


Age and growth in a European flagship amphibian: equal performance at agricultural ponds and favourably managed aquatic sites

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Abstract In human-modified landscapes, little is known about the influence of aquatic habitat types on the demographic structure of residing amphibian populations. In the present paper, we focus on a European flagship urodele species (the great crested newt *Triturus cristatus*) at the north-western range of its distribution, applying the method of skeletochronology to compare the ages of individuals retrieved from agricultural ponds with individuals retrieved from aquatic sites favourably managed for *T. cristatus* presence. Median ages ranged between 4.5 and 10.0 years depending on sex and population, and did not differ between the two site categories. Females were on average older than males at both agricultural ponds as well as favourably managed sites. Median ages at sexual maturity (3 years for females and 2 years for males) were 4 years below the most commonly observed age cohort in both sexes, suggesting that young adults regularly forgo reproduction. Mean body size did not differ between agricultural

ponds and favourably managed sites. However, the former were characterised by a higher variance in body size, which is possibly linked to more unstable ecological conditions in agricultural settings. Taken together, our findings confirm that under suitable conditions agricultural ponds can harbour sustainable populations, an important finding for the broad-scale conservation management of *T. cristatus* which does not usually take population demographics into account.

Keywords Demography · Great crested newt · Skeletochronology · *Triturus cristatus* · Urodeles

Introduction

The spatial distribution of populations can be shaped by suitable habitat patches surrounded by unsuitable terrain (for example, in a metapopulation framework, Hanski and Gaggiotti 2004), or can vary more gradually along biotic and abiotic clines (e.g. Endler 1977). Depending on their niche breadth and the spatial scale of investigation, given taxa can also be regarded as persisting in a range of different habitat types, which influence not only their abundance but also the demographic properties of residing populations (Dunning et al. 1992; Kareiva and Wennergren 1995). That population demographics vary across

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habitats is also embedded in the framework of life history theory, which predicts a differential allocation of resources to specific life stages depending on local environmental constraints (e.g. Stearns 2000).

Ponds in agricultural landscapes are important life-support ecosystems for a range of plants and animals which depend on stagnant water (e.g. Williams et al. 2004; Davies et al. 2008). Temperate amphibians are a good example for such a group, and their persistence in areas used for agriculture can indeed be directly related to the availability of ponds for reproduction (Curado et al. 2011; Arntzen et al. 2017). However, while the occupancy of specific agricultural ponds by amphibians can be predicted with information about aquatic and terrestrial habitat determinants (e.g. Denoël and Ficetola 2008; Hartel et al. 2011; da Silva et al. 2012; Boissinot et al. 2019), little is known about the demographic structure of residing populations (but see, for example, Zamora-Camacho and Comas 2017; Bionda et al. 2018). Such information would be useful to assess the long-term viability of amphibians in agricultural landscapes, where the suitability of specific breeding ponds can also be compromised by eutrophication through livestock, influx of agrochemicals, and altered hydroperiods (Beja and Alcazar 2003; Mann et al. 2009; Ferreira and Beja 2013; Koumaris and Fahrig 2016; Bókony et al. 2018), in addition to habitat matrix effects that lead to increased isolation (Joly et al. 2001; Sawatzky et al. 2019).

The age of amphibians exposed to seasonal environments can be determined through skeletochronology (the counting of lines of arrested growth in bone cross sections; for a review see, for example, Sinsch 2015), and a large body of literature using this method has revealed that demographic population structures can vastly differ across latitudes and altitudes both within as well as between species (e.g. Zhang and Lu 2012; Oromí et al. 2012; Hjernquist et al. 2012; Liao et al. 2016; Sinsch and Dehling 2017; Stark and Meiri 2018). Because time-limited growth determines size which in turn is related to fecundity, longevity in amphibians can be interpreted as the result of life history strategies to maximise reproductive output under given constraints (Sinsch et al. 2010). That age structures of neighbouring populations can markedly differ from each other when situated along steep ecological clines (e.g. Miaud et al. 2001; Cogălniceanu et al. 2017) suggests that mosaics of different habitats typical for human-modified landscapes could

also result in spatially heterogeneous demographics through differential local conditions.

Due to its requirement of rather large, well-vegetated ponds, the great crested newt (*Triturus cristatus*) is a typical inhabitant of traditionally managed agricultural areas as well as other landscapes in northern and central Europe (e.g. Hartel et al. 2010; Visser et al. 2016). Initially due to its status as a European protected species (listed in Annexes II and IV of the EU Natural Habitats Council Directive 92/43/EEC), *T. cristatus* has in the twenty-first century developed into a high-profile species for the use of translocation and habitat mitigation in species conservation (Edgar et al. 2005; Lewis et al. 2017; Matos et al. 2017), the use of habitat descriptors to predict occurrence and abundance in a management context (Unglaub et al. 2015, 2018; Miró et al. 2017; O'Brien et al. 2017), and the development of detection methods and associated analytical frameworks for large-scale monitoring (Biggs et al. 2015; Griffiths et al. 2015; Buxton et al. 2017; Harper et al. 2018). However, despite a disproportionate attention from conservation practitioners, *T. cristatus* continues to decline across most of its range (e.g. Jehle et al. 2011), among others questioning whether modern agricultural environments are suitable to form long-term demographically stable populations. The aim of the present study is to compare age at maturity, mean age, and growth of individuals residing in farm ponds with individuals breeding at aquatic sites which are favourably managed for *T. cristatus* presence.

Methods

The study took place across 13 ponds situated in Lancashire, North West England, in a roughly 36×138 km area (Table 1). All ponds were on flat or slightly hilly terrain. Six ponds were classed as favourably managed sites (ponds in local nature reserves or gardens managed to support *T. cristatus* populations), and seven ponds were classed as agricultural sites (Table 2). That the two site categories were spatially intermixed within the study area precluded any bias, for example, due to spatial autocorrelation. Geographic distances between ponds from the two site categories exceeded the migration capabilities of *T. cristatus*, preventing that, for

Table 1 Basic data across the 13 *Triturus cristatus* study populations

Pond	National Grid Reference	<i>n</i> (females)	<i>n</i> (males)	<i>N</i> (2013)	<i>N</i> (2014)	<i>N</i> (2015)	<i>N</i> (2016)
LHs	SD 54392 42647	23, 2	8, 4	–	–	–	–
LH	SD 53726 42767	3, 0	7, 0	110.1 ± 16.6	78.9 ± 13.4	39.3 ± 5.6	51.1 ± 5.6
Mhp	SD 59260 36544	8, 15	10, 10	32.9 ± 12.5	129.0 ± 170.7	127.9 ± 45.4	–
Marl	SD 59383 36262	22, 5	20, 9	331.4 ± 65.7	195.7 ± 74.3	261.7 ± 70.0	–
MS	SD 76775 08712	15, 12	19, 4	–	225.9 ± 92.6	245.3 ± 82.0	–
SF	SD 67940 07427	13, 12	14, 11	70.0 ± 13.8	123.6 ± 55.5	100.0 ± 16.2	85.8 ± 12.3
WH	SD 71951 19333	22, 7	22, 8	–	417.2 ± 159.4	193.0 ± 47.0	290.2 ± 20.5
AB	NY 61764 28207	0, 28	0, 25	–	–	282.1 ± 15.1	–
Bgp	SD 72943 13483	17, 1	4, 2	42.0 ± 5.9	31.9 ± 6.4	15.0 ± 2.2	19.0 ± 1.9
GH	SD 39741 07803	16, 3	16, 7	665.5 ± 381.1	753.0 ± 29.2	159.0 ± 9.2	–
HB	SD 56757 12708	18, 0	15, 0	–	–	–	–
RC	NY 46607 29327	22, 0	18, 0	–	–	–	–
R	SJ 68519 90135	18, 0	19, 0	–	–	–	–

The sites above and below the line represent agricultural ponds and favourably managed sites, respectively; *n*: number of samples for skeletochronology in the two study years 2014 and 2015; *N*: population size estimate ± standard errors, with years in brackets. Based on the National Grid Reference, ponds can be located, for example, on Google Maps using <https://gridreferencefinder.com/>

example, favourably managed ponds could harbour source populations for agricultural ponds.

Field work was conducted during the breeding season (March–June) between 2013 and 2016. Study individuals were captured using dip nets and, most commonly, mesh funnel traps following Madden and Jehle (2013). SCL (snout-cloaca length, in mm) was measured from the tip of the snout to the end of the cloaca using a ruler. For nine ponds (six farm ponds and three favourably managed sites), yearly population size estimates were obtained based on capture–recapture calculations using Begon’s weighted mean (Begon 1979), based on photographs of variable ventral spot patterns as a means for individual recognition. Because capture sessions took place at maximally 1-week intervals, we assumed closed populations and equal detectability among individuals.

Toe clips for skeletochronology were taken in 2014 and 2015, using a sharp scalpel to remove the third digit of the left and right foot in 2014 and 2015, respectively, stored in absolute ethanol in individual 1.5-ml Eppendorf tubes. The wound was sprayed with the antiseptic Bactine, and clipped newts were immediately released back into the pond; ventral spot patterns of individuals toe clipped in 2014 and 2015

were compared to prevent the sampling of identical individuals in both years. The scalpel was sterilised using a flame, and toe clipping was performed after the newts had been measured and photographed. The third segment of the toe was used to identify the lines of arrested growth (LAGs). Preparation of the toes largely followed the standard laboratory procedures detailed by Sinsch (2015) and Angelini et al. (2015). Soft tissue was gently scraped from the amputated toe, which was placed in 3% nitric acid for 75 min, followed by soaking in water overnight. Each toe bone was cut into sections of 10–16 µm using a cryostat microtome at a temperature of – 20 °C. The sections were stained with Ehrlich’s haematoxylin solution until growth marks became visible (e.g. Smirina 1972). Sections were stained and mounted onto slides, and LAGs were counted using 200×–400× magnification. Whenever possible, age at sexual maturity was considered as the youngest age with reduced inter-LAG spaces (“rapprochement”, see, for example, Francillon-Vieillot et al. 1990; Sinsch 2015).

The software PAST (Hammer et al. 2001) was used to conduct statistical tests. To characterise possible differences in growth rates between agricultural and favourably managed sites, we used the nonlinear regression option in Minitab 18 to construct von

Table 2 Verbal description of aquatic breeding sites used in this study

Site	Description
LHs	Tenanted farm managed for beef and dairy cattle. Six ponds in total, two with <i>T. cristatus</i> presence (see LH below). Pond size approximately 30 × 35 m
LH	On the same farm as LHs, at approximately 300 m distance from it separated by a road. Pond size approximately 15 × 15 m
Mhp	Tenanted farm managed for silage production with sheep grazing in winter. Including seven ponds, five of which occupied by <i>T. cristatus</i> . Approximately 25 × 20 m in size
Marl	On the same farm as Mhp, at approximately 400 m distance from it. Pond size approx. 15 × 15 m
MS	Tenanted farm, intensely grazed by beef cattle and horses. The farm includes a total of five ponds, four of which have been confirmed as <i>T. cristatus</i> breeding ponds. One of these is a temporary pool, and another is shallow and devoid of macrophyte vegetation
SF	Tenanted farm, grazed intensively by horses and beef cattle. Five ponds on the farm, only one suitable for <i>T. cristatus</i> due to the presence of fish
WH	Single pond on tenanted upland farm grazed by sheep
AB	Ornamental pond approximately 4 m in diameter, kept fish-free; situated in the parkland of a country house owned by the British National Trust
Bgp	Four ponds (10 × 2 m, 7 × 2 m, and twice 1.2 × 1.2 m) maximally 2 m apart in an urban garden managed for wildlife (terrestrial habitats include dry stone walls, log piles, and a large compost heap)
GH	A large pond (approx. 20 × 30 m) in a private nature reserve surrounded by managed woodland and meadows
HB	Pond on a private nature reserve originating from a former clay quarry. Main <i>T. cristatus</i> breeding pond in of a network of seven ponds within 100 m distance
RC	Former clay extraction site, recently managed by Natural England in conjunction with a proposal for a future holiday village
R	Disused brickworks site, designated SSSI (Site of Special Scientific Interest) due to prominent <i>T. cristatus</i> presence. One of at least 20 connected ponds managed by wardens

The sites above and below the line represent agricultural ponds and favourably managed sites, respectively

Bertalanffy growth curves (von Bertalanffy 1938). Following Arntzen (2000) and Hemelaar (1988), we used the equation $SUL_t = SUL_{max} - (SUL_{max} - SUL_{met})e^{-k(t-t_{met})}$, where SUL_t is the average SUL at the age of t years, SUL_{max} is the estimated average maximum SUL that can be reached, SUL_{met} is the average SUL at metamorphosis (fixed to 35.8 mm following Arntzen 2000), and t_{met} is the proportion of the first year of life already lapsed at metamorphosis (set as 0.6 given that oviposition peaks in April and metamorphosis takes place in late summer, see Arntzen 2000); k is the curvature parameter of the growth curve, describing the rate at which SUL_{max} is approached.

Results

Estimated population sizes ranged across more than one order of magnitude from 15 to 753 individuals, with differences between ponds vastly exceeding any differences between agricultural ponds and favourably managed sites (Table 1). In total, we determined the age of 282 female and 252 male *T. cristatus* (534 individuals, 305 of which from farm ponds and 229 from favourably managed sites). An example toe cross section highlighting the counted LAGs is shown in Fig. 1. We found no significant relationships between mean age and estimated population size in males or females (Pearson correlations, $p > 0.05$ in all cases, detailed data not shown), corresponding to a lack of marked temporal trends in median ages for those populations for which data from at least two successive years were available (Table 1). While our sampling dates were not sufficiently consistent to allow for

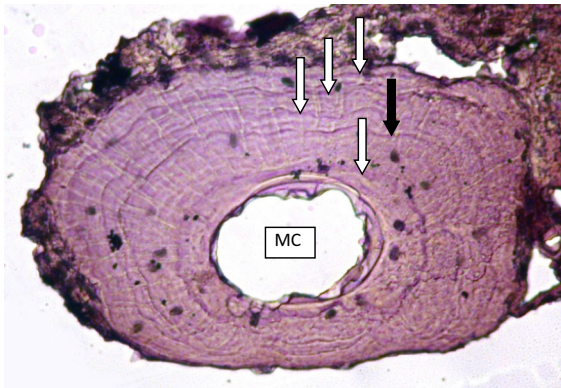


Fig. 1 Stained toe section from a male *Triturus cristatus* captured on May 2, 2014 (population RC). LAGs are indicated with arrows; this individual was 5 years old and sexually mature at 2 years of age (black arrow). MC medullar cavity

direct comparisons between ponds, we recorded a disproportionately high number of old individuals in captures early in the breeding season compared to later capture dates (age classes $\leq 5, 6, 7, 8,$ and > 8 years; Kruskal–Wallis test for differences in day of first capture, females: $\chi^2 = 26.94$, $d.f. = 4$, $p < 0.01$; males $\chi^2 = 15.79$, $d.f. = 4$, $p < 0.01$).

Age and size structure

For females, median ages ranged between 7 and 10 years at favourably managed sites, and between 6.5 and 10 years at farm ponds; corresponding numbers for males were 5–8 years and 4.5–8 years, respectively (Table 3). For both site categories, females were on average older than males (Mann–Whitney U tests: agricultural sites, $z = -3.21$, $p = 0.002$; favourably managed sites, $z = -3.05$, $p = 0.002$; see also Fig. 2). The maximum observed age was 15 years for females (one individual from a favourably managed site) and 12 years for males (one individual from the two site categories each). Median age at sexual maturity as determined by skeletochronology was 3 years in females (range 2–4 years), and 2 years in males (range 2–4 years), a difference which was highly significant (Chi-square test for independence, $d.f. = 2$, $\chi^2 = 80.81$, $p < 0.001$). Females were significantly larger than males in both site categories (farm ponds: average SCL females = 74.45 mm, average SCL males = 71.12 mm; favourably managed sites: average SCL females = 75.68 mm,

average SCL males = 71.29 mm; t tests, $p < 0.001$ in both cases).

Comparisons between agricultural ponds and favourably managed sites

Agricultural ponds and favourably managed sites did not differ in overall ages attained (Mann–Whitney U tests: females, $z = -0.12$, $p = 0.905$; males: females, $z = -0.17$, $p = 0.861$), at variances which were indiscernible from each other (F tests, females: $F = 1.20$, $p = 0.29$; males: $F = 1.10$, $p = 0.62$). Age at sexual maturity also did not differ between the two site categories (Chi-square tests for independence, females: $d.f. = 2$, $\chi^2 = 6.07$, $p = 0.05$; males: $d.f. = 2$, $\chi^2 = 3.54$, $p = 0.17$). Furthermore, mean SCL did not differ between favourably managed sites and agricultural ponds (t tests: females, $t = -1.55$, $p = 0.112$; males, $t = 0.21$, $p = 0.825$). Size differences could, however, also be due to differential degrees of size variation. Indeed, SCL data derived from farm ponds, where both the smallest as well as the largest individuals for both sexes were recorded, had a significantly higher variance than SCL data derived from favourably managed sites (F tests, females, $F = 1.50$, $p = 0.018$; males, $F = 1.66$, $p = 0.002$).

Age–size relationships characterised through von Bertalanffy growth curves reveal a large amount of variation in SCL for given ages in all categories tested (Fig. 3). Estimated asymptotic SCL was larger for agricultural ponds in both sexes, and the growth parameter k was larger in favourably managed sites in females but not in males.

Discussion

Although European amphibians regularly occupy a mosaic of farmland and more natural areas (Maes et al. 2008; Couto et al. 2017; Arntzen et al. 2017), the general value of agricultural ponds as breeding habitats to support self-sustaining populations remains a matter of debate. Population genetic studies, for example, regularly demonstrate that increased agricultural activities cause a decrease in overall genetic variation, likely resulting from a combination of habitat deterioration and lack of connectivity through disappearing stepping-stone networks of ponds (e.g. Crawford et al. 2016; Lenhardt et al. 2017). Such

Table 3 Median and range of average age across the 13 *Triturus cristatus* study ponds, with ranges shown in brackets

Pond	Sex	Median age (2014)	Median age (2015)
LHs	Females	10 (6–14)	8.5 (8–9)
	Males	8.5 (5–11)	4.5 (4–8)
LH	Females	10 (9–11)	–
	Males	8 (5–10)	–
Mhp	Females	6.5 (5–8)	7 (5–14)
	Males	5 (4–11)	7 (6–10)
Marl	Females	7 (4–11)	8 (7–12)
	Males	6.5 (4–10)	8 (5–11)
MS	Females	7 (5–10)	6 (4–7)
	Males	7 (5–9)	6 (5–7)
SF	Females	7 (3–8)	6 (5–8)
	Males	6 (4–10)	6 (5–7)
WH	Females	7 (3–12)	7 (5–9)
	Males	6 (4–12)	6.5 (5–9)
<hr/>			
AB	Females	–	10 (7–15)
	Males	–	8 (5–12)
Bgp	Females	7 (5–10)	7
	Males	6 (5–9)	7.5 (7–8)
GH	Females	7 (4–9)	7 (7–8)
	Males	6 (4–11)	7 (5–9)
HB	Females	6 (5–7)	–
	Males	5 (3–8)	–
RC	Females	7 (4–11)	–
	Males	5 (4–11)	–
R	Females	7 (5–9)	–
	Males	7 (4–9)	–

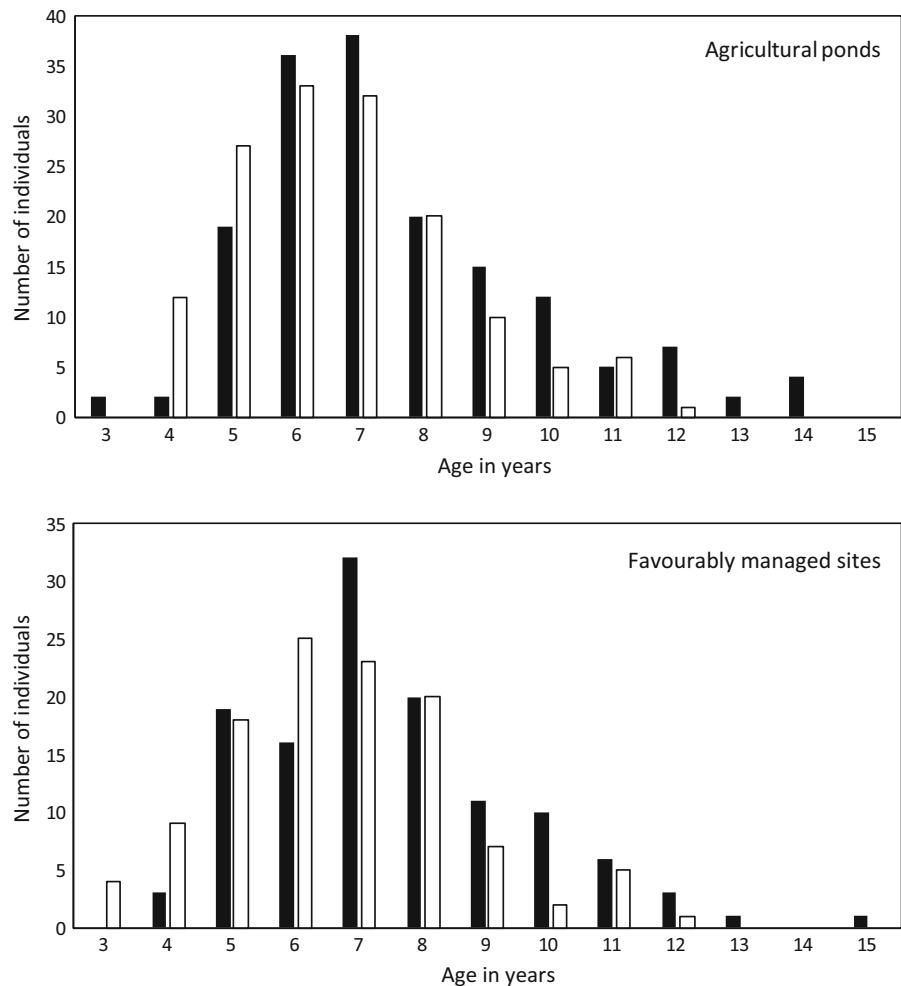
The sites above and below the line represent agricultural ponds and favourably managed sites, respectively. *n* refers to sample size

evidence is, however, contrasted by the general observation that farm ponds represent important life-support ecosystems for the local occurrence of many amphibians, particularly when allowing for spatial connectivity (e.g. Knutson et al. 2004; Hartel et al. 2011; Boissinot et al. 2019). The present paper reveals that individuals of the great crested newt *T. cristatus*, a European flagship species for amphibian conservation, attain comparable longevity and mean growth irrespective of whether they were derived from agricultural ponds or from favourably managed breeding sites.

Care is required when interpreting our findings because the selection of particularly agricultural ponds was based on the presence of sizable *T. cristatus*

populations rather than, for example, a randomisation process. As a consequence, the agricultural ponds under study represent particularly successful breeding sites in agricultural environments rather than an unbiased selection of typical ponds. Also, while skeletochronology is a well-established method to determine the age of amphibians, obtained data do not always represent truly attained ages (for example, due to endosteal resorption particularly in long-lived individuals, Wagner et al. 2011; Sinsch 2015). *Triturus cristatus* individuals from northern latitudes are generally characterised by higher longevity compared to individuals from southern latitudes, with mean ages ranging from 3 to 8 years depending on the population (Hagström 1977; Dolmen 1982; Francillon-Vieillot

Fig. 2 Age structure of *Triturus cristatus* populations across seven agricultural ponds (top) and six favourably managed sites (bottom). Black bars: females; white bars: males



et al. 1990; Miaud et al. 1993; Sinsch et al. 2003; Unglaub et al. 2018; Palau Daval et al. 2018). Our study site is situated at the north-western part of the *T. cristatus* distribution, conforming to median ages which are at the upper range of previously published studies.

At breeding ponds, the age class represented by the highest number of individuals was six (males) and seven (females) years of age (see Fig. 2 and Table 3), which is 4 years older than the median ages at maturity for both sexes as determined by reduced inter-lag spaces (2 and 3 years, respectively). One explanation for low numbers of young adults would be low levels of recruitment in the years before the study was conducted. However, given that the data stem from a range of ponds across > 100 km in latitude, we consider it unlikely that the study populations were

demographically coupled. Rather, our inferences suggest that young adults do not consistently partake in reproduction, highlighting a time lag between the onset of devoting energy to breeding to the actual participation in breeding activities. Capture–recapture studies across a range of amphibian species have revealed that particularly females do not participate in every reproductive opportunity, which is likely linked to high energetic requirements of producing eggs (Church et al. 2007; Muths et al. 2010; Cayuela et al. 2014). Our inferences suggest that not only females but also young adults regularly forgo reproduction, possibly biasing average ages as recorded at breeding ponds upwards. A combined age and sex bias of breeding frequencies might have contributed to the higher mean ages for females at our study site, which has not previously been recorded for *T. cristatus* (see

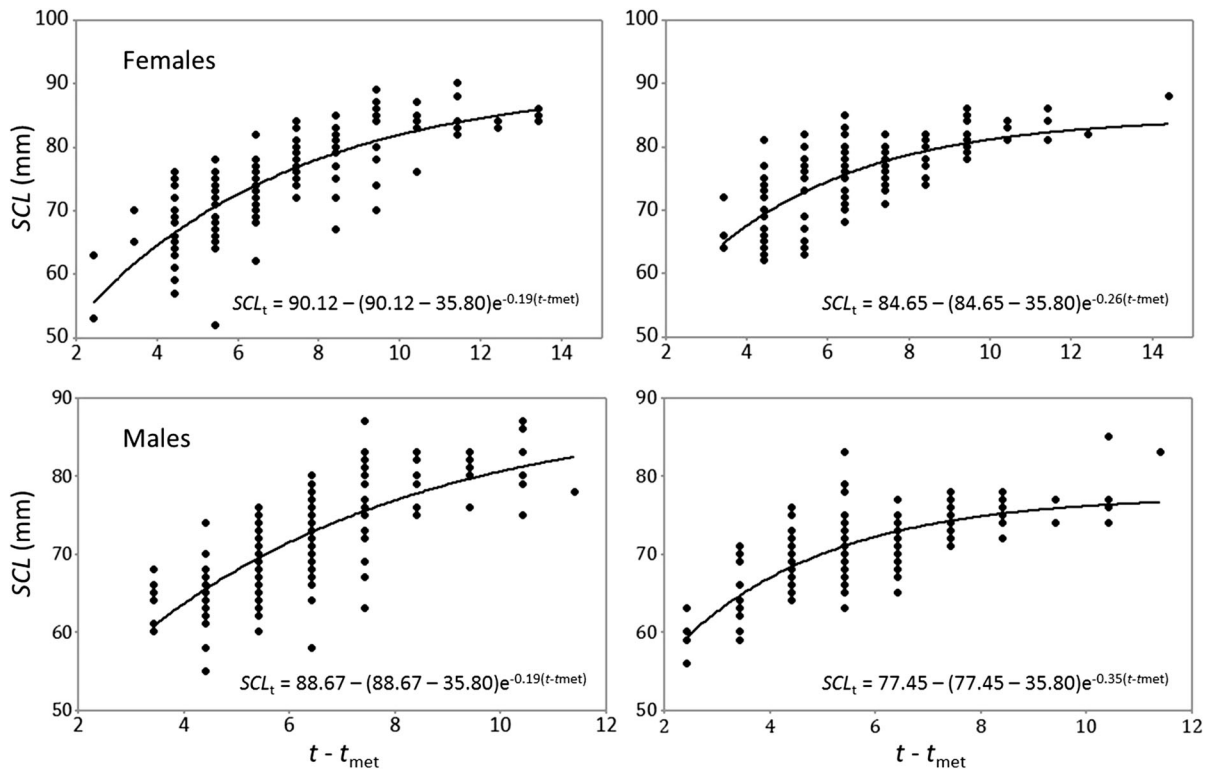


Fig. 3 Von Bertalanffy growth curve comparisons between agricultural ponds (left panel) and favourably managed sites (right panel) for *Triturus cristatus*. Top: females, bottom: males;

SCL: snout-cloaca length, *t*: age in years, *t*_{met}: age at metamorphosis (set at 0.6, for details see text)

Hagström 1977; Dolmen 1982; Miaud et al. 1993; Francillon-Vieillot et al. 1990; Sinsch et al. 2003). That older individuals tend to arrive before younger individuals has been previously reported (Sinsch et al. 2003), and Arntzen (2002) further showed that *T. cristatus* males tend to arrive at breeding ponds before females. Because tissue samples for skeletochronology were not evenly taken across the entire reproductive season, we are, however, unable to ascertain whether such phenomena have affected our inferences.

A main finding of the present study is that individuals stemming from agricultural ponds were characterised by a higher degree of variation in body size, leading to a higher estimated maximal body size in the growth models despite a lack of difference in average size. For another set of *T. cristatus* populations, body condition was inversely related to population size, which in turn was positively related to habitat suitability (Unghlaub et al. 2018). Because

population sizes did not differ between agricultural ponds and favourably managed sites, it is unlikely that they can be accounted for the observed differences in body size variation. Rather, the observed higher variation in body size in farm ponds might be due to higher within- and between-year fluctuations of ecological determinants for growth at early developmental stages (e.g. temperature: Griffiths and de Wijer 1994; water level to determine density: Unghlaub et al. 2018; Cayuela et al. 2018). In a similar investigation comparing urban and rural ponds, Jennette et al. (2018) found that urban storm water ponds are inhabited by on average smaller individuals at comparable age structures, which they also attributed to environmental conditions experienced at the larval and juvenile stage. Future studies could investigate whether habitat-dependent participation in breeding opportunities influences resource allocation to growth (for example, hybrid crested newts which are sterile or have low reproductive success attain larger sizes,

Arntzen et al. 2018), and whether terrestrial environments typical for agricultural areas have an influence on growth and size (distinct habitats provided by farmland are preferentially utilised by amphibians, e.g. Salazar et al. 2016).

What can we learn from the present study for the conservation management of *T. cristatus*? That suitable agricultural ponds, although not specifically managed for *T. cristatus*, can harbour populations with demographics which are indiscernible from, for example, local nature reserves reinforces their value for sustainable local occurrences. While we did not use quantitative approaches such as population viability analysis or spatial modelling to predict the viability of our demes (e.g. Auffarth et al. 2017; for examples on *T. cristatus* see Halley et al. 1996; Griffiths and Williams 2000), our data do not suggest that populations inhabiting agricultural ponds are exposed to higher demographic extinction risks than populations from favourably managed sites. This is particularly important, as management practices for *T. cristatus* are increasingly based on large-scale data such as derived from environmental DNA, which are as yet largely unable to take population sizes and demographics into account (Biggs et al. 2015; Buxton et al. 2017; Harper et al. 2018). It, however, needs to be taken into account that our study was unable to assess the negative consequences of habitat fragmentation and loss, which can reduce the population persistence of *T. cristatus* as it leads to a lack of pond connectivity (e.g. Halley et al. 1996). The high protection status of *T. cristatus* coincides with similar habitat requirements of more common syntopic amphibians (Denoël et al. 2013), suggesting that preventing suitable farm ponds from deteriorating or disappearing, for example, through pond restoration or the creation of new breeding sites through agro-environment schemes (Sayer et al. 2012; Maes et al. 2008), would benefit a range of other species.

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