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„Life-history variation in fire salamanders (*Salamandra salamandra*, Linnaeus, 1758) in the Vienna Woods“

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Abstract

In 2012 and 2013 we studied variation in life-history traits in three populations of *Salamandra salamandra* (Linnaeus, 1758). These populations use different aquatic habitats for larval deposition in the Vienna Woods, streams at “Neuwaldegg” and at “Moosgraben” and ponds at “Maurer Wald”. The aim of the study was to investigate if size and body condition differed between the study areas and if there was a correlation in size or body condition between adult fire salamanders and their larvae.

Females from “Neuwaldegg” were on average heavier than those from “Moosgraben”, whereas females from “Maurer Wald” were on average longer than those from “Moosgraben” and “Neuwaldegg”. Females from “Neuwaldegg” and from “Moosgraben” had a significantly higher body condition than those from “Maurer Wald”. Body mass and body condition at birth showed no significant differences between the areas. New born larvae at “Maurer Wald” were on average longer at birth than those from “Moosgraben”. Body mass at birth was weakly correlated ($R^2 = 0.12$) with maternal body mass; body length of female fire salamanders had less influence on body length of their new born larvae.

We assume that the differences in size and body condition between the areas are consequences of environmental conditions concerning food availability and temperature and are no adaptations.

Key words: size at birth, size correlates, Scaled Mass Index, *Salamandra salamandra*

Introduction

Life-history deals with development, reproduction and death of organisms (Nylin & Gotthard, 1998). Cost of reproduction is the most considerable trade-off, which consists of two essential parts, incurred for survival and for further reproduction (Stearns, 1989, Zera & Harshman, 2001). Food, energy and time are limited resources and play an important role for growth, health and reproduction (Rebelo & Leclair, 2003). If organisms invest more in one process, they have fewer resources for another process (Zera & Harshman, 2001). This principle influences the fitness of an organism (Stearns, 1989, Nylin & Gotthard, 1998). Trade-offs depend on environmental factors, such as temperature, rainfall, food availability, predation and competition, and genetic factors, e.g. pleiotropy (Zera & Harshman, 2001, Morrison & Hero, 2003).

Many organisms are able to accumulate fat reserves for a long time (Zera & Harshman, 2001), which they activate later for reproduction (Stearns, 1989). Maternal condition is important for offspring size (Bownds et al., 2010). As resources for reproduction are limited, females can either produce many small or fewer larger offspring (Morrison & Hero, 2003, Bownds et al., 2010). Given that environment affects offspring size, mothers should change the size of larvae according to local environmental conditions (Bownds et al., 2010). Selection works towards maximising maternal fitness rather than offspring fitness (Smith & Fretwell, 1974).

Salamandra salamandra (Linnaeus, 1758) have a complex life cycle with aquatic larvae and terrestrial adults (Alcobendas et al., 1996). They are nocturnal, if it is raining also diurnal (Westheide & Rieger, 2010, Leeb, 2013). If night temperature is higher than 4 °C, they show an increased activity (Zahn, 2007, Leeb, 2013). Temperature plays an important role for activity length in amphibians, as they accumulate energy during this period (Morrison & Hero, 2003).

Mating takes place from March to September on land (Westheide & Rieger, 2010). Steinfartz et al. (2006) and Rebelo & Leclair (2003) described multiple paternities in salamanders as females mate with different males.

The fertilization happens in the oviduct where the offspring develop to an advanced stage until the yolk of the egg is consumed (Kopp & Baur, 2000,

Alcobendas et al., 2004). Body condition of females and environmental factors such as temperature and food availability may play an important role for size of eggs (Alcobendas et al., 2004). Experiments with lizards showed a competition by developing eggs for limited yolk or place in the abdomen of the female (Zera & Harshman, 2001). Egg size is controlled by temperature and food availability (Alcobendas et al., 2004). The amount of energy existing for reproduction influences egg size as well (Morrison & Hero, 2003).

The product of egg size and the number of eggs produced is clutch size, which typifies number of possible offspring and is a trait that populations developed in adaptation to their habitat (Morrison & Hero, 2003). Variability in egg size, clutch size and size at birth occurs within and between populations (Rebelo & Leclair, 2003). With increasing number of fertilizations, females reduce their investment in eggs (Kopp & Baur, 2000). They produce smaller broods of larger individuals (Rebelo & Leclair, 2003).

Females start depositing their larvae normally after the first rainfall in spring (around March) and stop in the middle of May (Steinfartz et al., 2006). They give birth to between 10 and 72 well developed aquatic larvae (Warburg et al., 1979, Alcobendas et al., 2004). Larvae are born in an embryonic sac and sometimes they are born free of it (Warburg et al., 1979, Alcobendas et al., 1996). If conditions to breed are bad for the females, they can keep their larvae in the uterus for several months up to 5 years (Rebelo & Leclair, 2003, Warburg, 2010). For depositing larvae females prefer slow flowing streams with riffle pool sequences, but larvae can also be found in temporary, shadowed ponds, filled up from rain or melting snow. In Kottenforst in Germany larvae born in ponds had a significant higher body mass at birth than those born in streams (Schulte, 2008). Larvae with larger size at birth tended to have a shorter duration of development (Alcobendas et al., 2004). A higher body mass of new born larvae, which were deposited in ponds, is a maternal investment to develop faster in an unpredictable habitat and saves the offspring one week of eating (Weitere et al., 2004, Schulte, 2008). Often ponds get critical temperatures for larvae in summer or they even dry out. Other problems are the limiting food conditions, density of larvae, predation and the supply of oxygen. As temporary ponds and streams are unpredictable habitats, larvae have to develop adaptations to these varying conditions (Alcobendas, 2004, Weitere et al., 2004, Zahn, 2007, Schulte, 2008, Caspers et

al., 2009, Krause et al., 2011). The duration and temperature of the habitat, as well as food availability affect the available time to growth and metamorphosis (Warburg et al., 1979, Vences et al., 2002, Alcobendas et al., 2004). As an advance larvae born in ponds are larger at birth than those born in streams (Rebelo & Leclair, 2003, Weitere et al., 2004). We assume that larval body size at birth depends on the body size of females and is not adaptive, as older and thus larger females deposit larger offspring (Rebelo & Leclair, 2003). Furthermore, larvae born in ponds grow faster because of the higher water temperature and the short duration of the pond (Kopp & Baur, 2000).

Body condition is directly affected by the vitality of an animal (Peig & Green, 2010). Not only body mass and size but also body components such as fat, water protein and skeletal tissues should be used to make a statement about the condition of an animal (Schulte-Hostedde et al., 2005). Body condition indices show us a variation of body mass for a given length and are important indicators for fitness (Peig & Green, 2010). According to Stevenson & Woods (2006) and Peig & Green (2010) body mass is a good detection of condition because size is stable or mass is standardized by an arbitrary value of size (e.g. the arithmetic mean value of the population). The scaling exponent can be more or less than 3 which mean that individuals become more or less rotund at larger sizes (Stevenson & Woods, 2006).

Adult fire salamanders live in the forest floor of deciduous forests (Alcobendas et al., 1996). In the Vienna Woods – our study area – *Salamandra salamandra* is a character species for living in beech dominated forests depositing larvae in streams, but they can also be found in oak dominated forests using ponds as a breeding environment, both habitats differ in climatic conditions. Zutz (2012) used microsatellite genotyping to study the genetic diversity of fire salamanders in the Vienna Woods and showed that there were no genetic differences between the populations.

Even though salamanders are very common throughout Europe (except Britain), from Demark to North Africa and Israel (Degani & Warburg, 1978, Kopp & Baur, 2000), there are hardly any investigations of biology and ecology of this species occurring in Austria.

The aim of this study was to find out

- if there are differences in body mass and length of new born larvae between the areas,
- if there is a relationship between size of newborn larvae and size of their mothers,
- if there is a difference in body condition between the areas.

Material and methods

Study area

The field work took place in the Vienna Woods, Austria, part of the biosphere reserve. We examined three spatially disconnected areas (Fig. 1), which differed in habitat structure.



Figure 1: Study areas in the Vienna Woods. Sample sites are marked by red points.

At “Moosgraben” we examined 690 m stream upwards (starting at 48° 13' 19" N, 16° 15' 14" E, ending at 48° 13' 30" N, 16° 15' 30" E, Fig. 2 A). The stream is embedded in a flat terrain with a lot of riffle pool sequences, a preferred habitation of fire salamander larvae. As “Moosgraben” is located westwards of Wilhelminenberg it is raining very often there, leading to generally more humid and colder weather conditions at “Moosgraben”. Since it is a reservation of natural forest, the removal of deadwood is not allowed, which support a natural development of the ecosystem.

At “Neuwaldegg” (280 m a.s.l.) we investigated 410 m stream upwards (starting in Vienna, 48° 14' 59" N, 16° 16' 2" E, ending in Lower Austria, 48° 15' 5" N, 16° 15' 45" E. Fig. 2 B). The stream is encased by precipitous slopes containing holes, which salamanders use as hidings, and consists of longer, steeper riffles but less pools.

Both streams are surrounded by an old deciduous forest dominated by beech trees. The flow conditions can change after heavy rains and they also can dry - out.

The ponds are located at “Maurer Wald” (260 – 385 m a.s.l.), south-west of Vienna. As it is warmer and drier there, the hilly deciduous forest is dominated by oak trees.

“Steinbruch” (48° 9' 10" N, 16° 14' 34" E, Fig. 2 C), once a quarry of Vienna, is situated at the highest point of “Maurer Wald”. It is surrounded by slopes with holes, hidings for salamanders. “Molchtümpel” (48° 9' 8" N, 16° 14' 31" E, Fig. 2 D) is situated 130 m westwards from “Steinbruch”. It is most frequented from newts. “Jupiter” (48° 9' 17" N, 16° 14' 33" E, Fig. 2 E) is located next to the wall of Lainzer Tiergarten. Due to the fact that “Jupiter” is frequented by hikers, the amphibians there are often disturbed. “Saturn” (48° 9' 7" N, 16° 14' 10" E, Fig. 2 F) is also situated next to the wall of Lainzer Tiergarten, 590 m westwards from “Jupiter”.

The ponds were filled through rain and melting snow, except “Saturn”, which was spring-fed. “Steinbruch”, “Molchtümpel” and “Saturn” were vernal ponds because they dry out frequently, whereas “Jupiter” led water all year round. The water of “Jupiter” and “Molchtümpel” was muddy, whereas “Steinbruch” and “Saturn” contained clear water. “Molchtümpel” was the only pond, which is influenced directly by insolation.

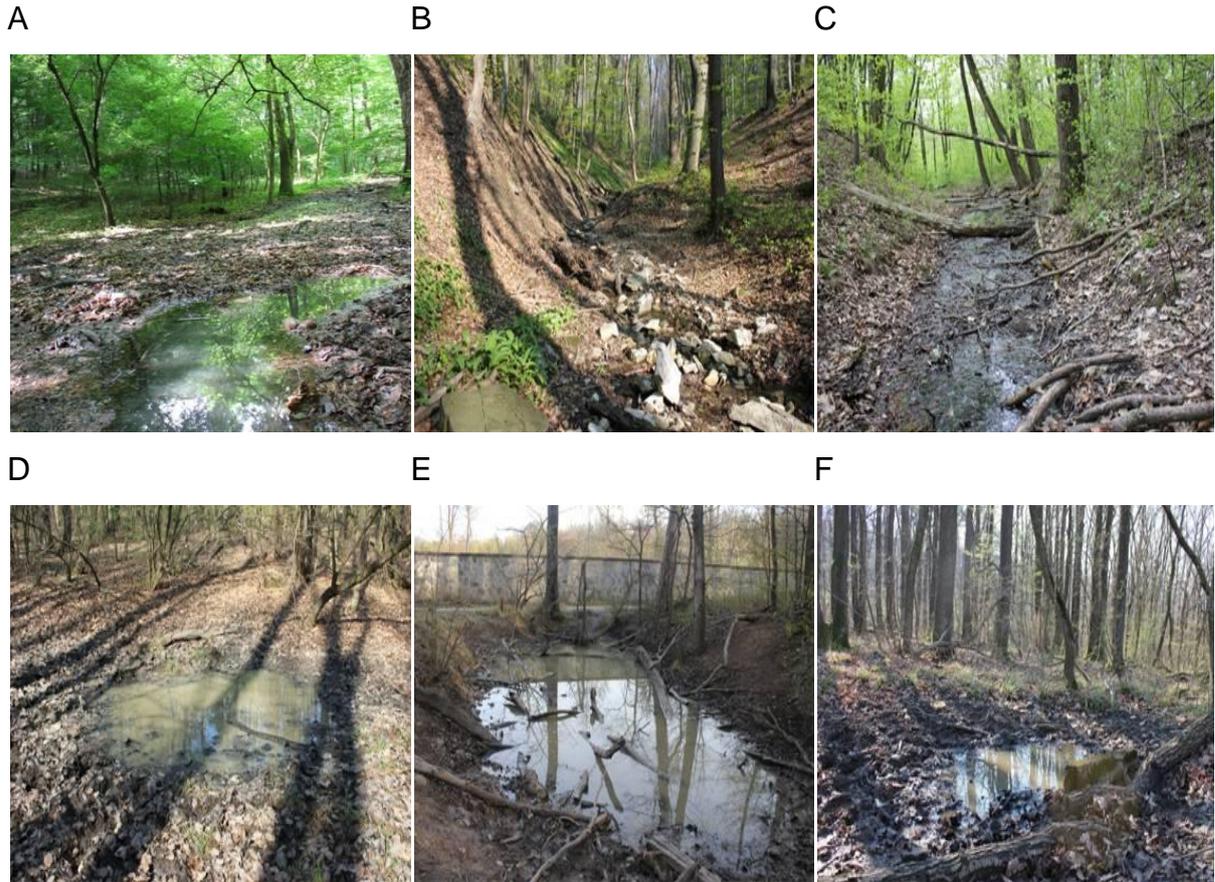


Figure 2: Study areas. A: Moosgraben. B: Neuwaldegg. C: Steinbruch. D: Molchtümpel. E: Jupiter. F: Saturn.

Data collection

Data were collected between March 14 and May 31, 2012 and between March 10 and April 25, 2013. Female fire salamanders were caught while depositing larvae or on their way to or away from the water body. If the tail of a larva was visible outside the cloaca of a female, it was animated to deposit larva via massage of their abdomen. If not, females were kept singly in a plastic box (Miraplast Universalwanne 35x24x14.5 cm, blue transparent and red, Fig. 3 A) with some water for the deposition of larvae and a piece of wood or a stone. The plastic box was placed on a slight slope and covered with a towel to minimize exterior stimuli. Females and larvae were photographed (from dorsal) on a scaled paper and weighed to the nearest 0.5 g, respectively larvae to the nearest 0.01 g. Females were put in a white linen bag (19x19 cm) to measure their body mass with a spring scale (PESOLA®, Micro-Line 20100, 100 g, d = 1.0 g, Fig. 3 B). Each larva was

transferred into a smaller plastic box (18x12 cm) with some water and millimetre paper to take a photo. After adhering water was blotted off carefully of larvae with a kitchen towel, they were weighed with a pocket scale (MH-Series Pocket Scale, MH-200, 200 g, d = 0.1 g, Fig. 3 C).



Figure 3: A: Larvae box. B: Spring scale for taking body mass of females. C: Pocket scale for taking body mass of larvae.

All the photographs were taken with a digital single lens reflex camera (Canon EOS 550D). Afterward the animals were released at the place of origin. Data collection was done with permits of Amt der Niederösterreichischen Landesregierung, Gruppe Raumordnung, Umwelt und Verkehr, Abteilung Naturschutz (RU5-BE-692/002-2012 and RU5-BE-692/003-2013) and MA 22 Bereich Naturschutz (MA 22 – 3726/2009).

Data analysis

The body length (measured from apex of snout to beginning of hind limbs and the tail length (measured from the beginning of hind limbs to the tip of the tail) of both, fire salamander females and larvae, were measured on the nearest millimetre using ImageJ (version 1.47, Fig. 4). A scale of 20 mm was defined as a reference to the millimetre paper.



Figure 4: Measuring larvae. Black line: 20 mm as a reference to millimetre paper; red line: body length, measured from apex of snout to the beginning of hind limbs; blue line: tail length, measured from the beginning of hind limbs to the tip of the tail. The sum of body length and tail length showed the total length.

The mean value of body length, total length, tail length and body mass of new born larvae from one female was calculated. Statistical analyses were done using R (version 2.15.2). Shapiro-Wilk test was used for testing normal distribution, ANOVA, respectively Kruskal-Wallis H-test to find out if there were differences in body mass, in size and body condition of the animals between the areas. Afterwards we used Tukey's HSD to look which areas differed. We used Pearson's respectively Spearman's correlation to determine the relationship between the measurements. The alpha level was set of 0.05 for all tests with Bonferroni as p-value adjustment.

According to Peig & Green (2009) the Scaled Mass Index can be computed with the following formula:

$$\hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$$

where M_i is the body mass and L_i linear body measurement of individual i , b_{SMA} is the scaling exponent which is estimated by Standard Major Axis regression of M and L , L_0 is the arithmetic mean of total length of all females respectively new born larvae. We decided us to use total length (the sum of body length and tail length showed the total length) instead of body length because tails are important storages for fat and perhaps offer energy during metamorphosis (MacCracken & Stebbings, 2012). As the relationship between body mass and total length is curvilinear, we used ln-transformed data for the Standard Major Axis regression, calculated using lmodel2 in R (version 2.15.2). For the calculation of the Scaled Mass Index we used raw data.

Results

We captured a total number of 255 female fire salamanders in the three study areas (“Maurer Wald” n = 60, “Moosgraben” n = 140, “Neuwaldegg” n = 55). Eighty-three of those females (“Maurer Wald” n = 22, “Moosgraben” n = 39, “Neuwaldegg” n = 22) deposited larvae (n = 203, 2.45 ± 1.93 larvae per female) in a “larvae box”.

Female fire salamanders had more time for depositing larvae in 2012 than in 2013 because of the long-lasting cold temperatures in 2013. In 2012 females started depositing their larvae at the end of March and stopped at the beginning of May. In 2013 they started in the middle of March at “Maurer Wald”, but they had to interrupt until the middle of April due to a cold snap. At “Moosgraben” and “Neuwaldegg” larval deposition started not until the middle of April.

Female characteristics

Females body mass ranged between 21 and 66 g ($36.6 \text{ g} \pm 7.3$), body length between 73.4 and 116.1 mm ($93.6 \text{ mm} \pm 8.2$) and total length between 141.4 and 223.5 ($181.7 \text{ mm} \pm 16.5$). Contrary to body mass (Shapiro-Wilk test, $W = 0.9829$, $p < 0.01$) body length and total length were normally distributed (Shapiro-Wilk test, body length: $W = 0.9963$, $p = 0.82$; total length: $W = 0.9922$, $p = 0.1968$).

Body mass, body length and total length significantly varied between the study areas (body mass: Kruskal-Wallis test, $n = 255$, $X^2 = 6.6$, $df = 2$, $p < 0.05$; body length: ANOVA, $n = 255$, $F_{2,252} = 16.18$, $p < 0.01$; total length: ANOVA, $n = 255$, $F_{2,252} = 12.85$, $p < 0.01$; Fig. 5). Females from “Neuwaldegg” were significantly heavier than those from “Moosgraben” (Tukey-HSD, $p < 0.05$, Tab. 1). Those from “Maurer Wald” and from “Neuwaldegg” had a significantly higher mean body length than those from “Moosgraben” (Tukey-HSD, $p < 0.01$, Tab. 1). Females from “Maurer Wald” had a significantly higher mean total length than those from “Moosgraben” and “Neuwaldegg” (Tukey-HSD, $p < 0.01$, Tab. 1).

Table 1: Characteristics of female fire salamanders. Data in each case are: top row: mean \pm standard deviation; bottom row: sample size. Values in the same row with identical superscripts are not significantly different.

	Maurer Wald	Moosgraben	Neuwaldegg
body mass [g]	37.9 \pm 1.12 ^{ab} n = 60	35.3 \pm 0.56 ^b n = 140	38.3 \pm 0.93 ^a n = 55
body length [mm]	97.7 \pm 1.09 ^a n = 60	91.2 \pm 0.67 ^b n = 140	95.7 \pm 0.9 ^a n = 55
total length [mm]	190.3 \pm 1.93 ^a n = 60	177.9 \pm 1.41 ^b n = 140	181.7 \pm 1.93 ^b n = 55

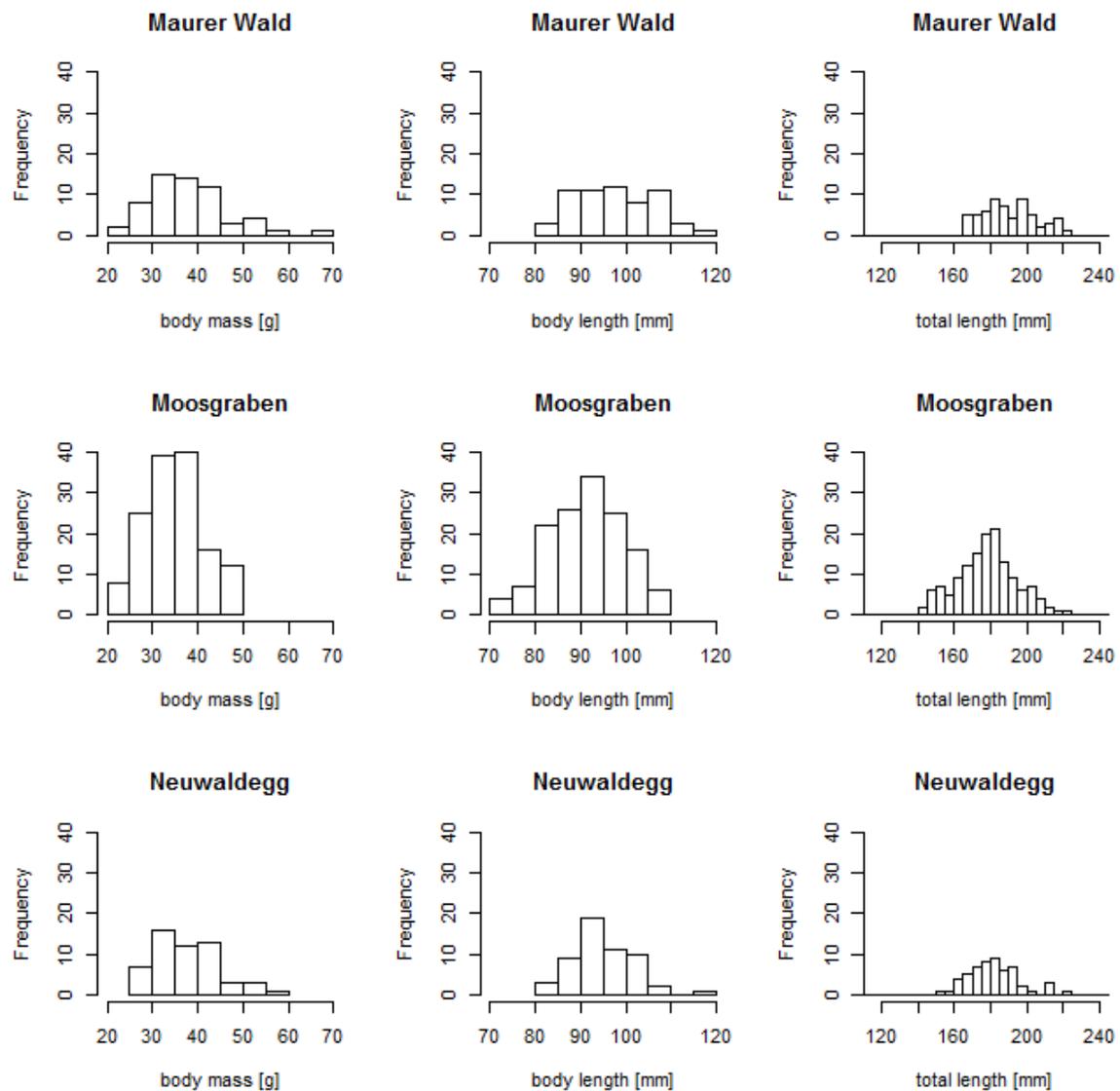


Figure 5: Body mass, body length and total length of female fire salamanders. In case of body mass the first bar includes all individuals between 20 and 25 g. Individuals with a body mass of 25.0 g belong to 20 – 25 g, those having 25.1 g to 25 – 30 g. In case of body length all individuals between 70 and 75 mm. Individuals measuring 75.0 mm belong to 70 – 75 mm, those measuring 75.1 mm to 75 – 80 mm. In case of total length the first bar includes all individuals between 120 and 125 mm. Individuals measuring 125.0 mm belong to 120 – 125 mm, those measuring 125.1 mm to 125 – 130 mm.

There was a significant correlation between body mass and body length of female fire salamanders (Spearman correlation, $y = 0.52x - 11.91$, $\rho = 0.592$, $R^2_{adj} = 0.34$, $t = 11.378$, $p < 0.01$, Fig. 6) as well as between body mass and total length (Spearman correlation, $y = 0.25x - 9.67$, $\rho = 0.587$, $R^2_{adj} = 0.33$, $t = 11.105$, $p < 0.01$, Fig. 7).

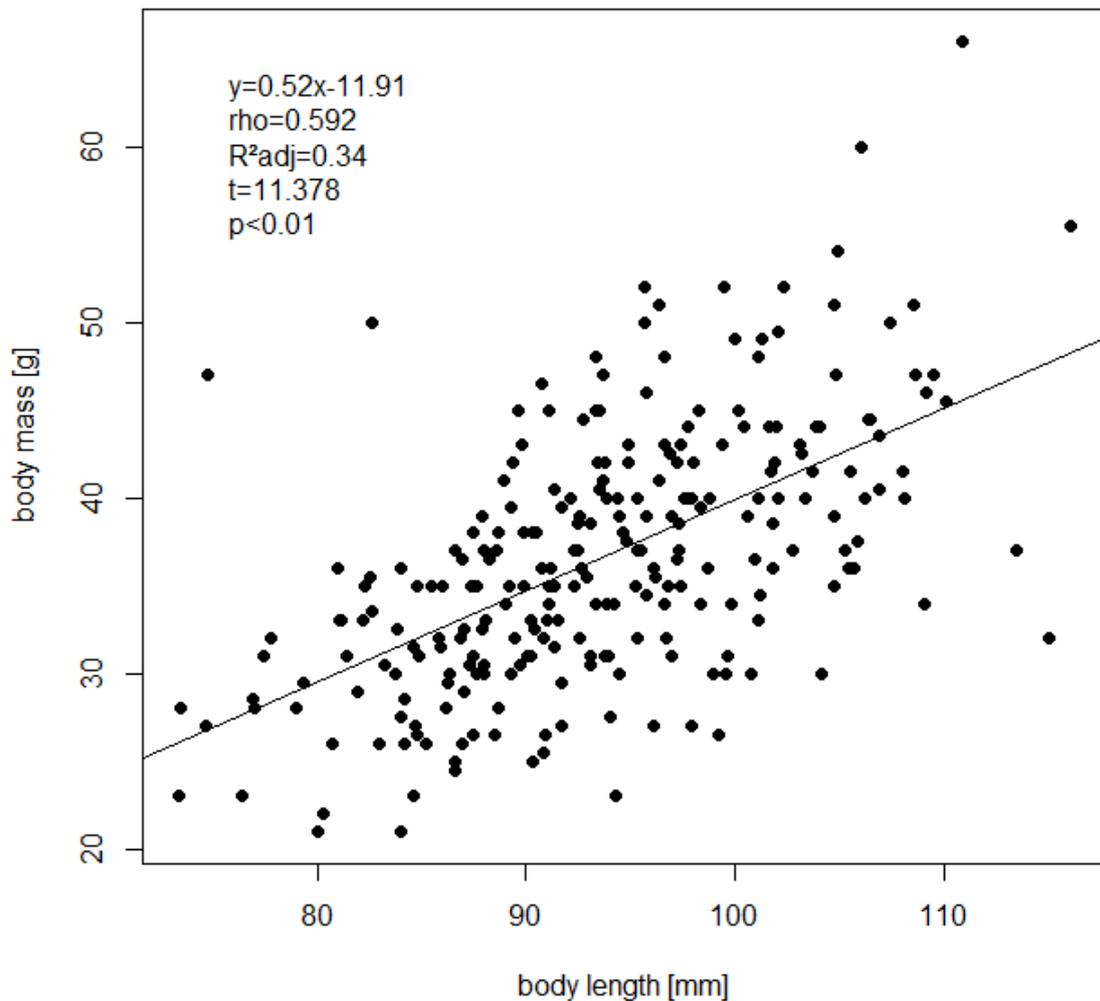


Figure 6: Body mass of female fire salamanders as a function of their body length.

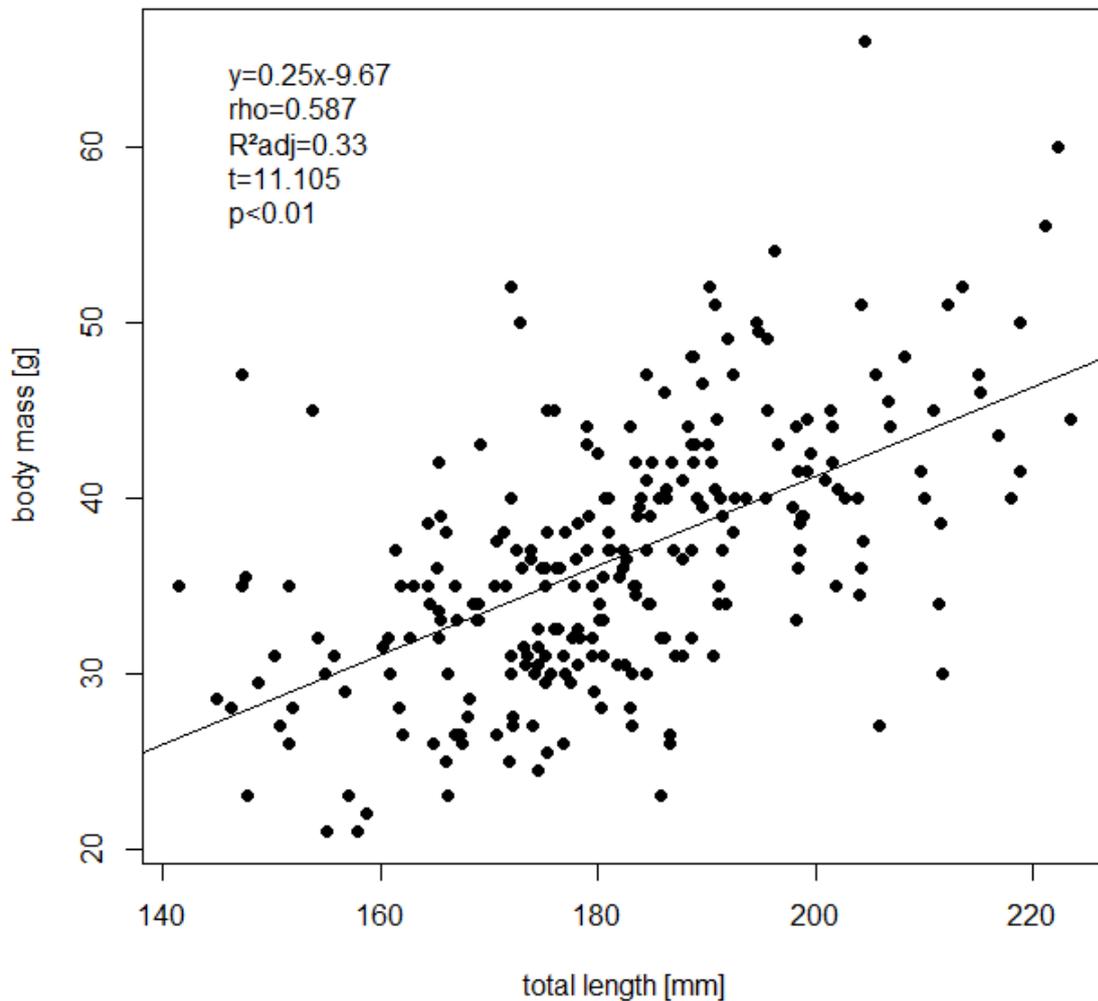


Figure 7: Body mass of female fire salamanders as a function of their total length.

Body condition

Body mass and body length were ln-transformed to calculate the Standard Major Axis (Fig. 8). We standardized the linear body measurement to $L_0 = 181.7$ mm, the arithmetic mean of total length. The scaling exponent of female fire salamanders was 2.2. They had a Scaled Mass Index between 20.54 and 74.65 g ($36.9 \text{ g} \pm 7.21$).

Area had a significant effect on the Scaled Mass Index (Kruskal-Wallis test, $n = 255$, $X^2 = 16.8755$, $df = 2$, $p < 0.01$, Fig. 9). Females from “Moosgraben” and “Neuwaldegg” had a significant higher Scaled Mass Index than those from “Maurer Wald” (Tukey-HSD, $p < 0.01$, Tab. 2).

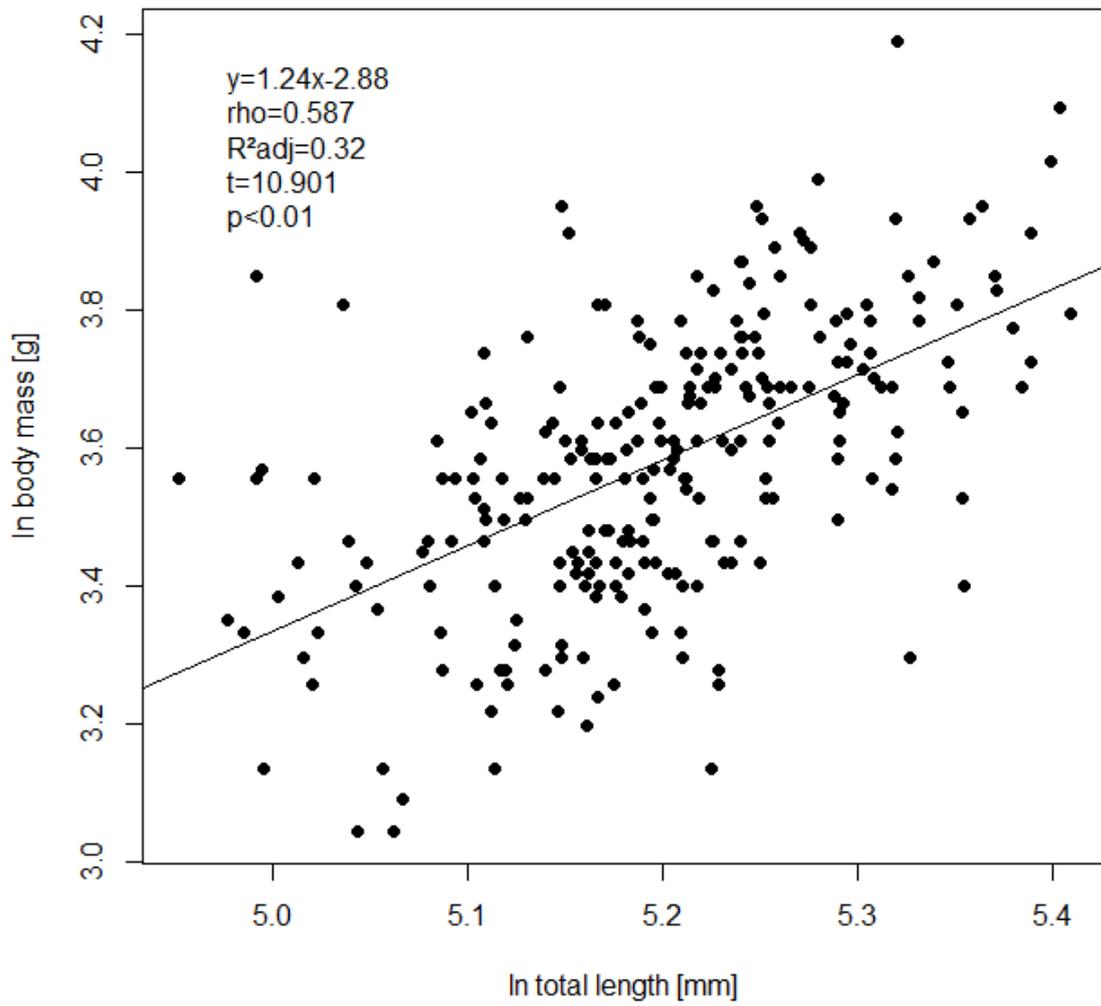


Figure 8: Correlation of the ln-transformed body mass and body length of female fire salamanders.

Table 2: Characteristics of Scaled Mass Index of female fire salamanders. Data in each case are: top row: mean \pm standard deviation; bottom row: sample size. Values in the same row with identical superscripts are not significantly different.

	Maurer Wald	Moosgraben	Neuwaldegg
SMI [g]	34.0 ± 0.69^b	37.4 ± 0.65^a	38.53 ± 0.93^a
	n = 60	n = 140	n = 55

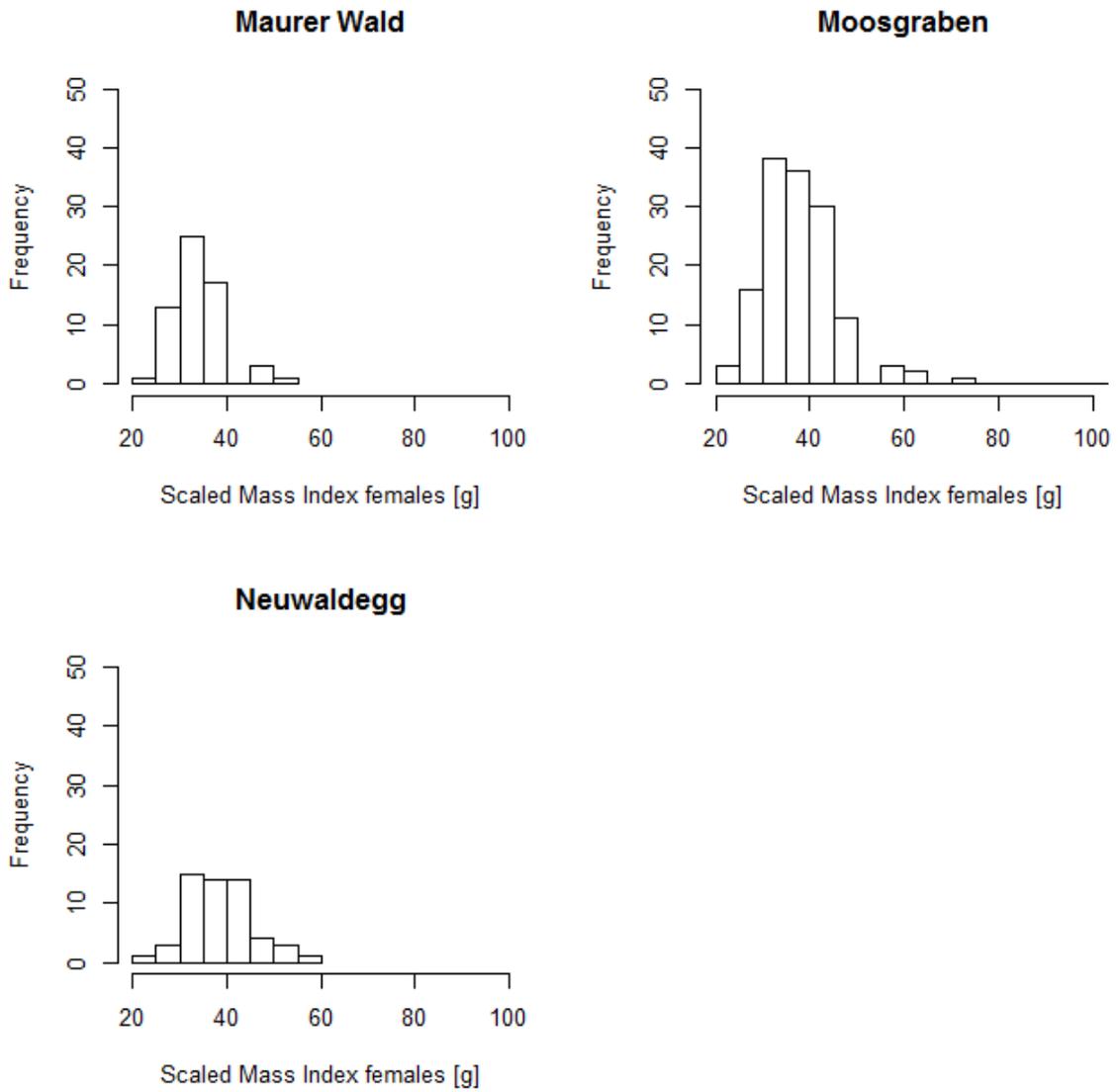


Figure 9: Histograms of the Scaled Mass Index (SMI) of female fire salamanders differing in origin. The first bar includes all individuals with a Scaled Mass Index between 20 and 25 g. Individuals with a Scaled Mass Index of 25.0 g belong to 20 – 25 g, those having 25.1 g to 25 – 30 g.

Larval characteristics

The body mass of new born larvae ranged from 0.07 to 0.32 g ($0.19 \text{ g} \pm 0.05$), the body length between 11.8 and 18.3 mm ($15.6 \text{ mm} \pm 1.35$), total length between 23.8 and 36.4 mm ($30.5 \text{ mm} \pm 2.78$) and tail length between 10.7 and 18.4 mm ($14.9 \text{ mm} \pm 1.56$).

Body mass, body length and tail length showed significant deviation from a normal distribution (Shapiro-Wilk test, body mass: $W = 0.9841$, $p < 0.05$; body length: $W = 0.9736$, $p < 0.01$; total length: $W = 0.974$, $df = 2$, $p < 0.01$; tail length: $W = 0.985$, $p = 0.028$). In contrast to body mass (Kruskal-Wallis test, $n = 203$, $X^2 = 5.7251$, $df = 2$, $p = 0.06$; Fig. 10), body length, total length and tail length differed significantly between the study areas (body length: Kruskal-Wallis test, $n = 203$, $X^2 = 9.3617$, $df = 2$, $p < 0.01$, total length: Kruskal-Wallis test, $n = 203$, $X^2 = 9.7059$, $df = 2$, $p < 0.01$; tail length: Fig. 10). Larvae born at “Maurer Wald” were significantly larger than those born at “Moosgraben” (Tukey-HSD, $p < 0.01$, Tab. 3).

Table 3: Characteristics of new born fire salamander larvae. Data in each case are: top row: mean \pm standard deviation; bottom row: sample size. Values in the same row with identical superscripts are not significantly different.

	Maurer Wald	Moosgraben	Neuwaldegg
body mass [g]	0.20 ± 0.01^a n = 44	0.18 ± 0.04^a n = 94	0.19 ± 0.01^a n = 65
body length [mm]	16.1 ± 0.18^a n = 44	15.4 ± 0.13^b n = 94	15.6 ± 0.19^{ab} n = 65
total length [mm]	31.5 ± 0.36^a n = 44	30.0 ± 0.26^b n = 94	30.7 ± 0.39^{ab} n = 65
tail length [mm]	15.38 ± 0.21^a n = 44	14.58 ± 0.15^b n = 94	15.1 ± 0.21^{ab} n = 65

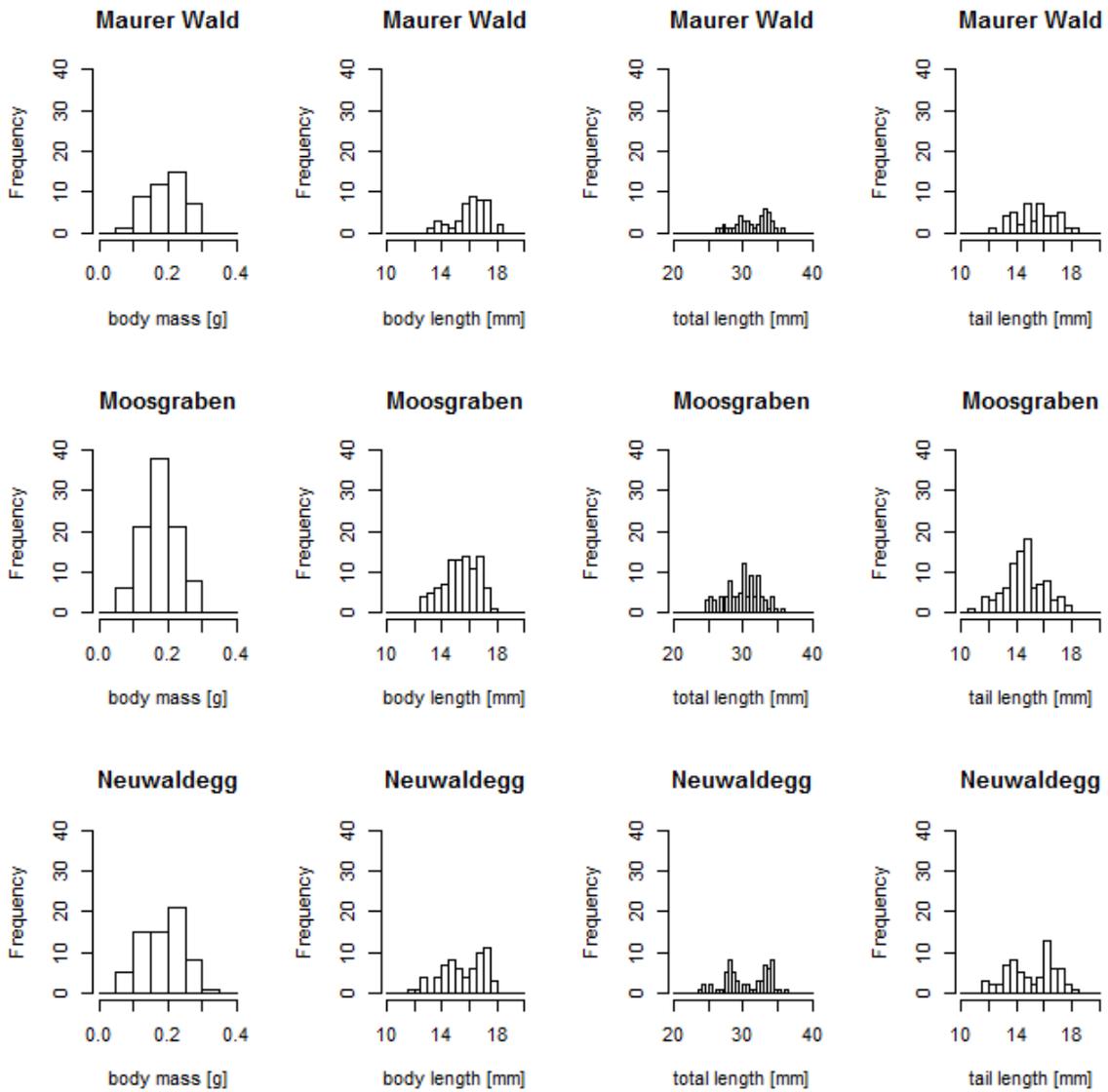


Figure 10: Histograms of body mass, body length and tail length of new born larvae. In case of body mass the first bar includes all individuals between 0 and 0.05 g. Individuals with a body mass of 0.05 g belong to 0 – 0.05 g, those with 0.051 g to 0.05 – 0.1 g. In case of body length the first bar includes all individuals between 10 and 10.5 mm. Individuals measuring 10.5 mm belong to 10 – 10.5 mm, those with 10.51 to 10.5 – 11 mm. In case of total length the first bar includes all individuals between 20 and 20.5 mm. Individuals measuring 20.5 mm belong to 20 – 20.5 mm, those with 20.51 mm to 20.5 – 21 mm. In case of tail length the first bar includes all individuals between 10 and 10.5 mm. Individuals measuring 10.5 mm belong to 10 – 10.5 mm, those with 10.51 mm to 10.5 – 11 mm.

There was a significant correlation between body mass and body length of new born larvae (Spearman correlation, $y = 0.02x - 0.27$, $\rho = 0.777$, $R^2_{adj} = 0.59$, $t = 16.909$, $p < 0.01$, Fig. 11) as well as between body mass and total length (Spearman correlation, $y = 0.01x - 0.26$, $\rho = 0.803$, $R^2_{adj} = 0.63$, $t = 18.49$, $p < 0.01$, Fig. 12).

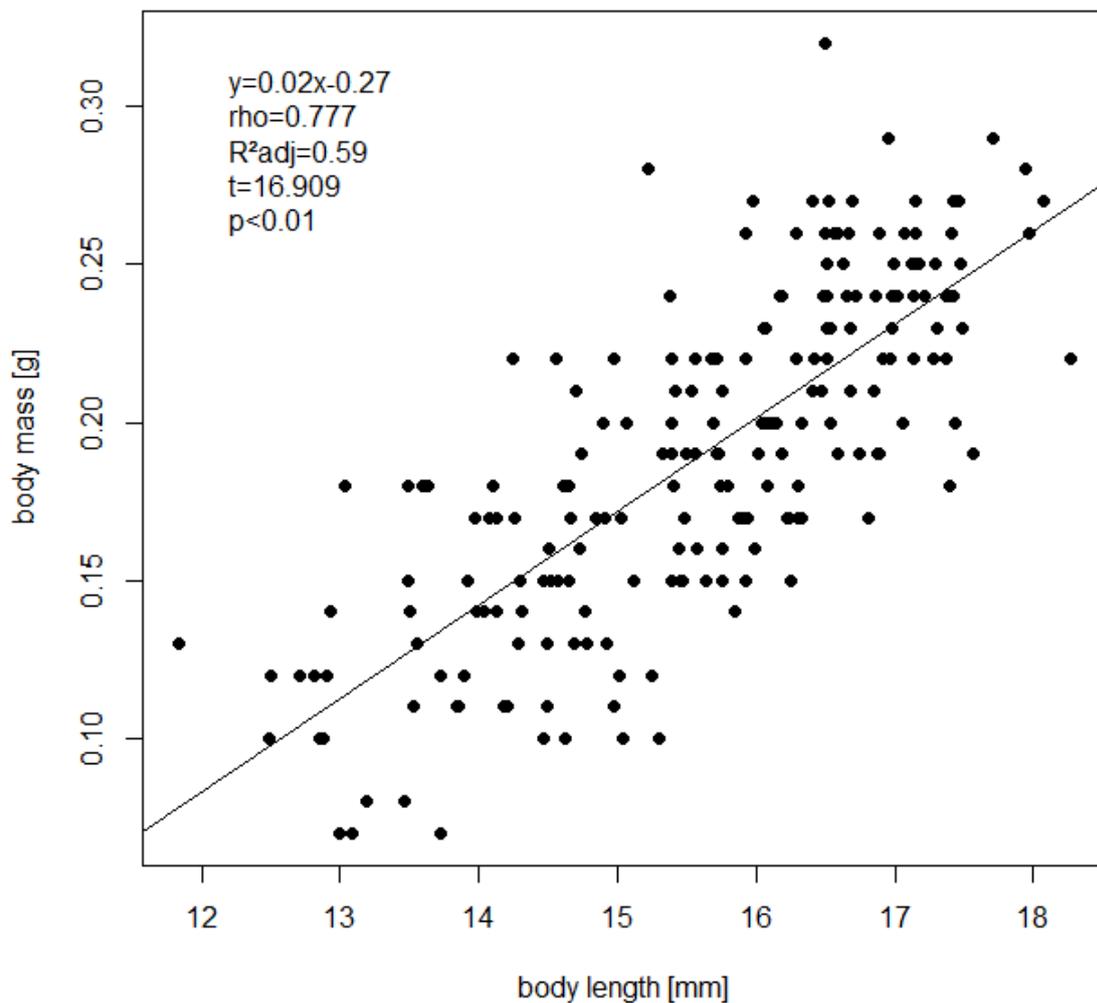


Figure 11: Body mass of new born larvae as a function of their body length.

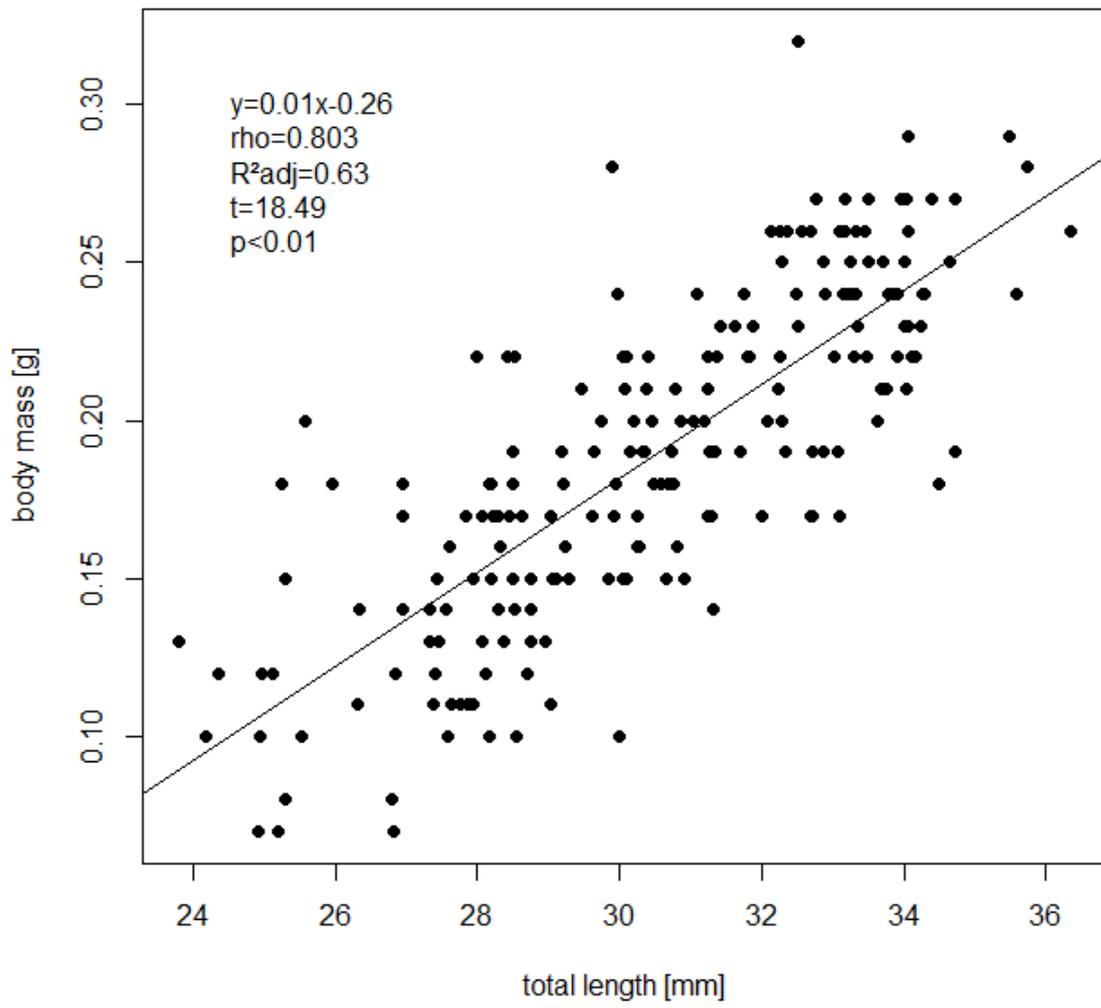


Figure 12: Body mass of new born larvae as a function of their total length.

Body condition

Body mass and total length were ln-transformed to calculate the Standard Major Axis (Fig. 13). The linear body measurement was standardized to $L_0 = 30.508$ mm, the arithmetic mean of total length. The scaling exponent of new born larvae was 3.29. They had a Scaled Mass Index between 0.11 and 0.36 g ($0.19 \text{ g} \pm 0.04$). The Scaled Mass Index of new born larvae did not differ between the areas (Kruskal-Wallis test, $n = 203$, $X^2 = 3.5183$, $df = 2$, $p = 0.1722$, Tab. 4, Fig. 14).

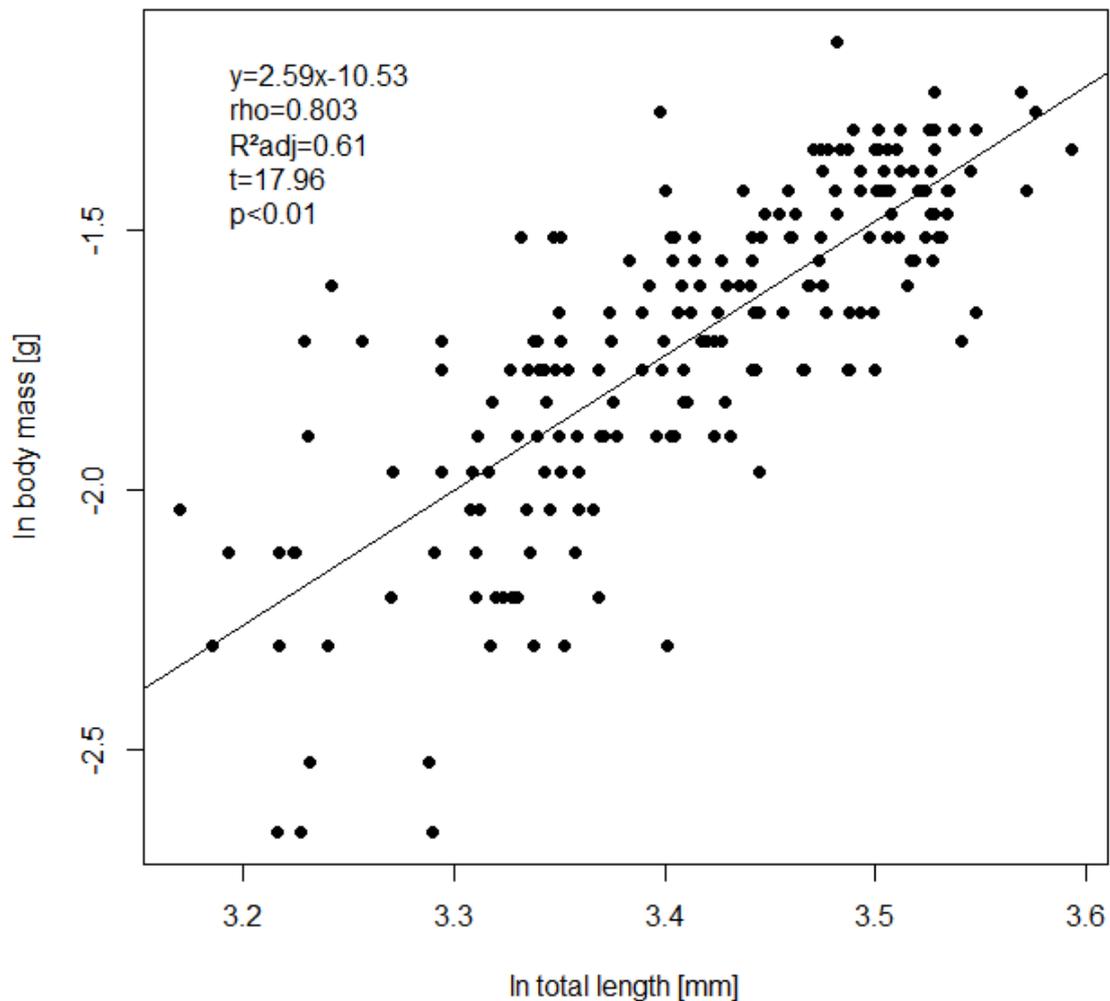


Figure 13: Correlation of the ln-transformed body mass and body length of new born larvae.

Table 4: Characteristics of the Scaled Mass Index of new born larvae. Data in each case are: top row: mean \pm standard deviation; bottom row: sample size. Values in the same row with identical superscripts are not significantly different.

	Maurer Wald	Moosgraben	Neuwaldegg
SMI [g]	0.18 ± 0.004^a	0.19 ± 0.004^a	0.19 ± 0.005^a
	n = 44	n = 94	n = 65

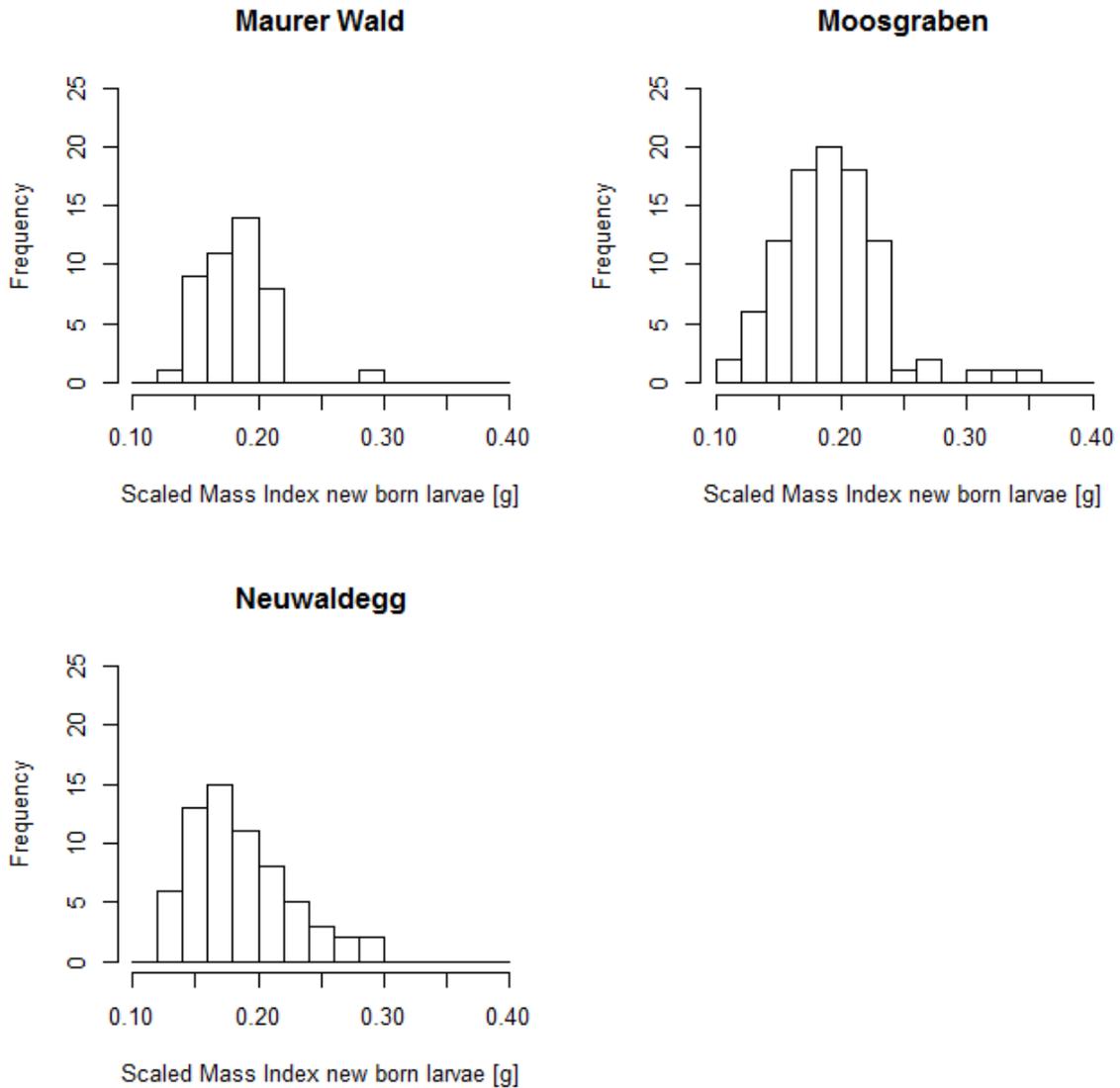


Figure 14: Histograms of the Scaled Mass Index (SMI) of new born larvae differing in their origin. The first bar includes all individuals with a Scaled Mass Index between 0.1 and 0.12 g. Individuals with a Scaled Mass Index of 0.10 g belong to class 0.1 – 0.12, those with 0.121 g to 0.12 – 0.14 g.

Correlation between females and their new born larvae

There was a significant correlation between mean body mass of new born larvae and body mass of females (Pearsons correlation, $y = 0.002x + 0.1$, $r = 0.356$, $R^2_{adj} = 0.12$, $t = 3.427$, $p < 0.01$, Fig. 15). Mean body length of new born larvae did not correlate with body length of their mothers (Pearsons correlation, $y = 0.04x + 11.87$, $r = 0.21$, $R^2_{adj} = 0.03$, $t = 1.935$, $p = 0.05$; Fig. 16). Mean total length of new born larvae did not correlate with total length of their mothers (Pearson correlation, $y = 0.034x + 23.62$, $r = 0.188$, $R^2_{adj} = 0.02$, $t = 1.719$, $p = 0.09$; Fig. 17). Mean Scaled Mass Index of new born larvae did not correlate with Scaled Mass Index of their mothers (Pearson correlation, $y = -0.0007x + 0.22$, $r = -0.099$, $R^2_{adj} = -0.002$, $t = -0.894$, $p = 0.37$; Fig. 18).

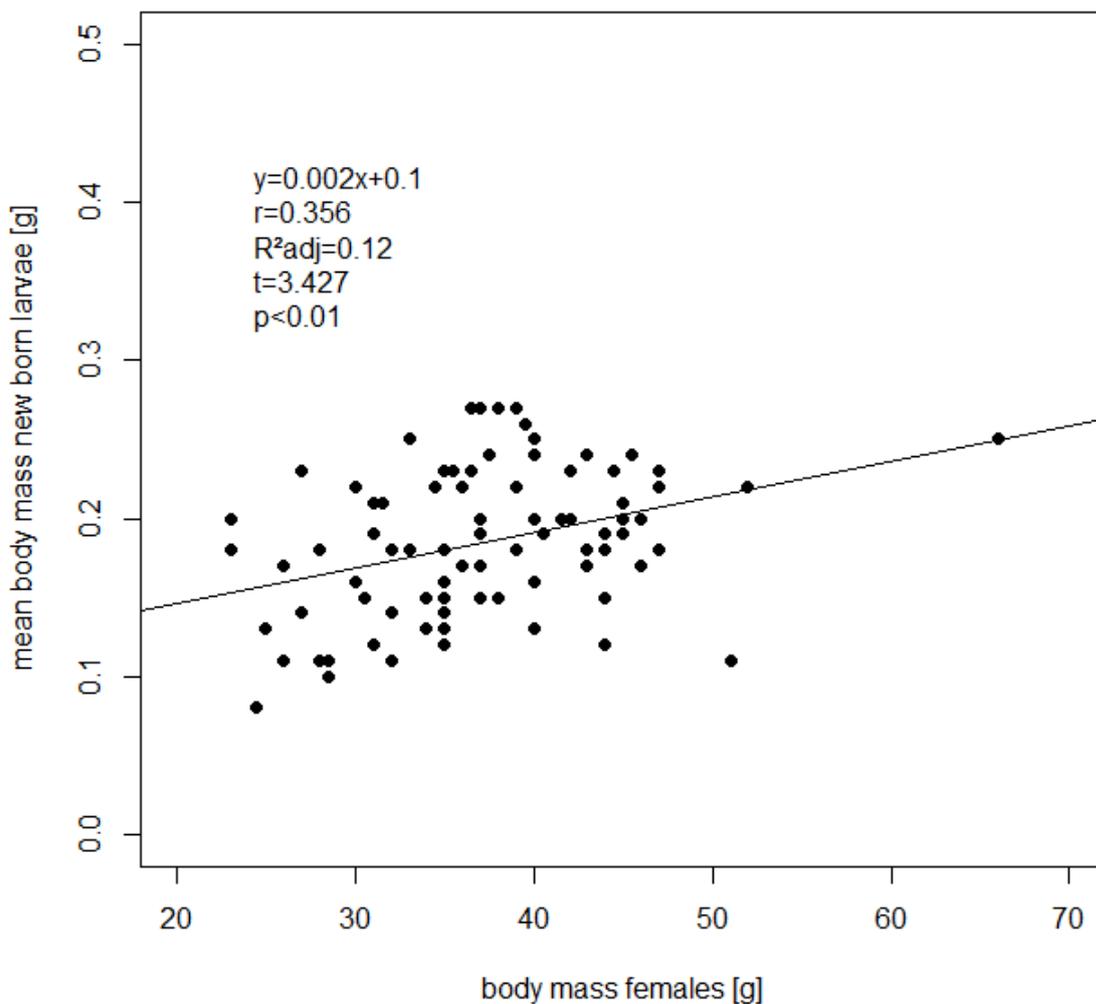


Figure 15: Mean body mass of newborn larvae as a function of body mass of their mothers.

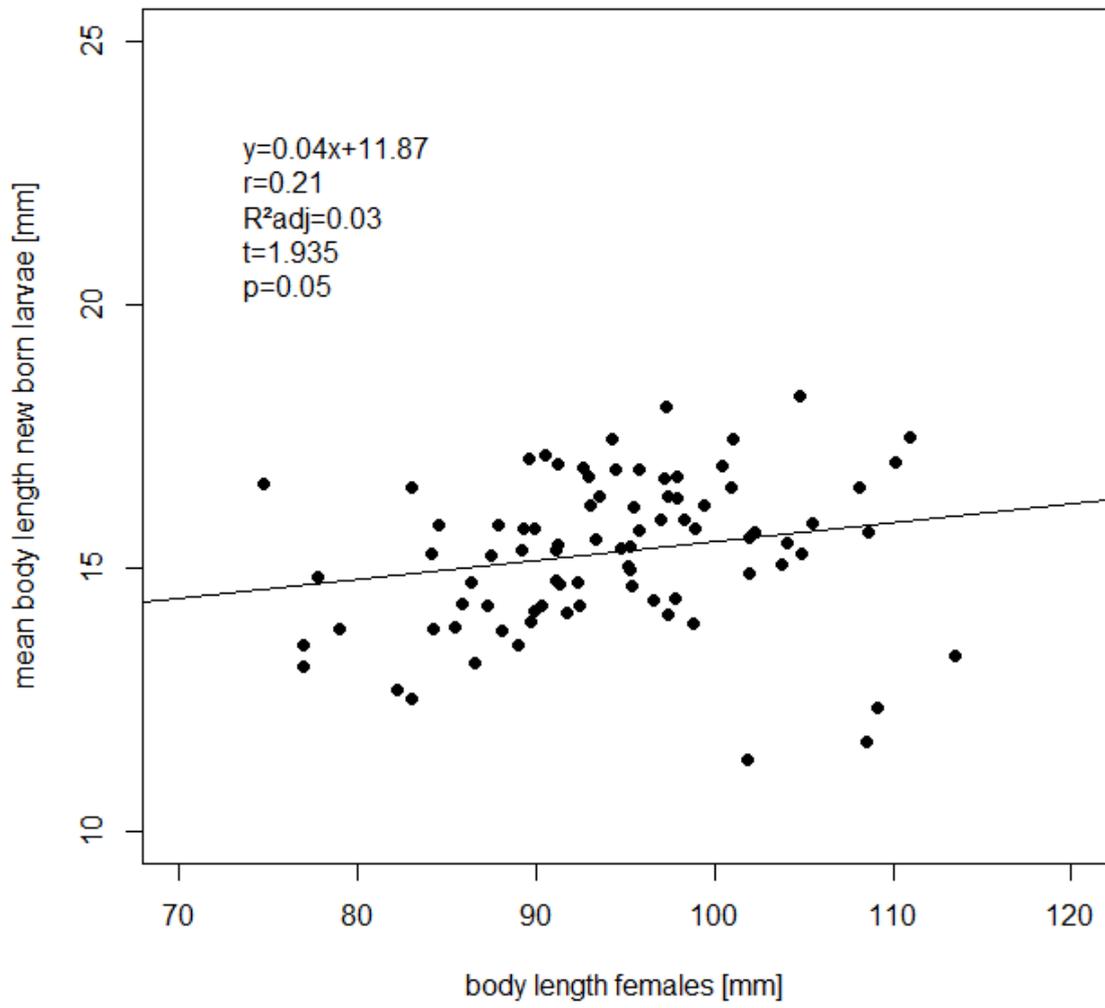


Figure 16: Mean body length of new born larvae as a function of body length of their mothers.

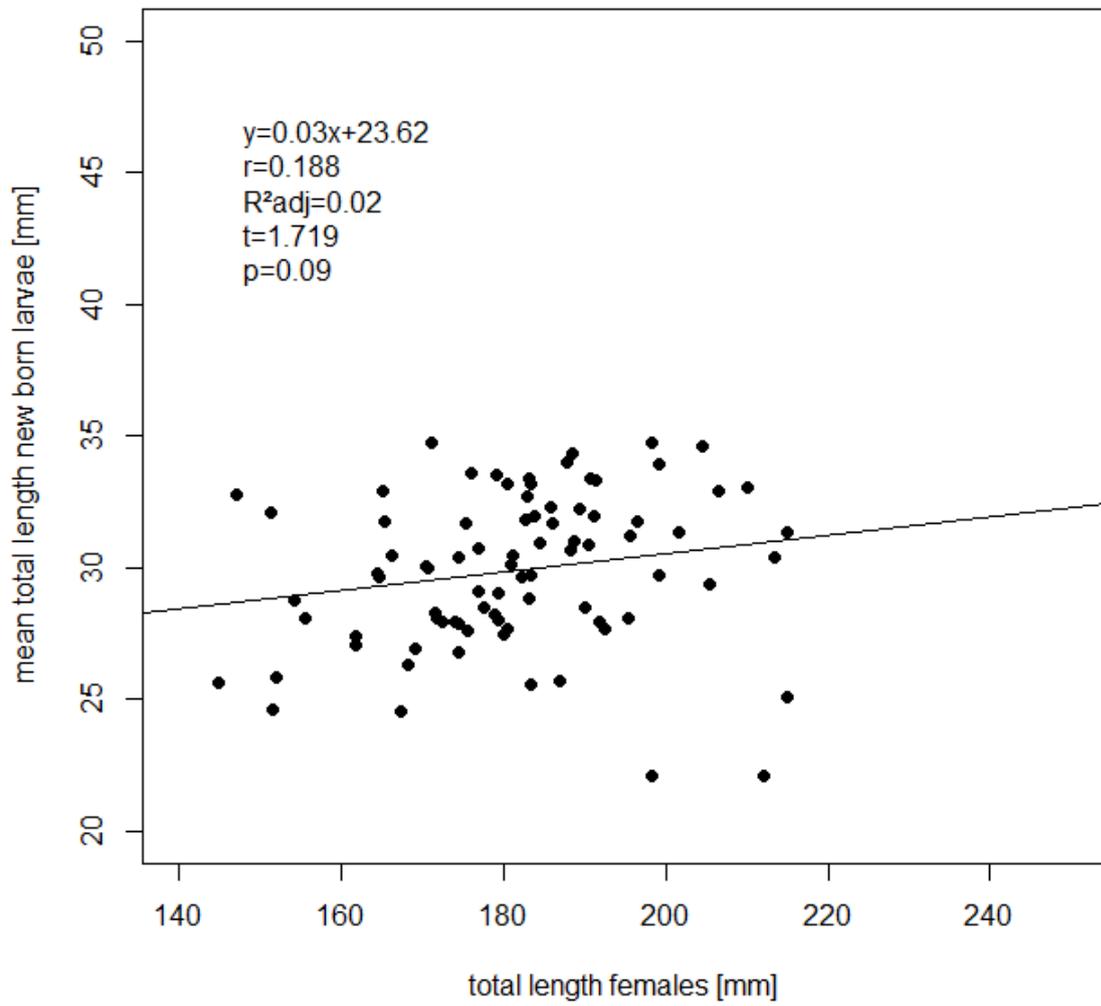


Figure 17: Mean total length of new born larvae as a function of total length of their mothers.

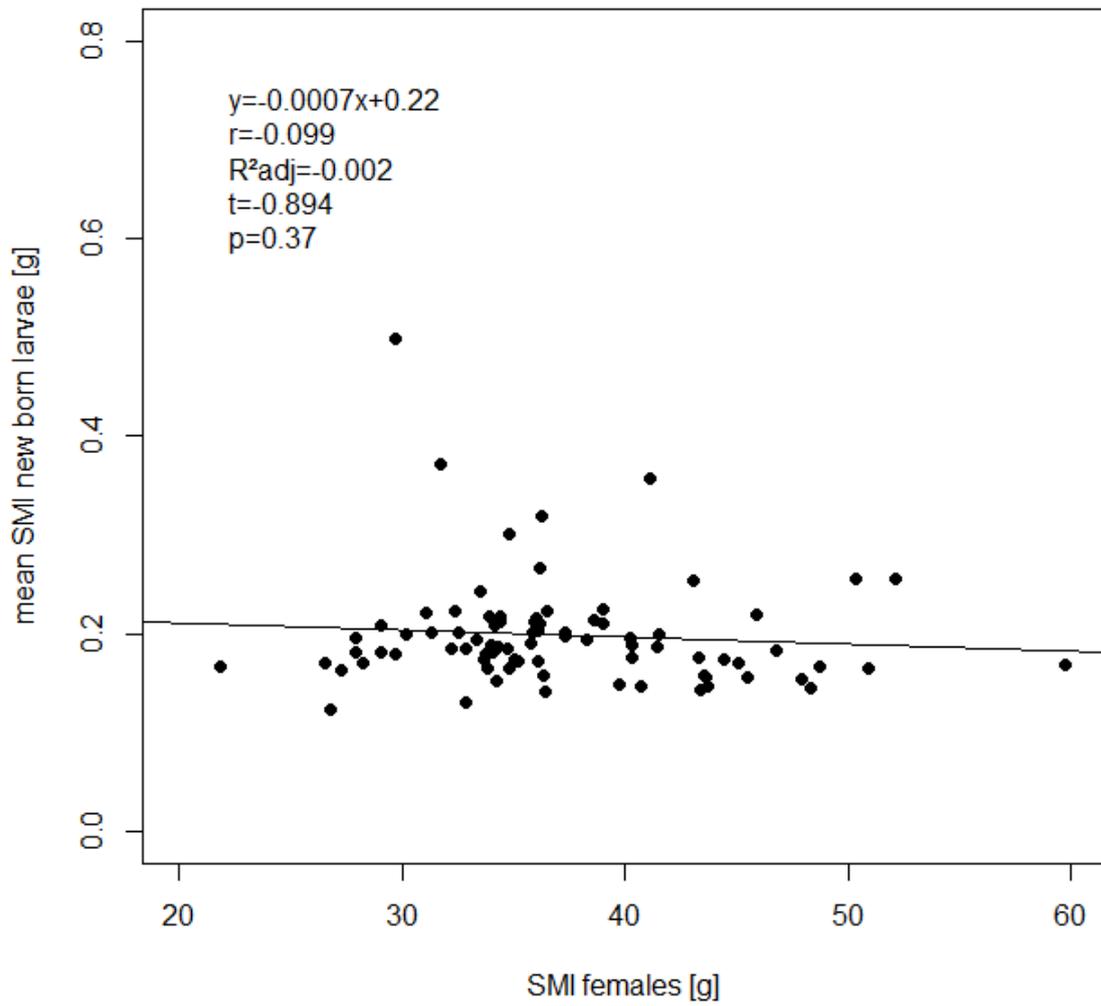


Figure 18: Mean Scaled Mass Index (SMI) of new born larvae as a function of Scaled Mass Index of their mothers.

Discussion

Female fire salamanders. Females had a body mass between 21 and 66 g which is in line with the findings of Degani (1981). The individuals with the highest mean body mass originated from “Neuwaldegg”. We cannot rule out that we sometimes weighed females with remaining larvae in their abdomen. Heavier animals can result from being structurally large, as body mass increases linearly with body size, or from carrying more fat or protein reserves or remaining larvae inside (Schulte-Hostedde et al., 2005). Female fire salamanders do not displace all their offspring at the same time at the same place (Segev et al., 2011).

Degani (1986) determined a mean body length between 109 and 113 mm of *Salamandra salamandra*, living in a moist habitat in Israel. Those from Vienna Woods had a mean body length of 93.6 mm and a mean total length of 181.7 mm. However, the individuals with the highest mean body length and total length were found at “Maurer Wald”, those with the least mean body length and mean total length at “Moosgraben”. We assume that the difference in length is due to a different age distribution among the areas, which may be affected by survival likelihood (cf. Angelini et al., 2008). It has been shown that salamanders, which use ponds for depositing their larvae, had a higher mean body length than those living next to streams, as flood water can drift them away (Angelini et al., 2008). The study of Romano & Ficetola (2010) illustrated that the type of aquatic habitat plays an important role for body length and survival, as animals reproduce in lotic waters have a higher mortality because of drifting away than those in lentic waters. Reaching sexual maturity later refers to larger body size in habitats with higher survival likelihood (Morrison & Hero, 2003, Angelini et al., 2008). Those with poor survival opportunities reach sexual maturity earlier with smaller body size (Angelini et al., 2008). In Europe larger salamanders are often found in warmer/southern areas (Romano & Ficetola, 2010).

We assume that females living at “Moosgraben” mature earlier, that’s why they are smaller. The higher mortality with selection reaching maturity earlier is less important than the more favorable land habitat in matters of activity periods and food availability. Consequently, they have enough resources for reproduction when they are younger. Females living at “Maurer Wald” reach maturity later because of the unfavorable land habitat. We suppose that reproduction at “Moosgraben” is more constant because of the advantageous environment for

larvae. We assume that at “Moosgraben” age distribution is equal because of continual reproduction every year and subsequently individuals are relatively small. At “Maurer Wald” reproduction alternate from year to year, e. g. in 2012 reproduction was close to zero because most of the ponds dried-out very early. Populations of some cohorts with prevailing older individuals dominate at “Maurer Wald”.

About one third of the females we captured deposited larvae. Depending whether females had already deposited some larvae prior to their capture, they placed varying number of larvae in the “larval box”.

New born larvae. New born larvae had a body mass between 0.07 – 0.32 g which is in line with the findings of Alcobendas et al. (2004) and Warburg (2010). They did not differ significantly in body mass between the areas, but in body, total and tail length. Larvae born at “Maurer Wald” had on average longer tails than larvae born at “Moosgraben”. It has been shown that larvae develop larger tails in shaded habitats and if they notice the presence of insect predators, e.g. through waterborne chemicals (Van Buskirk & McCollum, 2000, Van Buskirk & Schmidt, 2000, Keckeis, 2013). Another reason can be to redirect predators away from the prone body to the tail, because parts of the tail can be snapped in order to escape (Van Buskirk & McCollum, 2000). This confirms to the findings of Wilbur & Semlitsch (1990) where tail loss causes little cost in tadpoles and is an important method to decrease the effect of predation.

The results of size at birth showed similar patterns between the areas. The little differences in length of new born larvae may be associated with the difference in length of females from “Maurer Wald” and “Moosgraben”.

Correlation. Our results showed a weak correlation between mothers and their offspring in respect to body mass which correspond to the findings of Kopp & Baur (2000). Other studies however found that in some species of *Salamandra* larger females produce larger offspring, indicating a correlation between mothers and their offspring (e.g. Rebeleo & Leclair, 2003, Alcobendas et al., 2004).

We suppose that age of the females plays an important role for the investment in their offspring. Females that deposited larvae did not differ in their body mass as well as the body mass of new born larvae. We assume that the differences in body and total length at birth might be due to the size distribution of the females.

Body condition. The scaling exponent of female fire salamanders was 2.2 and of new born larvae 3.29. The origin of adult fire salamanders had a significant effect on their Scaled Mass Index. Salamanders reproducing in streams had a higher body condition. At “Neuwaldegg” females have to walk down an escarpment to deposit larvae and afterwards have to climb up again to get to their earth holes. We hypothesize that “Moosgraben” and “Neuwaldegg” are less disturbed habitats for salamanders. As it is more humid at “Moosgraben” the period of activity is longer. At “Maurer Wald” individuals show less activity in summer and more activity in winter (Leeb, 2013). Leeb (2013) described more activity on warm and humid days following colder periods at “Maurer Wald”. Female fire salamanders from “Maurer Wald” had a longer total length but had a poorer body condition than those from “Moosgraben”. We assume that the difference of microclimate plays an important role for the difference in body condition. Additionally, at “Moosgraben” the habitat of fire salamanders has improved, as deadwood is not removed. New born larvae from “Neuwaldegg” and “Moosgraben” had also a higher body condition than those from “Maurer Wald” but there was no significant difference. Larvae that were deposited in streams have better circumstances necessary for growth, because the water is colder and has a higher content of oxygen, but they need longer to reach metamorphosis. Larvae with poor body condition have a higher risk of predation than those with good condition (Krause et al., 2011). We suppose that the low difference of the Scaled Mass Index of new born larvae between the areas is due to the size distribution of their mothers.

Conclusion. The advance of being larger and heavier at birth when born in ponds is not relevant, as the difference in size of new born larvae between the areas was only marginal. We found a weak correlation between mean body mass of new born larvae and body mass of their mothers. Area had an important effect on body condition of the individuals, but the Scaled Mass Index did not correlate between new born larvae and their mothers. We assume that the differences in size and body condition are consequences of environmental conditions concerning temperature and food availability and are no adaptations.

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Zusammenfassung

2012 und 2013 wurde die Variation in life-history Merkmalen in drei Populationen von *Salamandra salamandra* (Linnaeus, 1758) untersucht. Diese Populationen verwenden verschiedene aquatische Lebensräume zum Absetzen ihrer Larven im Wiener Wald, Bäche in „Neuwaldegg“ und „Moosgraben“ und Tümpel im „Maurer Wald“. Ziel der Studie war es herauszufinden, ob es Unterschiede in der Masse, Größe und Kondition zwischen den Standorten gibt und ob es eine Korrelation zwischen dem Gewicht, Größe und Kondition von Feuersalamandern und deren neugeborenen Larven gibt.

Weibchen von „Neuwaldegg“ waren im Mittel schwere als jene vom „Moosgraben“, wohingegen Weibchen vom „Maurer Wald“ im Mittel länger waren als jene von „Neuwaldegg“ und „Moosgraben“. Weibchen von „Neuwaldegg“ und „Moosgraben“ hatten eine signifikant höhere Kondition als jene vom „Maurer Wald“. Körpermasse und Kondition bei der Geburt zeigten keinen signifikanten Unterschied zwischen den Standorten. Neugeborenen Larven vom „Maurer Wald“ waren im Mittel länger als jene vom „Moosgraben“. Die mittlere Geburtsmasse der Larven korrelierte nur schwach mit der Körpermasse ihrer Mutter ($R^2 = 0.12$). Die Körperlänge der Weibchen hatte wenig Einfluss auf die Körperlänge der Larven.

Wir gehen davon aus, dass die Unterschiede in der Größe und Kondition zwischen den Standorten Folgen von Umweltbedingungen in Bezug auf Nahrungsverfügbarkeit und Temperatur sind und keine Adaptation.

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