannot exist for a long time, and die of drought, predators, and other causes. However, under certain conditions the presence of paedomorphic individuals gives a number of advantages to the population (Whiteman, 1994). Kalezić et al. (1990) believe that these may be early maturation of individuals, better utilization of food resources, and also the advantage of feeding in a stable habitat of a permanent nonfreezing water-body. This is confirmed by our observations of *T. vulgaris lantzi* in Abkhazia. It appeared that paedomorphic individuals matured much earlier and attained the size of adults much quicker than metamorphosed newts. After the drought of 1987 the population could be quickly restored owing to its paedomorphic part, using the stability of water-body.

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