

# Age and body size of *Salamandrella keyserlingii* (Caudata: Hynobiidae): a difference in altitudes, latitudes, and temperatures

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**Abstract** The debate surrounding Bergmann's rule, in which the body size of animals is predicted to be larger in cooler environments, is still open concerning ectotherms. Our goal was to test this rule in the broadest ranging amphibian species *Salamandrella keyserlingii*. We determined age and body size in a cooler region (Darhadyn, Mongolia: mean yearly air temperature =  $-8.31^{\circ}\text{C}$ ) using skeletochronology, and compared their differences in altitude, latitude, and temperature with those of a warmer area (Kushiro, Japan:  $7.98^{\circ}\text{C}$ ). In Darhadyn, both sexes reached sexual maturity at 5–6 years of age (growth coefficient: male = 0.585, female = 0.266), 2–3 years later than those in Kushiro (male = 1.341, female = 1.129). Mean body size was smaller in Darhadyn (53.08 mm) than in Kushiro (57.63 mm) for males despite their constant metamorphic size around 30 mm. We also analyzed data available from published studies for 27 populations within the geographic range of this species from  $43$  to  $69^{\circ}\text{N}$  across a 2,900-km long latitudinal gradient. The analysis indicated an intraspecific tendency to decrease body size with increased latitude from  $43$  to  $57^{\circ}\text{N}$ , to increase size from  $57$  to  $69^{\circ}\text{N}$ , and to decrease body size with decreased temperature from  $8$  to  $-7^{\circ}\text{C}$  and increase size from  $-7$  to  $-15^{\circ}\text{C}$ . This pattern does not follow the intraspecific extension of Bergmann's rule and may follow the converse of Terentjev's optimum rule—a rule formulated to be an inverted-U shaped curve between increased latitude (or decreased temperature) and increased body size.

**Keywords** Age structure · Bergmann's rule · Ecogeography · Growth trajectory · Skeletochronology · Terentjev's optimum rule

## Introduction

Relationships between body size morphology and several key factors of climate, environment, and evolution potentially influence geographic patterns of body size variation of organisms at ecological and evolutionary time scales (Mayr 1965). Not only endotherms but also many ectotherms mature at larger size at lower rearing temperatures (Walters and Hassall 2006; Thomas 2009; Stillwell 2010). This has been termed the temperature–size rule, a pattern consistent with “Bergmann's (1847) rule” (hereafter “Bergmann's rule”). Bergmann's rule—a well-known ecogeographic pattern that predicts larger body size with increasing latitude or decreasing temperature—has received some degree of support in most tetrapod groups [e.g., mammals, birds, chelonian reptiles (turtles): Ashton 2004] and even in fish species (Thomas 2009). However, squamate reptiles (lizards and snakes) tend to decrease body size with high latitudes (Ashton and Feldman 2003). Geographic variation in body size is complex in North American squamates, whereas patterns in Europe are characterized by a clear latitudinal decrease in body size (Olalla-Tárraga et al. 2006). Amphibians also seem to follow Bergmann's rule (Ashton 2002), but Olalla-Tárraga and Rodríguez (2007) conducted an assemblage-based analysis (for details see Olalla-Tárraga et al. 2010) and revealed that, although anurans reach larger body size at colder climates in both Europe and North America, urodeles tend to be smaller in cooler areas. Adams and Church (2008) analyzed a great number of museum specimens of amphibians and concluded that, at the intraspecific level, Bergmann's rule does not apply to

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amphibians: 3 of 40 species of the genus *Plethodon* follow the rule, 7 show its converse, and 30 do not show any geographic trend. The temperature–size rule, which predicts a pattern consistent with Bergmann’s rule but relies on a different mechanism, will help elucidate the application of Bergmann’s rule to ectotherms (Stillwell 2010).

Bergmann’s rule, albeit originally defined as an interspecific pattern, was reformulated at the intraspecific level by Rensch in 1938 (Blackburn et al. 1999). At the intraspecific level, geographic variation in amphibian life-history traits, such as age and body size at sexual maturity or maximum longevity, occurs across altitudinal, latitudinal, and environmental gradients (Morrison and Hero 2003; Schauble 2004; Laugen et al. 2005). An altitudinal difference in age and body size is documented in many European species (e.g., Miaud et al. 2000; Krizmanic et al. 2005; Amat et al. 2010). For example, compared to maximum longevity of populations exposed to altitudinal gradients, *Ichthyosaura* (formerly *Triturus* or *Mesotriton*) *alpestris* reaches up to 20 years of age in highlands but is always less than 10 years old in lowlands (Miaud et al. 2000). Krizmanic et al. (2005) found that body size increases with high altitudes for *Ichthyosaura alpestris* and *Lissotriton* (formerly *Triturus*) *vulgaris* but not for *Triturus carnifex*. However, data on latitudinal differences in life-history traits are limited to a few species with a wide distribution range (e.g., *Bufo bufo*: Hemelaar 1988; Cvetkovic et al. 2009; *Rana temporaria*: Palo et al. 2003; Laugen et al. 2005; *Limnodynastes peronii* and *Limnodynastes tasmaniensis*: Schauble 2004; *Triturus cristatus*: Litvinchuk and Borkin 2009).

*Salamandrella keyserlingii* Dybowski, 1870 has the broadest range of any amphibian species worldwide (~12 million km<sup>2</sup> from 43 to 72°N), extending from eastern Europe through subarctic Siberia to Kamchatka Peninsula and Kurile Islands, including the northern portions of Kazakhstan, Mongolia, China, North Korea, and Japan (Borkin et al. 1984; Kuzmin 1994; Borkin 1999). This species is usually found in lowlands, but in the mountain range near Khovsgol Lake, Mongolia, an individual with the largest snout–vent length (76 mm) was found at the highest altitude (2,250 m elevation: Litvinov and Skuratov 1986). This observation has long supported the idea that *S. keyserlingii* follows Bergmann’s rule at the intraspecific level across altitudinal gradients. However, the recent collection of the largest female (80 mm) in Ekaterinburg (= Sverdlovsk in the former Soviet Union: 280 m elevation) challenges this idea (Vershinin 2007; V. L. Vershinin, unpublished). Because of its wide distribution, detecting age and body size among populations from different parts of the species’ range could contribute to a better understanding of altitudinal, latitudinal, and temperature-associated differences in life-history traits within ectothermic species.

In contrast to our knowledge of Bergmann’s rule, Allen’s (1877) rule (i.e., intraspecific tendency to shorten protruding

portions of the body such as ears, limbs, and tail with high latitudes or low temperatures) is relatively unknown in ectotherms (Ray 1960). Furthermore, the optimum rule, originally formulated by Terentjev (1946, 1947, 1951, 1966), does not seem to be known to the West, most likely because it is written in Russian (hereafter called “Terentjev’s optimum rule”). He agreed with Bergmann’s rule based on statistical analysis of intra- and inter-specific variation in body size of various vertebrate species such as mammals, birds, snakes, and anurans. However, he predicted that regression of body size on ambient temperature was not linear and instead followed an inverted-U shaped curve: decreases in the initial ambient temperatures corresponded to increased body size to some intermediate maximum, after which decreases in the next ambient temperatures corresponded to decreased body size. This pattern was predicted for both endotherms and ectotherms. Terentjev (1946, 1947, 1951, 1966) also cautioned against the use of incomplete geographic datasets (i.e., data deficiency). That is, increased body size with decreased temperatures in one case (Bergmann’s rule) and decreased body size with decreased temperatures in another case (converse of Bergmann’s rule) might be each of two different (i.e., increased and decreased) parts of the same nonlinear model, while a suggested mechanism of Terentjev’s optimum rule is still unknown.

In the context of the temperature–size rule with intraspecific versions of Bergmann’s rule and Terentjev’s optimum rule, our specific research questions were as follows: (1) Is body size at metamorphosis or after sexual maturity larger in a “northern, high altitudinal population” (NH: cooler area) than in a “southern, low altitudinal population” (SL: warmer area)? (2) Is age at sexual maturity older for males and females in NH than in SL? (3) Is maximum longevity greater in NH than in SL? (4) In which location is the growth coefficient smaller, in NH or in SL? (5) How applicable is the inverted-U shaped curve of Terentjev’s optimum rule to latitude/temperature–body size interaction? Regarding Allen’s (1877) rule, is tail length smaller in NH than in SL? To address these questions and to establish whether patterns of body size variation can be explained by a difference in age structure of a population, we generated data on “lines of arrested growth” (LAG) for age estimation by the use of skeletochronology, a method that can depict a growth trajectory of organisms without using nonindependent recapture data (for details see Hasumi 2010), in *S. keyserlingii*. We then compared age structure and body size morphology between a relatively northern, high-altitude (cool) population (Darhadyn, Mongolia: this study) and a southernmost, low-altitude (warm) population (Kushiro, Japan: Hasumi 2010). In addition, we used some data on age and body size at Shaamar, Mongolia (Hasumi et al. 2009). We then assessed relationships between latitude/temperature and maximum body size/longevity, using our data and other literature references within the geographic range

of *S. keyserlingii* from 43 to 69°N across a 2,900-km long latitudinal gradient (Fig. 1).

## Materials and methods

### Study area

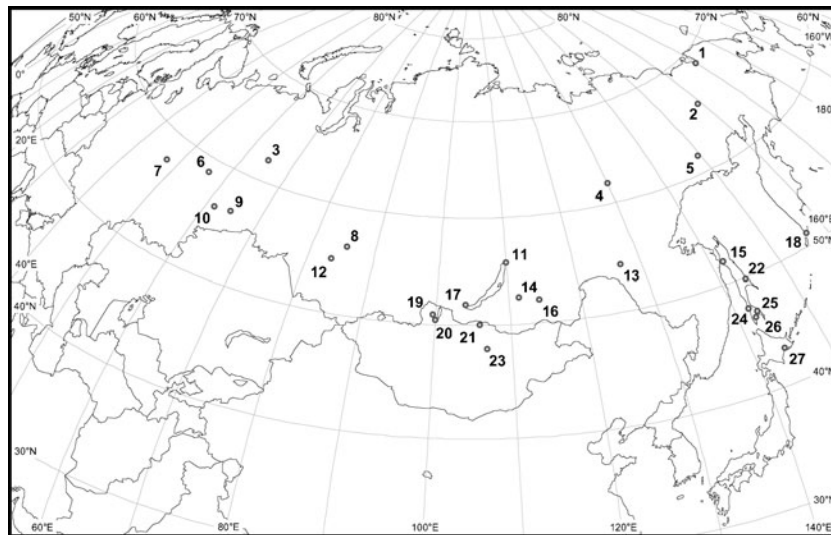
We conducted this study at a 20-ha forested zone comprising a single conifer species (*Larix sibirica*), several off-channel oxbow lakes, ephemeral and permanent pools, sedge meadows, and discontinuous grassland within a wetland complex in a floodplain (50°58'N, 99°25'E; 1,560 m elevation). The floodplain was developed along the Shish-khid River (40–60 m wide), winding through the southern part of Darhadyn Wetland. This wetland was widespread in Tsagaan Nuur, the western side of the Khovsgol Lake, Khovsgol Province, Mongolia (130 × 30 km area; 50°40'–51°40'N, 99°15'–99°45'E; 1,540–1,580 m elevation; sunset occurred at 21:30–23:00 in July–August: for a satellite picture see Hasumi et al. 2007). No broad-leaved trees were found within the study area. Those lakes and pools were breeding sites of *S. keyserlingii* (estimated breeding

season=late May or early June). Melting of the frozen soil around early June led to poor road conditions and hindered access to the study area, i.e., at Darhadyn, only a summer investigation was possible. Such locations generally exist in northern regions of the species' range (Borkin et al. 1984).

### Monitoring techniques

Salamanders of *S. keyserlingii* forage above ground at night and hide in cool, moist refugia during daytime (Grigoriev and Erdakov 1981; Hasumi and Kanda 2007). Available refugia were only downed logs or coarse woody debris, which were derived from naturally fallen trees. We conducted daily surveys from 19 to 23 July 2004 and from 8 to 17 August 2005. We turned over logs and thus searched for salamanders hidden under 40 logs selected previously. Immediately after finding an individual, we kept it temporarily in a cooler box with moist sphagnum moss to prevent desiccation.

We weighed each individual (body mass: BM) to within 0.05 g using a beam balance. We then measured broadest head width (HW), maximum tail height (TH), snout–anterior vent length (SAVL: distance from the tip of the snout to the anterior angle of the vent), snout–posterior vent length



**Fig. 1** Map of Eurasia, including 27 populations of *Salamandrella keyserlingii*, for which data on body size were available from our study and other literature references within its geographic range from 43 to 69°N across a 2,900-km long latitudinal gradient (population numbers were arranged in descending order of latitudes): 1 Chaun Lowland, Chukotka District (Russia); 2 Omolon River, Chukotka District (Russia); 3 Malaya Sos'va Nature Reserve, Khanty-Mansi Okrug (Russia); 4 Central Yakutiya (Russia); 5 Aborigen Biological Station, the left shore of Sibit-Tyellakh River, Kolyma River Valley, Ten'ka District, Magadan Province (Russia); 6 Verkhnyaya Kvazhva Biological Station, the right shore of Kama River, Dobryanka District, Perm Province (Russia); 7 Pizhma Village, Nizhniy Novgorod Province (Russia); 8 Tomsk City, Tomsk Province (Russia); 9 Talitsa Town, Sverdlovsk Province, West Siberian Lowland (Russia); 10 Ekaterinburg City, Sverdlovsk Province, Ural Mountains (Russia); 11 Nizhneangarsk

Settlement, northern Buryatia (Russia); 12 Novosibirsk City, Novosibirsk Province (Russia); 13 Zeya Nature Reserve, Amur Province (Russia); 14 Indola River, Buryatia (Russia); 15 Pogibi Village, Sakhalin (Russia); 16 Chita Province (Russia); 17 Kultuk Village, western Buryatia (Russia); 18 Lopatka Peninsula, southern Kamchatka (Russia); 19 Darhadyn, Khovsgol Province (Mongolia); 20 South slope of Khordil Saridag Mountains near Khovsgol Lake (Mongolia); 21 Shaamar, Selenge Province (Mongolia); 22 Poronai River, 53 km from the mouth, Sakhalin (Russia); 23 Bayanzurkh, the vicinity of Ulaanbaatar (Mongolia); 24 Slepikovsky Peninsula, Kostromskoe Village, Kholmsk District, Sakhalin (Russia); 25 Ozerki Village and Yuzhno-Sakhalinsk Town, Sakhalin (Russia); 26 Aniva Settlement and Kura River, Kril'on Peninsula, Aniva District, Sakhalin (Russia); and 27 Kushiro, Hokkaido Prefecture (Japan)

(SPVL: from the tip of the snout to the posterior angle of the vent), and tail length (TL: from the posterior angle of the vent to the tip of the tail) to within 0.01 mm using digital calipers by a modification of Wise and Buchanan's (1992) method without using anesthesia. We recorded age class, sex, and visual characteristics such as throat coloration and dorsal color pattern of each individual according to Hasumi (2001). These data were used to categorize all individuals into five classes: adult males, adult females, unsexed individuals, juveniles (over one year old), and metamorphs defined as individuals that completed metamorphosis within the last month (less than one year old). Adult males were identified as those with a pale-yellow throat, a "secondary sexual characteristic" (SSC) that appears late in the breeding season and does not usually appear in summer (Hasumi 2001). Adult females were identified as those with a beige ovisac (i.e., homologous uterus) visible through the skin of the ventral region of the torso near the hindlimbs, despite earlier reports that ovisacs are visible only in fall–spring (Hasumi 1996). The remnant of SSCs in both sexes indicated that at Darhadyn, summer came shortly after the cessation of the breeding season for *S. keyserlingii*. We defined unsexed individuals as those without SSCs but with larger body sizes than the smallest adult female. We chose this female as a threshold of the smallest unsexed individual because "sexual size dimorphism" (SSD) was evident in all females that were larger in size. Because of the difficulty in distinguishing metamorphs from juveniles by body size, we used skeletochronological results for the distinction.

To perform skeletochronology, we conducted a mark–recapture study. We individually marked large- and medium-sized salamanders ( $\geq 40$  mm SPVL) with a "passive integrated transponder" (PIT) tag ( $13 \times 2$  mm microchip, standardized by ISO: Datamars, Bedano, Switzerland) by injecting it intraperitoneally and marked small-sized salamanders including metamorphs ( $< 40$  mm SPVL) by using up to one toe clip per appendage (i.e., nonadditive toe clips). When using a PIT tag, we clipped the third toe from the left hindlimb of each individual or other appendages if the third toe was abnormal due to toe regeneration. We released marked salamanders at the site of capture under the log and attempted to reconstruct the log. We detected marked salamanders by reading an intraperitoneal PIT tag with a tag-reader or by reading a unique combination of the toe clips.

### Skeletochronology

We fixed the clipped toes in 10 % neutral buffered formalin in situ and conducted all skeletochronological procedures according to Hasumi and Watanabe (2007). We exploited a normal toe to prevent underestimation of the number of LAGs caused by toe regeneration. We counted the number

of LAGs (periosteal bones only) and estimated a practical age of each individual as

$$a + (b - c)/365,$$

where "a" was the number of LAGs, "b" the Julian date of capture, and "c" the Julian date of estimated completion of breeding (10 June=161).

Gathering data on altitudes, latitudes, longitudes, and temperatures

Altitudinal, latitudinal, and longitudinal data on 27 populations were usually omitted from the literature, many being attributed to military strategy in the Soviet time, with several recent exceptions (e.g., Hasumi et al. 2009; Hasumi 2010; this study). When these data were absent, we obtained altitude, latitude, and/or longitude from personal communications or estimated latitude and longitude to the degree level from the Times Comprehensive Atlas of the World (Anonymous 2007) by referring to a locality name described in each population. Since many formulations of Bergmann's rule explicitly stated that it is temperature rather than latitude per se that matters (Hawkins and Diniz-Filho 2004), we obtained available data on mean daily air temperatures from 1986 to 2004 for 19 populations in eastern Siberia ( $30\text{--}72^\circ\text{N}$ ,  $90\text{--}180^\circ\text{E}$ ;  $0.5 \times 0.5^\circ$  area) from the "Data Integration and Analysis System" (DIAS), "Japan Agency for Marine-earth Science and Technology" (JAMSTEC), on the basis of latitude and longitude of each population, except for Populations 3, 6–10, 12, and 23, which were out of this coverage. We used data from the nearest  $0.5 \times 0.5^\circ$  area to the longitudinal direction at most two degrees for Populations 19–21 because of lack of available data. We also obtained mean yearly air temperatures from published data based on long-term (over 100 years) observation series from the nearest Meteorological Stations for Populations 6 (Perm City: 171 m elevation), 7 (Vetluga: 133 m elevation), 8 (Tomsk City: 141 m elevation), 10 (Ekaterinburg City: 280 m elevation), and 12 (Ogurtsovo: 131 m elevation). We calculated mean annual air temperature from published monthly data from 1961 to 1990 at the nearest Meteorological Station for Population 23 (Ulaanbaatar: 1,306 m elevation). We could not obtain data on Populations 3 and 9.

We compared a difference between 19 years in 19 populations with a one-way analysis of variance (ANOVA) by the use of mean daily air temperatures as a within-group difference and then calculated each mean yearly air temperature. In the 19 populations examined, no difference in mean air temperatures was detected between the 19 years ( $F_{18,6921}=0.547\text{--}1.230$ ,  $P=0.2260\text{--}0.9364$ ; Appendix 1). Based on this homogeneity, mean yearly air temperature was used for these 19 populations. However, temperature data were heterogeneous for the 25 populations, consisting



of the 19 populations and 6 additional populations where only mean temperature was given. Because of this heterogeneity, we then considered using a global climatic dataset (Hijmans et al. 2005). However, our roughly estimated latitude and longitude included “fuzzy numbers” (i.e., a quantity whose value is imprecise rather than exact) in many cases, and therefore we did not use this dataset.

### Statistical analysis

Among 300 capture events, to ensure independence of data, we included only data on first capture for analysis ( $n=175$ ). SPVL ranged from 21.36 to 73.39 mm and was partitioned into 53 frequency categories of one mm each. We used a chi-square test to compare size-frequency data between groups to determine if they differed in population structure (i.e., the number of distinct groups) and to compare male to female age structure (in many skeletochronology papers, age at sexual maturity/first reproduction is expressed by minimum age of each sex). If a typical chi-square distribution was detected in age structure for either sex, its modal year would reflect age at sexual maturity in most individuals. We tested a normality of size-frequency SPVL distribution for sex/age classes with D’Agostino–Pearson normality test (D’Agostino et al. 1990). We calculated the index of SSD (Lovich and Gibbons 1992) as

$$a/b - 1,$$

where “ $a$ ” was the mean SPVL of females and “ $b$ ” the mean SPVL of males. To detect SSD, we compared male to female SPVL using a one-way ANOVA. We compared mean SPVL or mean TL for males, females, and/or metamorphs between Darhadyn (this study) and Kushiro (Hasumi 2010) with Student’s  $t$ -test for equal variances or Aspin–Welch test when exhibiting unequal variances. We then compared TL relative to SPVL for each sex between Darhadyn and Kushiro with analysis of covariance (ANCOVA) using SPVL as the covariate. We used lengths of only unelongated tails during the terrestrial-nonbreeding phase for Kushiro (Hasumi 2010). These comparisons were made by the use of the senior author’s raw data.

We calculated a sigmoid growth equation between age ( $x$ -axis: years) and SPVL ( $y$ -axis: mm) with a quasi-Newton method (Davidon–Fletcher–Powell algorithm; Zeleznik 1968), an algorithm without any constraints (Tarling and Cuzin-Roudy 2003). The starting point of the growth curve was the time at metamorphosis and growth during the aquatic larval stage was not considered (Hemelaar 1988; Arntzen 2000). The growth coefficient  $k$ —the rate at which maximum size is approached (asymptotic maximum size:  $SPVL_{\max}$ )—defines the shape of the curve (Charnov 1993). We calculated the parameters  $SPVL_{\max}$  and  $k$  from the definitive growth curve. We calculated 95 % support-plane “confidence interval” (CI)

for  $SPVL_{\max}$  and  $k$  and considered a difference between sexes or populations to be significant when these CIs did not overlap (Dunham 1978). We fitted a modified Bertalanffy’s (1938) equation according to Hemelaar (1988) where age at metamorphosis was added to growth parameters (Arntzen 2000; Hasumi 2010; hereafter called “Bertalanffy–Hemelaar”).

We used simple linear regression equations to test for a relationship between age ( $x$ -axis: years) and SPVL ( $y$ -axis: mm), between “maximum total length” [M-TOL ( $x$ -axis: mm)] and “maximum snout–vent length” [M-SVL ( $y$ -axis: mm)], between latitude ( $x$ -axis: °N) and temperature ( $y$ -axis: °C), and between latitude ( $x$ -axis: °N)/temperature in descending order ( $x$ -axis: °C) and maximum body size ( $y$ -axis: mm)/longevity ( $y$ -axis: years). Unlike long-term mark–recapture studies, in skeletochronological studies maximum longevity is used for longevity at a population level, and it is impossible to determine mean longevity or lifespan (multiple presence of the same maximum longevity does not indicate mean longevity). To optimize data, we present an algorithm that robustly computes a rational function approximation between latitude ( $x$ -axis: °N) and maximum body size ( $y$ -axis: mm) or a second order polynomial regression between temperature in descending order ( $x$ -axis: °C) and maximum body size ( $y$ -axis: mm) using a quasi-Newton method. This approximation or regression gives a closer fit over the entire range than when using linear regression with the same regression coefficient (King and Queen 1979), i.e., a rational function approximation or a second order polynomial regression is meaningful if its regression coefficient is higher than that of a given linear regression. We then used multiple regression equations to explore a relationship between maximum body size and two explanatory variables (altitude and latitude). We analyzed a difference in regression slopes between sexes with ANCOVA. All significance levels were tested at  $\alpha=0.05$  (two-tailed).

### Methodological considerations

There were seven difficulties when testing Bergmann’s rule with data on body size vs latitude/temperature from literature references on *S. keyserlingii*. First, accuracy of data on latitudes or temperatures was not the same in each population due to differences in data-collection (see “[Gathering data on altitudes, latitudes, longitudes, and temperatures](#)”). Second, only M-SVL and/or M-TOL were available for body size although we really wanted to use mean SVL for analysis. In Russian literature references, which account for most of the references related to body size of *S. keyserlingii*, mean body size (mean SVL or mean TOL) is not given. However, the use of maximum size may fit the assumptions of patterns of body size variation (Stamps and Andrews 1992). Third, males and females often were not distinguished from each other. TL is greater in terrestrial-phase males than in terrestrial-phase females and also in aquatic-phase males vs terrestrial-phase

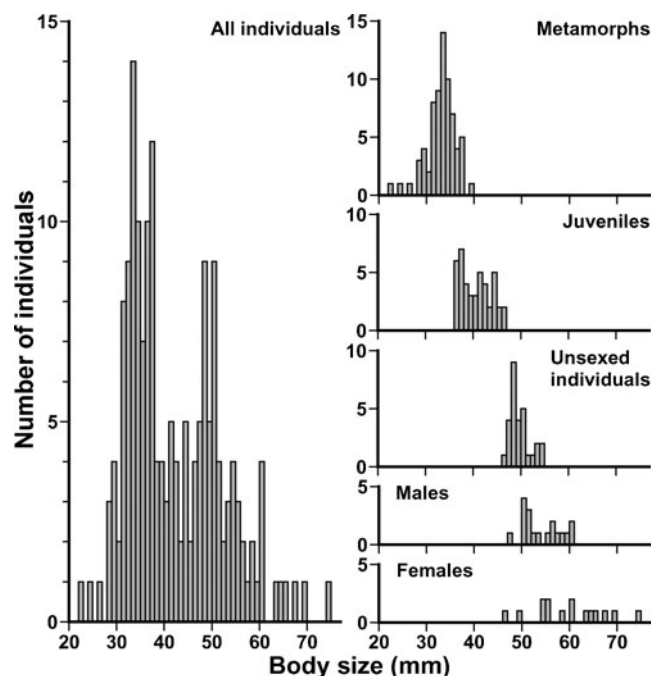
males (Hasumi 2010). Fourth, a few regions had small sample sizes, and when a large number of animals were examined the number included juveniles and/or metamorphs in many cases. Fifth, M-TOL might involve data on variable TL, including regenerated tails (Hasumi and Iwasawa 1987a), but most individuals examined did not seem to include regenerated tails. Sixth, it was unclear whether data expressed by M-SVL corresponded to maximum SAVL or maximum SPVL. It was also unclear whether SAVL or SPVL was used for SVL not only in *S. keyserlingii* but also in other salamanders of many published studies (Hasumi and Iwasawa 1987b). To overcome these difficulties, we tried to fit “hierarchical generalized linear models” (HGLM) for the analysis of data including fuzzy numbers, but we could not obtain a high significance from the preliminary analysis of these data with simple linear regression models (see “Latitude/temperature–body size interaction”). Hence, we did not fit HGLM and instead stated only tendency between parameters within a species.

Seventh, a sibling species (*Salamandrella schrenckii*) was recognized recently in southern continental Russian Far East (Berman et al. 2005a, b; Matsui et al. 2008). Its range covers southern regions of the Amur River (i.e., Primorskiy Kray and the southern part of Khabarovskiy Kray), but both species seem to occur in northeastern China (Berman et al. 2009). Therefore, we used only data associated with *S. keyserlingii* by excluding data from Primorskiy Kray (Bassarukin and Borkin 1984), Khabarovskiy Kray (Tagirova 1979), and Manchuria, China (Kostin 1934, 1942; Pavlov 1934), which should be allocated to sibling *S. schrenckii*. Accordingly, we provided the reasons why the nature of the fuzzy numbers was indeed unbiased in each of the seven cases, while some of those difficulties may be common to other taxa (i.e., unexpected use of fuzzy numbers would occur in other taxa).

## Results

### Body size distribution

Population structure analysis revealed two distinct groups in the overall histogram with sex/age classes pooled (Fig. 2): metamorphs ( $n=70$ ) and other individuals ( $n=105$ ) comprising juveniles ( $n=43$ ), unsexed individuals ( $n=29$ ), adult males ( $n=18$ ), and adult females ( $n=15$ ). A large number of unsexed individuals were due to the absence of identification of either sex during summer. Metamorphs were separated in their SPVL distribution from other individuals because of small body size ( $\chi^2=91.00$ ,  $df=52$ ,  $P=0.0007$ ). Size-frequency SPVL distribution showed skewness for all individuals ( $n=175$ ,  $K^2=11.972$ ,  $P=0.0025$ ) but did not deviate from normality for metamorphs ( $n=70$ ,  $K^2=5.199$ ,  $P=0.0743$ ), juveniles ( $n=43$ ,  $K^2=2.995$ ,  $P=0.2237$ ), unsexed individuals ( $n=29$ ,  $K^2=4.237$ ,  $P=0.1202$ ), juveniles plus unsexed individuals ( $n=72$ ,



**Fig. 2** Frequency distribution of body size for each sex or age class. Snout–posterior vent length (SPVL) was provided for body size of 175 first captures to ensure independence of data: 70 metamorphs (less than one year old), 43 juveniles (over one year old), 29 unsexed individuals, 18 adult males, and 15 adult females. Population structure analysis revealed two distinct groups with a first large peak by numerous metamorphs due to postmetamorphic emigration/dispersal resulted from early metamorphosis

$K^2=3.257$ ,  $P=0.1962$ ), males ( $n=18$ ,  $K^2=1.765$ ,  $P=0.4138$ ), and females ( $n=15$ ,  $K^2=0.332$ ,  $P=0.8471$ ). A normal distribution that was verified in the juveniles plus unsexed individuals suggested that they could be categorized as one size-class (i.e., they were not heterogeneous) because juveniles might include small-sized subadults. This led to a continuum of a growth trajectory for each sex (see Hasumi 2010). There were many small-sized juveniles relative to large-sized metamorphs, indicating low growth of juveniles after metamorphosis.

Mean SPVL was 53.08 mm for males and 59.05 mm for females (Appendix 2) with female-larger SSD (SSD index = 0.112,  $F_{1,31}=8.318$ ,  $P=0.0071$ ). Mean SPVL was 32.15 mm for metamorphs with postmetamorphic emigration/dispersal from mid-July. Mean TL was 32.62 mm for males and 33.54 mm for females. In comparison, at Kushiro (data from Hasumi 2010), mean SPVL was 57.63 mm for males (SD = 4.63, range = 46.21–71.52,  $n=276$ ) and 61.70 mm for females (SD = 4.56, range = 52.00–72.33,  $n=130$ ). Mean SPVL was 31.18 mm for metamorphs (SD = 3.05, range = 23.11–39.77,  $n=63$ ) with postmetamorphic emigration/dispersal from early September. When using data on terrestrial-phase individuals, mean TL was 46.89 mm for males (SD = 4.64, range = 32.04–58.32,  $n=247$ ) and 43.21 mm for females (SD = 3.92, range = 34.50–52.08,  $n=129$ ). Mean SPVL was smaller in Darhadyn than in Kushiro for males ( $t=4.070$ ,  $df=292$ ,  $P<0.0001$ ) but

did not differ between two populations for females ( $t=1.327$ ,  $df=15$ ,  $P=0.0242$ ) and metamorphs ( $t=1.861$ ,  $df=131$ ,  $P=0.0649$ ). Mean TL during the terrestrial phase was smaller in Darhadyn than in Kushiro for both males ( $t=12.354$ ,  $df=263$ ,  $P<0.0001$ ) and females ( $t=8.780$ ,  $df=142$ ,  $P<0.0001$ ). TL relative to SPVL was smaller in Darhadyn than in Kushiro for males (TL/SPVL ratio=0.614 vs 0.821;  $SS=135.835$ ,  $F_{1,261}=9.816$ ,  $P=0.0019$ ) but did not differ between two populations for females (TL/SPVL ratio=0.568 vs 0.701;  $SS=21.294$ ,  $F_{1,140}=1.809$ ,  $P=0.1808$ ). At Shaamar (data from Hasumi et al. 2009), mean SPVL was 62.28 mm for males (SD=5.09, range=51.80–68.17,  $n=9$ ), 61.53 mm for females (SD=5.92, range=54.35–66.82,  $n=4$ ), and 29.43 mm for metamorphs (range=28.30–30.56,  $n=2$ ).

### Age estimation

Mean age was 6.39 years for males (SD=1.17, range=5.11–9.16,  $n=18$ ) and 7.60 years for females (SD=2.99, range=5.11–11.17,  $n=15$ ). Males were younger on average than females ( $t=2.078$ ,  $df=22$ ,  $P=0.0496$ ). A typical distribution of chi-square values in age structure revealed that females reached sexual maturity at 5–6 years old (modal year=6;  $\chi^2=56.248$ ,  $df=14$ ,  $P<0.0001$ ), but males did not show a significant chi-square distribution (modal year=5;  $\chi^2=23.216$ ,  $df=17$ ,  $P=0.2847$ ). A female with maximum SPVL (73.39 mm) was estimated to be 11.17 years old, the eldest of all individuals. Extraordinarily rapid growth of aquatic larvae, an evolutionarily interesting phenomenon defined as “early metamorphosis” (Hasumi et al. 2011), occurred toward metamorphosis [“estimated premetamorphic period” (EPP)<1.5 months: M. Hasumi, T. Hongorzul, and M. Nakagawa,

unpublished]. At Kushiro (Hasumi 2010), males and females reached sexual maturity at 2–3 years old (modal year=3) and 3–4 years old (modal year=4), respectively, and minimum age at sexual maturity–maximum longevity were 1.92–9.99 years for males and 2.94–7.92 years for females (Table 1). When including 115 recapture data, maximum longevity was 10.37 years for males and 8.09 years for females (Hasumi 2010), i.e., males and females matured 2–3 years later in Darhadyn than in Kushiro, and maximum longevity was shorter in Darhadyn (9.16 years) than in Kushiro (10.37 years) for males and vice versa was longer in Darhadyn (11.17 years) than in Kushiro (8.02 years) for females. At Shaamar (Hasumi et al. 2009), minimum age at sexual maturity–maximum longevity were 5.14–9.13 years for males ( $n=9$ ) and 7.13–9.14 years for females ( $n=4$ ).

Maximum longevity of either sex ( $y$ -axis) decreased with increased latitude ( $x$ -axis) in eight populations with available age structure ( $n=8$ ,  $R^2=0.676$ ,  $P=0.0122$ ,  $y$  intercept=21.268, slope=−0.226). There was no significant relationship between temperature in descending order ( $x$ -axis) and maximum longevity of either sex ( $y$ -axis) in six populations with available age structure ( $n=6$ ,  $R^2=0.286$ ,  $P=0.2739$ ,  $y$  intercept=9.913, slope=−0.140: Table 1; Appendix 1).

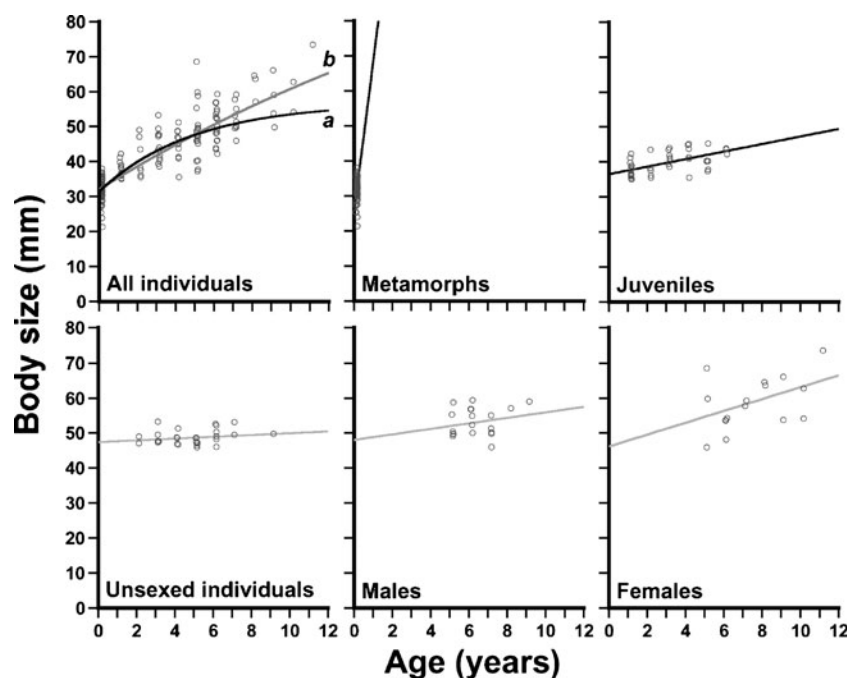
A sigmoid growth equation was fitted between age and SPVL in each sex (Fig. 3).  $SPVL_{max}$  was 56.70 mm ( $\pm 95\%$  CI=21.95) for males and 125.88 mm for females, and  $k$  was 0.585 ( $\pm 0.227$ ) for males and 0.266 for females. For 70 metamorphs, mean age and SPVL were 0.16 years and 32.15 mm, respectively. A Bertalanffy–Hemelaar equation between age ( $x$ -axis: years) and SPVL ( $y$ -axis: mm) was  $y=56.70 - (56.70 - 32.15) \exp(-0.585 \times (x - 0.16))$  for males and  $y=125.88 - (125.88 - 32.15) \exp(-0.266 \times (x - 0.16))$

**Table 1** Geographic variation in body size (snout–vent length: SVL) and age structure (minimum age at sexual maturity/first reproduction, maximum longevity, and growth coefficient) of adult males (M), adult females (F), and metamorphs (newly metamorphosed juveniles: N) among eight populations of *S. keyserlingii* (see Fig. 1 and Table 2 for

geographic positioning data). Sample size was taken from Ishchenko and Berman (1995) for Populations 3 and 13. Total sample size of 110 was given for both sexes in Population 5. Maximum longevity was in brackets when including 115 recapture data (Hasumi 2010)

Population	Range or mean SVL (mm) followed by $n$ in parentheses <sup>a</sup>			Age at maturity (years)		Longevity (years)		Growth coefficient ( $k$ )		Reference
	M	F	N	M	F	M	F	M	F	
(3) Malaya Sos'va	36.3–60.3 (14)	31.5–63.8 (39)	—	—	—	7	5	—	—	Ishchenko et al. (1995)
(5) Kolyma River	40.0–57.0	44.9–58.9	—	—	—	7	4	—	—	Ishchenko et al. (1995)
(9) Talitsa	44.7–62.5	48.8–64.7	—	—	—	7	9	—	—	Ishchenko et al. (1995)
(13) Zeya	48.3–66.8 (35)	—	—	—	—	8	—	—	—	Ishchenko et al. (1995)
(19) Darhadyn	53.08 (18)	59.05 (15)	32.15 (70)	5.11	5.11	9.16	11.17	0.585	0.266	Present study
(21) Shaamar	62.28 (9)	61.53 (4)	29.43 (2)	5.14	7.13	9.13	9.14	—	—	Hasumi et al. (2009)
(24) Kostromskoe	Maximum: 60.4 (21)	— (14)	—	3	3	12	6	—	—	Ishchenko and Berman (1995)
(27) Kushiro	57.63 (276)	61.70 (130)	31.18 (63)	1.92	2.94	9.99 [10.37]	7.92 [8.02]	1.341	1.129	Hasumi (2010)

<sup>a</sup> Snout–posterior vent length (SPVL) was used for body size in Hasumi et al. (2009), Hasumi (2010), and the present study, but there was no description about whether snout–anterior vent length or SPVL was used in other studies (also see “Methodological considerations”)



**Fig. 3** Nonlinear growth equations between age (x-axis: years) and body size [SPVL (y-axis: mm)] with 175 first captures [i.e., 18 adult males (M), 15 adult females (F), 29 unsexed individuals (U), 43 juveniles (J), and 70 metamorphs (N)]: (Equation a) males' class:  $y = 654.482 \times ((\exp(0.207172 \times (x + 18.9657)) - 1) / (\exp(0.207172 \times (x + 18.9657)) + 1)) - 597.777$  ( $n=160$ ,  $R^2=0.7862$ ,  $SPVL_{\max} \pm 95\%$  CI =  $56.70 \pm 21.95$ ,  $k \pm 95\%$  CI =  $0.585 \pm 0.227$ ); (Equation b) females' class:  $y = 420.226 \times ((\exp(0.0405108 \times (x + 51.2054)) - 1) / (\exp(0.0405108 \times (x + 51.2054)) + 1)) - 294.341$  ( $n = 157$ ,  $R^2=0.7743$ ,  $SPVL_{\max} = 125.88$ ,

$k = 0.266$ ). SPVL increased linearly with increased age in N ( $R^2=0.078$ ,  $P=0.0195$ ,  $y$  intercept=25.147, slope=42.884) and J ( $R^2=0.325$ ,  $P<0.0001$ ,  $y$  intercept=36.511, slope=1.077). There was no relationship between these parameters in U ( $R^2=0.037$ ,  $P=0.3174$ ,  $y$  intercept=47.419, slope=0.253), M ( $R^2=0.051$ ,  $P=0.3657$ ,  $y$  intercept=48.064, slope=0.785), and F ( $R^2=0.200$ ,  $P=0.0950$ ,  $y$  intercept=46.170, slope=1.693). The regression slope was greater in F than in M with male-larger body size at  $y$  intercept and a marginal significance (ANCOVA:  $SS=126.908$ ,  $F_{1,30}=4.120$ ,  $P=0.0513$ )

for females. No difference in growth parameters  $SPVL_{\max}$  and  $k$  could be detected between sexes because 95 % CI for females was not calculated in each parameter due to its fluctuation. At Kushiro (Hasumi 2010),  $SPVL_{\max}$  was 65.72 mm ( $\pm 95\%$  CI=2.96) for males and 71.38 mm ( $\pm 8.00$ ) for females, and  $k$  was 1.341 ( $\pm 0.060$ ) for males and 1.129 ( $\pm 0.126$ ) for females. Among those parameters, only a difference in  $k$  for males between Darhadyn and Kushiro was highly significant. SPVL increased linearly with increased age in metamorphs and juveniles but did not do so in unsexed individuals, males, or females (Fig. 3).

#### Latitude/temperature–body size interaction

Table 2 shows altitudinal and/or latitudinal differences in M-TOL and M-SVL among known populations of *S. keyserlingii*. There was no significant relationship between M-TOL and M-SVL ( $n=15$ ,  $R^2=0.169$ ,  $P=0.1282$ ). No relationship was found between latitude and M-TOL ( $n=18$ ,  $R^2=0.043$ ,  $P=0.4116$ ) or M-SVL ( $n=24$ ,  $R^2=0.020$ ,  $P=0.5097$ ; Fig. 4). A rational function approximation between latitude and M-TOL ( $R^2=0.202>0.043$  regression coefficient for a given linear regression) revealed an intraspecific

tendency to decrease maximum body size with increased latitude from 43 to 57°N and then increase size from 57 to 69°N, unlike M-SVL without any trend ( $R^2=0.022\approx 0.020$ ). This pattern of body size variation occurred despite decreased maximum longevity with increasing latitude (see “Age estimation”). A relationship was not found between M-TOL and explanatory altitude and latitude variables ( $F_{2,5}=4.975$ ,  $R^2=0.666$ ,  $P=0.0647$ , RMSE=7.753) and between M-SVL and the two variables ( $F_{2,6}=0.299$ ,  $R^2=0.091$ ,  $P=0.7519$ , RMSE=8.316). Apart from latitude–body size interaction, large-sized salamanders with M-TOL of 130 mm or more were found in southeastern parts of the species' range (i.e., Far East); namely, southern Sakhalin (Kostromskoe and Kura River, Russia) and neighboring Hokkaido (Kushiro, Japan), except for a recent finding in the Ural region (Ekaterinburg, Russia).

In the 19 years from 1986 to 2004, mean daily air temperatures ranged from  $-49.9$  to  $24.6$  °C for Darhadyn and from  $-14.5$  to  $26.3$  °C for Kushiro (see Appendix 1). Temperature (y-axis) decreased with increased latitude (x-axis) with a high significance ( $n=25$ ,  $R^2=0.481$ ,  $P<0.0001$ ,  $y$  intercept=30.815, slope= $-0.614$ ) even if altitudinal or longitudinal influence was present. The same trend as in latitude–



**Table 2** Geographic positioning data, maximum total length (M-TOL), and/or maximum snout–vent length (M-SVL) among 27 populations of *S. keyserlingii* within its geographic range (see Fig. 1). Population numbers were arranged in descending order of latitudes. In some cases, maximum altitude was applied when having a wide

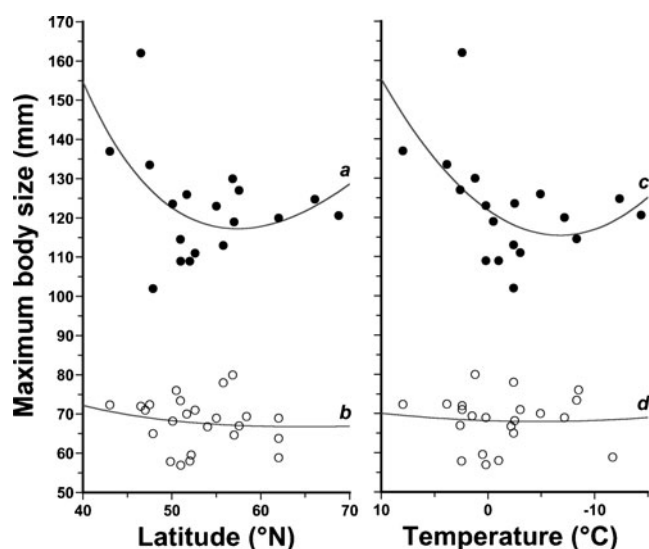
range of altitudes, and sample size was cumulative from multiple references. For analyzing latitude/temperature–body size interaction, when body size data were given for both sexes, maximum one was applied (see Fig. 4)

Population	Altitude (m)	Latitude (N)	Longitude (E)	Sex	<i>n</i>	M-TOL (mm)	M-SVL (mm)	References
(1) Chaun Lowland	3	68°46′	170°	Male Female	14 <sup>a</sup>	120.1 120.6	—	Dokuchaev et al. (1984), A. V. Andreev (unpublished)
(2) Omolon River	5	66°04′	159°	—	95	124.8	—	Dokuchaev et al. (1984), A. V. Andreev (unpublished)
(3) Malaya Sos'va	—	62°	64°	Male Female	14 39	— —	60.3 63.8	Ishchenko et al. (1995)
(4) Central Yakutiya	—	62°	130°	—	194	120	69	Larionov (1976), Borkin (1994), N. G. Ostashko (unpublished)
(5) Kolyma River	900	62°	149°	Male Female	110 <sup>a</sup>	— —	57.0 58.9	Ishchenko et al. (1995), D. I. Berman (unpublished), V. G. Ishchenko (unpublished)
(6) Verkhnyaya Kvazhva	—	58°23′	56°23′	—	12	—	69.4	Voronov et al. (1971)
(7) Pizhma	—	57°33′	47°11′	—	1	127	67	Ushakov (1978)
(8) Tomsk	—	57°	85°	—	—	119	—	Kashchenko (1896)
(9) Talitsa	130	56°59′	63°50′	Male Female	— —	— —	62.5 64.7	Ishchenko et al. (1995)
(10) Ekaterinburg	280	56°51′	60°42′	—	449	130 <sup>a</sup>	80 <sup>c</sup>	Vershinin (2007), V. L. Vershinin (unpublished)
(11) Nizhneangarsk	—	55°46′	109°32′	—	62	113	78	Shchepina et al. (2009), N. A. Shchepina (unpublished)
(12) Novosibirsk	—	55°	83°	Male Female	30 30	120.5 123	61 69	Borkin (1994), O. V. Grigoriev (unpublished)
(13) Zeya	—	54°	127°	Male	35	—	66.8	Ishchenko et al. (1995)
(14) Indola River	—	52°37′	111°27′	—	21	111	71	Shchepina et al. (2009), N. A. Shchepina (unpublished)
(15) Pogibi	—	52°10′	142°	—	6	—	59.6	Bassarukin and Borkin (1984)
(16) Chita Province	750	52°	113°40′	—	4	109 <sup>c</sup>	58 <sup>c</sup>	Shkatulova et al. (1978)
(17) Kultuk	—	51°40′	103°40′	—	5	126	70	Dybowski (1870)
(18) Lopatka Peninsula	—	51°	157°	—	46	109	57	Borkin (1994), A. M. Bassarukin (unpublished)
(19) Darhadyn	1,560	50°58′	99°25′	Male Female	18 15	102.32 114.57	59.38 73.39	Present study
(20) Khordil Saridag Mountains	2,250	50°30′	100°	—	10	—	76	Litvinov and Skuratov (1986)
(21) Shaamar	600	50°04′	106°07′	Male Female	18 4	123.61 110.36	68.17 66.82	Ledenzov (1986), Ishchenko et al. (1995), Hasumi et al. (2009), M. Hasumi (unpublished)
(22) Poronai River	—	49°50′	143°	—	22	—	57.9	Bassarukin and Borkin (1984)
(23) Bayanzurkh	1,317	47°53′	107°05′	—	45	102	65	Obst (1963), Munkhbayar (1967, 1976), L. J. Borkin (unpublished)
(24) Kostromskoe	—	47°30′	142°	—	71	133.5 <sup>c</sup>	72.4 <sup>c</sup>	Bassarukin and Borkin (1984), Ishchenko and Berman (1995)
(25) Ozerki and Yuzhno-Sakhalinsk	—	47°	143°	—	55	—	71	Shurygina (1969)
(26) Kura River	—	46°30′	142°20′	—	148	162.0 <sup>b</sup>	72.0 <sup>b</sup>	Bassarukin and Borkin (1984)
(27) Kushiro	4	43°01′	144°18′	Male Female	276 130	136.97 122.09	71.52 72.33	Hasumi (2010), M. Hasumi (unpublished)

<sup>a</sup> both sexes, <sup>b</sup> male, <sup>c</sup> female

body size interaction also occurred in temperature–body size interaction (Fig. 4). A significant relationship was not found between temperature and M-TOL ( $n=18$ ,  $R^2=0.127$ ,  $P=0.1464$ ), and neither relationship nor trend was found between temperature and M-SVL ( $n=22$ ,  $R^2=0.001$ ,  $P=$

0.8804). A polynomial regression also appeared to decrease M-TOL ( $R^2=0.304>0.127$  regression coefficient for a given linear regression) with decreased temperature from 8 to  $-7$  °C, and then increase in size from  $-7$  to  $-15$  °C. No trend was shown for M-SVL ( $R^2=0.003\approx0.001$ ).



**Fig. 4** Fittest equations (rational function approximation or second order polynomial regression) between latitude (x-axis: °N)/temperature in descending order (x-axis: °C) and maximum body size (y-axis: mm). No relationship was found between latitude and M-TOL (solid circle:  $n=18$ ,  $R^2=0.043$ ,  $P=0.4116$ ,  $y$  intercept=144.876, slope=-0.414) or M-SVL (open circle:  $n=24$ ,  $R^2=0.020$ ,  $P=0.5097$ ,  $y$  intercept=77.240, slope=-0.175). Rational function approximations indicated an intraspecific tendency to decrease M-TOL (Equation a:  $y = 4.98338 \times x - 454.274 + 16386.0/x$ ,  $R^2 = 0.202 > 0.043$  regression coefficient for a given linear regression) with increased latitude from 43 to 57°N and then increase the size from 57 to 69°N (U shaped curve), unlike M-SVL (Equation b:  $y = 0.351151 \times x + 21.1776 + 1478.83/x$ ,  $R^2 = 0.022 \approx 0.020$ ). A significant relationship was not found between temperature and M-TOL ( $n=18$ ,  $R^2=0.127$ ,  $P=0.1464$ ,  $y$  intercept=124.426, slope=-0.857), and neither relationship nor trend was found between temperature and M-SVL ( $n=22$ ,  $R^2=0.001$ ,  $P=0.8804$ ,  $y$  intercept=68.330, slope=-0.048). Polynomial regressions also appeared to decrease M-TOL (Equation c:  $y = 0.142278 \times x^2 + 1.91652 \times x + 121.877$ ,  $R^2 = 0.304 > 0.127$  regression coefficient for a given linear regression) with decreased temperature from 8 to -7 °C and then increase the size from -7 to -15 °C (U shaped curve), but they did not show any trend for M-SVL (Equation d:  $y = 0.00965508 \times x^2 + 0.0919399 \times x + 68.1711$ ,  $R^2 = 0.003 \approx 0.001$ )

## Discussion

Almost all endotherms and numerous ectotherms follow Bergmann's rule, in which body size of animals increases with high latitudes or low temperatures (Walters and Hassall 2006; Thomas 2009). Amphibians seem to follow this rule (Ashton 2002), but Olalla-Tárraga and Rodríguez (2007) and Adams and Church (2008) did not find support for it in urodeles. The broadest ranging amphibian species (*S. keyserlingii*) had an intraspecific decrease in body size with high altitudes, high latitudes, and low temperatures when compared to populations from Darhadyn (cooler area; mean yearly air temperature=-8.31 °C) and Kushiro (warmer area; 7.98 °C), although mitochondrial DNA differences might influence these populations (Malyarchuk et al. 2010). This result is consistent with the converse to Bergmann's rule at the

intraspecific level. Likewise, the analysis of published studies on *S. keyserlingii* indicated an inverted Bergmann's rule of an intraspecific tendency to decrease M-TOL with high latitudes or low temperatures when considering a simple linear regression equation. The application of this equation might support Olalla-Tárraga and Rodríguez's (2007) assemblage-based analysis of body size variation that urodeles tend to be smaller in cool areas. In *S. keyserlingii*, Borkin (1994) demonstrated that M-TOL is correlated negatively with latitude. Within Sakhalin Island, Russia (46°30'–52°10'N), adult salamanders are larger size in southern than in northern regions (Bassarukin and Borkin 1984), suggesting that this species also has an intra-island tendency to decrease body size with high latitudes. The converse to Bergmann's rule at the intraspecific level (i.e., decreased body size with increased latitude or decreased temperature) has often been found in urodeles, but also in anuran species such as *Bufo bufo* (Cvetkovic et al. 2009). These references also support our results.

On the other hand, a rational function approximation between latitude and M-TOL detected that size decreases with increasing latitude from 43 to 57°N, and then increases from 57 to 69°N. Consistently, size decreased with temperature from 8 to -7 °C and then increased from -7 to -15 °C (U shaped curves: see Fig. 4). This is just the converse of Terentjev's optimum rule and some other inverted-U shaped curves shown in anurans (Laugen et al. 2005); on the contrary, anurans generally reach large body size in low temperatures (Olalla-Tárraga and Rodríguez 2007). In addition, in our study the U shaped pattern of body size variation with increased latitude or decreased temperature occurred despite lower maximum longevity with increased latitude. All the results suggest that patterns of body size of *S. keyserlingii* vary with complexity of increase and decrease across latitudinal and temperature-associated gradients.

Geographic variation occurs in life-history traits such as age and body size (Morrison and Hero 2003). In *S. keyserlingii* studied herein, maturation was delayed with age estimation of 5–6 years for each sex (i.e., ecogeographically predicted pattern for “delayed sexual maturity”) but with smaller body size (mean SPVL: male=53.08 mm, female=59.11 mm; i.e., unpredicted pattern against “larger body size”). Compared to high larval growth, growth after metamorphosis was very low ( $k$ : male=0.585, female=0.266), which influenced the delay of age at sexual maturity of both sexes. In comparison, at Kushiro (Hasumi 2010), males and females reached sexual maturity at 2–3 and 3–4 years of age, respectively, with larger body size (mean SPVL: male=57.63 mm, female=61.70 mm). Mean metamorphic size was similar to that in Darhadyn, but growth after metamorphosis was greater ( $k$ : male=1.341, female=1.129). The case of constant metamorphic size around 30 mm (Darhadyn=32.15 mm, Kushiro=31.18 mm, Shaamar=29.43 mm) relative to variable adult-body size suggests the

existence of genetic determinants of metamorphic size between populations in the evolution of amphibian size-determinants (e.g., *Rana temporaria*: Laugen et al. 2005). Independently of the possible existence of genetic determinants, a difference in age structure of a population seems to explain patterns of body size variation within the geographic range of *S. keyserlingii*, according to Stamps et al. (1994).

Although comparable data on age structure are definitely limited to *S. keyserlingii*, maximum longevity is 12 years for males and 6 years for females with 3 years of minimum age at sexual maturity in Kostromskoe, Sakhalin, Russia (Ishchenko and Berman 1995: see Table 1). In another Shaamar population, Mongolia, 17 individuals comprising 8 juveniles and 9 adults are estimated to be 1–5 years of age with 31–55 mm SVLs (sex or age class is not indicated in each year: Ledenzov 1986); Ishchenko et al. (1995) judged all of the 17 individuals to be a male, which could be sexed by the dissection of stored specimens (V. G. Ishchenko, unpublished). It is unknown why a difference in maximum longevity occurs between Shaamar populations of Ledenzov (1986: 5 years) and Hasumi et al. (2009: 9.14 years). In the Ural Mountain Range, Sverdlovsk Province, Russia (no detailed locality is shown), 72 individuals are estimated to be 1–7 years of age with 35–59 mm SVLs (Ledenzov 1986); in another Russian population (unknown locality), maximum longevity is 8 years (Smirina 1994). Nonetheless, our age structure and body size morphology suggest rigorous and severe climate/environmental conditions for this species to survive at Darhadyn, to which the salamanders have adapted and evolved (minimum value of mean daily air temperatures from 1986 to 2004 = −49.9 °C), while their natural freezing tolerance has been documented against ambient air temperatures down to −40 °C during winter (Storey and Storey 1992). Survival of *S. keyserlingii* in extremely cold environments may well be the reason behind the nonlinear relationship between temperature and body size. That is, below a temperature threshold of around −7 °C, body size may play a secondary role in determining the occurrence of the species, whereas a size-independent physiological trait (i.e., freezing tolerance) plays the leading role.

In contrast to maximum longevity of around 10 years (e.g., *Triturus pygmaeus*: Diaz-Paniagua et al. 1996; *Hynobius leechii*: Lee and Park 2008; *Lissotriton helveticus*: Amat et al. 2010; *S. keyserlingii*: Hasumi 2010; this study), extremely high and low longevity are estimated in some populations or species (e.g., *Salamandra lanzai*: 24 years, Miaud et al. 2001; *Triturus dobrogicus*: 4–5 years, Cogalniceanu and Miaud 2002, 2003; *Hynobius tokyoensis*: 21 years, Kusano et al. 2006). These differences may depend on specific characteristics or environmental conditions (e.g., low maximum longevity is influenced by periodic floods: Cogalniceanu and Miaud 2002, 2003) and different interpretations of LAGs (Wagner et al. 2011). In such terms,

*S. keyserlingii* decreased maximum longevity with high latitudes, suggesting that this species has lower survival in cool areas than in warm areas. This is contrary to that of *Ichthyosaura alpestris*, which reaches higher maximum longevity up to 20 years of age in cooler areas (Miaud et al. 2000), and also to intraspecific extension of Bergmann's rule. However, *Lissotriton helveticus* populations do not include the predicted pattern of higher maximum longevity despite their higher altitude (2,300 m elevation: Amat et al. 2010), and this pattern supports our results. In addition, we detected smaller  $k$  (male = 0.585, female = 0.266) at cooler Darhadyn (mean yearly air temperature = −8.31 °C). These values resembled those of other species, many being European species such as *Triturus marmoratus* (0.26–0.36: Caetano and Castanet 1993), *Triturus cristatus* (0.30–0.92: Arntzen 2000), *Ichthyosaura alpestris* (0.24–0.27: Miaud et al. 2000), *Salamandra lanzai* (0.173–0.296: Miaud et al. 2001), *Lyciasalamandra* (formerly *Mertensiella*) *luschani* (0.171–0.173: Olgun et al. 2001), and *Lissotriton vulgaris* (0.703) and *Triturus dobrogicus* (0.20–0.27: Cogalniceanu and Miaud 2002, 2003). By contrast, greater  $k$  (male = 1.341, female = 1.129) was detected at warmer Kushiro (7.98 °C) due to earlier sexual maturity at a lower age and more rapid growth before sexual maturity (Hasumi 2010). Thus, our study provides a new ecogeographic factor, concerning life-history correlates of differences in body size, that a growth coefficient is smaller in a cool area than in a warm area if a species does not follow intraspecific extension of Bergmann's rule.

When considering TL in urodeles, there still remains an unresolved puzzle whether the tail is the part of the body (Bergmann 1847) or the protruding portion of the body (Allen 1877). Litvinchuk and Borkin (2009) documented an intraspecific tendency to increase TL toward the North in *Triturus cristatus* with a wide distribution range in temperate Europe. They documented the same tendency in forelimbs and hindlimbs of only females. Hasumi and Iwasawa (1987a) stated for 19 localities of *Hynobius lichenatus* distributed in northeastern Japan that TL relative to body size tends to be greater with high latitudes when comparing data on individuals having unregenerated tails. By contrast, in our study, mean TL during the terrestrial phase was smaller in cool Darhadyn than in warm Kushiro for both males and females. It is unclear whether this observation means that *S. keyserlingii* follows Allen's (1877) rule. However, when considering a difference in body shape or morphology, ectothermic vertebrates with thin bodies seem to decrease body size with high latitudes or low temperatures at both intra- and inter-specific levels (e.g., urodeles: Olalla-Tárraga and Rodríguez 2007; this study; lizards and snakes: Ashton and Feldman 2003; Olalla-Tárraga et al. 2006) unlike those with thick bodies (e.g., anurans: Laugen et al. 2005; Olalla-Tárraga and Rodríguez 2007; turtles: Ashton 2004). We thus suggest that thermal physiology of

ectotherms with thick bodies, specifically anurans and turtles, evolutionarily resembles that of endotherms.

## Conclusions

Latitudinal and temperature-associated patterns of body size variation are very complex in the broadest ranging amphibian species (*S. keyserlingii*), but may follow an intraspecific tendency to decrease maximum body size with increased latitude from 43 to 57°N, and then to increase in size from 57 to 69°N. These patterns also may follow an intraspecific tendency to decrease maximum body size with decreased temperature from 8 to −7 °C and then increase size from −7 to −15 °C (i.e., 57°N or −7 °C is the optimum part of its range or a threshold for body size). This study reaffirms the

complexity of body size gradients and the limitations inherent to simple explanations, as suggested by Terentjev's optimum rule.

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## Appendix 1

**Table 3** Mean yearly air temperature (°C) from 1986 to 2004 ( $n=19$ ) in each population. Each temperature was calculated based on the absence of a significant difference between 19 years with a one-way ANOVA by the use of mean daily air temperatures as a within-group difference. In Populations 6–8, 10, 12, and 23, only mean temperature was shown

Population	$F_{18,6921}$	$P$	Mean±SE (Range)
(1) Chaun Lowland	1.230	0.2260	−14.35±0.25 (−16.92 to −12.87)
(2) Omolon River	1.038	0.4122	−12.33±0.22 (−14.56 to −10.93)
(3) Malaya Sos'va	—	—	—
(4) Central Yakutiya	0.808	0.6928	−7.16±0.18 (−9.10 to −5.73)
(5) Kolyma River	0.727	0.7861	−11.69±0.18 (−13.77 to −10.53)
(6) Verkhnyaya Kvazhva	—	—	1.5
(7) Pizhma	—	—	2.6
(8) Tomsk	—	—	−0.5
(9) Talitsa	—	—	—
(10) Ekaterinburg	—	—	1.2
(11) Nizhneangarsk	0.623	0.8848	−2.39±0.14 (−3.96 to −1.25)
(12) Novosibirsk	—	—	0.2
(13) Zeya	0.547	0.9364	−2.16±0.13 (−3.65 to −1.29)
(14) Indola River	0.576	0.9192	−3.01±0.14 (−4.51 to −2.09)
(15) Pogibi	0.658	0.8550	0.50±0.13 (−0.82 to 1.36)
(16) Chita Province	0.548	0.9361	−0.99±0.13 (−2.39 to −0.18)
(17) Kultuk	0.708	0.8061	−4.90±0.16 (−6.45 to −3.77)
(18) Lopatka Peninsula	0.801	0.7013	0.20±0.14 (−1.21 to 1.13)
(19) Darhadyn	0.894	0.5863	−8.31±0.20 (−10.00 to −6.90)
(20) Khordil Saridag Mountains	0.927	0.5447	−8.48±0.21 (−10.14 to −7.02)
(21) Shaamar	0.645	0.8665	−2.49±0.14 (−3.89 to −1.49)
(22) Poronai River	0.633	0.8769	2.49±0.12 (1.33–3.32)
(23) Bayanzurkh	—	—	−2.4
(24) Kostromskoe	0.594	0.9067	3.85±0.11 (2.82–4.66)
(25) Ozerki and Yuzhno-Sakhalinsk	0.567	0.9250	2.43±0.11 (1.37–3.25)
(26) Kura River	0.567	0.9250	2.43±0.11 (1.37–3.25)
(27) Kushiro	0.732	0.7810	7.98±0.10 (7.21–8.74)



## Appendix 2

**Table 4** Morphometric variables of body size characteristics for each sex or age class. These variables are expressed by mean measurements±SD (range) of body mass (BM), head width (HW), tail height (TH), snout–anterior vent length (SAVL), snout–posterior vent length (SPVL), and tail

length (TL) in adult males (M), adult females (F), unsexed individuals (U), juveniles (J: over one year old), and metamorphs or newly metamorphosed juveniles (N: less than one year old)

Class	n	BM (g)	HW (mm)	TH (mm)	SAVL (mm)	SPVL (mm)	TL (mm)
M	18	3.69±0.87 (2.40–5.30)	9.29±0.84 (7.98–10.67)	5.94±0.62 (4.94–7.08)	49.10±3.91 (42.45–55.57)	53.08±4.05 (46.02–59.38)	32.62±5.85 (24.02–43.57)
F	15	5.23±1.79 (2.65–9.80)	9.87±1.01 (8.19–11.86)	6.05±0.85 (4.92–7.53)	54.40±8.24 (40.35–69.07)	59.05±7.59 (45.93–73.39)	33.54±4.99 (26.04–41.18)
U	29	2.60±0.45 (2.00–4.25)	8.60±0.54 (7.57–10.01)	5.27±0.51 (4.57–6.46)	45.50±2.14 (42.45–50.07)	48.67±2.14 (45.93–53.28)	26.19±5.02 (7.54–35.23)
J	43	1.54±0.37 (1.00–2.30)	7.47±0.74 (6.06–9.29)	4.52±0.53 (3.40–5.90)	36.72±3.21 (31.38–43.07)	39.61±3.17 (35.03–45.26)	21.12±3.25 (12.50–27.51)
N	70	0.80±0.19 (0.15–1.25)	6.39±0.47 (4.78–7.38)	3.68±0.41 (2.86–4.74)	29.70±2.79 (20.23–35.29)	32.15±2.99 (21.36–38.09)	17.46±3.15 (8.27–25.30)

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