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Morph switching in a dimorphic population of *Triturus alpestris* (Amphibia, Caudata)

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Abstract

The usual life cycle of Alpine newts comprises an aquatic larval stage and a terrestrial juvenile and adult stage. However, some populations differ from this pattern in exhibiting facultative paedomorphosis where some individuals reach sexual maturity while retaining larval traits such as gills and gill slits. While paedomorphic newts can, in some circumstances, initiate metamorphosis, once a newt has commenced metamorphosis, the state is irreversible. Because the frequency of this switching from one morph to the other has never been quantified in the wild, we attempted to estimate switching rate and survival by carrying out a 3-year monitoring survey of a population inhabiting an alpine lake. While morph switching did occur in this population, it involved a relatively low proportion of the paedomorphs (approx. 12%), suggesting that metamorphosis is not favoured in the study population. The hypothesis of paedomorphic advantage was not supported since neither survival nor body condition differed between morphs. The ontogenetic pathway of wild Alpine newts is thus characterised by two forks in the developmental pathway. The first occurs during the larval stage (metamorphosis vs. paedomorphosis), and the second occurs in paedomorphic adults (switching for metamorphosis vs. continuation of the paedomorphic lifestyle). Such a two-level decision process may allow individuals to cope with environmental uncertainty.

Keywords: Body condition - Facultative paedomorphosis - Growth rate - Metamorphosis - Survival - *Triturus alpestris*

Introduction

In species with complex life cycles, ontogeny is marked by abrupt jumps, such as metamorphoses, that are usually associated with a drastic change in habitat use (Wilbur 1980; Nielsen 1998; Shi 2000). A two-phase ontogenetic course allows an individual to optimise habitat use since (1) growth modifies the match between body size and current resource availability and (2) the availability of resources might be temporary. However, differences in the variability of resource availability between the aquatic and terrestrial habitats carries with it contrasting selective pressures that favour the plasticity of ontogenetic pathways. Basically, plasticity is expressed by the length of the larval period and animal size at metamorphosis (Wilbur and Collins 1973). More complex forms of plasticity are the polyphenisms that result in the emergence of different morphological forms, as in the metamorphic/paedomorphic system. Facultative paedomorphosis can indeed be viewed as a plastic ontogenetic pathway since a single juvenile may mature either with a metamorphosed soma or with a paedomorphic soma that retains larval characteristics (Semlitsch and Wilbur 1989; Whiteman 1994; Denoël et al. 2005b). Moreover, while metamorphosis is irreversible, paedomorphosis is reversible since the metamorphosis of an adult paedomorph remains possible (Breuil 1992; Denoël and Poncin 2001; Denoël 2003b).

Facultative paedomorphosis occurs in several urodele species when individuals retain larval traits while becoming sexually mature (Gould 1977; Wilbur 1996; Denoël 2003a). These paedomorphs have gills, gill slits and other somatic larval traits that allow them to cope with an aquatic lifestyle. Numerous studies have attempted to define the environmental conditions that govern the ontogenetic course of newts and salamanders. The degradation of conditions in the aquatic habitat (pond drying, high density, low food availability) has been shown to favour metamorphosis, while contrasting conditions favour paedomorphosis (Harris 1987; Semlitsch 1987; Denoël and Poncin 2001; Denoël 2003b, 2006). Paedomorphosis is also suspected to be favoured when ponds are surrounded by harsh terrestrial habitats (Wilbur and Collins 1973; Whiteman 1994), such as in arid regions. In this situation, paedomorphs are expected to have a higher fitness than metamorphs because they avoid the costs of tissue restructuring during metamorphosis and the risks coincident with switching from one habitat to another. Indeed, several studies have

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reported that paedomorphs exhibit earlier age at maturity (Ryan and Semlitsch 1998; Denoël and Joly 2000) or higher scores of breeding events (Whiteman 1997) than metamorphs. However, harsh aquatic conditions have also been assumed to favour paedomorphosis when the energetic cost of metamorphosis is not bearable by slow-growing larvae that then opt to accelerate sexual maturation at the expense of somatic transformations (i.e. the 'best-of-a-bad-lot' hypothesis, Whiteman 1994). Whatever the ontogenetic determinants of paedomorphosis, little attention has been paid to the asymmetry of developmental pathways since the occurrence of ontogenetic switching has rarely been quantified in the wild. Only two studies have provided data on Ambystomatids obtained from monitoring studies that have continued over several years (Whiteman et al. 1996; Whiteman 1997; Ryan and Swenson 2001). These studies, however, mainly focused on breeding frequencies and growth rates. To date, there is a lack of data on other key life history parameters, such as adult survival and the frequency of morph switching.

The aim of the present study was to establish the frequency of morph switching, growth rates, body condition and survival in a dimorphic population of Alpine newts that has been monitored for several years.

Materials and methods

Study site

We performed the study at La Cabane Lake (Alpes-de-Haute-Provence, France, 44°24'N / 6°24'E Greenwich; 1950 m a.s.l.). This lake is usually free of ice from May to November. It retains water all the year round, but the water level drastically decreases during the summer so that the maximum depth – 7 m – is in June and the minimum depth –2 m – is in October. However, because the lake is formed by two depressions, in August it splits into two basins that differ by their depth, with the shallower basin usually drying up completely by the end of summer. The lake substratum consists of rocks and sediment, which are devoid of any riparian and floating vegetation. The Alpine newt (*Triturus alpestris*) is the only vertebrate in this lake with the exception of occasional common frogs (*Rana temporaria*) and grass snakes (*Natrix natrix*) (Breuil 1986; Denoël et al. 2001a; Denoël 2003b).

Sampling Scheme

All analyses were performed on a sample population first marked in 1997 and monitored for three successive years. For this purpose, 386 adult newts (82% of paedomorphs) were caught in July, August and October 1997 using landing nets. All of the newts were anaesthetised using phenoxyethanol prior to measurements and marking. They were allowed to recover in fresh water before being returned to the lake. Both paedomorphic and metamorphic newts used in this study were mature individuals (Denoël et al. 2001b). We marked 159 newts by means of PIT-tags (Passive Integrative Transponders; Trovan, UK). We introduced the transponder under the skin by perforating the belly skin at the border of the flank close to the hindlimb. The tag was then pushed up to the forelimb (Faber 1997). We also marked 227 newts by tattoo in October 1997 following the procedure described in Joly and Miaud (1989). The two marking techniques have similar effects and do not affect survival nor body condition (Perret and Joly 2002). All of the newts were measured to the nearest 1 mm (snout-vent length: SVL) and weighed to the nearest 0.1 g.

To examine whether growth and survival differed between paedomorphic and metamorphic newts, we monitored animals marked in 1997 during five recapture sessions: May 1998, October 1998, May 1999, October 1999 and May 2000. Each sampling session lasted a couple of days. Animals were caught with landing nets. All of the newts were measured as described and then released at the end of each capture session.

Statistical analyses

The large size of the lake precluded high recapture efficiency within each sampling period. We therefore pooled the two seasonal sampling sessions within each year to obtain four capture occasions: newts marked in 1997, newts recaptured in 1998, newts recaptured in 1999 and newts recaptured in 2000. Pooling successive sampling sessions is usually not recommended since increasing the time of the sampling period relative to the interval over which survival is to be estimated could result in higher heterogeneity of capture histories (Lebreton et al. 1992; Williams et al. 2001). However, the duration of the sampling period is not as relevant as mortality rate during the interval (Williams et al. 2001). As revealed by preliminary analyses, apparent survival between the spring and fall sampling periods was always estimated at the upper bound so that this bias should be minimised.

Capture-recapture data were analysed with the program SURGE ver. 1.41 (Choquet et al. 2004) to estimate morph switching and survival rates and with the program UCARE ver. 2.0 (Choquet et al. 2003) to control for the adequacy of a multi-state model used to analyse our data. More specifically, we used a multi-state capture-recapture model (i.e. classical Arnason-Schwarz type model; see, for example, Williams et al. 2001) that allowed us to estimate separately the transition probability from a state *i* to a state *j* between a capture occasion and the next one ($\psi_{i \to j}$), the survival of animals in the state i during the same interval (ϕ_i) and the capture probability of animals in that state j at the recapture occasion (P_j). Because metamorphosis is an irreversible process, only $\psi_{p \to m}$ was estimated (i.e. $\psi_{m \to p}$ fixed to 0 with m for the metamorphic status and p for the paedomorphic one). Two starting models were constructed: one for which the morph switching was kept constant across the recapture occasions but varied between sex ($\psi_{[p \to m]\ (S)}$), the other one for which the morph switching was kept constant across sex but varied between the recapture occasions ($\psi_{[p \to m] \cdot (T)}$). For each model, an additive effect of the sex and of the time on the survival and on the capture probabilities was introduced. The above two models are expressed respectively as:

$$\{\psi_{[p \to m] \cdot (S)}, \phi_{i \cdot (S+T)}, p_{j \cdot (S+T)}\} \text{ and } \{\psi_{[p \to m] \cdot (T)}, \phi_{i \cdot (S+T)}, p_{j \cdot (S+T)}\}.$$

All of the nested models within one or both of these two structural models were then constructed (total of 507 models). For each model, ten repeated minimisations with random initial values were performed to avoid the problem of local minima, as recommended by Choquet et al. (2004). Both the parameter numbers estimated at the boundary and the rank of the Hessian matrix were used to check the rank of the model, as suggested by Choquet et al. (2004) and Gimenez (2003). We compared the support between models by means of their weighted A.I.C.$_c$ (i.e. $\omega_{A.I.C._c}$, see for detailed information: Buckland et al. 1997; Burnham and Anderson 1998; Williams et al. 2001). Estimates of real (i.e. transition probabilities, apparent survivals and recapture probabilities) and structural (i.e. hypothesised effects on the apparent survival and/or the recapture probability) parameters were derived from the best-supported model. The 95% confidence interval (95% CI) of the estimated parameters ($\hat{\theta}_i$) were constructed using their profile deviance, as recommended in the case of a small data set (Lebreton et al. 1992; Gimenez 2003). The estimates of real parameters were obtained by back-transformation of the structural parameters using the exponential function. Since the structural parameters are nominal variables, these transformed estimates correspond to the odds ratio of survival (or capture) between the two categories being compared. For example, in the case of morph effect on the apparent survival, the odds ratio is the ratio between the odds of survival instead of death for metamorphs (i.e. $odds_{meta.} = \frac{\phi_{meta.}}{1-\phi_{meta.}}$) and the one for paedomorphs (i.e. $odds_{paedo.} = \frac{\phi_{paedo.}}{1-\phi_{paedo.}}$)(Agresti 2002).

We performed two-way ANOVA to test for an effect of morph, sex and their interaction on growth rates. Growth rates were obtained by the difference in snout-vent length between the first and last capture dates, divided by the number of months separating these two dates. We measured body condition by computing the residuals of the regression of $\log_{10}$(body mass) on $\log_{10}$(snout-vent length) (Jakob et al. 1996) in the autumns of 1997 and 1998. To increase the sample size, which was decreasing with years in the set of marked newts, we measured and weighed unmarked newts. Data were analysed by a three-way ANOVA. Previous analyses on the study population validated the use of body condition as a reliable estimation of the storage of biological reserves because of the positive relationships between fat contents and body condition (Denoël et al. 2002).

Results

Of the 386 adult newts that were marked in 1997 (319 paedomorphs and 67 metamorphs), a total of 94 newts (71 first caught as paedomorphs and 23 as metamorphs) were recaptured at least once during the study period (see Table 1 for individual capture histories). Among the newts first caught as paedomorphs, 12 were recaptured at least one time as metamorphs.

Goodness-of-fit tests did not indicate any evidence of lack of fit [Test 3G respectively for males and females: $\chi 2_{2df} = 0.45$, nonsignificant (ns); $\chi 2_{1df} = 1.40$, ns; Test M respectively for males and females: $\chi 2_{1df} = 1.68$, ns; $\chi 2_{1df} = 1.64$, ns].

The subset of models well supported by the data (i.e. those models with a ΔA.I.C.$_C$ <2) is indicated in the Table 2. The best-supported model is the structural model $\{\psi_{p \to m}, \phi_{i+S}, p_C\}$(see Table 2). Given this model, neither sex nor time affect morph switching, but an additive effect of both morph and sex influences apparent survival, while the capture probabilities are kept constant across time, sex and morph status. Based on this model, morph switching is estimated at 0.12 (95% CI: 0.07–0.25), the survival odds of metamorphs are 1.56-fold higher (95% CI: 1.13–2.18) than those of paedomorphs and the survival odds of males are 1.92-fold higher (95% CI: 2.08–4.75) higher those of females. Nevertheless, this model is only 1.20-fold more supported, given the data, than the third best-supported model for which morph switching varies between sex $\{\psi_{[p \to m].S}, \phi_{i+S}, p_C\}$. Conditioned to a sex effect, morph switching would be 0.16 for males and 0.08 for females. The best-supported model is also only 1.08-fold more supported, given the data, than the second-best supported model for which survival is kept constant across morph (i.e. model $\{\psi_{p \to m}, \phi_S, p_C\}$, see Table 2). There is, therefore, also weak evidence for a morph effect on newt survival, but this effect is lower than that of sex. Indeed, the best-supported model among those for which no sex effect was introduced in the survival estimates [i.e. model $\{\psi_{p \to m}, \phi_C, p_S\}$] has a ΔA.I.C.$_c$ equal to 2.93. Moreover, this model is 4.33-fold supported given the data than the one ranked with the lowest A.I.C. c [i.e. model $\{\psi_{p \to m}, \phi_{i+S}, p_C\}$].

Table 1. Summary of capture-recapture (HCR) data

HCR[a]	Male	Female
1000	50	198
1001	0	2
1002	1	1
1010	2	8
1011	2	2
1020	3	1
1100	10	24
1101	1	0
1110	2	6
1200	2	4
2000	18	26
2002	1	0
2020	3	4
2022	2	0
2200	4	4
2202	1	0
2220	1	3

[a] The first number of the HCR capture-recapture code indicates morph status: 1, paedomorph; 2, metamorph. The three following characters indicate the number of times the animal was seen during the three successive years respectively, with 0 indicating that the animal was not seen in that year

Morph ($F_{1,73}$=0.520, p=0.47), sex ($F_{1,73}$=3,016, p=0.09) and their interaction ($F_{1,73}$=1.432, p=0.24) did not significantly influence growth rates. Mean growth rates were slightly negative in both females (paedomorphs: $\bar{x}$ ± SE = - 0.11 ± 0.02 mm/month; metamorphs: −0.05±0.04 mm/month) and males (paedomorphs; −0.01±0.04 mm/month; metamorphs: −0.03±0.02 mm/month).

Body condition was influenced by year (p<0.001), but not by morph, sex or their interactions (Tables 3 and 4; Fig. 1). Residuals were indeed higher in 1997

Table 2. Best-supported models[a] (with a ΔA.I.C.$_c$ < 2)

A.I.C.$_c$	Model	df	$W_{A.I.C._c}$
755.592	$\{\psi_{p\to m}, \phi_{i+S}, p_C\}$	5	0.0329
755.746	$\{\psi_{p\to m}, \phi_{S}, p_C\}$	4	0.0305
755.954	$\{\psi_{p\to m}\cdot S, \phi_{i+S}, p_C\}$	6	0.0275
756.139	$\{\psi_{p\to m}\cdot S, \phi_{S}, p_C\}$	5	0.0250
756.378	$\{\psi_{p\to m}, \phi_{i+S}, p_T\}$	7	0.0222
756.748	$\{\psi_{[p\to m]\cdot S}, \phi_{i+S}, p_T\}$	8	0.0185
756.815	$\{\psi_{p\to m}, \phi_{S}, p_T\}$	6	0.0179
756.847	$\{\psi_{p\to m}, \phi_{i+S+T}, p_C\}$	7	0.0176
756.874	$\{\psi_{[p\to m]}\cdot T, \phi_{S}, p_C\}$	5	0.0173
757.035	$\{\psi_{p\to m}, \phi_{S+T}, p_C\}$	6	0.0160
757.229	$\{\psi_{[p\to m]\cdot S}, \phi_{S}, p_C\}$	7	0.0145
757.251	$\{\psi_{[p\to m]\cdot S}, \phi_{i+S+T}, p_C\}$	8	0.0144
757.320	$\{\psi_{p\to m}, \phi_{S}, p_i\}$	5	0.0139
757.449	$\{\psi_{[p\to m]\cdot S}, \phi_{S+T}, p_C\}$	7	0.0130
757.460	$\{\psi_{p\to m}, \phi_{i+S}, p_i\}$	6	0.0129
757.541	$\{\psi_{p\to m}, \phi_{i\cdot S}, p_C\}$	6	0.0124

[a] This table shows the best-supported models (i.e. those having a ΔA.I.C.$_C$ < 2) among the set of 507 fitted models. See the Material and methods for the definitions of the model formulas and symbols used. All of these models include a sex effect on survival, revealing a relatively good support for a sex-biased survival of newts. Although the first better supported model also includes a morph effect on survival, one-half of the best-supported models (including the second-best supported model) do not include such an effect, indicating relatively weak evidence for a morph-biased survival of newts

Table 3. Snout-vent length and mass of Alpine newts

		Snout-vent length		Mass	
		Paedomorph	Metamorph	Paedomorph	Metamorph
Female	1997	53.3 ± 0.2 (81)	53 ± 0.5 (23)	3.77 ± 0.06 (81)	3.45 ± 0.09 (23)
	1998	51.7 ± 0.3 (64)	51.4 ± 0.6 (15)	2.51 ± 0.05 (64)	2.50 ± 0.12 (15)
Male	1997	49.9 ± 0.4 (16)	49 ± 0.5 (12)	2.93 ± 0.08 (16)	2.62 ± 0.10 (12)
	1998	47.9 ± 0.4 (42)	46.7 ± 0.3 (15)	2.05 ± 0.05 (42)	1.89 ± 0.07 (15)

than in 1998. Although no main effect of morph was detected; pair-wise comparisons indicated a significantly higher body condition in female paedomorphs than in metamorphs in autumn 1997 (p<0.05), but no significant difference was detected for females in 1998 or for males in the 2 years.

Discussion

In our multi-year study 12% of paedomorphs were estimated to metamorphose each year, so that a total of 17% of the released cohort were found to be metamorphosed during the 3 years of monitoring. Consequently, our results clearly indicate that switching from a paedomorphic lifestyle to a metamorphic lifestyle is not uncommon in the studied population. However, the frequency of such a switching remains relatively low. First, as only one cohort was released, it is likely that the erosion of sample size along time largely contributed to the better selection of those models for which the morph switching was constant across years than for those models that allowed time variation in morph switching. In particular, one may expect that morph switching decreases with the age of the monitored cohort. Indeed, fixing the transition probabilities after the year 1998 to zero gives a better supported model [$\{\psi_{[p\to m]_{98}}, \phi_{i+S}, p_C\}$, A.I.C.$_c$ = 754.5] than the model for which the transition probabilities are kept constant across years [$\{\psi_{p\to m}, \phi_{i+S}, p_C\}$, A.I.C.$_c$ = 755.6]. Second, even under the hypothesis of a sex-biased morph switching, no more than 16% of males (the sex with the highest switching rate) are estimated to become metamorphosed. This larger value in males than in females (8%) may partly explain the female-biased sex ratio, but other factors are probably acting because larger biases in sex ratio have been found in other populations (Breuil 1992; Whiteman 1997; Denoël, 2003a, b).

These switching rates suggest that most of paedomorphic newts in this population remain paedomorphic throughout their lifetime. Several observations lead us to assume that the dispersal of newly metamorphosed adults is weak, thereby supporting our hypothesis that the likelihood of underestimation is low. First, dispersal is believed to occur mainly at immature stages (Joly and Grolet 1996). Second, if most of the newly metamorphosed adult newts were prone to disperse from the sampled site, one should expect some of them to settle in nearby lakes. However, fish introduction in these lakes makes them unsuitable for newts (Smith et al. 1999; Denoël 2003a; Denoël et al. 2005a). Thirdly, the hypothesis of high dispersal in metamorphs would be inconsistent with the results of our survival analysis and field observations (Denoël and Joly 2001): we did not detect lower survival or lower capture probability in metamorphs when compared to paedomorphs. In addition, both field observations and laboratory experiments performed on this population suggest that the paedomorphs undertake metamorphosis to avoid drying condition only when they cannot reach another aquatic site (Denoël 2003b). Paedomorphs have been observed to be capable of moving from the basin of the lake that dries out during the summer to the second basin where water is permanently present (Denoël 2003b). In this population, metamorphosis would be therefore mostly favoured only in the case of a total drying out of the lake, an exceptional phenomenon but a possible one during very dry summers (Breuil 1992). In this context, metamorphosis can be seen as an adaptive response to environmental stress (Denver 1997). However, most of the time the potential interest of switching from one lifestyle to the other is probably limited because of the short adult life expectancy of newts in this population (Denoël and Joly 2000).

Our analyses did not detect any difference in growth rate between the two morphs. This result confirms those of transversal studies showing that growth rates are strongly reduced after sexual maturation regardless of life cycle (Denoël and Joly 2000; Denoël et al. 2001b). Our longitudinal survey also indicated that most individuals became shorter with age. Whiteman et al. (1996) also detected such negative growth in *Ambystoma tigrinum*, but only in paedomorphic individuals, as all the metamorphs gained size across years. We have also observed such slightly negative growth rates in fasting experiments involving adult Alpine newts, although growth rates were high when prey were provided in abundance (Denoël and Poncin 2001). Temperature has also been experimentally shown to influence growth rates (Knight 1937), therefore it does seem likely that both the cold temperatures prevailing in the studied lake (Denoël 2003a) and low prey availability (Denoël and Joly 2001) impaired newt growth in our population.

The 'Best-of-bad-lot' rather than a 'paedomorph advantage' is usually the hypothesis suggested to explain a low metamorphosis rate in harsh aquatic conditions (Whiteman 1994). Our results partially support the 'Best-of a-bad-lot' hypothesis as our analyses did not reveal that paedomorphs had a consistently higher survival rate than metamorphs (Denoël et al. 2002; this study). Because only one annual cohort was monitored to perform the survival analyses, it might be suggested that this absence of effect simply results from a lack of statistical power due to low recapture probability. However, this is unlikely to be the case, since our results indicate that if the two morphs differ in survival, this difference should be in favour of the metamorphs. A lack of statistical power would limit the probability of detecting a metamorphic advantage rather than the opposite effect. Further longitudinal studies are thus needed to confirm and precisely evaluate survival differences between the two morphs within the framework of prevailing environmental conditions. Moreover, niche specialisation of both morphs could also greatly contribute to the maintenance of their coexistence (Whiteman et al. 1996). The study of diet and micro-habitat use in La Cabane Lake suggests that this hypothesis could also apply to the population studied here on the scale of the lake (Denoël and Joly 2001; Denoël 2004; Denoël et al. 2004). In this context, annual variations in resource availability in the aquatic environment could differently affect the fitness of each morph (Denoël and Joly 2001). For example, paedomorphs may benefit from higher prey abundance than metamorphs when the terrestrial ecological conditions are not favourable (Denoël and Poncin 2001). In agreement with this hypothesis, Denoël et al. (2002) showed that the body condition (a reliable indicator of fat reserves) of paedomorphs from different populations was significantly higher than in that of metamorphs. However, paedomorphs might

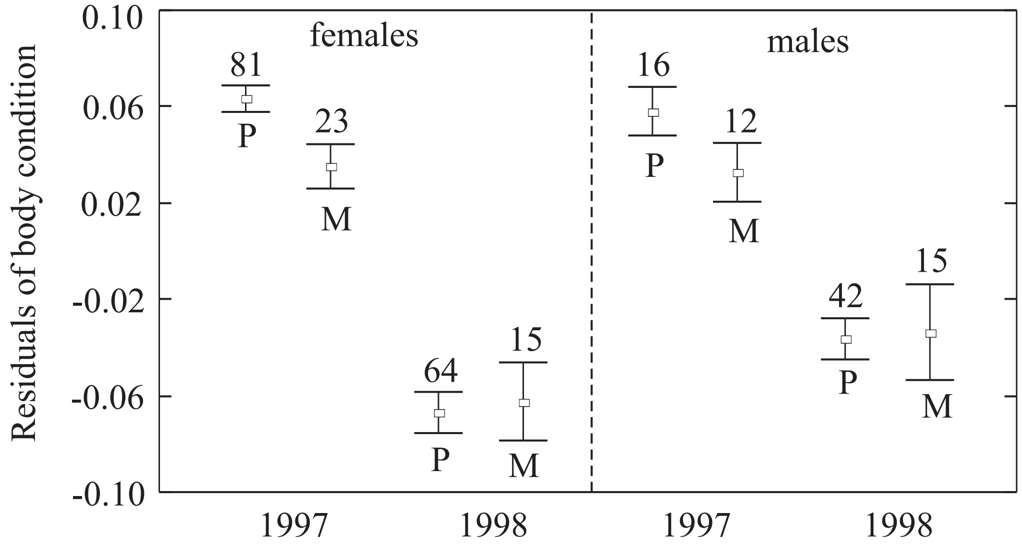

Fig. 1. Residuals (mean ± standard error) of the linear regression of log(body mass) on log(snout-vent length) between the two morphs (P paedomorphs, M metamorphs) and the 2 years (1997, 1998) in female and male Alpine newts. See Table 2 for the results of the ANOVA. Newt numbers are indicated.

Table 4. Three-way ANOVA on the residuals of linear regression of log(body mass) on log(snout-vent length) in Alpine newts

	d.f.	MS	*F*	*p*
Year	1	0.408	124.892	< 0.001
Morph	1	0.005	1.492	0.22
Sex	1	0.008	2.362	0.13
Year x Morph	1	0.009	2.688	0.10
Year x Sex	1	0.011	3.435	0.07
Morph x Sex	1	0	0.013	0.91
Year x Morph x Sex	1	0	0.040	0.84
Error	260	0.003268		

obtain less benefit from their lifestyle when aquatic conditions deteriorate (Denoël and Joly 2001). In support of this hypothesis is our result that the body condition of the paedomorphs showed a significant decrease after 1997 (this study). Thus, because paedomorphs may metamorphose in response to stressful environmental conditions and because metamorphosis is a costly event (Shi 2000; Denoël and Poncin 2001; Denoël 2003b), the survival of the paedomorphs might have been affected in that time interval, as indicated by the large decrease in body condition. Long-term studies are needed to increase our understanding of paedomorphosis evolution with regard to the impact of ecological conditions on the fitness of each morph.

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