The giant salamanders (Cryptobranchidae): Part B. Biogeography, ecology and reproduction

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Abstract - The Chinese (*Andrias davidianus*) and Japanese (*A. japonicus*) giant salamanders far exceed any other living amphibians in size, with the North American giant salamander (Hellbender; *Cryptobranchus alleganiensis*) also being one of the world's largest amphibians. The sustainable management of cryptobranchids requires knowledge of cryptobranchid biogeography, ecology and reproduction in concert with other scientific fields. Cultural, political, and economic factors also contribute to the design of optimal strategies for sustainable management. Cryptobranchids are biologically similar in many ways including extreme longevity, a highly conserved morphology, low metabolism, males brooding of eggs, and large larvae. However, there are differences in cryptobranchids' habitats and diets, reproductive behaviors and seasonality, fecundities, egg sizes, mating strategies and paternities. In "The giant salamanders (Cryptobranchidae): Part A" we reviewed cryptobranchid paleontology, phylogeny, genetics, and morphology. Here we review cryptobranchid range and distribution, demography and growth, population density and size, habitat, territoriality and migration, diet, predators, and reproduction.

Introduction. The amphibian family Cryptobranchidae, known as giant salamanders, consists of two genera with three currently recognized species. The Chinese giant salamander (*Andrias davidianus*: Peng et al. 1998; Zhao 1998) with a total length (TL) of ~2.0 m and up to 59 kg in weight, and the closely related but slightly smaller Japanese giant salamander (*A. japonicus*; Kawakami et al. 2005; Figure 1), far exceed any other amphibians in size. The North American giant salamander (Hellbender; *Cryptobranchus alleganiensis;* Collins and Taggart 2009) although reaching only ~30% of the TL, and 9% of the weight of the *Andrias* species (Petranka 1998), is still one of the largest extant amphibians, rivaled in weight only by the goliath frog (*Conraua goliath*), which can weigh up to 3.3 kg (Sabater-Pi 1985), and in maximum recorded TL by *Amphiuma* species (116 cm), greater sirens (*Siren lacertian,* 97 cm; Petranka 1998), and some caecilians (ie. *Caecilia thompsoni*, 152 cm; Salgar 2007).

Cryptobranchids have a highly conserved morphology that has remained relatively unchanged since their earliest fossil records from 160 million years ago. *Cryptobranchus* likely became isolated from *Andrias* ~70 million years ago (Roelants et al. 2007), with the two *Andrias* species becoming isolated ~7 million years ago (Wiens 2007; review see Browne et al. 2012). The Critically Endangered *A. davidianus* (Wang and Xie 2009), and the Near Threatened *A. japonicus* (Tochimoto 1995) and *C. alleganiensis* (Briggler et al. 2007, 2010; Nashville Zoo 2012), are subject to expanding initiatives for their sustainable management.

Although much has been published on giant salamanders, this literature has previously been scattered, with many important articles only in the national languages of the bio-political regions where the species are found; (*A. davidianus*, Peoples Republic of China, Mandarin Chinese; *A. japonicus,* Japan, Japanese; *C. alleganiensis*, United States of America, English). Here we provide information that may facilitate the sustainable management of cryptobranchids through a review of their biogeography, ecology and reproduction.

Figure 1. The massive size of *Andrias* species is illustrated in this photograph of a large Japanese giant salamander (*Andrias japonicus*). *Image by Michael Ready: http://michaelready.photoshelter.com*

Range and Distribution. Cryptobranchid species range over the cooler temperate zones of China, Japan, and North America (Dai et al. 2010; Tao et al. 2004; Wang et al. 2004; Tochimoto 2005; Okada et al. 2008; Tochimoto et al. 2008; Nickerson et al. 2009). Within this range their distribution is generally in oligotrophic streams and rivers with lithoid substrates and steep banks.

Andrias davidianus: The original lowland range of *A. davidianus* has been estimated to extend throughout central, south-western, and southern China (Wang et al. 2004). *Andrias davidianus* may have previously been distributed in 17 Chinese provinces and autonomous regions based on stream or river types and climate; Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hebei, Henan, Hubei, Hunan, Jiangxi, Qinghai, Shanxi, Shaanxi, Sichuan (including Chongqing), Yunnan, and Zhejiang (Dai et al. 2010).

Populations of *A. davidianus* may still be found in a fragmented distribution in the mountainous areas of the middle and lower tributaries of the Yangtze River, Huang He River (Yellow River), and Zhu Jiang River (Pearl River), from Qinghai and Sichuan to Guangxi, Guangdong and Jiangsu Provinces (Liu and Liu 1998; Wang et al. 2004; Dai et al. 2010; Figure 2). However, in lowland areas most rivers are highly modified and *A. davidianus* only lives in isolated sections of tributaries, lakes, and source streams (Wang et al. 2004; Dai et al. 2010). A population of uncertain taxonomic status is recorded from 4,200 m elevation (Chen 1989), with the site now probably too

polluted to support *A. davidianus* (Pierson et al. 2014).

We could not find information to support the rumored existence of introduced *A. davidianus* in Taiwan. However, an incidentally introduced population of *A. davidianus*, probably originating from illegal importation for food, are hybridizing with *A. japonicus* in the Kamogawa River, Kyoto Prefecture, Japan (Okada, pers. comm.).

Andrias davidianus
range type
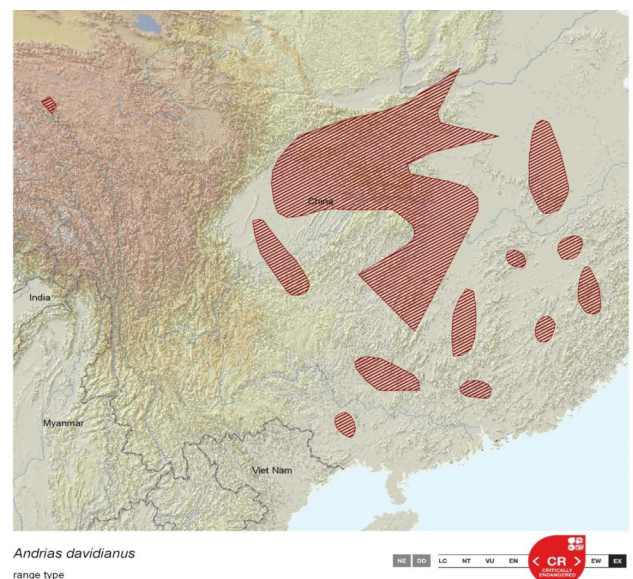
Figure 2. The current distribution (red shading) of the Chinese giant salamander (*Andrias davidianus;* (IUCN 2010). The location on the high plateau to the far left of the figure may now be uninhabitable by *A. davidianus* (Pierson et al. 2014).

Andrias japonicus: The distribution of *A. japonicus* extends from the south-west of the island of Honshu to the northeastern prefecture of Gifu, Shikoku Island, and only in the prefecture of Oita on Kyusyu Island. Their main habitat is in the Chugoku Mountains (westernmost part of Honshu); however, there are many populations in Gifu, Mie, and Oita prefectures (Tochimoto et al. 2008; Figure 3). There is a continuing decline in the extent and quality of *A. japonicus* habitat and consequently their populations are highly fragmented (Tochimoto 2005).


Andrias japonicus
range type
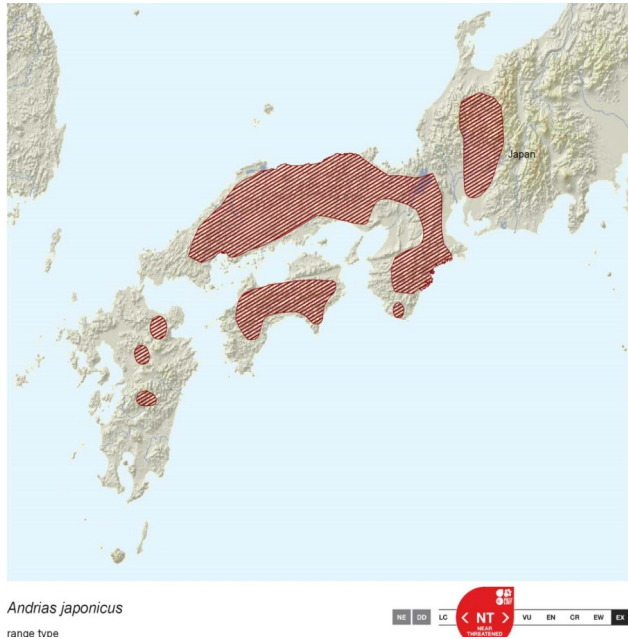
Figure 3. The current distribution (red shading) of the Japanese giant salamander (*Andrias japonicus*) is mainly limited to the Chugoku Mountains (westernmost part of Honshu), however, there are many populations in Gifu, Mie and Oita prefectures (IUCN 2010).

Cryptobranchus alleganiensis: The distribution of *C. alleganiensis* comprises two disjunct regions of North America; western populations (centered in the Ozark Highlands) and eastern populations (in streams and rivers within the Ohio and Tennessee River basins and along the Appalachian Mountains; Figure 4). Currently, these two groups are considered subspecies; *C. a. bishopi* as the southern Ozark subspecies and *C. a. alleganiensis* as the eastern subspecies. However, recent genetic evidence has shown that these subspecific designations do not accurately reflect the evolutionary history of this group and that lineage boundaries within this genus are in need of further resolution (Sabatino and Routman 2009; Tonione et al. 2011).

Historic records show *C. a. bishopi* occurred in southern Missouri, and northern Arkansas (Nickerson and Mays 1973a). *Cryptobranchus a. alleganiensis* inhabited a large range from New York State, through Pennsylvania, patchily in Ohio, in West Virginia, throughout Kentucky, western and central and eastern Tennessee, western North Carolina and the central Ozark Highlands in Missouri (Phillips and Humphries 2005). Records of *C. alleganiensis* from south-eastern Kansas are likely from introduced individuals

(Collins 1993), and there are unreliable reports of *C. alleganiensis* in Iowa (Nickerson and Mays 1973a), the Great Lakes drainage, and New Jersey (Harding 1997).

Cryptobranchus a. alleganiensis were once abundant in the Appalachian Mountains, and throughout the Ohio River Valley and central Missouri, however, large populations are now mainly found in New York, Pennsylvania, West Virginia, Virginia, Tennessee, North Carolina, and Georgia. Since the 1970's and 1980's, populations of *Cryptobranchus* have been estimated to have suffered declines of 40 to 100% (Wheeler et al. 2003; Foster et al. 2009; Nickerson et al. 2009).

Cryptobranchus alleganiensis
range type
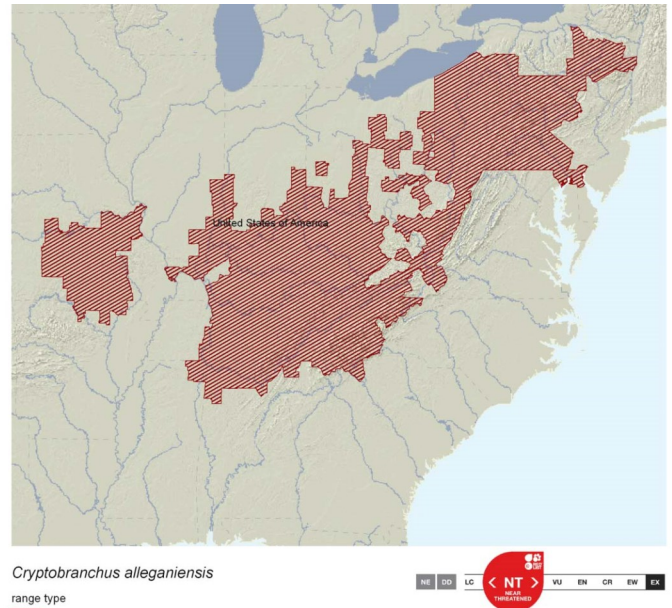
Figure 4. The current distribution of the North American giant salamander (*Cryptobranchus alleganiensis*) comprises two disjunct populations in North America; a western group of populations centered in the Ozark Highlands and an eastern group of populations in streams and rivers throughout the Appalachian Mountains (IUCN 2010).

Habitat, Micro-habitat, and Water Quality. Cryptobranchids typically inhabited cool, fast flowing, well oxygenated, and unpolluted streams and rivers. They also require rocks, holes in banks, crevices in bedrock or other similar sites for shelter or for their dens. Although cryptobranchids mainly inhabit streams and rivers with fast to moderate flow they can also inhabit still water bodies (Nickerson and Mays 1973a; Tao et al. 2004; Wang et al. 2004; Okada et al. 2008; Tochimoto et al. 2008; Dai et al. 2010).

Andrias davidianus: The habitat of *A. davidianus* mainly consists of rocky mountain streams and lakes at moderate elevations between 300 and 800 m above sea level but have been recorded at 1500 m (Wang et al. 2004; Figure 5), with a population reported from 4,200 m elevation (Pierson et al. 2014). In some regions almost all *A. davidianus* only persist in underground rivers, where their presence is indicated by their larvae emerging from springs (Dai et al. 2010).

Figure 5. The steep rocky stream habitat of the Chinese giant salamander (*Andrias davidianus*) in the Qin Ling Mountains, southern Shaanxi Provence, Peoples Republic of China. The image shows the border of a national park where habitat restoration, including reforestation and rehabitation of *A. davidianus* is occurring. *Image Robert Browne.*

Andrias davidianus lives in rocky dens ranging from 0.4 to 4.0 m in width, small crevices between large rocks or under rocks, or in caves in river banks (Luo 2009; Wu 2009). Tao et al. (2004) showed among 8 rivers that water depth, den width, water speed, and river substrate were the main correlates of den selection by *A. davidianus*, and that den elevations from the river bottom and den height were insignificant. *Andrias davidianus* inhabited creeks, U-shaped, flat, and interior rivers. From recent surveys of emerging larvae in springs, most adult *A. davidianus* were considered to be living in underground rivers in the Xingwen, Jiangyou, Zhangjiajie, Wuxi, Yangxian, and Qinba Mountain ranges. In these regions polluted streams may no longer support *A. davidianus* (Dai et al. 2010).

Lou and Kang (2009) found in Zhangjiajie province that the reaches of streams inhabited by *A. davidianus* were characterized by modest elevation (~380 m), a small river width (~6.4 m) and depth (~1.1 m), high to moderate flow rates (~0.3 m/s), high dissolved oxygen (~7.2 mg/L), low carbon oxygen demand (~4.0 mg/L), low total nitrogen (~0.1 mg/L), and moderate total hardness (~140 mg/L). The

streams had a lithoid substrate of gravel or rock, with a steep stony river bank of ~60 degrees gradient and more than 50% cover of bankside scrubby vegetation.

In captivity, *A, davidianus* juveniles were relatively tolerant of low oxygen levels and showed no signs of hypoxia at dissolved oxygen levels of 4 mg/L, however at 3 mg/L, growth rate declined, and at 2 mg/L behavior became erratic and mortality occurred after 48 hours (Liu et al. 2006). Luo et al. (2007) reported that the ideal breeding locations for *A. davidianus* are in clean shallow rivers less than 1 m in depth, with a substrate of gravel or rocks and a moderately slow flow of ~0.25 m/s. There was little anthropogenic influence with high dissolved oxygen of ~8.0 mg/L and low carbon oxygen demand of ~8.5 mg/L. The average density of food organisms in the stream was ~50 g/m^2 of substrate. Luo et al. (2007) recorded ~4 dens per 100 m and considered a stream with the following attributes as providing an ideal location for the rehabilitation of *A. davidianus*; a lithoid bottom and bank with a high gradient of ~80º, high vegetation coverage of ~95%, a water velocity of ~0.35 m/s, with ~30 potential den sites per km.

The temperature of streams inhabited by *A. davidianus* varied from a 10ºC winter minimum to a 25ºC summer maximum in a low elevation stream, and from a 3ºC winter minimum to a 20ºC summer maximum in a two moderate elevation streams (Figure 6). Liu et al. (2006) tested the effect of high water temperatures in an experiment on the feeding activity of *A. davidianus*. In temperatures from 20 to 22ºC, 35% of *A. davidianus* fed, from 26 to 28ºC only 10% fed, from 28 to 30ºC feeding had almost ceased, and death occurred above 35ºC.

Under future global warming scenarios, this sensitivity to higher water temperatures may pose a threat to *A. davidianus* and other cryptobranchid species. Therefore, possible changes in the distribution of suitable habitats due to climate change should be included in plans for the sustainable management of cryptobranchids.

Sodium chloride at levels of 0.04% or below did not inhibit growth of wild sampled juvenile *A. davidianus*. Among captive bred individuals, skin disease appeared in ~65% of F1 and ~50% of F2 juveniles kept at pH 9 for 30 days. Alkalinity also had a pronounced effect on growth; however, the juveniles were more tolerant of high acidity than high alkalinity (Liu et al. 2006).

Andrias japonicus: The distribution of *A. japonicus* extends through elevations from 200 to 1,000 m above sea level. Their habitats range from rivers 20 to 50 m wide and 4 m in depth, to mountain streams one to 4 m wide and 0.3 m in depth (Kawamichi and Ueda 1998; S. Okada, unpubl. data). The mountain streams have clear cool water flowing through granite and schist substrates, and usually have rocky or gravel bottoms (Tago 1927). The spawning nests and larvae of *A. japonicus* are often found in very small streams at the upper reaches of tributaries and in some catchments these streams may provide essential habitat (Kobara 1985; Kawamichi and Ueda 1998; Okada et al. 2008).
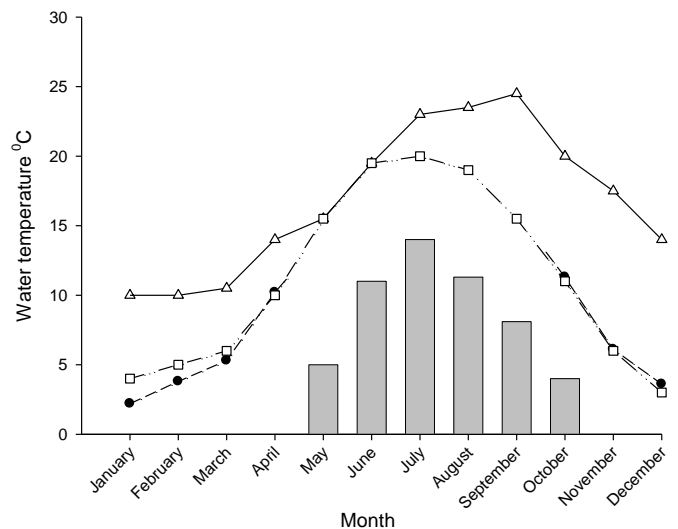
Figure 6. Water temperatures of the habitat of the Chinese giant salamander (*Andrias davidianus*) measured over one year at one low altitude stream (triangle), and on two different years at a moderate altitude mountain stream (closed circle, square) . The bars represent the average gonadal maturity in females (Adapted from Zhang et al. 2006).

Figure 7. Japanese giant salamander (*Andrias japonicus)* urban habitat. Many rivers in Japan are now heavily modified with concrete for flood protection and irrigation. This prevents the males finding the nesting burrows they need, normally found along the stream bank. *Image by Sumio Okada.*

The terrestrial vegetation of rural catchments that support *A. japonicus* include broadleaf forest and tree plantations with areas of clear-cut forest, and agricultural areas. Adult *A. japonicus* also occupy a wide variety of habitats and are occasionally found in urban areas, for instance, irrigation canals, creeks, and pools near towns in the middle section of rivers (Okada et al. 2008; Figure 7). However, breeding would prove difficult in these habitats due to the lack of suitable den sites unless den sites are artificially provided (Tochimoto 1995).

The seasonal temperatures of two small tributary streams in Hiroshima Prefecture, western Honshu, Japan, inhabited by *A. japonicus* range from nine to 21ºC (Okada et al. 2008). Spawning dens and larvae are often found in very small streams at the upper reaches of tributaries, and in some catchments these may provide essential habitat (Kobara 1985; Kawamichi and Ueda 1998; Okada et al. 2008).

Cryptobranchus alleganiensis: Historically, within their range *C. alleganiensis* were abundant in rivers and streams below 750 m elevation, with a high density of bank vegetation and canopy cover, and a substrate of large flat rocks, bedrock shelves, crevices, and logs (Bishop 1941; Nickerson and Mays 1973a; Figure 8). Adult and juvenile *C. alleganiensis* have been observed in water as shallow as 16 cm in depth.

Humphries and Pauley (2005) showed that *Cryptobranchus* size did not correlate with the size of rock shelters. Larval *C. alleganiensis* are rarely reported during standard surveys of large rock cover but have been found in the interstices of gravel in an area of subsurface percolation, small stones, and litter (Nickerson et al. 2003; Foster et al. 2008).

The small lungs in adult *C. alleganiensis* are used for buoyancy and their folded and extensive skin provides ~ 90% of oxygen for respiration (Guimond and Hutchison 1973). Year-round water quality data from a Missouri stream with historically large *Cryptobranchus* populations had undetectable carbon dioxide, with fluctuations of dissolved oxygen concentrations between eight and 14 ppm, alkalinity between 122 and 289 ppm, and temperatures between 10 and 22ºC (Nickerson and Mays 1973b).

Growth, Size, Longevity, and Demography. The growth rate of individuals within an amphibian species is highly labile and depends on diet and prey availability, temperature, and their sex. Therefore, growth rates for amphibians may vary between those in nature and in captivity, mainly due to differences in the availability of food and temperature (Browne et al. 2003).

Both *Andrias* species grow rapidly under favorable conditions until reaching about 60% of their final TL when growth rates decline (Zheng and Wang 2004; CITES 2009). Cryptobranchid species appear to generally mature, whether in captivity or in nature, by an age of five to seven years and a TL of 30 to 40 cm, at which stage growth of *C. alleganiensis* slows markedly.

Maximum longevity of all cryptobranchid species has only been estimated from specimens held in captivity. All captive specimens have, until recent decades, been wild captured

and are therefore of undetermined initial age. However, even with this limited knowledge it is clear that *A. davidianus* and *A. japonicus* can live for more than 60 years. The size of some individuals of *C. alleganiensis* suggests they may have lived for 30 years in nature (Taber et al. 1975; Petranka 1998), and Nigrelli (1954) noted an individual living 29 years in captivity.

Cryptobranchus alleganiensis (Bishop 1941) and *A. japonicus* (CITES 2009) reach 20 cm TL after three years of age, with *A. davidianus* reaching 30 cm TL over the same time period (Cheng 1998; Zheng and Wang 2004; Niwelinski 2007; Wu et al. 2010).

Andrias davidianus: *Andrias davidianus* is the largest extant amphibian reaching a TL of ~200 cm and a weight of ~50 kg (Peng et al. 1998; Zhao 1998). In Zhangjiajie City, an *A. davidianus* of 180 cm TL and 59 kg weight was recorded in 2007 in the Furong Bridge *Andrias davidianus* Farm (GSPIW 2005).
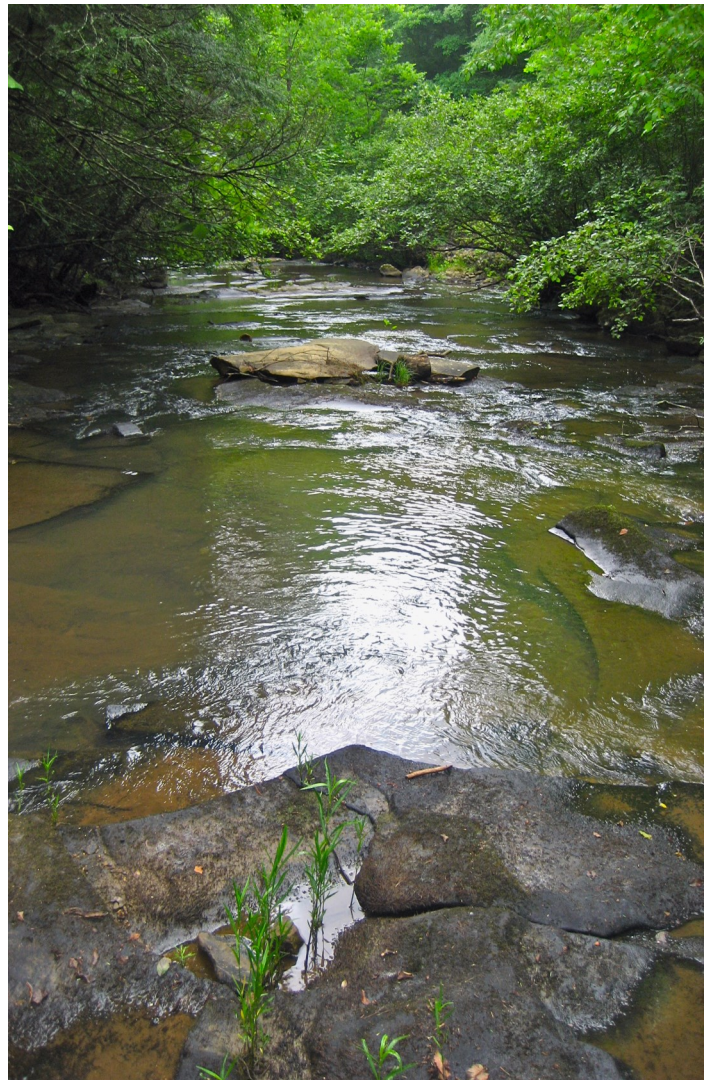
Figure 8. Typical habitat of the North American giant salamander (*Cryptobranchus alleganiensis*) showing high stream flows and the large flat rocks that provide shelter. *Image by Paul Hime.*
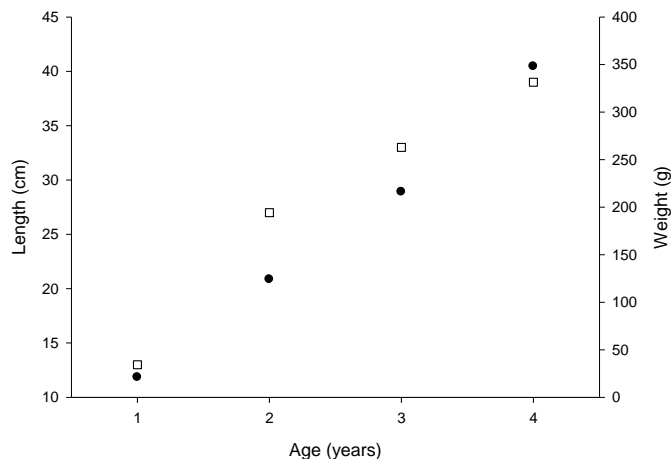
Figure 9. The growth in weight and length of Chinese giant salamanders (*Andrias davidianus*) in aquaculture. White squares length (cm), black circles weight (g) (Adapted from Wu et al. 2010).

Andrias davidianus grow from 3 cm TL and 0.7 g at hatching to 6 cm TL after 3 months, then grow approximately 10 cm TL a year to 40 cm TL and 3.5 kg at four years, 50 cm TL and 4.0 kg at five years, and reach ~100 cm TL and 6.0 kg at eight years of age (Cheng 1998; Niwelinski 2007; Wu et al. 2010; Figure 9). Using cluster analysis of weight and length, a demographic survey of *A. davidianus* from 1990 to 1991 in Lushi County, Henan Province, showed eight significant yearly age classes; however, only five were confidently identified and confirmed from the growth rates of captive bred individuals (Zheng and Wang 2004; Figure 10). A sex ratio of 1:1.2 (males to females; m:f) was found in natural population of 205 *A. davidianus* in 1991 (Zheng and Wang 2004).

Andrias japonicus: *A. japonicus* is the second largest extant amphibian and reaches a maximum TL of 150 cm and a weight of 45 kg (Kawakami et al. 2005). An *A. japonicas* hatched at Asa Zoo grew from 7 cm TL at yolk absorption to 20 cm TL after 3 years, and 26 cm TL after 4 years, and to 42 cm TL after 9 years (CITES 2009). From 1945 to 1992, a captive *A. japonicus* in the Tottori Prefecture, Japan, grew from 50 cm to 132 cm TL and reached 31 kg in weight; by 2005 was 143 cm TL and 44 kg in weight; and in 2008 weighed 55 kg. If this individual was at least 10 years old at capture by 2008 it had survived for 72 years.

Other records for the TL and weight of *A. japonicus* individuals are 150 cm and 28 kg, 149 cm and 22 kg, 148 cm and 35 kg, and 142 cm and 19.6 kg (Kawakami et al. 2005). The record longevity of *A. japonicus* in captivity outside of Japan was 52 years for an individual that was born in 1903 in the Natura Artis Magistra ("Nature is the Teacher of Art"), Amsterdam, Netherlands (Tago 1927).

Cryptobranchus alleganiensis: The sizes of mature *C. alleganiensis* generally range from 29 to 51 cm TL with a record of 74 cm (Fitch 1947; Figure 11). *Cryptobranchus alleganiensis* have survived 55 years in captivity (Nigrelli 1954), with the length of a 25 to 30 year old individual
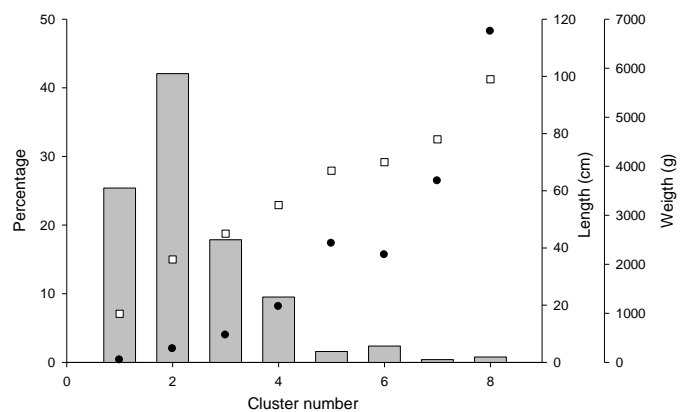
Figure 10. Cluster analysis of weight and length in a demographic survey of the Chinese giant salamander (*Andrias davidianus*) from 1990 to 1991, in Henan Province, Peoples Republic of China. Eight groups were identified from the cluster analysis; however, the first 5 (cluster 1 to 4) yearly age classes were confidently identified and confirmed with captive bred individuals. White squares total length (TL, cm), black circles weight (g) (Zheng and Wang 2004).

increasing only by 1 cm per year (Peterson et al. 1988; Taber et al. 1975), suggesting that a 74 cm TL individual found in nature may have been more than 40 years in age. The TL of *C. alleganiensis,* 1.5 to two years after hatching was 13 cm and after three years was 20 cm (Bishop 1941; Peterson et al. 1983).

Humphries and Pauley (2005) showed the m:f sex ratio of *C. alleganiensis* as 1.2:1.0, Hillis and Bellis (1971) 1.6:1.0 m:f., Peterson (1988) recorded equal numbers of males and females in a sample of 50 *C. alleganiensis* in an Ozark population, and Foster et al. (2009) found a m:f ratio of 1.8:1.0 in 159 *C. alleganiensis* captured in seven sites in the Allegheny River drainage.

Figure 11. Adult *Cryptobranchus a. alleganiensis* from the Gasconade River, Missouri. *Image by Jeffrey T. Briggler.*

Population Density. Past and present population densities of all cryptobranchid species are difficult to accurately assess because cryptobranchids are aquatic and primarily nocturnal, seek deep shelter, are cryptic and well camouflaged, and many surveys only use capture rates and not mark recapture estimates of population size (Browne et al. 2010). Nevertheless, observational or capture rates of all three species show high population densities before declines occurred (Tochimoto 1995; Wheeler et al. 2003; Zheng 2006; Wang and Xie 2009).

Populations of all three species have declined, with *A. davidianus* suffering an almost total loss of natural populations since the 1980s (Wang et al. 2004; Dai et al. 2010). *Andrias japonicus* populations are stable where their natural habitat and nest sites are protected, but in many areas populations have declined due to habitat loss (Tochimoto 1995; 2005). *Cryptobranchus alleganiensis* populations have been extirpated, are declining, or only comprise old individuals over much of their range due to a lack of recruitment (Rogers 2001; Wheeler et al. 2003; Foster et al. 2009).

Andrias davidianus: The natural populations of *A. davidianus* were rapidly declining through overharvesting and habitat loss before estimates of populations began (Wang et al. 2004; Luo et al. 2009; Wang and Xie 2009). Consequently, estimations of their original population densities are hard to determine. However the numbers of *A. davidianus* harvested annually before protection, relied on very large populations thus inferring high population densities (Wang and Xie 2009).

Andrias japonicus: We found only one specific reference to the population density of *A. japonicus*. Tochimoto (1995) found 10 *A. japonicus* measuring 30 to 50 cm TL over 100 m of stream length, and 300 over 12 km of stream length of the Ichi River in Hyogo Prefecture.

Cryptobranchus alleganiensis: Before the recently documented declines, surveys revealed large and ecologically significant populations of both *C. a. alleganiensis (*Burgmeier et al. 2011) and *C. a. bishopi* (Briggler et al. 2007). Records include ~1,100 *C. a. bishopi* in a 2.5 km stretch of the White River drainage of the North Fork River in 1969 (44/100 m of river; Nickerson and Mays 1973b), between one and 6/100 m^2 (Peterson et al. 1988), 269 in a 4,600 m^2 riffle (5/100 m^2; Nickerson and Mays 1973b), and 4/100 m^2 (Peterson 1985).

Cryptobranchus a. bishopi was found to be a dominant organism in streams that Nickerson and Mays (1973b; reviewed in Nickerson and Krysko 2003) surveyed with between 341 and 570/km of stream bed. In the 1980s, Gottlieb (1991) found up to 6 *C. a. alleganiensis* per 10 m^2 of habitable area in New York streams.

There have been losses of 60 to 80% of *Cryptobranchus* populations over much of their current range, and extirpations over a substantial part of their historic range (see Burgmeier et al. 2011 for a comprehensive summary table of previous studies reporting *Cryptobranchus* population densities), and USFWS (2011) has considerable information on estimates for *C. a. bishop*).

Territoriality, Migration, and Circadian and Seasonal Activity. Adult cryptobranchids are territorial, with territoriality and movement being more pronounced during the breeding season (Kobara 1985; Humphries 1999; Zheng and Wang 2010). Movement outside of shelters is mostly nocturnal (Noeske and Nickerson 1979; Kobara 1985; Humphries 1999; Liang and Wu 2010); however, large numbers of *C. a. alleganiensis* were shown to be active during daytime by Humphries (2007).

In a limited number of studies, home ranges of female *A. davidianus* (Zheng and Wang 2010) and female *C. alleganiensis* (Peterson and Wilkinson 1996) have been shown to be smaller than those of males. A tendency for upstream movement to find mates or dens was recorded with *A. davidianus* (Zheng and Wang 2010) and with *C. alleganiensis* (Topping and Peterson 1985; Humphries 1999).

Andrias davidianus: Zheng and Wang (2010) conducted a 160 day home range study of two male and two female captive-reared *A. davidianus* between May and October. Ten days after release the longest distance travelled was ~760 m, with an average movement of ~300 m, and an average area of activity of 1,150 m^2. Individual areas of activity increased with the size of occupied pools.

After establishing a shelter, an individual's activity area was confined to the vicinity of the shelters and averaged ~40 m^2 for males and ~30 m^2 for females. Both males and females showed strong territoriality with frequent conflicts. After dislodgement by a flood, the *A. davidianus* on average covered a 310 m stretch of stream over 7.5 days to find permanent shelters.

Liang and Wu (2010) studied the circadian activity and reproductive behavior of captive *A. davidianus*. Foraging occurred from mid-evening at 20.30 hours, shortly after at 21.00 hours their activity peaked, and between 01.00 hours and 03.00 hours activity ceased. Peak activity of *A. davidianus* in nature corresponded with the reproductive season from August to September (Wu 2009, 2010).

Andrias japonicus: Both male and female *A. japonicus* have overlapping home ranges and are generally sedentary except during the breeding season when they will migrate up to 600 m to find suitable nests. The largest males attempt to monopolize occupancy by guarding a 2 to 3 m radius around the nest (Kobara 1985). Agonistic behavior during nest guarding sometimes results in dead and injured males during September (Kawamichi and Ueda 1998).

Cryptobranchus alleganiensis: Shelters are generally occupied by only one *C. alleganiensis* (Smith 1907; Hillis and Bellis 1971; Nickerson and Mays 1973a; Peterson 1988) and are vigorously defended (Peterson and Wilkinson 1996; Hillis and Bellis 1971). In some populations, recently vacated shelters will be rapidly occupied and may indicate that shelter availability limits the density of populations (Hillis and Bellis 1971; Peterson and Wilkinson 1996; Humphries 1999).

The home ranges of individual *C. alleganiensis* overlap (Peterson and Wilkinson 1996), and during the breeding season the home range of males show greater overlap than those of females (Blais 1996). Except for the breeding season, individual male and female *C. alleganiensis* can exist in close proximity (Humphries 1999) and avoid contact or conflict when foraging (Coatney 1982). However, during the breeding season males show a high level of territoriality in defense of breeding sites (Smith 1907; Peterson 1988). The exceptional numbers of injuries on adult male and female *C. alleganiensis* found during the breeding season, including missing digits or truncated limbs, are likely the result of intraspecific conflicts (Miller and Miller 2005).

Studies of *C. alleganiensis* show a wide variation in home range sizes of between 28 and 90 m^2 (Coatney 1982; Peterson and Wilkinson 1996). The average home range size of *C. a. bishopi*, using minimum area convex polygons, was 28 m^2 for females and 81 m^2 for males (Peterson and Wilkinson 1996). Coatney (1982) calculated an average elliptical home range of 90 m^2.

Peterson (1987) detected no net movement upstream or downstream in the Niangua River, Missouri, USA. However, other studies have shown migratory behavior of *C. alleganiensis*. Nickerson and Mays (1973a) showed more movement upstream and downstream on the North Fork River. Topping and Peterson (1985) showed size specific upstream movements between two to 26 m/day, and Humphries (1999) showed an average one month linear movement in a West Virginia stream of 20 m, which ranged between individuals from one to 70 m. During a mark-recapture study a female moved >1 km upstream in the Allegheny drainage of New York (Foster et al. 2009).

Large numbers of *C. alleganiensis* in a North Carolina population were found to be active during bright daylight hours (Humphries 2007). Up to 30 sightings per person hour were recorded, with aggregations of five and 13 individuals around two nest rocks. Noeske and Nickerson (1979) showed activity was most pronounced 2.5 hrs after dark . Temperature directly affects the activity and behavior of *C. alleganiensis* with migration to overwintering sites and torpor occurring during the cold of winter; overwintering sites typically include pools more than 2 m deep (Blais 1996). Green (1935) showed that in West Virginia *C. alleganiensis* also moved to deeper and cooler habitats in summer.

Diet. Cryptobranchids are mainly ambush predators that feed through buccal suction (Cundall et al. 1987). The composition of a cryptobranchid's diet depends on the species, individual's size, and prey type and availability. Cannibalism may include the consumption of oocytes, eggs, and conspecifics (Nickerson and Mays 1973a; Song 1994; Humphries et al. 2005; Shimizu 2008). Cryptobranchids may predate invertebrates, such as spiders, millipedes, insects, and crustaceans, or vertebrates including mammals, reptiles, amphibians, and fish (Song 1994; Okada et al. 2008; Tables 1, 2). Large cryptobranchids such as adult *Andrias* consume all the above prey (Song 1994; Okada et

al. 2008), while *C. alleganiensis* has been reported as consuming mainly freshwater crayfish (Figure 12; Peterson et al. 1989).

However, there are major *Cryptobranchus* populations in several streams in the eastern U.S. where crayfish populations are very low. Diet samples from these localities either don't exist or are from larvae. There are instances where lamprey or carrion represent the major component of diet samples (Nickerson and Ashton 1983; Nickerson, pers. comm.).

Figure 12. Freshwater crayfish are a major component of the diet of some *Cryptobranchus* populations.

Cryptobranchids typically have a low dietary intake relative to body mass, reflecting their very low metabolic rates and calorie requirements. Song (1994) showed that 40% of *A. davidianus* had empty stomachs, and Peterson et al. (1989) found that 12% of *C. alleganiensis* had empty stomachs. The ratio of the weight of stomach contents to cryptobranchid weight was less than 2% with *A. davidianus* (Song 1994), and ~1% with *A. japonicus* (Okada et al. 2008). With all cryptobranchid species, twigs and gravel are ingested along with prey (Peterson et al. 1989; Song 1994; Okada et al. 2008).

Andrias davidianus: Song (1994, Table 1) showed that *A. davidianus* was highly cannibalistic with 27% of their diet by weight consisting of conspecifics. Other major dietary components by weight were crabs (23%), frogs (12%), and water shrews (9%). Fish comprised 9% of diet and invertebrates represented 6%. Twigs, leaves and gravel comprised 9% of weight of stomach contents. In contrast, Luo and Kang (2009) found in Zhangjiajie Province that crabs were the most important food organisms followed by shrimp.

Andrias japonicus: Adult *A. japonicus* have been reported to be cannibalistic during reproduction (Shimizu 2008). However, dietary studies of *A. japonicus* outside of breeding season have not provided evidence of cannibalism (Okada et al. 2008; Table 2). Okada et al. (2008) conducted a dietary study of *A. japonicus* in the Ikuridani River and Ouchi River (Table 2). The Ikuridani River almost entirely passes through forested areas. The Ouchi River passes

through about 35% of disturbed and agricultural areas including rice paddies, clear-cuts, and broadleaf forests. Fish provided a similar ~25% of prey by weight in both rivers. However, in the Ikuridani River a high percentage of other prey by weight ~25% were aquatic crabs, and in the Ouchi River prey included a large percentage of frogs (56%) and snakes (12%). There was 4% weight of twigs and rocks as stomach contents.

Cryptobranchus alleganiensis: The current geographic range of *C. alleganiensis* is approximately congruent with the highest global biodiversity of freshwater crayfish (Taylor et al. 1996). Abundant freshwater crayfish (*Orconectes* spp., *Camberas* spp.) are the dominant food of *C. alleganiensis* and comprise ~70 to 100% of diet by

weight (Smith 1907; Green 1935; Peterson et al. 1989). Other food items include mostly small fish (minnows, darters, sculpin, lampreys) and also insects, earthworms, snails, tadpoles, and fish eggs.

Cryptobranchus alleganiensis is frequently reported as being cannibalistic in nature (Smith 1907; Bishop 1941; Nickerson and Mays 1973a; Peterson 1985) and in captivity (D. McGinnity, pers. comm.). Smith (1912) recorded cannibalism between larvae as small as 12 cm TL. *Cryptobranchus alleganiensis* have also been reported to ingest large numbers of oocytes and eggs from nests (Nickerson and Mays 1973a; Humphries et al. 2005) and will also cannibalise juveniles (Miller and Miller 2005).

Taxon	Family/Order	Common Name	No	TW (g)	TW (%)	% Salam.
A. davidianus	Crytobranchidae	Chinese giant salamanders	5	190	28	17
Potamon sp.	Potamidae	Freshwater crabs	19	157	23	28
Rana sp.	Ranidae	Bullfrogs	4	85	12	9
Chimarrogale sp.	Soricinae	Water shrews	2	63	9	6
Saurogobio sp., *Cobitis* sp.	Cyprinidae, Cobitidae	Minnows/ carps, loaches	4	61	9	9
Julus sp.	Julidae	Millipedes	1	27	4	2
Lepidoptera, Odonata		Moths, Butterflies, Dragonflies	9	23	3	7
Locusta sp.		Locusts	5	11	2	6
Coleoptera	Coleoptera	Beetles	10	4	1	2
Gordius sp.	Gordioidea	Horsehair worms	2	5	1	1
Twigs			2	9	1	0.
Leaves			7	14	2	3
Gravel			9	43	6	12
TOTAL			79	692		

Table 1. The stomachs of 71 specimens of sub-adult (40) and adult (31) *A. davidianus* collected in the Qinling Dabashan Mountains within Shaanxi Province over a 10 month period from 1995 - 1988. Adapted from; Song (1994). No = Number of *A. davidianus* with the food category in their stomachs; TW = Total weight of each food type, % Salam. = Percentage of *A. davidianus* with each food category in their stomachs.

River (number of salamanders)	Salamander Wt (g)	PI	TW (g)	Prey (% No/% TW)	Prey Wt. (% aquatic/% terrestrial)
Ikuridani River - forest (12)	1800	44	51	Crabs 92/35 Fish 46/29 Insects 23/9 Twigs, rocks 22/4	97%/3%
Ouchi River - agriculture (11)	690	45	188	Fish 27/24 Frogs 64/56 Snakes 9/12 Terrestrial insects 27/36	28%/72%

Table 2. Diet composition (%) of the Japanese giant salamander (*Andrias japonicus*) in the Ikuridani and Ouchi Rivers, the average salamander weight, number of prey items (PI), total weight of prey (TW), the percentage of individual prey (% No) and percentage of total prey weight (% TW), and the percentage of aquatic (% aquatic) and terrestrial (% terrestrial) prey by weight (Okada et al. 2008).

In captivity, *C. alleganiensis* larvae begin to feed at two to four months after hatching (Bishop 1941, J. Briggler, pers. comm.). Captive larvae initially feed on a variety of live food items including blackworms (*Lumbriculus variegates*), mayfly nymphs (*Stenonema* spp.), cladocerans (*Ceriodaphnia* spp., *Simocephalus* spp.), and chopped earthworms (*Lumbricus terrestris*). Once larvae reach a TL of 6 to 8 cm they readily consume small crayfish (*Orconectes* spp.), and from eight to 10 cm they feed on small fish (e.g., *Etheostoma* sp., *Cottus* sp.) and crayfish (*Orconectes* sp.) ~4 cm in TL (Unger 2003; Briggler et al. 2012).

Predators. Dependent on their biogeographic region, size, behavior, and habitat, cryptobranchids may be subject to predation by invertebrates, fish, reptiles, birds, and semi-aquatic mammals (Nickerson and Mays 1973a). *Cryptobranchus alleganiensis* are preyed upon by large turtles, water snakes including *Nerodia*, North American river otters (*Lontra canadensis*), as well as native and exotic fish (Nickerson and Mays 1973a). In 2012 a *C. alleganiensis* in the Allegheny drainage in New York State was found with a sea lamprey wound (M. Jensen, pers. comm.).

All cryptobranchids exude milky skin secretions that have a complex variety of functions including the repelling of predators. The biochemistry (Lai et al. 2002; Lan et al. 1990) of the acrid, milky and sticky skin secretions from *A. davidianus* have been investigated for medicinal purposes. *Andrias japonicus* produce an acrid skin secretion in large amounts until they turn white (S. Okada, pers. comm.) *Cryptobranchus alleganiensis* also produce skin secretions that may be repellent to some predators (Brodie 1971; Gall and Mathis 2010). Nickerson and Mays 1973a observed water soluble secretions that caused fish to vigorously react, and dogs grab or licked live hellbenders immediately releasing them and withdrawing.

Reproduction.
Age and size at reproduction. *Andrias davidianus* mature at five to six years in age (Cheng 1998; Table 3), and *A. japonicus* at a minimum age of eight years (Kuwabara et al. 1989), with both species maturing at 40 to 50 cm TL, and *Cryptobranchus* mature at a slightly lower TL of 30 to 40 cm (Petranka 1998). Therefore, *Andrias* species mature at ~20% of attainable body length and ~ 4% of maximum body weight, whereas *C. alleganiensis* mature at ~ 60% of maximum body length and ~30% of maximum body weight.
Andrias japonicus: CITES (2009) states that the larval period for *A. japonicus* from hatching to metamorphosis (external gill absorption) is ~ 4 to 5 years and another 10 years to reach maturity. At Asa Zoo, an individual *A. japonicus* first spawned at 18 years of age (Kuwabara et al. 1989).
Cryptobranchus alleganiensis: *C. alleganiensis* reach maturity at four to six years of age when approximately 40 cm TL (Nickerson and Mays 1973a: Taber et al. 1975), with males generally sexually maturing at a smaller size than females (Petranka 1998). Smith (1907) gave a maturation age of three to four years, and Bishop (1941) of five to six years for both males and females of *C. a. alleganiensis*.

Age (years)	Body length (cm)	Body feature
1	5	external gills presents
2	15	external gills begin to degenerate
3	30	external gills absents
4	40	sexual maturation
5	50	sexually mature

Table 3. In captivity *A. davidianus* mature at ~five years age at ~50 cm body length (Cheng 1998).

A maturation age of five to six years for *C. a. bishopi* was given by Dundee and Dundee (1965) and Nickerson and Mays (1973a). However, Rogers (2001) considered that *Cryptobranchus* did not mature before seven years of age.
*Hormonal cycle, gonadal development, and breeding season.* Important extrinsic factors that may affect the seasonal cycling of gonadal development in amphibians are temperature, day length, precipitation, and prey availability. However, these factors are often highly correlated and uncoupling their individual influences can be challenging (Duellman and Trueb 1994).
The reproductive cycle of cryptobranchids follow a seasonal cycle ; 1) gonad maturation during the period of increasing water temperature, declining water flows, and high food productivity from spring to summer (Zhang et al. 2006); 2) spawning by *A. davidianus* (Zhang et al. 2006) and *A. japonicus* (Kobara et al. 1980) from summer to late summer with the highest water temperatures, and spawning by *Cryptobranchus* as water temperatures decrease in late summer and winter (Peterson 1988); 3) brooding and larval development to early winter; and 4) a period of inactivity during the coldest part of winter with larvae leaving the den at yolk absorption and finding shelter interstitially in gravel or organic debris (Bishop 1941; Kuwabara et al. 2005; Wu 2010).
Andrias davidianus: The seasonal reproductive cycle in *A. davidianus* begins when water temperatures rise to ~20 ºC during spring and summer from May to late July. The gonads of both female and male *A. davidianus* then reach full development and spawning occurs from August to mid-September (Figure 13).
Andrias japonicus: *A. japonicus* spawns in late July to early September as water temperatures increase (Kobara et al.1980). Water temperatures are lower at spawning (due to lower seasonal maximums) than with *A. davidianus* (Okada et al. 2008) and spawning earlier in the season than with *A. davidianus* (Zhang et al. 2006).
Cryptobranchus alleganiensis: The spawning season of *C. alleganiensis* has been shown to vary within and between different populations of *C. a. bishop* and *C. a. alleganiensis*. *Cryptobranchus a. alleganiensis* in the Appalachian Mountains (New York, Pennsylvania, Alabama, and Tennessee) mainly spawn in September and October, with some spawning extending to December and January.
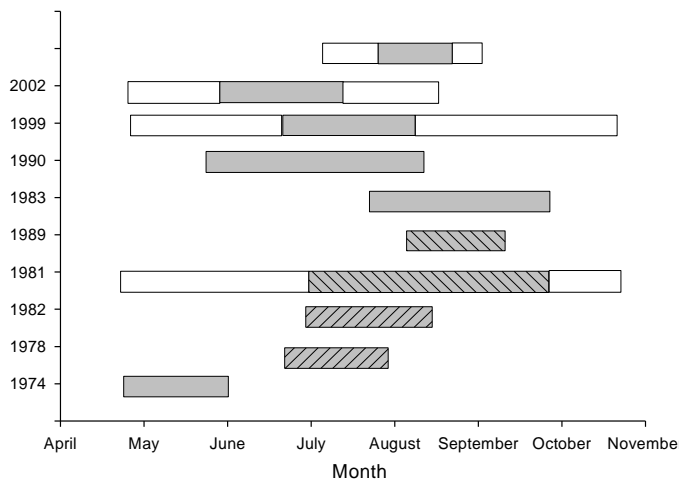
Figure 13. The period of gonadal recrudescence (white fill), then maximal gonadal maturation (grey fill), then gonadal decline (white fill), of the Chinese giant salamander (*Andrias davidianus*). The shadings represent the same stream on different years (Adapted from Zhang et al. 2006).

However, *C. a. alleganiensis* from Indiana, eastern parts of Ohio, and Missouri populations mainly spawn in September (Peterson 1988). *Cryptobranchus a. bishopi* in the Ozarks typically have short breeding seasons mainly from early October to late October (Dundee and Dundee 1965). However the Spring River, Arkansas, populations of *C. a. bishopi* spawn in December and January (Peterson 1988).

Mating and spawning. All cryptobranchids are external fertilizers in the aquatic environment. Mating and spawning behaviors vary widely between the three cryptobranchid species, and both monogamous and polygynous mating systems exist. Characteristic of cryptobranchids are frequent multiple paternities of an egg clutch, eggs laid by several females in one nest site (spawning dens for *Andrias* species), and the brooding of eggs and larvae by dominant males (Kobara et al. 1980, 1985; Kuwabara et al. 2010, Peterson 1988; Liang and Wu 2010).

The spawning dens of *Andrias* are large hollows under rocks or in river banks, with the nest sites of *Cryptobranchus* in hollows under rocks and in crevices (see refs. above). The spawning dens of *A. japonicus* are often found in very small streams at the upper reaches of tributaries; a characteristic not observed in *A. davidianus* or *C. alleganiensis* (Kawamichi and Ueda 1998; Okada et al. 2008).

Andrias davidianus: Liang and Wu (2010) recorded a sequence of breeding behaviors by males including sand-pushing, courting, head-washing, and spawning and fertilisation, then egg-safeguarding. Mating behavior comprised of females entering the spawning den, head exposing, inspection, trailing, cloacal scenting, mouth contact, and mounting the females back. Wu (2010)

reported that during the breeding season, several male *A. davidianus* followed a female with egg strings extending from her cloaca to her spawning den. But then only one male followed the female into her spawning den.

After fertilization the dominant male guarded the eggs and the female left the spawning den. Sometimes more than one mass of eggs, with different developing stages, was observed in the same breeding nest showing that the guarding male mated with more than one female. Therefore, *A. davidianus* displays both monogamous and polygynous mating systems.

Andrias japonicus: Spawning dens are 100 to 150 cm long burrows in or near the river bank with a single underwater entrance (Kobara et al. 1980). Spawning dens may be used during successive years, and both males and females may use more than one spawning den during a breeding season. Females can enter the same spawning den repeatedly to spawn (Kuwabara et al. 2005). During spawning several other males may enter the den and fertilise eggs, and 5 females spawned in the same spawning den over 3 days (Kobara et al. 1980).

Kobara (1985) observed a den owner male accepting other males in the nest in the presence of a gravid female. The owner male bit the upper jaw of the female and 10 minutes before spawning occurred both salamanders started turning and spinning together, with another male joining the pair after three minutes. Two minutes before spawning activity accelerated and the female arched her back and spawned ~100 eggs. Then the dance slowed down and after two minutes a third male entered the nest and joined the activity and within three minutes another 100 eggs were spawned. Then five and again six minutes after the initial spawning all males shed semen and the water became cloudy. In the 12th minute one of the males left the nest. Spawn was again deposited at about 30 minutes and 45 minutes after the initial spawning, and observation ceased as the water was too cloudy with sperm.

Cryptobranchus alleganiensis: With the approach of the breeding period, the sexually mature male *C. alleganiensis* leave their regular shelters and explore hollows under flat rocks, in crevices, usually in moderate to fast currents for suitable nesting sites (Smith 1907; Peterson 1988) where the male prepares a saucer-shaped depression as a nesting site (Bishop 1941). Males wait at their nest sites for females with their head pointing outward, sometimes exposed, and females approaching the spawning nest may enter voluntarily or be guided by the male. Male *Cryptobranchus* may be attracted to chemical cues from females prior to spawning and males have been observed converging around rocks where females are preparing to spawn.

Humphries (2007) observed five and 13 hellbenders at two spawning nest sites within an area approximately 5 m diameter. The male moves alongside or slightly above the spawning female and sways his tail and moves his hind limbs to envelop the eggs with white semen, which is expressed as a cloud or as coagulated strings (Smith 1907). After spawning the male drives the female away from the

spawning nest and then guards the eggs from predation including cannibalism from other *C. alleganiensis* (Petranka 1998).

Egg size and numbers. To facilitate readability we use egg to refer to both eggs and oocytes. A characteristic of cryptobranchids is the relatively constant number of spawned eggs irrespective of species or female size, and a slightly larger egg size in *Andrias* than *Cryptobranchus*. After sexual maturity, as *Andrias* species continue to grow to maximum size, egg numbers only increases slightly, even with an eight fold increase in body weight (Topping and Ingersol 1981; Xiao et al. 2006). This suggests that both egg numbers and size are constrained in cryptobranchids, although the reasons for this are unclear.

The eggs of *Andrias* when spawned are ~5 to 8 mm diameter and then hydrate to ~15 to 20 mm (Cheng 1998) and increase in volume by 185% over the first 5 days of development (Liu et al. 1999). Slightly smaller are *Cryptobranchus* eggs, spawned at ~ 6.5 mm diameter. Eggs of all cryptobranchids are spawned as a gel string consisting of three gel layers. The outer layer forms the cord, with eggs and the two gel layers surrounding them spaced about 3 cm apart and suspended within the cord (Smith 1907; Figure 14). Egg numbers show little variation between cryptobranchid species, with *Cryptobranchus* spawning an average of 350, *A. davidianus* 350, and *A. japonicus* 450.

Andrias davidianus: *A. davidianus* spawn ~300 to 560 eggs of ~ 7 to 8 mm diameter (Ge and Zheng 1994; Xiao et al. 2006; Liu et al. 1999). As *A. davidianus* females age

between five to eleven years old and body weight increases from of 2 to 5 kg, the average egg numbers increase from 300 to 560, then egg numbers remain fairly constant (Xiao et. al. 2006). *Andrias japonicus*: Niwelinski (2007), with captive *A. japonicus*, recorded ~2,400 eggs from three females in one nest (~800 per female), and in another nest ~340 eggs from one female. Kuwabara et al. (1989, 2005) recorded *A. japonicus* as spawning 300 to 700 eggs of 5 to 8 mm diameter.

Cryptobranchus alleganiensis: A single female *C. alleganiensis* deposits approximately 200 to 550 eggs (Nickerson and Mays 1973a; Topping and Ingersol 1981). Several females may use the same nest and produce a combined clutch of more than 2,000 eggs (Bishop 1941; Crowhurst et al. 2009). Smith (1907) reported that an average sized female *C. a. alleganiensis* spawns approximately 450 eggs, while Nickerson and Mays (1973b) reported that three female *C. a. bishopi* maintained in the laboratory laid an average of 270 eggs each.

Correlations between female TL and fecundity as shown by mature gonadal eggs (>3.5 mm diameter) show that fecundity increases with female length, where females ~40 cm length spawn about ~230 eggs and when ~55 cm length spawn ~550 eggs (Topping and Ingersol 1981). Females can take up to two days to spawn (Bishop 1941). Unger (2003) recorded egg numbers of *C. alleganiensis* of 155 to 330 from four nests with the smallest guarding male 35 cm in body length and the largest 49 cm; larger males guarded greater numbers of eggs.

Figure 14. The oocytes of *Cryptobranchus* when spawned are ~6.5 mm diameter. Oocytes of all cryptobranchids are spawned as a gel string consisting of three gel layers. The outer layer forms the cord, with oocytes and the 2 gel layers surrounding them spaced about 3 cm apart and suspended within the cord. *Image by Jeffrey T. Briggler.*

Cryptobranchus eggs are yellow or white and average 6.5 mm in diameter, the gel surrounding the eggs is 1.8 cm thick, the connecting cord 0.5 cm in length, and the distance between eggs is 3 cm (Smith 1907; Figure 14). Topping and Ingersol (1981) estimated that only 50% of the mature eggs in a population were spawned in a given year, as 30% of females did not spawn, and females that did spawn retained on average 25% of their mature eggs.

Brooding and Larval Development. Eggs and larvae of cryptobranchids are guarded by males until the larvae leave the nest (Bishop 1941; Kuwabara et al. 2005; Wu et al. 2010). Hatching periods are dependent on temperature, with higher temperatures more than halving hatching periods for *C. alleganiensis* from ~80 to ~35 days (Bishop 1941).

Larval size at hatching can vary considerably and the eggs hatch over periods of up to one week. Similarly, the time to yolk sac absorption and exogenous feeding is reduced by lower temperatures (Niwelinski 2007). The larvae of *Andrias* hatch at ~3.0 cm TL (Ge and Zheng 1990; Kawamichi and Ueda 1998; Figure 15) and those of *Cryptobranchus* at ~2.5 cm TL (Unger 2003). *Andrias* larvae remain in an embryonic state with external gills until about 3.0 years of age and 20 cm TL (Cheng 1998; Table 3; Figure 15), while gills are lost in *Cryptobranchus* at 1.5 to 2.0 years of age and 12 cm TL (Bishop 1941; Smith 1907; Figure 16,17).

Figure 15. The larvae of the Chinese giant salamander (*Andrias davidianus*) in aquaculture after absorption of the yolk sac and the formation of limbs. *Image Robert Browne.*

Andrias davidianus: In Lushi County, eggs spawned from early to mid-August are guarded by males until they hatch in late September to early October and larvae are then brooded in the nest until exogenous feeding. During early brooding guarding males do not feed, but as the juveniles grow, the males increase foraging and feeding behavior (Wu et al. 2010). Larvae hatch at 2.6 to 3.0 cm TL, start exogenous feeding after 30 days, and hibernate when they reach 4 to 5 cm TL (Ge and Zheng 1990; Figure 14). By the end of the next year, juveniles are 7 to 13 cm TL and 4 to 15g. Haker (1997) reported that metamorphosis gill loss begins when the larvae are 20 to 25 cm TL and 2.5 years old; similarly, Fei et al. (2006) reported that external gills disappear when total length reaches 17 to 22 cm. Considerably faster growth can occur in optimal aquaculture conditions where *A. davidianus* can reach 24 to 30 cm TL after the first year (Wu et al. 2010; Table 3).

Andrias japonicus: After spawning is completed during August and early September, the dominant male remains at the spawning den for over four months to guard the eggs and larvae (Kuwabara et al. 2005). Larvae hatch from eggs in 40 to 60 days at a water temperature from 13 to 20ºC and at 3 cm TL (Kobara et al. 1980; Kobara 1985; Kuwabara et al. 1989; Kawamichi and Ueda 1998). Absorption of the yolk sac and the initiation of exogenous feeding occur about 80 days post-hatch in water temperatures of 3 to 13ºC, but take place in about 30d at an elevated temperature of 16ºC (Niwelinski 2007). By January, the larvae intermittently disperse and have been recorded as far as 600 m downstream from their brooding den (Kobara et al. 1980).

Cryptobranchus alleganiensis: Brooding male *C. alleganiensis* consistently direct oxygen rich currents of water over the developing eggs with their tail and by undulating their lateral folds. Males will also vigorously protect the nest and eggs from cannibalistic conspecifics (Smith 1907; Bishop 1941). Peterson (1988) estimated that eggs hatched in 45 to 84 days depending on the region and water temperature. Bishop (1941) estimated the time to hatching at 68 to 84 days for populations in western New York and Pennsylvania, with eggs hatching over a period of a week. Smith (1912) provides comprehensive data on embryonic development stages.

Figure 16. The yolk sac larvae of the North American giant salamander (*Cryptobranchus a. alleganiensis*) a week after hatching. *Image Sheri Reinsch.*

Figure 17. The larvae of *Cryptobranchus a. bishopi* from the North Fork of the White River, Missouri after absorption of the yolk sac and formation of the limb. *Image by Jeffrey T. Briggler.*

In captivity, the larvae of *C. alleganiensis* at hatching were 2.5 cm TL and grew consistently to 7.0 cm TL at 25 weeks (Figure 17; Unger 2003). The larvae are strongly pigmented dorsally and caudally, and have a prominent yolk sac. Hatchlings have conspicuous mouth and eyes, gills are short and flattened, front limbs terminate in two lobes, and hind limbs are paddle-shaped and unlobed (Bishop 1941). *Cryptobranchus alleganiensis* larvae gills that are not lost until 1.5 to 2 years of age and 10 to 13 cm TL (Bishop 1941, Nickerson and Mays 1973a).

Conclusion. Cryptobranchids are obligatory aquatic and inhabit oligotrophic streams and rivers with temperatures seasonally ranging seasonally from 5 to 25ºC. Cryptobranchids are primarily opportunistic ambush predators with many populations of *C. alleganiensis* living almost entirely on abundant freshwater crayfish, while *Andrias* species generally have a more varied diet, with at least some populations of *A. davidianus* being highly cannibalistic, and *A. japonicus* being cannibalistic during reproduction. Cannibalism particularly with oocytes, has also been shown with *C. alleganiensis*.

All three cryptobranchid species typically mature at an age of five to seven years old and a length of 30 to 40 cm. However, these similar sizes at maturation represent markedly different ratios of size at maturation to species maximum size; in *Andrias* the ratio at maturation is ~20% of attainable body length and 4% of attainable body mass, and in *C. alleganiensis* maturation at ~60% of attainable body length and 30% of attainable body mass. Consequently, a main growth characteristic of *Andrias*, when compared to *Cryptobranchus*, is continued growth well beyond maturation size.

Characteristic of cryptobranchids is the relatively constant number of spawned oocytes irrespective of species or female size, and only a slightly larger oocyte size in *Andrias* than *Cryptobranchus*. After sexual maturity, as *Andrias* species continue to grow to maximum size, oocyte numbers only increase two-fold, even with an eight-fold increase in body weight (Topping and Ingersol 1981; Xiao et al. 2006; Niwelinski 2007). This suggests that egg numbers are constrained in cryptobranchids, although the reasons for this are unclear. Characteristic of cryptobranchids are frequent multiple paternities of an egg clutch, including both monogamous and polygynous systems, with oocytes laid by several females in one nest site (spawning dens for *Andrias* species), and the brooding of eggs and larvae by dominant males (Kobara et al. 1980; Petranka 1998; Liang and Wu 2010).

The eggs and larvae in the nests of *Andrias* and *Cryptobranchus* are attended by males for up to four months. The large larvae then occupy sheltered cryptic microhabitats under small stones or within debris. *Andrias* spawn in late spring and summer when water temperatures are highest, but *Cryptobranchus* spawns as water cools in early autumn and winter. The significance of this difference in reproductive strategies is unknown.

In the final article of this series we will review how knowledge of the evolutionary histories, life histories and ecology of cryptobranchids (presented in Part A and Part B of these reviews) can be used to support their sustainable management both in regional and international arenas. Recent conservation initiatives include increased emphasis on conservation breeding programs combined with rehabitation and supplementation, genetic resource banking, conservation genetic analysis, and greater public engagement through media and events.

We will also discuss how the conservation of cryptobranchids is linked with the conservation of other freshwater stream species, the surrounding habitats and watersheds, basic and applied scientific research, and economic benefits for communities.

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