

Age structure and growth rates of two Korean salamander species (*Hynobius yangi* and *Hynobius quelpaertensis*) from field populations

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We studied and compared the age structure, body size, and growth rates of field populations of two Korean salamander species (*Hynobius yangi* and *Hynobius quelpaertensis*) to elucidate important aspects of basic population dynamics of these two endemic *Hynobius* species. In both populations, females were sexually mature at three years of age, while *H. yangi* and *H. quelpaertensis* males matured at two and three years of age, respectively. Both males and females of *H. yangi* and *H. quelpaertensis* attained a maximum age of 11 years and 10 years, respectively. In both species, the snout-vent length (SVL) and body weight (BW) of the females were greater than those of the males. The SVL, BW, and asymptotic SVL of both male and female *H. yangi* were smaller than those of *H. quelpaertensis*, possibly resulting in the smaller body size of the former, although overall growth coefficients were not significantly different between the two species. We also compared the age structure and growth rates of three Korean and three Japanese species of *Hynobius*.

Keywords: Urodela; sexual dimorphism; skeletochronology; age structure; annual survivorship; growth coefficient

Introduction

Life history traits such as the age structure and growth rates of amphibian populations can assist us in understanding basic population dynamics (Stearns 1989; Misawa and Matsui 1999). In Urodela, age at maturity and growth rate are determined by the combined effects of environmental factors including food resources, competition, temperature, latitude and altitude and genetic factors such as developmental constraints (Olgun et al. 2001; Cogălniceanu and Miaud 2003). In Urodela, females are often larger than males, and female body size is usually correlated with fecundity. This sexual size dimorphism may be caused by the slower growth rate and delayed sexual maturation of females (Trivers 1972; Caetano and Leclair 1996; Marzona et al. 2004).

Several methods are available for determining the age of individual amphibians. One can use the relationship between age and the size frequency distributions of individuals, conduct a mark and recapture study, or initiate a skeletochronology study (Halliday and Verrell 1988; Eden et al. 2007; Matsuki and Matsui 2009). Of these techniques, skeletochronology has been used most frequently because it provides reliable data about

the sexual maturity, growth rate, and longevity of a species (Castanet and Smirina 1990; Cheong et al. 2007; Lee and Park 2008). In Urodela, one can determine the age of a specimen by counting the number of lines of arrested growth (LAGs) in the periosteal bones of the phalanges.

In South Korea, there are five different urodele species. The largest genus, *Hynobius*, includes three endemic species, *H. leechii*, *H. yangi*, and *H. quelpaertensis* (Kim 2009). *Hynobius leechii* is distributed over most of South Korea, with the exception of regions where *H. yangi* and *H. quelpaertensis* are found. Age structure and growth in a population of *H. leechii* were previously studied in Chuncheon, Kangwon (Lee and Park 2008). *Hynobius yangi* is primarily distributed in Gijang-gun near Busan and in surrounding areas. *Hynobius quelpaertensis* is mainly found on Jeju Island and in parts of the southern Korean peninsula (Yang et al. 2001). The age and growth of *H. yangi* and *H. quelpaertensis* have not been investigated in any field population. It has been reported that *H. yangi* has a smaller body size than *H. quelpaertensis* (Kim et al. 2003), but the factors responsible for the smaller size are not known.

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In this study, we determined the age structure and growth rates of *H. yangi* and *H. quelpaertensis* in a field population of each species and compared the results for the two species. This work was undertaken in order to elucidate important aspects of basic population dynamics of these two Korean endemic *Hynobius* species and to identify the factors responsible for the small body size of *H. yangi*. We also compared the age structure and growth rates of three Korean and three Japanese species of *Hynobius*.

Materials and methods

Animal collection

Between 22 February and 10 April 2006, we collected 508 *H. yangi* (288 males and 220 females) from a breeding population present in a mountain wetland (N 35°19'55.6", E 129°19'28.0", 10 m long × 10 m wide × 0.3 m deep, altitude 40 m) near Hyoam-ri, Jangan, Busan, South Korea. The animals were collected by setting up a drift fence with pitfall traps surrounding the wetland. The wetland is often dry in mid-summer. On Jeju Island between 16 February and 19 March 2008, we collected 123 *H. quelpaertensis* (76 males and 47 females) from a breeding population formed in a mountain pond (N 33°31'06.3", E 126°42'53.7", 5 m long × 4 m wide × 1 m deep, altitude 150 m) located at Deokcheon-ri, BukJeju, Jeju, South Korea. Most of the salamanders were found under rocks and among water plants and fallen leaves. The pond was located in a deciduous forest and does not dry up on a yearly basis.

We anesthetized the salamanders by submerging them in 0.1% MS-222 (3-aminobenzoic acid ethyl ester, Sigma) for 5–10 min. We measured the snout-vent length (SVL, the distance from the tip of the snout to the posterior margin of the cloaca) and body weight (BW) of each individual to an accuracy of 0.1 mm using digital calipers (CD-15CPX, Mitutoyo, NV) or to an accuracy of 0.1 g using a digital field balance (CB-1200, Sartorius, MA), respectively. For purposes of the skeletochronology study, two joints of two digits (approximately 1–3 mm of each digit) were removed from each animal and individually preserved in 10% neutral formalin (Junsei Chemical). To reduce the probability of infection, antiseptic solution (Povidone iodine topical solution, Green Pharmacy Co., Korea) was applied to the digits after cutting. Though they did not directly study the adverse effects of toe clipping in the field, Lee and Park (2008) successfully used toe clipping for individual identification in their field study of *H. leechii*. The salamanders were released into the wetland or pond after they had recovered from the anesthetic.

Skeletochronology

The skeletochronology study was conducted following the methods of Cheong et al. (2007) and Lee and Park (2008). We washed the preserved digits in tap water for 24 h, decalcified the bone by submerging the digits in 5% nitric acid (Daejung Chemical, Seoul) for 2–3 h, and washed the digits again in tap water for 24 h. The digit samples were then dehydrated, paraffin-embedded, sectioned (8–10 µm, Microtome-530, Erma), stained using the Harris eosin-hematoxylin method (Presnell and Schreiber 1997), and observed under a microscope (X 400, Eclipse-50i, Nikon).

Because endosteal bone resorption was observed in both *H. yangi* and *H. quelpaertensis*, we determined the age of these species using a back calculation method (Castanet et al. 1993). Applying this method was necessary because in specimens in which such resorption occurred, we were unable to detect a metamorphosis line. To adjust the age in such individuals, we compared the mean diameter of the first LAG in individuals that had a metamorphosis line with the diameter of the first LAG in an individual that had lost the metamorphosis line. If the first LAG diameter of the latter individual was larger than that of the former, we added an additional year to the estimate of the first animal's age (Rozenblut and Ogielska 2005; Üzüm 2009).

Annual survivorship and adult life expectancy

Annual survivorship and adult life expectancy are important components of basic population dynamics. We calculated the annual adult survival rate (S) based on Robson and Chapman (1961), as follows: $S = T / (R + T - 1)$, where $T = N_1 + 2N_2 + 3N_3 + \dots$, $R = \sum N_i$, and N_i = the number of individuals in age group i . The adult life expectancy (LEP, the expected total longevity of individuals that have reached maturity) was calculated for each population of *H. yangi* and *H. quelpaertensis* using Seber's (1973) formula: $ESP = 0.5 + 1 / (1 - S)$.

Growth curve

To calculate a growth curve, we fitted the SVL and age data of *H. yangi* and *H. quelpaertensis* to the von Bertalanffy equation (1938): $S_t = S_m - (S_m - S_0) e^{-k(t-t_0)}$, where S_t = the average SVL at age t , S_m = the asymptotic SVL, S_0 = the SVL at metamorphosis, t = the number of growing seasons experienced, t_0 = the age at metamorphosis, and K = the growth coefficient (the shape of the growth curve). To obtain data for S_0 and t_0 , we collected one clutch of eggs of each species that had been newly oviposited at the wetland or pond in March 2006 and

2008, respectively. The eggs were hatched and reared in a laboratory aquarium (90 cm long \times 30 cm wide \times 45 cm deep, 5 L water) that included both aquatic and terrestrial conditions. Fallen leaves were provided in the aquarium as shelter for the animals; the air temperature and photoperiod were not manipulated. Blood worms were provided for food and half of the water was changed weekly. A total of 16 larvae of *H. yangi* and 22 larvae of *H. quelpaertensis* successfully metamorphosed. We measured the SVL of each metamorphosed individual after anesthetizing the animals as described above.

Data analysis

The SVL of recently metamorphosed and adult individuals and the BW of male and female *H. yangi* and *H. quelpaertensis* did not pass the normality test (Shapiro-Wilk normality test, $P < 0.05$). Comparisons of these parameters between sexes in each species and between the two species were therefore assessed using a more conservative Mann-Whitney U test. To compare the growth coefficient and the asymptotic SVL between sexes and between species, we used the independent sample t -test. All analyses were performed with SPSS (ver. 11.0); the data are presented as mean \pm SE.

Results

Endosteal resorption, age structure, annual survivorship, and adult life expectancy

We determined the age of 414 of 508 *H. yangi* salamanders and of 114 of 123 *H. quelpaertensis* salamanders (Figure 1). Endosteal resorption was observed in 397 *H. yangi* (95.9%) and 107 *H. quelpaertensis* (93.9%, Figure 1C). We observed both a metamorphosis line (Figure 1A) and the first LAG (Figure 1B) in 17 *H. yangi* and 7 *H. quelpaertensis*; the mean diameters of the first LAG of these specimens were $85.1 \pm 12.1 \mu\text{m}$ ($n = 17$, range = 66.5–106.5) and $86.4 \pm 14.7 \mu\text{m}$ ($n = 8$, range = 69.0–106.1), respectively. Comparing these mean values to the diameter of the first LAG in each individual, we added one year to the calculated age of 27 *H. yangi* and 13 *H. quelpaertensis* whose first LAG diameter was larger than that of individuals having both a metamorphosis line and a first LAG.

Hynobius yangi males and females become sexually mature at 2 and 3 years of age, respectively; both sexes commonly attain a maximum age of 11 years (Figure 2A). In our sample, the mean age of females was higher than that of males (Mann-Whitney U test: $Z = -4.18$, $P < 0.01$, Table 1). *Hynobius quelpaertensis* males and females most often mature sexually at three years of age

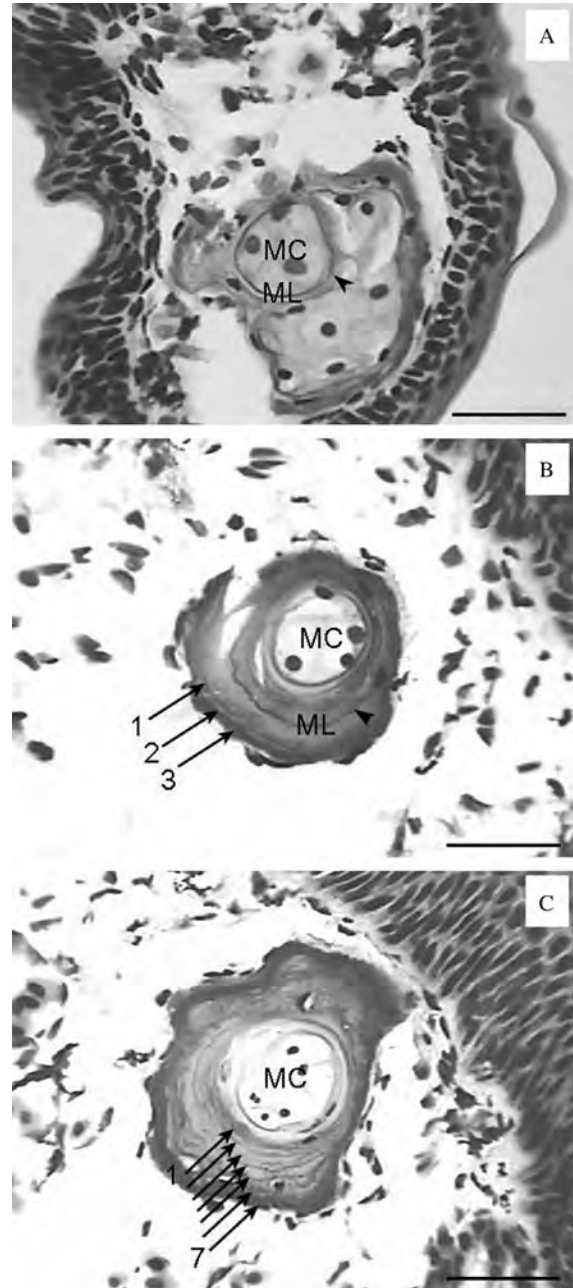


Figure 1. Phalangeal cross-sections of *Hynobius yangi* and *Hynobius quelpaertensis*. An arrowhead indicates a metamorphosis line, and arrows indicate the lines of arrested growth (LAGs). MC = marrow cavity, ML = metamorphosis line. (A) A juvenile (SVL = 23.8 mm) of *H. quelpaertensis* caught in February 2008. Only a metamorphosis line was observed. (B) A female of *H. yangi* (SVL = 59.2 mm) caught in March 2006. A metamorphosis line and three LAGs were observed. This individual was three years old. (C) A male of *H. quelpaertensis* (SVL = 63.3 mm) caught in March 2008. Seven LAGs were observed. This individual was seven years old. The scale bars represent 50 μm .

and attain a maximum age of ten years (Figure 2B). The mean ages of males and females were not significantly different (Mann-Whitney U test: $Z = -1.52$, $P = 0.12$, Table 1). The mean ages of both male and female *H. yangi* were lower than those of *H. quelpaertensis* (Mann-Whitney U test: $Z = -4.55$, $P < 0.01$ for males; Mann-Whitney U test: $Z = -2.19$, $P = 0.028$ for females).

The annual survivorship and adult life expectancy of male *H. yangi* were 0.70 and 3.87, respectively, while those of females were 0.67 and 3.55. The annual survivorship and adult life expectancy of male *H. quelpaertensis* were 0.69 and 3.74, respectively; those of the females were 0.72 and 4.10.

Body size and growth

In both species, females were longer and heavier than males (Mann-Whitney U test: $Z = -9.59$, $P < 0.01$ for SVL; Mann-Whitney U test: $Z = -5.61$, $P < 0.01$ for BW in *H. yangi*; Mann-Whitney U test: $Z = -2.04$, $P = 0.041$ for SVL; Mann-Whitney U test: $Z = -3.01$, $P < 0.003$ for BW in *H. quelpaertensis*; Table 1). The

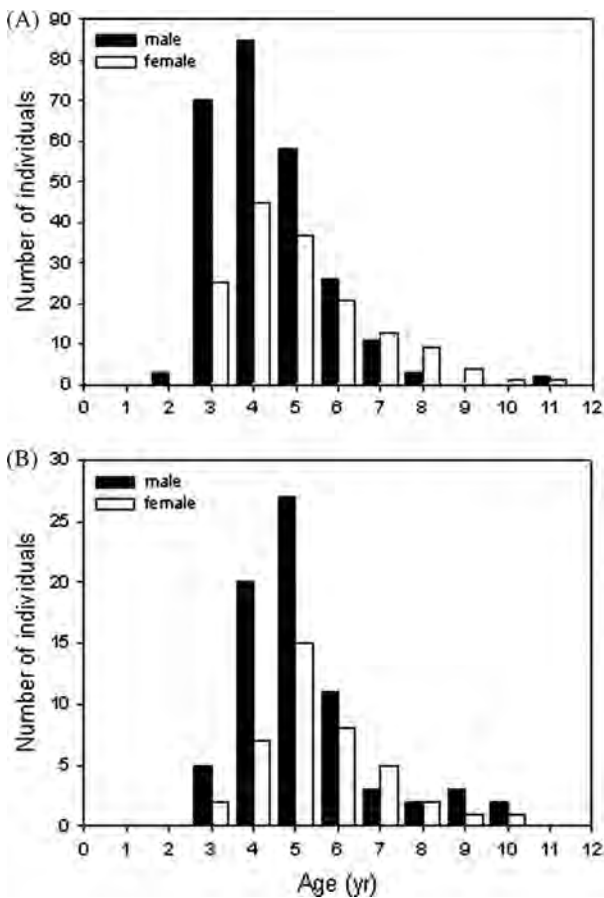


Figure 2. Age distributions in populations of *Hynobius yangi* (A) and *Hynobius quelpaertensis* (B).

SVL and BW of both male and female *H. yangi* were less than those of male and female *H. quelpaertensis* (Mann-Whitney U test: $Z = -11.38$, $P < 0.01$ for SVL; Mann-Whitney U test: $Z = -8.85$, $P < 0.01$ for BW between males; Mann-Whitney U test: $Z = -7.84$, $P < 0.01$ for SVL; Mann-Whitney U test: $Z = -6.86$, $P < 0.01$ for BW between females; Table 1).

The larvae of both species metamorphosed approximately three months after hatching. The mean SVLs of recently metamorphosed *H. yangi* and *H. quelpaertensis* were 23.5 ± 0.2 mm ($n = 16$, range = 19.4–28.5) and 23.3 ± 0.8 mm ($n = 22$, range = 20.9–25.3), respectively; the difference was not significant (Mann-Whitney U test: $Z = -0.59$, $P = 0.55$). Therefore, in applying the von Bertalanffy growth equation, we used $t_0 = 0.3$ and $S_0 = 2.3$ for both *H. yangi* and *H. quelpaertensis*.

The growth coefficients of males and females were not different in either species ($t = 0.41$, $df = 412$, $P > 0.05$ in *H. yangi*; $t = 0.24$, $df = 112$, $P > 0.05$ in *H. quelpaertensis*, Table 1). The asymptotic SVL of *H. yangi* females was greater than that of males ($t = 3.23$, $df = 412$, $P < 0.05$), but there was no difference in this variable between genders in *H. quelpaertensis* ($t = 0.16$, $df = 112$, $P > 0.05$). The growth coefficients of males and females did not differ between the two species ($t = 0.83$, $df = 195$, $P > 0.05$ between males; $t = 1.86$, $df = 329$, $P > 0.05$ between females, Figure 3). However, the asymptotic SVLs of both male and female *H. yangi* were smaller than those of male and female *H. quelpaertensis* ($t = -3.15$, $df = 195$, $P < 0.05$ between males; $t = -5.70$, $df = 329$, $P < 0.05$ between females, Figure 3).

Discussion

In Urodela, more than 60% of the species show larger SVLs in females than in males (Shine 1979), and large SVL in females is directly related to high fecundity (Trivers 1972; Kaplan and Salthe 1979). Body size dimorphism between the sexes can be influenced by several factors including the growth rate before metamorphosis, the adult growth rate (different energy allocations between growth and reproduction), age at sexual maturity, and the age structure (mean age) of the population (Marzona et al. 2004). In several salamander species including *H. leechii* and *H. kimurae*, low sexual maturation and high mean age of a population have been shown to contribute to large female SVLs (Misawa and Matsui 1997, 1999; Miaud et al. 2001; Lee and Park 2008). However, other factors cannot be neglected as possible causes of this type of dimorphism.

In Alpine newts (*Triturus alpestris*), large SVLs of females have been shown to result from a higher growth rate in females than in males before sexual maturation (Miaud et al. 2000). In our study, we could not

Table 1. Snout-vent length (SVL), body weight (BW), mean age, age at maturity, adult survivorship (S), life expectancy (LEP), asymptotic SVL, and growth coefficient in populations of *Hynobius yangi*, *Hynobius quelpaertensis*, and *Hynobius leechii*. The data for *H. leechii* were calculated from published data (Lee and Park 2008) for comparison among three Korean species in the genus *Hynobius*.

| Species name | Sex | SVL (mm) | BW (g) | Mean age (yrs) | Age at maturity (yrs) | S (no./year) | LEP (yrs) | Asymptotic SVL (mm) | Growth coefficient |
|--------------------------|-----------------------|------------------------|----------------------|----------------|-----------------------|--------------|-----------|---------------------|--------------------|
| <i>H. yangi</i> | Male (n = 288*/258) | 52.8 ± 0.2 (41.0–67.2) | 4.8 ± 0.1 (2.6–8.2) | 4.82 (2–11) | 2 | 0.70 | 3.87 | 54.6 ± 0.7 | 1.0 ± 0.1 |
| | Female (n = 220*/156) | 56.8 ± 0.3 (48.1–73.2) | 5.5 ± 0.1 (3.0–9.9) | 5.04 (3–11) | 3 | 0.67 | 3.55 | 58.1 ± 0.9 | 1.1 ± 0.2 |
| <i>H. quelpaertensis</i> | Male (n = 76*/73) | 61.7 ± 0.6 (47.1–75.7) | 6.5 ± 0.2 (3.2–11.0) | 5.21 (3–10) | 3 | 0.69 | 3.74 | 66.0 ± 3.0 | 0.6 ± 0.2 |
| | Female (n = 47*/41) | 64.2 ± 0.8 (56.7–79.2) | 7.7 ± 0.4 (3.5–14.1) | 5.54 (3–10) | 3 | 0.72 | 4.10 | 66.8 ± 4.0 | 0.7 ± 0.3 |
| <i>H. leechii</i> | Male (n = 43) | 61.3 ± 1.0 (47.0–71.0) | 6.8 ± 0.2 (3.5–9.8) | 4.49 (1–9) | 1 | 0.70 | 3.89 | 63.6 ± 1.7 | 0.7 ± 0.1 |
| | Female (n = 32) | 65.1 ± 0.8 (56.8–72.0) | 8.3 ± 0.3 (5.4–12.1) | 5.31 (3–9) | 3 | 0.78 | 5.07 | 65.1 ± 1.4 | 0.8 ± 0.2 |

* indicates the sample size for the SVL and BW data only.

discriminate the sex of recently metamorphosed *H. yangi* and *H. quelpaertensis*. Although the growth rate of female *H. yangi* tended to be lower than that of the males, this is unlikely to be the primary causative factor of large female SVLs in this species because the differences in growth rates between the sexes were not significant. Instead, the slower sexual maturation and higher mean age of female *H. yangi* may be responsible for the larger SVLs and BWs observed in females. In *H. quelpaertensis*, on the other hand, the causes of the larger SVLs observed in females are not clear because the mean age and age at sexual maturity were not significantly different for the two sexes.

Another question we addressed in this study was why the body sizes (SVL and BW) of male and female *H. yangi* are smaller than those of their *H. quelpaertensis* counterparts. The earlier sexual maturation and lower growth rate after sexual maturation (i.e. greater *K*) of male and female *H. yangi* might cause these differences. Several previously mentioned factors that determine body size, including a greater growth coefficient and a lowered growth rate after sexual maturation, might explain the smaller body size in *H. yangi*. Although the differences were not statistically significant, the growth coefficients (*K*) of male and female *H. yangi* were greater (1.0 and 1.1) than those of male and female *H. quelpaertensis* (0.6 and 0.7). However, the growth rates of male and female *H. yangi* after sexual maturation were lower than those of their *H. quelpaertensis* counterparts. If the growth rates of the two species before sexual maturation are not different but the overall growth coefficient is greater in one species than in the other, the adult growth rate after sexual maturation in the species with the lower growth coefficient should be smaller, resulting in a smaller body size. Similar growth patterns have been reported in several amphibian species including *H. nebulosus*, *Bombina bombina*, and *Hyla annectans chuanxiensis* (Ento and Matsui 2002; Cogălniceanu and Miaud 2003; Liao and Lu 2010).

Amphibians show indeterminate growth patterns in which an individual grows continuously, even after sexual maturity (Kozłowski and Uchmanski 1987; Cichon 1999). The observation that the growth rate of *H. yangi* decreases after sexual maturation suggests that adult *H. yangi* allocate more energy to reproduction than to growth (Kozłowski and Uchmanski 1987; Hemelaar 1988). Although we do not know the clutch size of *H. quelpaertensis*, the clutch size of female *H. yangi* was found to be the same as that of *H. leechii* (66 eggs per clutch), despite the fact that the SVL of female *H. leechii* was greater than that of female *H. yangi* (Park and Park 2000; Lee 2007). This difference indicates that the smaller *H. yangi* might channel relatively more energy towards reproduction than growth. Similar

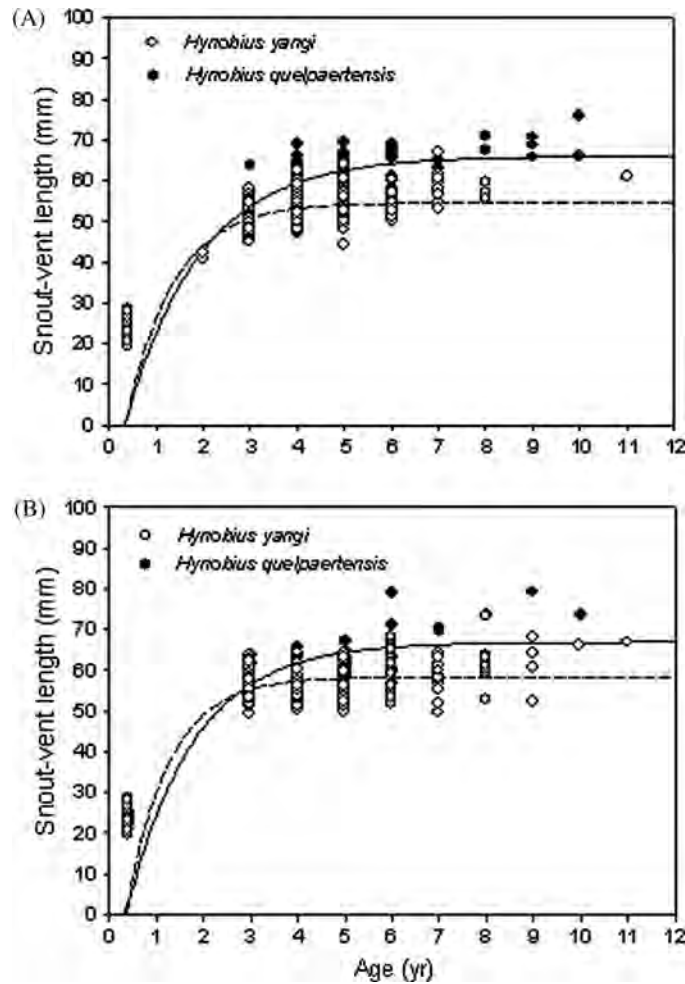


Figure 3. Growth curves for males (A) and females (B) of *Hynobius yangi* (open dots and dotted line) and *Hynobius queipaertensis* (solid dots and solid line). The growth curves were fitted to von Bertalanffy's growth equation.

results have been reported in *B. bombina* (Cogălniceanu and Miaud 2003, 2004), a species that has a low growth rate after sexual maturation because females put greater energy into reproduction, laying more than 500 eggs per year. It is known that individuals in a species will channel less energy towards growth when adult survivorship is low due to limited food resources, high predator pressure, reproductive competition, and highly fluctuating environmental conditions (Diaz-Paniagua et al. 1996; Olgun et al. 2001). However, our results are not easily explained by this phenomenon because the annual survivorship rates of *H. yangi* and *H. queipaertensis* were not significantly different. In animals, the intrinsic growth rate of a species can be determined by the combined effects of both environmental and genetic variables including nutrient stress, temperature, and developmental constraints (Arendt 1997). To elucidate which factors contribute to the low growth rate of *H. yangi* after sexual maturation, further studies focusing

on both environmental and genetic factors should be conducted.

In our analysis, the mean age and growth rate of all three Korean species in the genus *Hynobius* (*H. leechii*, *H. yangi*, and *H. queipaertensis*) were determined for a field population of each species. Males and females of Korean *Hynobius* species mature sexually at 1–3 years and 3 years, respectively, and attain a maximum age of 9–11 years. The females of Korean *Hynobius* species tend to have larger SVLs than males. In Japan, the age and growth rate of three species in the genus *Hynobius* (*H. nebulosus*, *H. tokyoensis*, and *H. kimurae*) have been studied. The females of all three Japanese species show later sexual maturation and greater mean age than the males. Male and female *H. nebulosus* mature sexually at 3 and 4 years, respectively, and attain maximum ages of 10 and 6 years, respectively (Ento and Matsui 2002). In *H. tokyoensis*, both males and females start to breed at 4 years of age, and longevity

ranges from 13 to 21 years (Kusano et al. 2006). Male and female *H. kimurae* mature sexually at 5–6 and 7 years respectively and attain a maximum age of 12 to 20 years (Misawa and Matsui 1999). Unlike Korean *Hynobius*, in which the females invariably have larger SVLs, sexual dimorphism as measured by SVL is not consistent in the Japanese species. Male *H. nebulosus* have larger SVLs than the females, the SVLs of male *H. tokyoensis* do not differ from those of the females, and female *H. kimurae* are larger than their male counterparts. Previous studies suggest that variability in sexual size dimorphism may be caused by several different factors including differences between lentic and lotic habitats (Ento and Matsui 2002), differences in air temperature at various latitudes and altitudes (Caetano and Castanet 1993; Üzüüm and Olgun 2009; Liao and Lu 2010), and different mortality rates resulting from variable environmental conditions (Shine 1979; Olgun et al. 2001). Overall, Korean *Hynobius* species begin to breed early, at 1–4 years of age, but their longevity is similar to or shorter than that of Japanese *Hynobius* species by approximately 10 years.

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