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Population ecology of endangered white-clawed crayfish (*Austropotamobius pallipes* s. str.) in a small rhithral river in Germany

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ABSTRACT

Key-words: *population dynamics, imperiled species, white-clawed crayfish, stone crayfish, Austropotamobius*

Sound knowledge on distribution and ecology of imperiled species is an essential prerequisite for effective conservation planning. Here, we report the distribution and autecological traits of a newly discovered population of critically-endangered white-clawed crayfish (*Austropotamobius pallipes* s. str.) in a small river in southwestern Germany. Using an established crayfish survey protocol, we detected white-clawed crayfish in a river stretch of 4.5 km, with an estimated abundance of 1.4 ± 0.2 indiv.$\cdot$m^{-2}. The sex ratio was even and sexual maturity was attained at approximately 25 mm carapace length (*CL*). Life-history traits, as assessed using Von Bertalanffy's growth function, indicate a life history most similar to populations in France, with longevity, asymptotic size, and growth performance index being higher in males than in females (11 y, 46 mm *CL*, and 2.8 and 9 y, 41 mm *CL*, and 2.7, for males and females, respectively). Estimated fecundity ranged from 9 to 135 eggs$\cdot$female^{-1} (mean: 90 ± 28). White-clawed crayfish were also found in lower reaches of small tributary streams, of which one also featured endangered stone crayfish (*Austropotamobius torrentium*). A syntopic occurrence of both species was recorded for the first time within a short stretch. Implications for species conservation are discussed.

RÉSUMÉ

Écologie de la population d'écrevisses à pattes blanches, en danger (*Austropotamobius pallipes* s. str.) dans un petit torrent en Allemagne

Mots-clés : *dynamique des populations, espèces en péril, écrevisse à pattes blanches,*

Une bonne connaissance sur la distribution et l'écologie des espèces en péril est une condition essentielle pour la planification d'une conservation efficace. Ici, nous rapportons la distribution et les traits autécologiques d'une population nouvellement découverte d'écrevisses à pattes blanches en danger critique (*Austropotamobius pallipes* s. str.) dans une petite rivière du sud-ouest d'Allemagne. Utilisant un protocole standard de suivi de l'écrevisse, nous avons détecté l'écrevisse à pattes blanches dans un tronçon de la rivière de 4,5 km, avec une abondance estimée de 1,4 ± 0,2 indiv$\cdot$m^{-2}. Le sexe ratio était de un et la maturité sexuelle est

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écrevisse de torrent, Austropotamobius

atteinte à environ 25 mm de longueur de carapace (CL). Les traits de vie, évalués en utilisant la fonction de croissance de Von Bertalanffy, indiquent une histoire de vie très semblable à celle des populations en France, avec la longévité, la taille asymptotique, et l'indice de performance de croissance plus élevés chez les mâles que chez les femelles (11 ans, 46 mm CL, et 2,8 et 9 ans, 41 mm CL, et 2,7, pour les mâles et les femelles, respectivement). La fécondité estimée variait de 9 à 135 oeufs·femelle^{-1} (moyenne : 90 ± 28). L'écrevisse à pattes blanches a également été trouvée dans les tronçons inférieurs de petits affluents, dont l'un a également présenté des écrevisses des torrents en danger (*Austropotamobius torrentium*). Une occurrence syntopique des deux espèces a été enregistrée pour la première fois dans un court tronçon. Les implications pour la conservation des espèces sont discutées.

INTRODUCTION

Freshwater crayfish (Crustacea: Decapoda: Astacida) represent the largest mobile invertebrates in temperate inland waters and are often considered as keystone species (Nyström, 1999; Holdich, 2003; Stenroth *et al*., 2008). Native crayfish are a vital part of intact freshwater ecosystems and represent flagship species for conservation efforts (Füreder and Reynolds, 2004; Reynolds and Souty-Grosset, 2012). In this context, they can be used as "umbrellas" for the conservation of sympatric species with similar habitat requirements (Füreder *et al*., 2003; Reynolds and Souty-Grosset, 2012).

White-clawed crayfish (*Austropotamobius pallipes* species complex) is the naturally rarest species among the three native crayfishes in Germany. In contrast to the widespread noble crayfish (*Astacus astacus*) and the stone crayfish (*Austropotamobius torrentium*), which occurs throughout most of southern Germany (Souty-Grosset *et al*., 2006; Chucholl and Schrimpf, 2015), the native range of the white-clawed crayfish is naturally restricted to a few catchments of the Upper Rhine drainage in the southwesternmost part of Germany. These occurrences are situated along the western and southern slopes of the Black Forest and represent the northeastern distribution limit of white-clawed crayfish in central Europe (Troschel, 1997; Souty-Grosset *et al*., 2006). They belong to the western lineage of white-clawed crayfish (*A. pallipes* s. str.) and exhibit relatively deep divergence to the southern clade, which is considered a distinct species ("*A. italicus*") by some authors (*cf*. Trontelj *et al*., 2005; Chucholl *et al*., 2015).

White-clawed crayfish are ecologically demanding and mostly occur in pristine or semi-natural small streams (1–8 m in width) with a mosaic of microhabitat patches at moderate elevations of 200 to 550 m a.s.l in Germany. They are usually restricted to areas without intensive riparian land-use and are frequently associated with natural riparian vegetation composed of broad-leafed trees (Troschel, 1997; Chucholl and Dehus, 2011). Since its discovery in the late 1980s in Germany (Troschel and Dehus, 1993), several white-clawed crayfish populations have disappeared and a recent assessment against the IUCN red list criteria yielded a critically-endangered status for Germany (Chucholl and Dehus, 2011). This coincides with a regression of white-clawed crayfish throughout most of its native range, including an estimated decline of somewhere between 50–80% in England, France and Italy in the last decade (Füreder *et al*., 2010).

White-clawed crayfish are generally threatened by human-induced environmental change, including deterioration of habitats and water pollution (Füreder *et al*., 2010, and citations therein). An additional, imminent threat is the ongoing spread of non-indigenous crayfish species (NICS) in combination with crayfish plague. NICS of North American origin frequently outcompete native crayfish for habitats and act as reservoir hosts for the crayfish plague agent, *Aphanomyces astaci*, which causes devastating mass mortalities among native crayfish (Souty-Grosset *et al.*, 2006; and citations therein). Particularly dangerous for white-clawed

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crayfish is the North American signal crayfish (*Pacifastacus leniusculus*), which actively invades remaining refuges (Chucholl and Dehus, 2011; Holdich *et al*., 2014).

Given the critically-endangered status of white-clawed crayfish in Germany, species conservation projects have been initiated (Chucholl and Dehus, 2011). Among other efforts, these include habitat protection, restocking of suitable and safe habitats, and efforts to halt the spread of NICS (*cf*. Chucholl, 2014). An essential prerequisite for all of these conservation efforts is sound knowledge on distribution, population dynamics, and life history of white-clawed crayfish (*cf*. Souty-Grosset *et al*., 2006; Ghia *et al*., 2015). Previous studies on white-clawed crayfish suggest high latitudinal variation in population ecology (summarized in Ghia *et al*., 2015) and very little is known about its life history and populations dynamics in Germany.

The aim of this study was therefore to assess the distribution, abundance, and life-history traits of a white-clawed crayfish population in a small river in southwestern Germany in order to further our understanding of this highly endangered species and to facilitate its conservation. In particular, we used an established crayfish survey protocol to explore the spatial extent and abundance of the population, and estimated life-history traits from size-frequency distributions by means of the Von Bertalanffy's Growth Function (VBGF) (*cf*. Scalici *et al*., 2008; Ghia *et al*., 2015).

MATERIALS AND METHODS

> *STUDY SITE*

The study was carried out in the River Brugga, which is a small summer-cool river near the city of Freiburg (southwestern Germany). The white-clawed crayfish population within the river was only recently discovered (unpubl. data Nagel, 2013), although it has been a long known fact that a small tributary stream of the river features an abundant white-clawed crayfish population (Biss, 1996).

The River Brugga has a total length of 15.4 km and is one of the major tributaries in the headwater area of the Dreisam catchment, which discharges into the Rhine system. It arises at an altitude of 1305 m a.s.l. from two spring-fed brooks, and flows in a northwestern direction through a basin-shaped valley until its confluence with the River Dreisam at an altitude of 326 m a.s.l. (Figure 1). The River Brugga represents a rhithral river that is characterized by a high flow-rate, a stony river bed and a mean summer temperature below 20 °C (Illies, 1961). The investigated stretch was 8.5 km long and started below the headwater section with high gradients (Figure 1). Width averaged 4.5 m and depth ranged from 0.1 m in riffles to 1.2 m in pools. Mean flow rate in June, 2014 varied from 0.12 $\text{m}\cdot\text{s}^{-1}$ to 1.14 $\text{m}\cdot\text{s}^{-1}$ (Schiltknecht flow measuring device Mini Air 2).

Throughout most of the investigated stretch, the River Brugga features pristine or close to natural conditions with riparian vegetation consisting of deciduous trees, mostly alder (*Alnus glutinosa*), shrubs and grassland. The structure of the river bank is dominated by alder roots and rocks, often forming overhanging banks. The sparse submerged vegetation in the summer months was dominated by willow moss (*Fontinalis spp.*). The benthic invertebrate fauna was mostly composed of stonefly (Plecoptera), mayfly (Ephemeroptera) and caddisfly (Trichoptera) larvae, as well as gammarids (*cf*. Biss, 1996). Amphibians, salmonid fish and bullhead (*Cottus gobio*) were sporadically noticed.

Physico-chemical water parameters (pH, conductivity, water temperature, and dissolved oxygen levels) were weekly measured from mid-April to mid-June, 2014 (WTW sensors, onset T-Logger). The levels of pH ranged from 6.2 to 7.0 and conductivity was low with values between 74 and 173 $\mu\text{S}\cdot\text{cm}^{-1}$. The recorded water temperature increased from 8.0 °C in April to 16.1 °C in June with dissolved oxygen ranging from 5.5 to 14.6 $\text{mg}\cdot\text{L}^{-1}$.

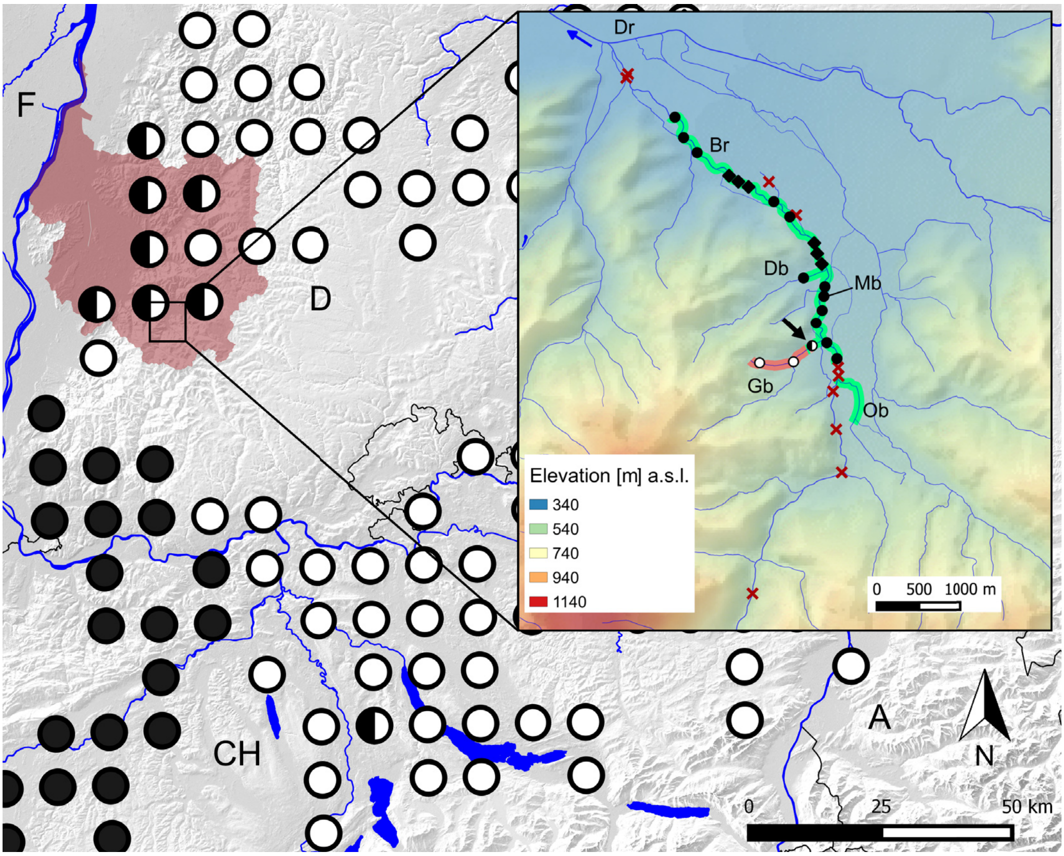

Figure 1
Distribution of A. pallipes s. str. (black dots) and A. torrentium (white dots) in southwestern Germany and neighboring territories shown as presence in 10 × 10 km grid cells (EEA reference grid) (background map). The red colored area highlights the River Dreisam/Elz catchment, which represents the only natural range overlap between A. pallipes s. str. and A. torrentium. The detail map shows the distribution of A. pallipes s. str. (green line) and A. torrentium (red line) within the Brugga (Br) catchment. The arrow indicates the short stretch of syntopic co-occurrence. Red ‘x’ mark sampling sites where no crayfish were detected, dots indicate sites with crayfish presence, and diamonds indicate the stretches used for fixed-area sampling. Abbreviations are as follows: Dr – Dreisam; Db – Dietenbach; Gb – Geroldsbach; Mb – Mühlbach; and Ob – Oberriederbach. Distribution data for the background map were compiled from Chucholl and Dehus (2011) and Stucki and Zaugg (2011).

> *CRAYFISH SURVEY*

The first goal was to determine the upstream and downstream limits of the newly discovered white-clawed crayfish population. For this purpose, we surveyed a total of 29 sampling sites for presence of crayfish by way of selective hand capture (*cf*. Peay, 2003). Sampling sites were selected in areas where conditions are suitable for crayfish. At each sampling site, at least 20 potential shelters (usually boulders or large stones) were carefully searched for hiding crayfish during daytime using hand-held nets. Shelters were selected for large bearing surface area, which increases the probability of occupancy by crayfish (Streissl and Hödl, 2002), and accessibility. To estimate the effectiveness of the sampling strategy, we calculated the probability of capturing at least one crayfish at a sampling site as: $P\text{ (capture)} = (1 - (1 - F)^N)$, where F is the frequency of crayfish capture at sites where crayfish are present, and N is the number of inspected shelters per sampling site. Although this estimate does not exclude the possibility of false negatives at sites with very low crayfish density, it can be useful to assess the detection probability at sites with representative abundance (*cf*. Chucholl and Schrimpf, 2015).

To assess the population status and life-history traits, we used an established crayfish survey protocol, which was developed for crayfish monitoring within the framework of the EU Habitats Directive (Council Directive 92/43/EEC). This scheme combines fixed-area (point-abundance) with selective (shelter-related) hand-capture by day. In comparison to passive surveying methods (night observation or trapping) this method provides a less biased sample and does not depend on crayfish activity (Pratten, 1980; Peay, 2003). Furthermore, detection of juveniles is rarely possible by way of passive surveying methods. To determine abundance of white-clawed crayfish we selected two river stretches of 150 m in length. These river stretches were subdivided into three sections of 50 m in length, ensuring that one of the sections (intensive stretch) offers suitable conditions to crayfish. The two remaining sections (selective stretches) were located downstream and upstream of the intensive stretch. Within the intensive stretch we selected the three most suitable and surveyable areas (habitat patches), ranging in area from 5 to 10 m^2. In these habitat patches we did a fixed-area sampling by searching all potential refuges for crayfish. According to Peay (2003) fixed-area sampling gives the closest approximation to local density of crayfish. The selective stretches were surveyed by selective hand capture as outlined above. Shelter use was subsequently calculated as the total number of captured crayfish divided by the total number of inspected shelters. Shelter use correlates with the density of crayfish and can be considered a measure of crayfish abundance (Pearson correlation with logarithmic model: $N = 10$, $R = 0.85$, $P < 0.001$). Sampling according to this survey protocol was done on a total of 26 occasions from mid-April to mid-June, and again from mid-September to mid-October, 2014, to assess life-history traits across one growth season.

> MORPHOMETRIC MEASUREMENTS AND FECUNDITY

Captured crayfish were sexed, and chelae (propodus) length (*PL*) and carapace length (from the tip of the rostrum to the posterior margin of the carapace; *CL*) were measured to the nearest 0.1 mm using a slide caliper. Lost or regenerated chelae and other injuries were noted and crayfish were inspected for colonization of branchiobdellid worms. Females were checked for attached eggs and, if present, we took a photograph of the ventral side of the pleon to estimate the total number of eggs following the rationale of Stucki (2002). Because the eggs are attached to the pleopods in several layers, not all of the eggs were visible. Therefore, the number of eggs counted on the photograph was multiplied by the estimated number of egg layers (Stucki, 2002). The number of egg layers was estimated from lateral photographs. Subsequently, the visible part of the eggs in each photograph was re-assessed to identify the multiplier needed for correction. After the examination all crayfish were carefully released near their finding place to avoid downstream drift following sampling.

> GROWTH AND LIFE-HISTORY TRAITS

To estimate life-history traits, growth was described using the Von Bertalanffy's Growth Function (VBGF), adjusted for seasonal growth in summer and no growth in winter (Pauly and Morgan, 1987; Scalici *et al.*, 2010; Ghia *et al.*, 2015):

$$CL(t) = CL_\infty \left\{ 1 - \exp\left[-k(t - t_0) - (Ck/2\pi)\sin(2\pi(t - t_s)) \right] \right\}$$

where $CL(t)$ is the CL at age t, CL_∞ the asymptotic length (*i.e.* the theoretical possible *CL*), k the curvature parameter (which determines how fast CL_∞ is approached) and t_0 the initial condition parameter (*i.e.*, the hypothesized age at which *CL* is zero). The summer point (t_s) refers to the onset of the first oscillation relative to $t = 0$. For practical purposes it was replaced by the winter point ($WP = t_s + 0.5$), *i.e.* the time of the year when growth is slowest. The *WP* was set to mid-winter, and the parameter expressing the amplitude of the seasonal growth oscillation (*C*) was set arbitrarily to 1, allowing for no growth in winter (*cf*. Ghia *et al.*, 2015). CL_∞ and k were estimated for each sex from the obtained 1 mm size-frequency distributions within the ELEFAN I module (non-parametric scoring of the VBGF fit) in the FAO-ICLARM Stock Assessment Tools software (FiSAT 2 v.1.2.2; Pauly and David, 1981; Gayanilo and Pauly, 1997; Scalici *et al*., 2010), and t_0 was assessed by non-linear regression analysis. Longevity (t_{max}) was estimated by $t_{max} = (3/k) + t_0$ (Gayanilo and Pauly, 1997; Scalici and Gherardi, 2007). Finally, the growth performance index (ϕ') was derived from k and CL_∞ by applying the equation $\phi' = \log(k) + 2\log(CL_\infty)$ (Pauly and Munro, 1984). ϕ' allows comparison of different stocks' growth performance in terms of length but can also be used to detect biased growth parameter estimates, because populations of the same species show similar values of ϕ' (Pauly and Munro, 1984).

> *STATISTICAL ANALYSES*

All statistical analyses were performed in the software R 3.1.3. (R Core Team, 2015) and SigmaPlot 11.0, except for the life-history analysis, which was performed in FiSAT 2 as outlined above. Prior to statistical analyses, all variables were checked for normality and non-parametric tests were used when appropriate. To assess the effects of crayfish size (*CL*), sex, and sexual maturity on chelae length (*PL*), we constructed a multiple linear regression model (MLM) with *PL* as response variable. *CL* was implemented as continuous predictor, and sexual maturity and sex were included as factors with two levels. To account for sex-specific growth pattern upon attaining sexual maturity, we included an interaction term between *CL*, sex, and sexual maturity. To reduce model complexity and to arrive at the minimum adequate model, the full model was subjected to stepwise backward selection based on Akaike's information criterion (AIC). The AIC is a model selection tool that measures MLM fit, with a penalty for model complexity (Chambers and Hastie, 1992). The significance of the predictors in the final model was subsequently assessed by analysis of variance (Type II tests) and the partial eta-square statistic (η^2) was given as a measure of effect size. R^2, adjusted for model complexity, was calculated as a measure of goodness of fit. The relationship between female *CL* and the estimated pleopodal fecundity was described by linear regression, with *CL* as independent variable. Finally, we used principal component analysis (PCA) to plot different populations of the white-clawed crayfish species complex according to life-history traits (ϕ', k, t_{max}, and CL_∞; as summarized in Scalici *et al*., 2010 and Ghia *et al*., 2015).

RESULTS

> *DISTRIBUTION*

White-clawed crayfish were detected at 15 of the 29 sampling sites along a continuous river stretch of 4.5 km (Figure 1). Frequency of capture at presence sites was 0.42 (95% *CI*: 0.24–0.59). The probability of capturing at least one crayfish at a positive sampling site was 1.0 (95% *CI*: 0.996–1.000), which indicates a negligible probability of false negatives.

The upper distribution limit (371 m a.s.l.) was approximately 300 m downstream the confluence of the small tributary stream Oberrieder Bach (Ob; Figure 1), which features a previously known abundant white-clawed crayfish population (Biss, 1996; Beyerle, 2000). The lower distribution limit (346 m a.s.l.) was situated in a settlement area, where artificial bank structures gradually replace the natural riparian vegetation.

Apart from the River Brugga, we detected white-clawed crayfish in a short stretch of one artificial outflow, the canal Mühlbach, and in lower reaches of two small tributary streams, the Dietenbach and the Geroldsbach (Db and Gb, respectively; Figure 1). In Gb we also detected a population of endangered stone crayfish (*Austropotamobius torrentium*). Stone crayfish exclusively inhabited the headwater section of Gb, followed by a short overlap zone with a syntopic co-occurrence of both *Austropotamobius* species (Figure 1).

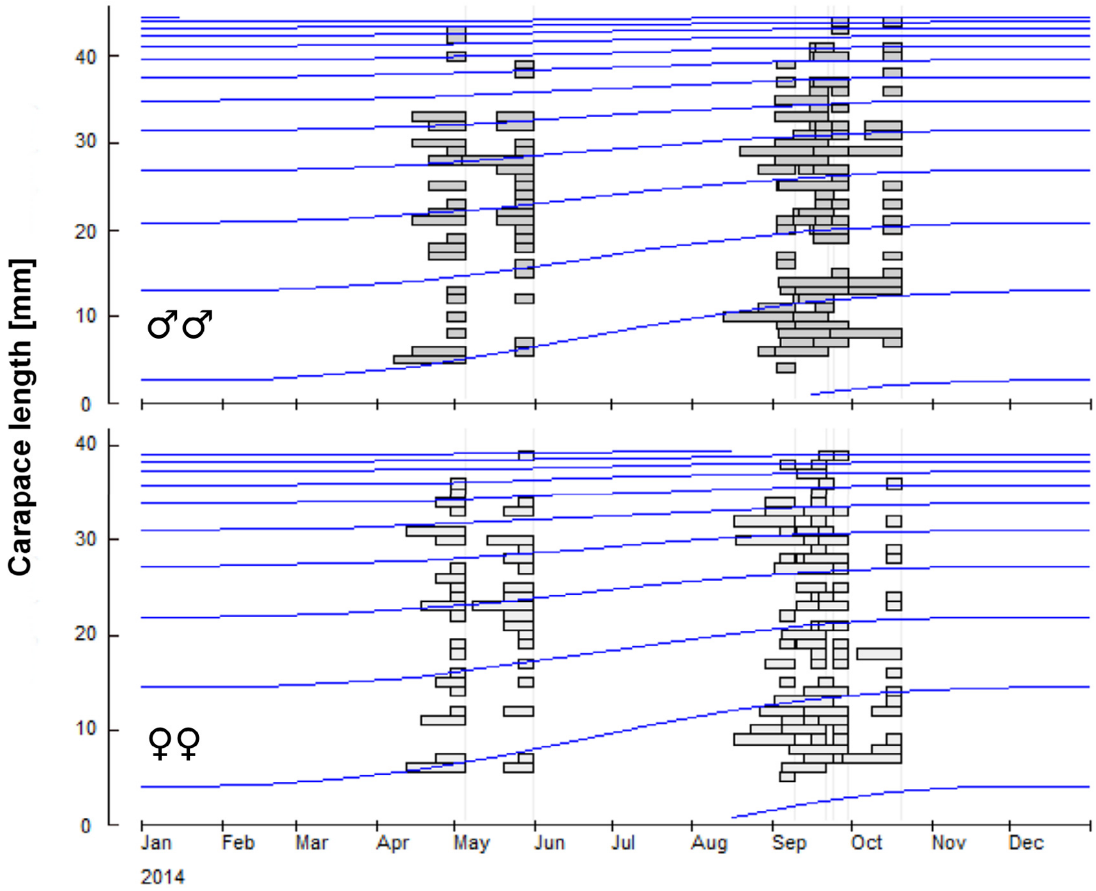

Figure 2
VBGF (blue line) and size frequency distribution (horizontal grey bars) of male (top) and female (bottom) A. pallipes in the River Brugga, southwestern Germany (N = 452). VBGF parameters are summarized in Table I.

> POPULATION STRUCTURE, ABUNDANCE AND ESTIMATED POPULATION SIZE

A total of 455 white-clawed crayfish were captured from the River Brugga during the study period. The sex ratio was even (1.02 males: 0.98 females, Fisher exact test: $P = 1.00$) and there was no size difference between sexes (Mann-Whitney U test: $U = 23\,879$, $P = 0.15$). *CL* ranged from 4 to 44 mm in males ($N = 230$) and from 5 to 39 mm in females ($N = 225$). Five percent of the sampled individuals had lost or regenerated chelae, other injuries were found in 3% of the crayfish. Colonization by branchiobdellid worms was noticed in 3% of the individuals.

Mean abundance of white-clawed crayfish, as assessed by fixed-area sampling, was 1.4 (range: 1.1–1.6) ± 0.2 indiv.$\cdot$m^{-2} (95% CI: 1.2–1.6 indiv. $\cdot$m^{-2}). Shelter occupancy averaged 0.42 (range: 0.35–0.60) ± 0.1 indiv.$\cdot$shelter^{-1}.

> GROWTH AND LIFE-HISTORY TRAITS

Seasonal growth was described by using Von Bertalanffy's Growth Function (VBGF) and the resulting seasonal growth pattern . Size-frequencies of the Brugga-population are shown in Figure 2 for each sex. The obtained VBGF-parameters (CL_∞, k, and t_0) and their derivatives (t_{max} and ϕ') are summarized per sex in Table I.

Table I
VBGF-parameters (asymptotic size, CL_∞, curvature parameter, k, and initial condition parameter, t_0), longevity (t_{max}) and growth performance index (ϕ') of the A. pallipes population in the River Brugga, distinguished per sex.

sex	CL_∞	k	t_0	t_{max}	ϕ'
Males	46.2	0.27	–0.20	10.9	2.8
Females	41.0	0.33	–0.19	8.9	2.7

Table II
*Predictors of chelae length, as assessed by multiple linear regression analysis (adjusted $R^2 = 0.96$). CL means carapace length and SE indicates the standard error of the coefficient estimate. F and P are given by analysis of variance (Type II tests) and indicate whether inclusion of the predictor significantly improves model fit. Partial eta-square (η^2) gives the effect size. Asterisks show the significance level: * – $P < 0.05$ and *** – $P < 0.001$. Coefficients printed in grey are part of an interaction term and should be carefully interpreted. Please refer to Figure 3B-E for details.*

Predictor	Coefficient	SE	η^2	F	P	
CL	0.56	0.03	0.84	2409.8	<0.001	***
Sex	–0.69	0.57	0.15	77.0	<0.001	***
Maturity (*CL* ⩾ 25 mm)	–7.06	1.73	0.01	6.5	0.011	*
***CL*:sex[male]**	0.07	0.04	0.05	23.6	<0.001	***
CL:maturity[adult]	0.32	0.06	0.35	234.7	<0.001	***
Sex[male]:maturity[adult]	–8.90	2.08	0.00	0.0	0.92	
***CL*:sex[male]:maturity[adult]**	0.34	0.07	0.05	20.8	<0.001	***

> RELATIONSHIP BETWEEN CHELAE LENGTH AND CARAPACE LENGTH

No interaction term or predictor variable was dropped from the MLM during stepwise backward selection based on AIC and the full model was therefore considered as minimum adequate model (AIC = 523.3, residual standard error = 1.77, $F_{7/444} = 1480$, $P < 0.001$, and adjusted $R^2 = 0.96$). *PL* was positively related to *CL*, but depended also on sex and maturity (analysis of variance: $P < 0.05$; Table II; Figure 3). The interaction between *CL*, sex, and sexual maturity was highly significant, which indicates that chelae length increases significantly faster in adult males (Figure 3A) than in females and juvenile crayfish (Figure 3B–3E). Based on effect size (η^2), *PL* mostly depends on *CL*, followed by the interaction between *CL* and maturity, and sex (*cf*. Table II).

> SIZE AT MATURITY, REPRODUCTION AND FECUNDITY

The smallest captured female with attached eggs had a *CL* of 25 mm and all females ⩾27 mm *CL* captured during the spring sampling period (mid-April to mid-June) were ovigerous. From Figure 3 and the MLM analysis of the relationship between *PL* and *CL* it can be concluded that males also mature at approximately 25 mm *CL* or slightly below. Fifty-two percent of the sampled crayfish featured a $CL < 25$ mm and were therefore considered as juveniles.

During the spring sampling, when females carry eggs (Souty-Grosset *et al*., 2006), we captured a total of 29 females, which were considered as sexually mature ($CL \geqslant 25$ mm). Twenty-four (83%) of these females had attached eggs. The *CL* of ovigerous females averaged 31 mm (range: 25 to 39 mm) and the number of estimated pleopodal eggs averaged 90 ± 28 (range: 60–135) per female. There was a significant correlation between *CL* and the estimated number of eggs attached to the pleopods (Pearson correlation: $N = 22$; $R = 0.79$; $P \leqslant 0.001$; Figure 4). Two clutches were excluded from the correlation, because the eggs had an orange color, which indicates that they were not viable (Pöckl, 1998a).Throughout the study period, none of the captured females featured hatchlings, albeit embryos were almost fully developed by mid-June.

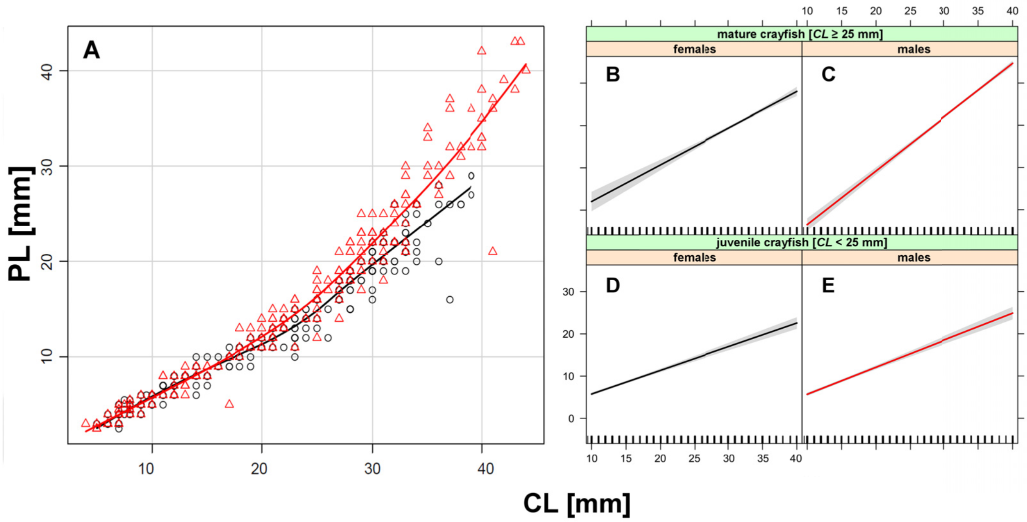

Figure 3
A – Relationship between carapace length (CL) and chelae length (PL) in male (triangles) and female (circles) white-clawed crayfish (N = 452). Solid lines represent trend lines given by locally weighted scatterplot smoothing (LOESS). B-E – Effects plot of the MLM used to describe the data with sex, maturity (CL $\geqslant$ 25 mm) and CL as independent variables (adjusted R^2 = 0.96): B – mature females; C – mature males; D – juvenile females; and E – juveniles males. See Table II for MLM statistics.

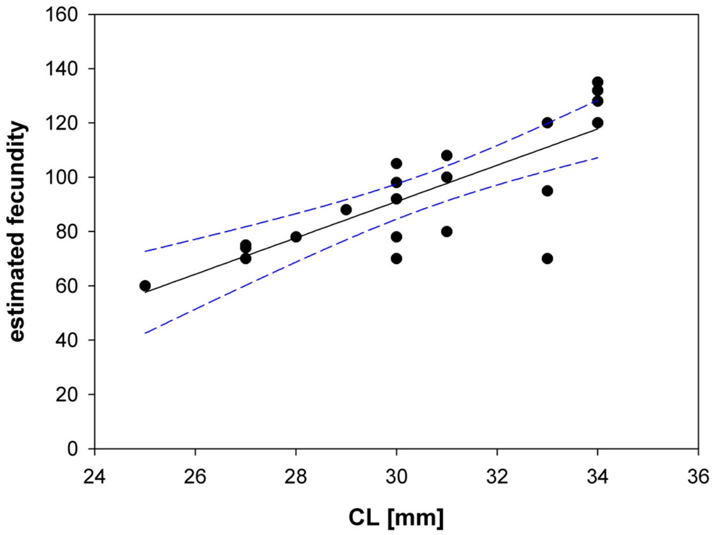

Figure 4
Fecundity of A. pallipes females captured from the River Brugga in relation to carapace length. Trend line is given by linear regression (R^2 = 0.62; $P \leqslant 0.001$) and hatched lines represent the 95%-confidence interval.

DISCUSSION

> *DISTRIBUTION AND ABUNDANCE*

Owing to the cryptic lifestyle of crayfish and the fact that the River Brugga represents a complex water body with many hiding places, the *A. pallipes* population investigated in our study had remained undetected until recently. Nonetheless, in the course of the investigation we discovered a large, widespread population (*cf*. Figure 1).

The colonized stretch started below the high-gradient headwater section of the River Brugga featuring a torrential character and ended where the river enters a settlement area. High water currents and low temperatures are presumably important factors in limiting the upstream distribution of the population. In particular, upstream of the population we measured water currents of up to 0.65 $\text{m}\cdot\text{s}^{-1}$ near the river bank, which clearly exceeds the range preferred by crayfish (up to approximately 0.30 $\text{m}\cdot\text{s}^{-1}$; Bohl, 1989; Beyerle, 2000; Gilly, 2002) and the values measured within the colonized stretch (up to 0.43 $\text{m}\cdot\text{s}^{-1}$). Moreover, Biss (1996) reported that the headwater section of the River Brugga is subject to substrate mobilization during high water flow events, which prevents permanent colonization by white-clawed crayfish (Laurent, 1988). The downstream limit of the population coincides with a settlement area, where artificial bank structures gradually replace the natural riparian vegetation. Here, the banks were directly surrounded by human dwellings with gardens and orchards, *i.e.* riparian land-use types which were previously shown to be negatively associated with white-clawed crayfish presence probability in a French population (Souty-Grosset *et al*., 2010).

Interestingly, we detected no crayfish in a 300-m stretch between the confluence of the stream Oberriederbach (Ob, Figure 1), which holds the previously known population, and the upstream limit of the newly discovered population in the River Brugga (*cf*. Figure 1). Although we cannot exclude the possibility of a false negative, *i.e*. due to very low crayfish density, the estimated detection probability of the used sampling method was fairly high and we suggest that crayfish were indeed absent from this 300-m stretch, probably due to high water currents. Exchange of individuals, and therefore gene flow between both populations seems likely, though, and suggests a meta-population structure. This is of relevance from a conservational point of view, because meta-population structure can decrease extinction risk (Hanski, 1998). In the case of the local extinction of a subpopulation, the vacant habitat can be re-colonized by immigrants from the remaining subpopulations. This offers, in theory, some protection against local extinction events that are caused by short-term deleterious forces, such as droughts during extreme climate events or point-source water pollution. However, further field data or genetic evidence is necessary to validate the hypothesis of a meta-population structure.

The mean crayfish abundance in the River Brugga, (1.4 $\text{crayfish}\cdot\text{m}^{-2}$), as assessed by fixed-area sampling, falls within the range of densities reported from other white-clawed crayfish populations in Germany (0.8–2.3 $\text{crayfish}\cdot\text{m}^{-2}$; unpubl. monitoring data, Fisheries Research Station, C. Chucholl) and the densities known from Ireland and France (0.2–10 $\text{crayfish}\cdot\text{m}^{-2}$; Matthews and Reynolds, 1995; Reynolds, 2002). Moreover, the collected data on distribution and abundance concordantly indicate that the population in the River Brugga ranks among the largest remaining populations in Germany (*cf.* Chucholl and Dehus, 2011) and could be used as a donor stock for re-stocking efforts – both aspects warrant a high conservation priority.

> GROWTH AND LIFE HISTORY

Using size-frequency distributions to estimate age cohorts and thereby growth in crayfish requires an adequate sample size. The dataset of our study exceeded the minimum of 200 specimens suggested by France *et al*. (1991) and the estimated life-history parameters are in good accordance with previous studies on white-clawed crayfish (*cf*. Scalici *et al*., 2010). In particular, the obtained growth performance indexes were identical to the values reported by other studies (Table III), which indicates that our growth parameter estimates are not biased (Pauly and Munro, 1984). Moreover, the sex ratio of the captured crayfish was even and there was no size difference between sexes, which suggests no sex-specific sampling bias.

Compared to the life-history parameters of populations in other European localities, the population in the River Brugga features a life history most similar to a population in France (summarized in Table III and Figure 5). White-clawed crayfish in the UK tend to grow larger and older than populations in France, Germany and central Italy, which is in accordance with latitudinal clines as suggested by Scalici *et al*. (2008). Interestingly, however, white-clawed crayfish in

Table III
Comparison of life-history parameters of different A. pallipes populations in Europe (cf. Figure 5).

Country/region	Taxon	Sex	ϕ'	CL_∞	k	t_{max}	Reference
UK, Central South England	*A. pallipes* s. str.	m	2.8	54.2	0.21	14.3	Pratten (1980)#
		f	2.7	45.6	0.26	11.5	
UK, East of England	*A. pallipes* s. str.	m	2.8	55.1	0.23	13.0	Hogger (1984)#
		f	2.8	51.4	0.25	12.5	
NW France, Normandy	*A. pallipes* s. str.	m	2.9	48.7	0.30	10.0	Neveu (1996)#*
		f	2.7	40.4	0.33	9.1	
Central Italy, Tuscany	'*A. italicus*'	m	3.1	57.9	0.34	8.8	Brusconi *et al.* (2008)
		f	3.0	52.1	0.37	8.1	
Central Italy, Lazio	'*A. italicus*'	m	2.8	42.4	0.35	7.8	Scalici *et al.* (2008)
		f	2.8	39.0	0.41	7.1	
Northern Italy	'*A. italicus*'	m	2.8	63.0	0.16	17.9	Ghia *et al.* (2015)
		f	2.7	52.0	0.19	15.1	

\# VBGF parameters derived by Scalici et al. (2008)
* Carapace length estimated from total length data using linear regression

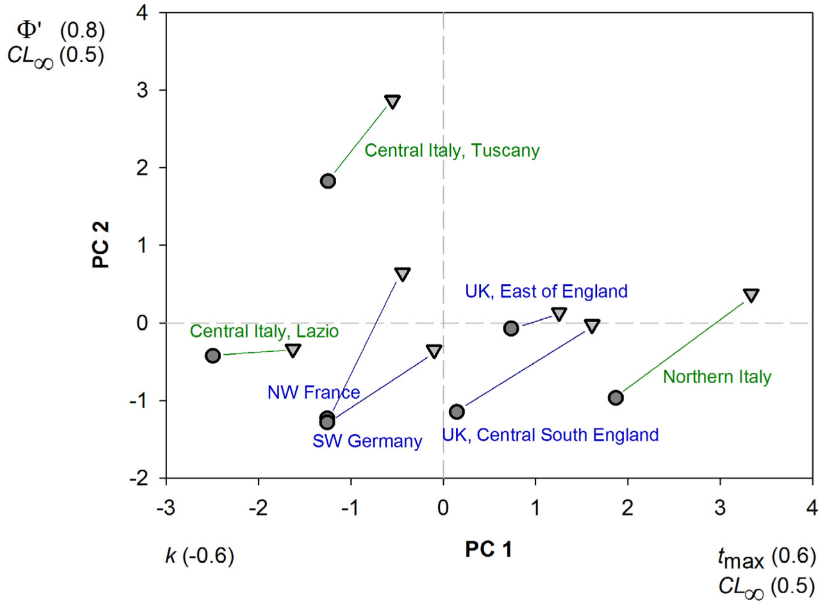

Figure 5
Ordination from PCA of white-clawed crayfish populations according to life-history traits (as summarized in Table III). Males are shown as triangles, dots represent females. Populations of the western lineage (A. pallipes s. str.) are depicted in blue, populations of the southern lineage (A. 'italicus') are shown in green. Life-history traits with loadings ⩾|0.5| are shown at the corresponding axes (loading in brackets). Cumulative proportion of explained variance = 0.99.

the Alpine climatic zone in northern Italy were recently shown to grow even larger and older than in the UK (Ghia *et al*., 2015), with an estimated longevity in males of up to 18 y, as opposed to values between 10 and 13 y reported for French, German and UK populations, and values between 8 and 9 y in central Italy (Table III, Figure 5). This strongly points to temperature as the primary factor governing white-clawed crayfish life history (Lowery, 1988; Ghia *et al*., 2015).

Growth of crayfish is generally influenced by temperature and increases with temperature up to a species-specific optimum (Reynolds, 2002). In reared *A. pallipes* the optimal growth occurs at a temperature of 20 °C whereas lowest was observed at 13 °C (Policar *et al*., 2010); at water temperatures below 10 °C growth ceases (Pratten, 1980). Water temperatures in the River Brugga exceeded 10 °C in May and reached 16 °C in summer, which, according to Arrignon (1996), is the optimum for the species in France. In a comparative study of habitat parameters of 11 German streams with white-clawed crayfish, Gilly (2002) found mid-summer temperatures between 17 and 20 °C, *i.e.* slightly above those observed in the River Brugga.

Climate-induced variability in growth is likely to affect other life-history traits, such as the onset of sexual maturity (Reynolds, 2002). Irish and British populations of *A. pallipes* attain sexual maturity between 22 and 27 mm *CL* (Moriarty, 1973; Brewis and Bowler, 1982; O'Keeffe, 1986; Woodlock and Reynolds, 1988) and Alpine populations in northern Italy mature at 27 mm *CL* (Ghia *et al*., 2015). The *A. pallipes* from the River Brugga in Germany were sexually mature at 25 mm *CL*, which corresponds to the previously reported values. Ghia *et al*. (2015) suggested that maturity in white-clawed crayfish is mostly related to size rather than age. Populations experiencing different growth rates may therefore also exhibit a different age at maturity and cold temperatures may delay maturity (Reynolds, 2002). For instance, under controlled conditions with optimal temperatures, some *A. pallipes* females had been able to lay eggs at an age of 16 months (Policar *et al*., 2010), whereas age at maturity in Alpine populations with slow growth rates was estimated at three years (Ghia *et al*., 2015). Based on the estimated growth parameters, white-clawed crayfish in the River Brugga probably mature at an age of 2+, which coincides with the age at maturity reported for Irish, British, and French populations (Pöckl, 1998b, and citations therein).

Apart from climate-induced variability in life-history traits, Figure 5 also illustrates the well-known phenomenon of larger asymptotic size and higher longevity in males, which also involves a higher growth performance. Sex-specific growth patterns are known from a number of crayfish species, including white-clawed crayfish, and are probably driven by slower growth of adult females due to a lower moult frequency because female crayfish cannot moult while bearing eggs (Reynolds, 2002; Scalici *et al*., 2010; Ghia *et al*., 2015). Furthermore, moult increments of mature females are smaller than those of males because of the high energetic demands of egg production coupled with a feeding inhibition while bearing eggs (Reynolds, 2002).

Finally, the estimated pleopodal fecundity of the ovigerous white-clawed crayfish females captured from the River Brugga (60–135 eggs·female^{-1}) is in good accordance with the fecundity ranges reported by Pöckl (1998a) and Souty-Grosset *et al*. (2006), namely 50–120 and 50–200 eggs· female^{-1}, respectively. The linear increase of fecundity with female size represents a well-documented phenomenon in crayfish (Souty-Grosset *et al*., 2006). The presence of almost fully developed embryos by mid-June suggests a hatching period of mid to late June, similar to populations in northern Italy (Ghia *et al*., 2015) and southern England (Holdich, 2003), but a little later than populations in central Italy (Gherardi *et al*., 1997) and earlier than in populations in northern England, releasing their juveniles in August (Holdich, 2003). Overall, the obtained size-frequency distributions, life-history traits and fecundity estimates, as well as the high proportion of ovigerous females concordantly suggest the presence of a well-structured, vital white-clawed crayfish population in the River Brugga.

> OVERLAP WITH STONE CRAYFISH

A surprising finding of the crayfish survey was the short syntopic co-occurrence of stone crayfish and white-clawed crayfish in the small tributary stream Geroldsbach (Gb; Figure 1). Stone crayfish exclusively inhabited the headwater section of Gb, whereas white-clawed crayfish were found in the lower reach, where we also detected the overlap zone (*cf*. Figure 1).

This is remarkable because, according to our knowledge, there exist no previous reports of a natural overlap between the western lineage of white-clawed crayfish and stone crayfish. The rare cases of synoptic co-occurrence between white-clawed crayfish and stone crayfish that we are aware of either originate from introduction of white-clawed crayfish, such as in a small pond in Switzerland (Stucki and Zaugg, 2011) and Lake Plansee in Austria

(Füreder and Machino, 1995), or refer to the southern lineage of white-clawed crayfish, such as in the River Krka on the Dalmatian coast in Croatia (Laurent, 1988). This is despite the fact that both species have largely comparable habitat requirements (Gilly, 2002) and occur in close proximity in Switzerland and Germany, as well as possibly in Alsace, France (Laurent, 1988). While there is a well-defined, distinct distribution border between both species in Switzerland, with *A. pallipes* s. str. inhabiting the western part of the country (*cf*. Figure 1), the situation in southwestern Germany seems unique because of a sympatric range overlap in a whole catchment area (highlighted in red in Figure 1). Within this catchment both species occur in tributary streams of the same rivers, in some areas even in alternating sequence in adjacent tributaries (*cf*. Chucholl and Dehus, 2011). But even within this sympatric range, there has yet been no record of both species from the same stream (*cf*. Gilly, 2002).

In fact, the distribution pattern, both at the stream and catchment level, strongly points to competitive exclusion between the sister taxa. This notion is supported by the displacement of resident stone crayfish by introduced *A. "italicus"* in Tyrol, Austria (Sint *et al*., 2006). Gilly (2002) compared hydro-morphological and physico-chemical properties of white-clawed crayfish and stone crayfish streams in the sympatric German range and found high overlap in all habitat features. The only significant differences related to stone crayfish occurring at higher slopes and at shorter distance to springs. This finding is corroborated by the situation encountered in our study and a similar case in another small stream of the River Dreisam catchment that became known in the meantime. Overall, stone crayfish may be better adapted to extreme conditions in headwater streams, despite considerable niche overlap with white-clawed crayfish (*cf*. Gilly, 2002).

CONCLUSION

In summary, our study provides first insights into the population ecology of critically-endangered white-clawed crayfish in Germany and documents for the first time a short natural overlap zone with stone crayfish. The estimated life-history traits emphasize the *K*-selected life history of white-clawed crayfish, *i.e.* a slow life cycle, high longevity and low fecundity. This becomes particularly apparent when compared to the more *r*-selected NICS, which, by contrast, feature a rapid life cycle and high fecundity (*cf*. Souty-Grosset *et al*., 2006; Chucholl, 2012). The syntopic occurrence with stone crayfish raises the question of ecological niche competition. Finally, our results may serve as a basis for monitoring and conservation of the species in the River Brugga, which features one of the largest remaining occurrences in Germany.

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