A multi-year and multi-site population study on the life history of *Salamandrina perspicillata* (Savi, 1821) (Amphibia, Urodela)

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Abstract. We studied nine populations of *Salamandrina perspicillata* for two to nine years and described the life history variation among these population. Despite experiencing similar climatic conditions, populations differed in mean body size: populations using still water bodies for oviposition were larger body-sized than those using brooks. One semi-natural pond was used by particularly small individuals and was probably recently colonised. The mean body size of ovipositing females varied from year to year. Measurements of individuals in successive years showed that the tail grew more than the trunk and this differential growth increased with age. Females did not oviposit every year and, within a given population, the number of ovipositing females varied widely from year to year.

Keywords: body-size correlates, inter-population variability, population study, *Salamandrina*.

Introduction

Salamandrina (Fitzinger, 1826) is a salamander genus endemic to peninsular Italy. This previously monotypic genus was recently divided into two species: *S. perspicillata* (Savi, 1821), the Northern Spectacled Salamander, occurs in central and northern Italy, and *S. terdigitata* (Lacépède, 1788), the Southern Spectacled Salamander, is found only in southern Italy (Mattoccia, Romano and Sbordoni, 2005; Nascetti, Zangari and Canestrelli, 2005). Andreone and Luiselli (2000) used multidimensional analysis of ecological, distributional, demographic and taxonomic information and from this concluded that *Salamandrina* should be considered endangered. While *S. perspicillata* (sub. *S. terdigitata*) is relatively well-studied in terms of anatomy and physiology (for a review see Vanni and Zuffi, 2001), little is known regarding its population ecology, biometry and life history (Vanni, 1980; Angelini, Antonelli

and Utzeri, 2001; Della Rocca, Vignoli and Bologna, 2005; Romano and Mattoccia, 2005; Angelini, 2006; Angelini, Cari and Utzeri, 2006). Also, information on among-population variation in the life history of this species is missing. This seriously hampers any attempt to evaluate species status and develop appropriate conservation strategies. The requirement of these types of medium-long-term and multi-site population studies for making informed conservation decision has been emphasized (Collins and Storfer, 2003; Storfer, 2003). In this paper we report on demographic and life history features of nine populations of *S. perspicillata* from central Italy, which we studied for a minimum of two and a maximum of nine years.

Materials and methods

Study sites

Site Acqua della Chiesa (AdC) is a $2 \times 1.8 \times 0.8$ m trough (roughly 2800 litres), built onto a rocky, natural wall, in a mesophilic forest at 908 m a.s.l. (see fig. 1 for this and all site locations). The trough is spring-fed and water persists throughout the year. Data were collected from 1998 to 2006.

Site Belle Facce dell'Ariano (BF) is a flooded tuff tunnel, 15 m long, 1 m wide and 0.6 m maximum water depth (6500 litres) located at 810 m elevation a.s.l. It is a permanent water body and is located in a mesophilic forest. Data were collected in 2002 and 2003.

Site Castellone (CA) is a rocky, roughly ellipsoid spring pond with a 1.8×1.3 m surface area and a maximum depth

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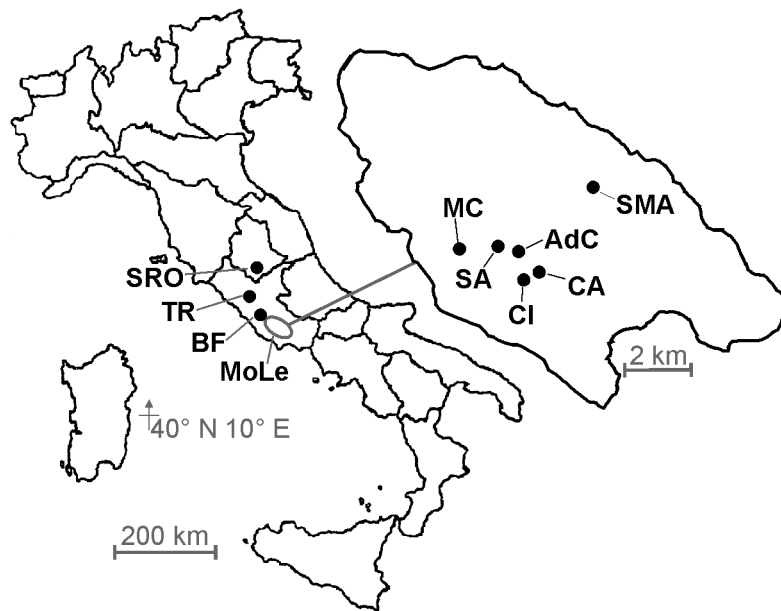
Figure 1. Location of the research sites (full names in the text). The Monte Lepini area (= MoLe) is enlarged at the right.

of about 0.3 m (330 litres). It is located at 910 m a.s.l., on grassy ground, and usually dries from July through to the first half of September. Data were collected from autumn 1998 to autumn 1999, from autumn 2001 to spring 2002 and from autumn 2003 to spring 2005.

Site Ciccopano (CI) consists of three rocky spring ponds 20-86 m apart located at about 680 m a.s.l. in a mixed deciduous forest. The ponds are very small (total surface area ca 0.8 m^2; maximum depth ca 37 cm; estimated water volume about 75 litres) and usually dry between July and August-October. Data were collected from autumn 1998 to spring 2000, from autumn 2001 to spring 2002 and from autumn 2003 to spring 2005.

Site Monte Carbolino (MC) is a brook falling from 410 m to 350 m a.s.l. and has a total length 160 m. It is located in a mixed deciduous forest and experiences summer drought. Data were collected in 2004 and 2005.

Site Sant'Angelo (SA) is a brook which flows for about 350 m, falling from 980 to 890 m a.s.l., along a karstic moderately steep sided valley. This brook undergoes winter-spring floods and dries in the summer (July-September). Data were collected in 2003 and 2004.

Site San Martino (SMA) is $2.5 \times 0.8 \times 0.3$ m trough (600 litres) located at 816 m elevation a.s.l. in a mixed deciduous forest. Data were collected from spring 2004 to spring 2005.

Site San Rocco (SRO) is a $2.5 \times 2 \times 1.5$ m (one meter maximum water depth, 1500 litres) water body created in 1982 to receive the water from a shallow water-bed. The site is in a private garden, at 200 m a.s.l.; the summer drought lasts from July to late autumn. Data were collected from 1996 to 1999.

Site Rigo (TR) is a brook located in a mixed deciduous forest. A stretch of 650 m between 265 and 220 m a.s.l. was surveyed. Data were collected in 2002 and 2003.

With the exception of SRO, that is placed in a rural area, all sites are located far from anthropogenic influences (no roads, houses, farming, logging and very little cattle grazing occur). At all sites, oviposition was recorded in late winter-spring and at CA, CI and SMA in autumn as well (at CA we captured females only during the autumn oviposition).

Methods

We visited each site at intervals of one to six days during the oviposition season, but we visited less frequently AdC in 2002, CA from autumn 2001 to spring 2002, and CI from autumn 2001 to spring 2003. At each site we photographed the ventral pattern of all the salamanders we found and used these pictures to identify all recaptures on the basis of unique and persistent marking (Vanni, Nistri and Zagaglioni, 1997). We measured snout-vent length (SVL, from the tip of the snout to the anterior margin of the cloaca) and total length (TL) with a ruler (to the nearest mm) once every oviposition season. We also measured body weight, with a Pesola dynamometer (to the nearest 0.05 g), each time a specimen was captured. The tail length (tL) was obtained as the difference between TL and SVL. We also recorded the eventual abdominal swelling as an index of pregnancy. Due to some missing measurements, analyses do not always include the same number of samples. In particular, at AdC in 2006 and SRO in 1999 we did not record measurements.

Salamandrina perspicillata does not exhibit any distinct secondary sexual characters. Nevertheless, we could assign sex to females when observed depositing eggs, or by their presence in water, as only females enter the water (Lanza, 1983; Zuffi, 1999). Females could further be distinguished by abdominal swelling and by observed weight decline on subsequent captures within the same oviposition season

(during oviposition, females lose 20-40% of their weight [Antonelli, 1999]). We could not sex the salamanders which did not meet these requisites. Vanni (1980) examined dissected salamanders and found that males have both statistically smaller SVL and a greater tL/SVL ratio than females. Below, we tentatively treated the non-sexed individuals as males.

We bimonthly recorded the TL and the developmental stages of limbs of larvae hatched from eggs deposited at AdC (1999), BF (2001), CA and CI (autumn 1998 and spring 1999). Larvae were collected by dip-netting and then measured in a Petri dish gridded with a sheet of graph paper. The measurements were recorded to the nearest millimetre (approximation of 0.5 mm). Larvae were inspected in the field using a 10× magnifier and only those with undamaged limbs and tails were included in the samples. Manipulation of both adults and larvae never caused mortality or injuries to study animals.

Statistical analyses

Where possible and appropriate we applied parametric statistical techniques. We applied non-parametric statistics in those cases in which the data failed to meet the assumptions of parametric statistics even after their transformation. Both ratio and percent data were angularly transformed.

We used nested ANOVA to evaluate the difference in female SVL between sites and between years within each site (both site and year were treated as random factors). Since some individuals were measured in more than one year, this creates some non-independence in the data set. However, when we kept only data from one capture per individual in five randomized data sets, then the results did not change. As to TL and tL/SVL ratio, we applied an ANOVA to evaluate differences between sites using only the first measurements of each female. Unsexed individuals were measured only once.

We computed the average yearly individual growth rate as the ratio of the increase in SVL, i.e. the difference between the first and last SVL measurements, over the years elapsed between them. All statistical analyses were carried out using Statistica 5.1 (StatSoft Inc.).

Results

We captured 977 female salamanders at AdC, 52 at BF, 152 at CA and 40 at MC; at CI we captured 323 salamanders of which 179 were females, at SA 595 (559 females), at SMA 431 (417 females), at SRO 325 (207 females), and at TR 212 (192 females). Several salamanders were recorded in more than one year, each time at the same site in which they had been recorded the first time. At each site, a variable fraction of the females counted in a given year was recaptured in the next year; at the still water sites we recaptured on average 55.3%, whilst in brook sites we recaptured on average 14% (32% at MC, 1.9% at SA and 8.5% at TR). At AdC, CA, CI and SRO about one half of the females sampled still oviposited three years after their first capture and at AdC seven out of 101 still oviposited eight years after their first capture.

Biometric features and growth

Nested ANOVA was performed to test female SVL differences (table 1) among populations and among years within populations. Female body size differed among populations ($F_{8,20.3} = 65.4$, $P < 0.001$) and among successive years ($F_{22,3361} = 4.3$, $P < 0.001$). Variation among sites (49.7%) was much higher than among years (1.6%). At AdC, CA and CI among-year variation showed no temporal trend; at SRO the average SVL increased in successive years. TL and tL/SVL% of females were different among populations (respectively: $F_{8,2141} = 243.1$, $P < 0.001$; $F_{8,2140} = 33.9$, $P < 0.001$).

Samples of indeterminate sex were also different among population (table 1; ANOVA: SVL: $F_{4,280} = 85.1$, $P < 0.001$; TL: $F_{4,215} = 50.7$, $P < 0.001$; tL/SVL%: $F_{4,215} = 3.9$, $P < 0.01$). These samples exhibited both a smaller SVL and a larger tL/SVL% than females of the same population at CI, SMA and SRO (Mann-Whitney U test, $P < 0.001$ in all cases). Two-way ANOVA revealed significant effects of both population ($F_{2,854} = 609.3$, $P < 0.001$) and sex ($F_{1,854} = 378.9$, $P < 0.001$) on body size (SVL), and a significant interaction between these two effects ($F_{2,854} = 17.2$, $P < 0.001$) (the post-hoc test indicated that there were no significant differences between SRO females and SMA unsexed individuals) (fig. 2a). We also detected significant effects of both sex ($F_{1,686} = 47.6$, $P < 0.001$) and population ($F_{2,686} = 14.7$, $P < 0.001$) on tL/SVL% but did not detect any significant interaction between these two variables ($F_{2,686} = 0.2$, $P > 0.5$) (fig. 2b).

Table 1. Biometric features (mm) of the surveyed populations. TL = total length; SVL = snout-vent length; tL/SVL% = tail length/snout vent length %-ratio. Last column reports homogeneousness groups (Spjøtvoll/Stoline test, $\alpha = 0.05$) relative to female SVL.

Site	Sex	Trait	n	Mean $\pm$ SE	Range	Group
AdC	female	TL	649	99.2 $\pm$ 0.2	83-122	c
		SVL	839	38.5 $\pm$ 0.1	33-45	
		tL/SVL%	649	157.3 $\pm$ 0.3	118.4-186.8	
BF	female	TL	50	98.5 $\pm$ 0.9	83-113	c
		SVL	52	38.8 $\pm$ 0.3	33-43	
		tL/SVL%	50	154.1 $\pm$ 1.5	125.6-181.6	
CA	female	TL	146	103.6 $\pm$ 0.4	89-118	d
		SVL	148	41.7 $\pm$ 0.1	37-47	
		tL/SVL%	146	148.2 $\pm$ 0.8	120.4-172.9	
CI	female	TL	108	107 $\pm$ 0.6	92-123	d
		SVL	147	42.1 $\pm$ 0.2	36-48	
		tL/SVL%	108	152.2 $\pm$ 1	115.9-178	
	non-sexed	TL	33	93.1 $\pm$ 1.1	79-105	
		SVL	97	35.8 $\pm$ 0.2	29-45	
		tL/SVL%	33	161 $\pm$ 0.6	141.2-177.1	
MC	female	TL	36	97 $\pm$ 1.2	84-111	b, c
		SVL	39	38.2 $\pm$ 0.4	35-44	
		tL/SVL%	36	153.3 $\pm$ 1.5	133.3-178.9	
SA	female	TL	559	93.8 $\pm$ 0.3	75-118	b
		SVL	559	36.7 $\pm$ 0.1	27-44	
		tL/SVL%	559	155.9 $\pm$ 0.5	120-196.9	
	non-sexed	TL	36	83.4 $\pm$ 1.4	52-98	
		SVL	36	32.8 $\pm$ 0.6	21-38	
		tL/SVL%	36	154.8 $\pm$ 2.3	121-181.8	
SMA	female	TL	216	107.6 $\pm$ 0.6	85-134	d
		SVL	277	42 $\pm$ 0.2	35-50	
		tL/SVL%	215	156.2 $\pm$ 0.6	126.2-180.9	
	non-sexed	TL	13	96.2 $\pm$ 1.1	90-102	
		SVL	14	36.2 $\pm$ 0.3	34-38	
		tL/SVL%	13	165.1 $\pm$ 1.9	152.6-174.3	
SRO	female	TL	207	83.9 $\pm$ 0.5	70-109	a
		SVL	207	33.6 $\pm$ 0.2	29-43	
		tL/SVL%	207	149.4 $\pm$ 0.7	97.2-173.3	
	non-sexed	TL	118	76.8 $\pm$ 0.6	60-96	
		SVL	118	29.9 $\pm$ 0.2	25-34	
		tL/SVL%	118	156.9 $\pm$ 1	121.9-190.9	
TR	female	TL	179	91.3 $\pm$ 0.7	62-114	b
		SVL	192	37 $\pm$ 0.3	25-48	
		tL/SVL%	179	145.4 $\pm$ 1.4	80-180	
	non-sexed	TL	20	83.1 $\pm$ 2.1	68-95	
		SVL	20	32.8 $\pm$ 0.7	26-37	
		tL/SVL%	20	153.4 $\pm$ 2	134.5-175.7	
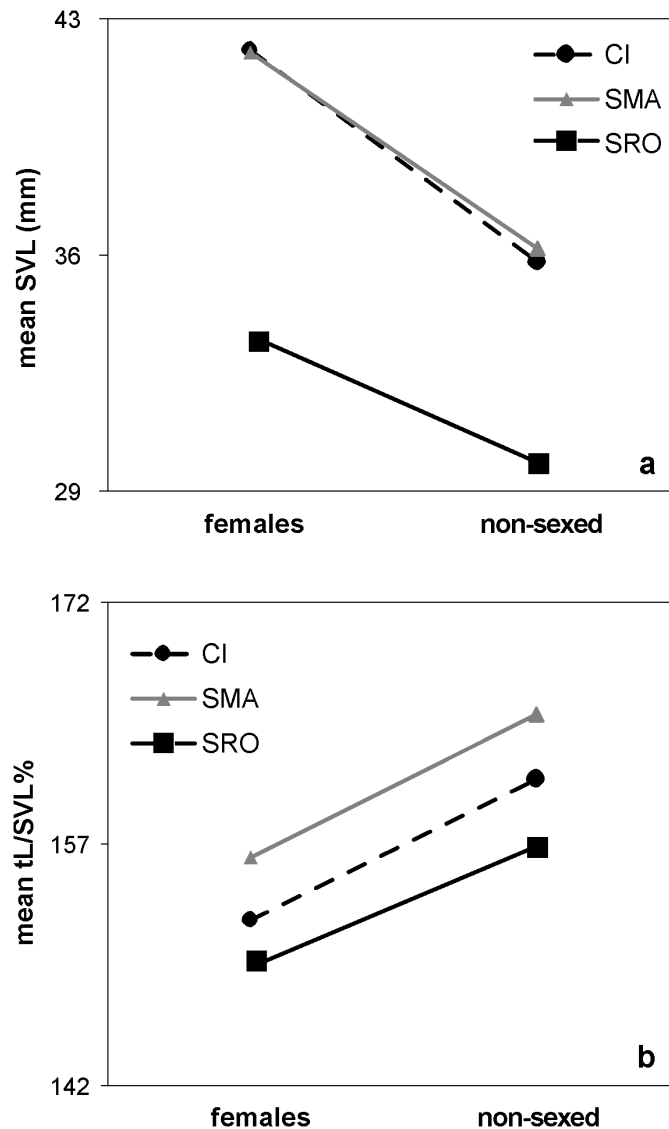
Figure 2. (a) Snout-vent length (SVL) and (b) tail length (tL)/SVL% mean values of females and non-sexed samples in sites CI, SMA and SRO.

Table 2 reports the average yearly growth rates. Annual growth was negatively correlated with body size and this correlation was significant at AdC, SRO, CA and SMA. The relative yearly growth rate (the ratio between yearly SVL increase and initial SVL) varied among years at each site (fig. 3) and this variation was significant at AdC (ANOVA$_{K-W}$: $H_{6,336} = 53.9$, $P < 0.001$) and at SRO ($U_{70,91} = 1939.5$, $P < 0.001$). SRO females, on average much smaller

than females of other sites, grew more than females of AdC, CA and CI (ANOVA $F_{3,511} = 37.02$, $P < 0.001$) (table 2). However, ANCOVA with SVL as covariate ($F_{3,510} = 0.01$, $P > 0.5$) showed that the difference in growth rate was due to body size differences (reported in table 1).

A comparison between individual SVL and tL yearly growth of females from AdC and SRO (the sites for which we dispose of a

Table 2. Average yearly individual growth rate (mm) of females and its correlation with initial SVL.

Site	n	Range	Mean $\pm$ SE	r_s LMC
AdC	320	0-3	0.58 $\pm$ 0.03	−0.39 $P < 0.001$
BF	14	0-4	1.43 $\pm$ 0.33	−0.41 $P = 0.15$
CA	38	0-1	0.24 $\pm$ 0.04	−0.47 $P < 0.01$
CI	40	−0.17-1.5	0.36 $\pm$ 0.06	−0.23 $P = 0.15$
MC	8	0-2	0.62 $\pm$ 0.26	0.6 $P = 0.11$
SA	9	0-2	1.11 $\pm$ 0.26	−0.04 $P > 0.9$
SMA	40	0-3	0.6 $\pm$ 0.13	−0.38 $P < 0.05$
SRO	118	0-4	1.11 $\pm$ 0.07	−0.53 $P < 0.001$
TR	5	0-2	1 $\pm$ 0.45	−0.4 $P = 0.5$

fairly large number of salamanders) revealed that tL increased significantly more than SVL (repeated measures ANCOVA, covariate: initial SVL; AdC: $F_{1,134} = 27.32$, $P < 0.001$; SRO: $F_{1,69} = 10.43$, $P < 0.01$) and both SVL and tL growths decreased in larger females, but SVL decreased more markedly than tL (fig. 4).

Pre- and post-metamorphic body size

Total length of pre-metamorphic larvae (four digits on both fore and hind limbs) differed significantly among populations: AdC (mean $\pm$ SE): 23.4 $\pm$ 0.3 mm ($n = 101$); BF: 17.7 $\pm$ 0.2 ($n = 314$); CA: 18.3 $\pm$ 0.3 mm ($n = 81$); and CI: 17.7 $\pm$ 0.2 mm ($n = 97$) (ANOVA$_{\text{K-W}}$: $H_{3,593} = 182.5$, $P < 0.001$). Nineteen newly metamorphosed salamanders (with no obvious ventral pattern colouration) from CI, SMA, SA and TR, measured 24.99 $\pm$ 1 mm in TL and 0.88 $\pm$ 0.02 in tL/SVL ratio.

Discussion

Body size varied greatly among populations, with differences when females were considered alone and when samples of indeterminate sex were analysed (table 1, fig. 2). Wide inter-population differences in body size were even detected within the Monti Lepini area, where study sites are geographically proximate. Body sizes reported by Vanni (1980), Della Rocca, Vignoli and Bologna (2005) and Romano and Mattoccia (2005) fall within the range herewith reported. Several ecological factors may cause inter-population differences in adult body size and we address these in turn. Caudate species with aquatic larvae and terrestrial adults may exhibit dissociation between adult body size and larval body size (Lima, Arntzen and Ferrand, 2000; Trenham et al., 2000). When we compared body size among life history stages at sites with still water, we could detect no clear relationship between larval and adult body size. Lima, Arntzen and Ferrand (2000) and Trenham et al. (2000) have attributed such a pattern to the unpredictability of the terrestrial feeding habitat relative to the aquatic one. However, in *S. perspicillata* analysed in this study, adult growth rate was negatively correlated with body size and did not differ across populations. Furthermore, adult body size is independent of oviposition effort (Angelini, Antonelli and Utzeri, 2001). This suggests that food in the terrestrial habitat is not greatly restricted and probably is not responsible for body size differences
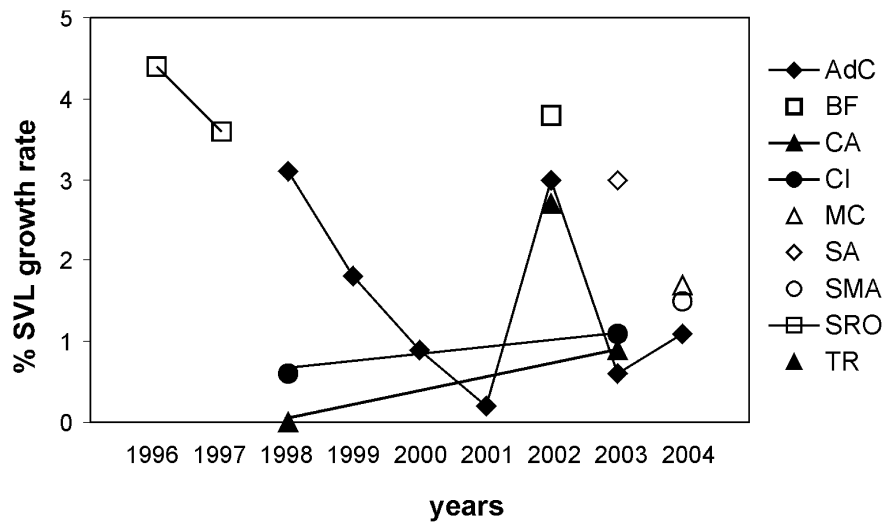
Figure 3. Variation of annual growth rate (snout-vent length SVL). X-axis report the first of two consecutive years.

among populations. Variation of climatic conditions between sites has also been proposed as a factor leading to intra-specific adult body size differences (Halliday and Verrell, 1988; Caetano and Castanet, 1993; Esteban and Sanchiz, 2000). We think that this would be unlikely to influence body size among our study populations as climate is fairly homogeneous across the range encompassed by our study (Accordi and Lupia Palmieri, 1987; Blasi, 1994). We believe that body size variation among our study populations is dictated primarily by variation in age distribution among our sites, which may be influenced by different survival probabilities. Body size is known to vary with age in ectotherms, and Bovero, Angelini and Utzeri (2006) showed that in *S. perspicillata* age is correlated to body size. In *Desmognathus monticola*, survival is increased by the availability of cover objects (Bruce and Hairston, 1990). In the Monti Lepini, *S. perspicillata* occurs in habitats characterized by limestone rock outcrops and debris (Angelini, 2006) which afford salamanders numerous shelters: the populations we studied with largest body sizes (CA, CI and SMA) are from the Monti Lepini. Populations utilizing still water exhibited larger average body sizes than brook populations and brooks represent less safe habitat, as sudden

flooding can displace adults (besides to eggs and larvae). This last is supported by the low recapture rates we reported for the brooks populations. In habitats where survival is high, sexual maturity is attained later (Bruce and Hairston, 1990), which leads to a larger adult body size (Halliday and Verrell, 1986). Thus, poor survival should lead to a relatively smaller body size, a pattern we recorded in brooks SA and TR (table 1). In *S. perspicillata*, larger females oviposit earlier than the smaller ones (Angelini, Antonelli and Utzeri, 2001; Della Rocca, Vignoli and Bologna, 2005; Angelini, 2006; Angelini, Cari and Utzeri, 2006). In brooks, this exposes larger females to floods, which occur early during the spring oviposition season (Blasi, 1994). Mortality at sites such as SA and TR may then be size/age specific, which would also generate the observed pattern. Consistently with this scenario, site MC, in which the higher percent of females recaptured suggests a lower mortality compared to SA and TR, harbours the largest body-sized brook population. SRO does not meet the expectations of our hypothesis regarding water permanence and body size variation: salamanders were the smallest at this site although it is a still-water, semi-natural pond. This population (table 1) was probably composed mostly of young individuals, as is sug-
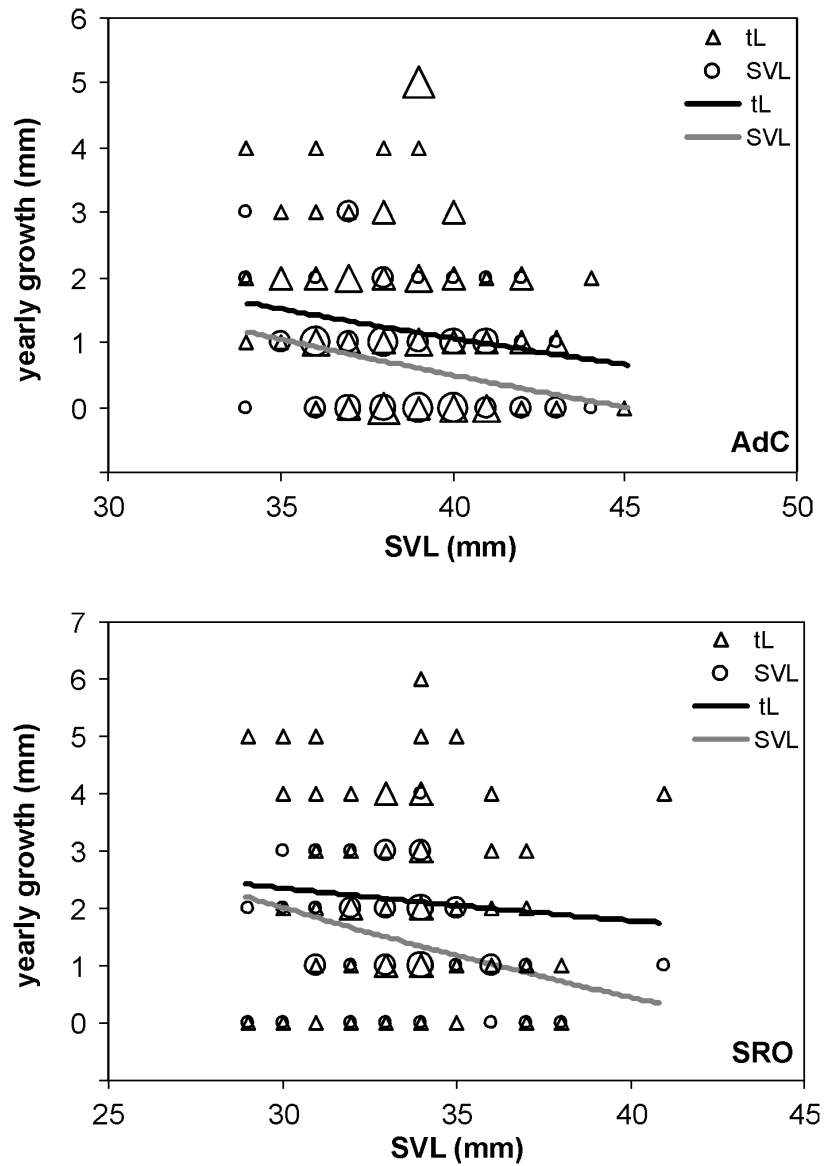
Figure 4. Correlation between snout-vent length SVL (mm) and yearly growth (mm) of SVL and tail length tL at two selected sites (AdC and SRO). The size of symbols is proportionate to the number of individuals.

gested by the steady increase in average SVL across the course of the study. The pattern of small body size, consistent growth and the fact the pond was artificially created in 1982 suggest that this site was recently colonized, although lack of recordings of inter-site dispersal suggests that colonization of a new site by salamanders should be a fairly rare occurrence. However, since this pond is placed in a garden, its

colonization might have resulted from unaware human introduction.

According to Vanni (1980), *S. perspicillata* is sexually dimorphic in both size and shape (tL/SVL ratio, some head features). Nevertheless, the intersexual differences outlined by Vanni are statistical and do not permit sexing individuals in the field. Since at CI, SMA and SRO our non-sexed samples exhibited both

smaller SVL and greater tL/SVL ratio when compared to female samples, these fit part of Vanni's criteria for males. The tL/SVL dimorphism was consistent across populations despite the inter-population SVL variation (fig. 2); that is, in larger body-sized populations, the tL/SVL inter-sexual difference is roughly the same than in smaller body-sized ones. This suggests that post-metamorphic growth is allometric throughout life. In fact, tail length of recently metamorphosed individuals is almost the same as, or shorter than, the body length, while in adults the tail is much longer (table 1). Further, at least in females, the difference between tail growth and trunk growth increases with increasing body size (fig. 4). When comparing the larger sized (and probably older) CI and SMA populations to the smaller (and probably younger) SRO (table 1 and fig. 2), similarity of the tL/SVL ratio of CI and SMA females with that of SRO "males" is evident.

Andreone and Luiselli (2000) state that *Salamandrina* should be considered as endangered. Monitoring and conservation planning requires basic life history and demographic data (Pullin, 2002; Storfer, 2003). We found 1) that high variability of both population structure and reproductive ecology occurs among and within our populations; 2) interannual variation in the number of ovipositing females, as detected in other species (Loredo and Van Vuren, 1996; Meyer, Schmidt and Grossenbacher, 1998; Trenham et al., 2000; Vaira, 2005); and 3) strong evidence for oviposition site fidelity. According to Vanni (1980) and Della Rocca, Vignoli and Bologna (2005), brook females tend to oviposit in the same brook stretch year after year, and Angelini (2006) reports that adults do not displace far from the oviposition sites. Consequently, we believe an effective conservation plan for this species should include ongoing long term studies and mark-recapture analyses that adjust for detection probabilities (Schmidt, 2003), with conservation actions focused particularly on water bodies and their close vicinities.

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