Structure and population dynamics of the secondary burrower crayfish *Procambarus acanthophorus* from a tropical Mexican wetland

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Procambarus acanthophorus from a tropical Mexican wetland

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Summary

Structure and population dynamics of the secondary burrower crayfish

Procambarus acanthophorus from a tropical Mexican wetland

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The catch-size, sex-ratio, structure and dynamics, and mortality of a population of the secondary burrower crayfish *Procambarus acanthophorus* Villalobos, 1948, from tropical wetland La Mixtequilla, Veracruz, Mexico, were examined. Monthly samples were taken from artisanal commercial captures. A total of 2,141 individuals were caught. Although the total female:male ratio was 0.86, variation in sex ratios have also been found in monthly catches. Monthly polymodal frequency distributions of Cephalothorax Length (CL) were analyzed by the Bhattacharya method. Population catches consisted of six CL-classes. The CL-class dynamic may show adaptations to the flood period. Growth parameters were estimated using the von Bertalanffy model. For females, $K = 0.39 \text{ year (yr)}^{-1}$, $CL_{\infty} = 57.30 \text{ mm}$, $\Phi' = 3.11$, and $t_{\max} = 6.73 \text{ yr}$, and for males, $K = 0.40 \text{ yr}^{-1}$, $CL_{\infty} = 59.00 \text{ mm}$, $\Phi' = 3.14$, and $t_{\max} = 6.59 \text{ yr}$ were found. We also examined whether water temperature influences catches or sex ratio.

Keywords: *Procambarus acanthophorus*, secondary burrower crayfish, tropical wetland.

Introduction

Crayfish play several roles in many freshwater ecosystems at different trophic levels (Nyström et al. 1996; Correia 2001; Huner et al. 2002; Marion 2013; Boyle et al. 2014). They can change physical-habitat characteristics (Usio and Townsend 2004; Usio et al. 2009). Some crayfish species exert such a large impact on ecosystems (cf. Power et al. 1996) that they may be identified as keystone species (Nyström et al. 1996; Magoulick 2014).

Associated with longitudinal or latitudinal gradients in species diversity, biological processes may be similar and/or different in the tropics from those in temperate regions (Paine 1966). From this viewpoint, crayfish could provide model organisms for comparative research on life-history traits (Scalici et al. 2008; Chucholl 2011). The major groups of freshwater crayfish, *Astacoidea* and *Parastacoidea*, have centers of species richness in tropical or temperate areas. *Astacoidea* is divided into the families Astacidae and Cambaridae, and *Parastacoidea* has a single family. Parastacidae, both astacoids and parastacoids, occur in the Neotropical realm, with cambarids concentrated in Mexico (Lodge et al. 2012). However, in this country, there is a lack of basic natural-history information on wild populations. With regard to what Stearns (1992) identifies as primary life-history traits, some research has only been conducted on the structure and dynamic of the population, morphometry, and the growth pattern of *Cambarellus montezumae* (de Saussure, 1857) (Álvarez and Rangel 2007), *Procambarus acanthophorus* Villalobos, 1948 (Signoret-Poillon et al. 2008), *Procambarus bouvieri* (Ortmann, 1909) (Gutiérrez-

Yurrita and Latournerié-Cervera 1999), *Procambarus clarkii* (Girard, 1852) (Rodríguez-Almaraz 1992; Sánchez-Saavedra et al. 1993), and *Procambarus digueti* (Bouvier, 1897) (Gutiérrez-Yurrita and Latournerié-Cervera 1999). Thus, while there are at least 53 crayfish species in Mexico (Hernández et al. 2008), relatively little attention has been paid to such matters in other members of the Cambaridae family.

The crayfish *Procambarus acanthophorus* is endemic in Southeast Mexico. This Neotropical crayfish has been recorded in the states of Chiapas (Hobbs 1989), Oaxaca (Villalobos 1948), Tabasco (Bueno et al. 2005; Barba-Macías et al. 2015), and Veracruz (Villalobos 1983; Torres-Corona 2007; Díaz-Jiménez et al. 2012). The specimen Type was collected in a small lake, which becomes dry at times (Villalobos 1983). *Procambarus acanthophorus* spends much of its life inside its burrows during the dry season, but wanders into open waters during the floodplain period (Bueno et al. 2005; Signoret-Poillon et al. 2008). It is an allogenic engineer (cf. Jones et al. 1994). Its burrows are simple and are connected to the water table at depths ranging from 1.5–2.0 m. This crayfish can build chimneys at the entrances of their burrows, which are sometimes covered (Torres-Corona 2007). According to the classification of Hobbs (1942; 1981), this endemic crayfish can be considered a secondary burrower (Torres-Corona 2007).

Hobbs (1942; 1981) recognized three categories of burrower crayfishes: primary burrowers, restricted to burrows; secondary burrowers, that spend much of their lives in burrows but wander into open water during rainy seasons, and tertiary burrowers, crayfish that live in open water and burrow only during drought periods

or occasionally. Although the structure and dynamics of populations of these latter categories tend to be well described (Rodríguez-Almaraz 1992; Anastácio and Marques 1995; Gutiérrez-Yurrita and Montes 1999; Fidalgo et al. 2001; Chiesa et al. 2006; Dörr et al. 2006; Jones et al. 2007; Scalici and Gherardi 2007; Anastácio et al. 2009; Scalici et al. 2010; Chucholl 2011, 2012; Huang et al. 2012; Dörr and Scalici 2013), they are poorly understood in secondary (Fontoura and Buckup 1989; Jones et al. 2007) and primary burrowers (Jones et al. 2007; Miller et al. 2014), this mainly due to sampling difficulty and small sample size (Miller et al. 2014).

To help fill this gap, the aim of the present study was to address knowledge on the structure and dynamics of a population of *P. acanthophorus*, a secondary burrower crayfish (sensu Hobbs 1942; 1981) that, in the tropical wetland of La Mixtequilla in Mexico, is only accessible during the rainy season. We also examined whether water temperature influences catches or sex ratio.

Methods

Study site

The Mixtequilla, a seasonally flooded wetland, is located in Veracruz State, Mexico, within the Sistema Lagunar Alvarado (Fig. 1), designated as Ramsar Site 1355 (Portilla-Ochoa 2003; The Ramsar Convention on Wetlands 2014). This wetland is traversed by the Río Blanco River. The climate is warm: Aw2(i')w" type.

Average annual temperature is 25.9°C, and in the coldest month, it is 22.6°C, while the hottest months are May and June (28.3°C). Average annual rainfall is 1531.8 mm, with rain beginning in June and ending in October; in addition, there is the presence of a heat wave (García 2004). Generally, the dry season runs from January to June.

Soils from La Mixtequilla correspond to Gleysols (Vela-Correa et al. 2011). The La Mixtequilla site is localized within a popal-tular herbaceous vegetation marsh (cf. Rivera-Becerril et al. 2008; Moreno-Casasola et al. 2012). In La Mixtequilla, the aquatic bird group comprised 50 species, among these the Black-Crowned Night-Heron (*Nycticorax nycticorax* L., 1758) and the White Ibis (*Eudocimus albus* L., 1758).

Trapping and measurements

Samples were from commercial captures, which were carried out by local crayfish-catchers (Signoret-Poillon et al. 2008) at El Llanete, a site in the wetland. La Mixtequilla wetland is a flooded ecosystem full of weeds, any agitation makes the water turbid. This limits the efficiency of techniques such as manual capture or hand-nets for catching *P. acanthophorus*. Thus, captures were effected employing artisanal traps constructed of 3-mm mesh galvanized screening (Signoret-Poillon et al. 2008). These traps were of two types: rectangular traps (33.5 × 28 cm) with a single entrance funnel (cf. Momot 1967), and horizontal cylindrical traps (50 cm long and 21 cm diameter), with two opposed-access funnels, each 3 cm in diameter (cf. Rodríguez-Almaraz 1992; Scalici et al. 2010; Huang et al. 2012). The

two trap types may differ in capture efficiency and selectivity in terms of size and sex ratio (cf. Momot 1967; Pfister and Romaine 1983; Scalici et al. 2008; Chucholl 2011; Paillisson et al. 2011). Our samples were obtained following Signoret-Poillon et al. (2008). The traps only catch animals outside of their burrows, reflecting the population structure of individuals that remain in open water during the rainy season. Twenty traps were baited with fish meat. After that, these were set out at dusk and harvested at the following dawn. Six samplings were performed from September 2011 to February 2012 as follows: 1) September 24–25; 2) October 15–16; 3) November 12–13; 4) December 10–11; 5) January 14–15, and 6) February 25–26.

Each specimen was sexed and weighed to the nearest 0.01 g. Cephalothorax Length (CL) measurements were taken along the dorsal midline of the carapace, from the tip of the rostrum to the posterior edge. Measurements were carried out with a Vernier caliper to the nearest 0.1 mm.

Physicochemical parameters of the water

Water samples were taken at El Llanete, the same area where the crayfish was caught. Using a Hydrolab DS5 (Hach Company, Loveland, CO, USA) multi-parameter water quality instrument, we registered temperature, pH, dissolved oxygen concentration, and ammonium (NH_4^+). Data were recorded every hour (36 recordings/6 min) during 6 h (11:00 to 17:00 hours) on each day that crayfish were sampled. Additionally, four samples per day were collected for orthophosphate

determination (PO_4^-) using the 4,500-P E ascorbic acid method (American Public Health Association et al. 2005); water depth was determined with a wooden ruler.

Analytical procedure and statistical analysis

Means of CL among monthly catches and between sexes were compared using two-way Analysis of Variance (ANOVA). When significant p values (<0.05) were obtained by ANOVA, multiple comparisons of means were computed with the Tukey and the Kolmogorov-Smirnov post hoc tests. The Chi square test was used to compare the sex ratio balance.

With the Bhattacharya (1967) method, using FiSAT (FAO-ICLARM Stock Assessment Tools) software (Gayanilo et al. 2005), CL-frequency distributions for the females and males of each monthly catch were decomposed into their Gaussian components; each of these was identified as one CL-class, which were 1-mm class intervals. In addition, means, Standard Deviations (SD), numbers of individual crayfish, R^2 determination coefficients for each CL-class, and the Separation Index (SI) value for each pair of adjacent groups were calculated. When two adjacent CL-classes were separated ($\text{SI} \geq 2$), a chi-square test for determining the significance of the decomposition was applied.

Growth rates were described according to von Bertalanffy (1938) for each sex:

$$CL(t) = CL_{\infty}\{1 - \exp[-K(t-t_0)]\}$$

where $CL(t)$ is Cephalothorax Length at time t , CL_{∞} is the asymptotic length, K is the curvature parameter, and t_0 is age at zero length. Growth models were estimated from CL-frequency distributions using Electronic Length Frequency ANalysis (ELEFAN), and the K -value, by the scan method. Other parameters calculated included the following: (a) total mortality index Z , the sum of natural mortality and mortality due to trapping, obtained by the Powell-Wetherall plot equation (modified by Pauly and Soriano 1986), which computed CL_{∞} and the Z/K ratio using CL-frequency distributions; (b) natural Mortality (M), calculated by the following formula:

$$\text{Log}M = -0.0066 - 0.279\text{Log}CL_{\infty} + 0.6543\text{Log}K + 0.463\text{Log}T \text{ (Pauly 1980)}$$

where $T = 26.16^{\circ}\text{C}$ is the mean value of the water temperature recorded during sampling months; (c) mortality due to catching (F), obtained by subtracting M from Z (expressed as percentage of Z), and (d) expected mean lifetime ($t_{1/2}$) and expected longevity ($t_{\max}$) were computed from the equations

$$t_{1/2} = \sum\{[n(t)*t]\}/N \text{ and } t_{\max} = (3/K) + t_0$$

where $n(t)$ is the number of individuals at time t and N is the total number of individuals, and (e) the growth performance index (*phi prima* ϕ') was calculated as $\phi' = \text{Log}(K) + 2\text{Log}(CL_{\infty})$.

Results

Catch Size and Sex Ratio

The results of catch sizes and sex ratios throughout the monthly captures are summarized in Figure 2. A total of 2,141 individual *P. acanthophorus* were caught during the study. In October, there was one catch peak of 467 crayfish when the temperature decreased from 30.1 ± 0.4 to $27.5 \pm 0.1^{\circ}\text{C}$ (Fig. 2; Table 3). From this point, catches dropped to 262 individuals in January when the temperature decreased to $21.4 \pm 0.2^{\circ}\text{C}$, and this increase was again observed when the temperature rose to $25.3 \pm 1.5^{\circ}\text{C}$ (Fig. 2; Table 3).

The pooled data of the sex ratio was 0.86 (988 females and 1,153 males); this proportion showed significant differences from the expected 1:1 sex ratio ($\chi^2 = 13.09$; $p < 0.05$). The proportion of females was highest in September, and males predominated in October, December, and January. In November and February, catches exhibited a balanced sex ratio ($\chi^2 = 0.38$; $p < 0.05$ and $\chi^2 = 3.7$; $p < 0.05$, respectively).

Cephalothorax Length

For females, CL increased from 29.5 ± 3.2 mm in September to 37.8 ± 2.8 mm in January, and decreased to 29.0 ± 4.9 mm in February (Fig. 3). The dynamic was similar for males: CL ranged from 29.9 ± 3.8 mm– 37.0 ± 4.0 mm, and fell to $29.6 \pm$

5.3 mm during the same months (Fig. 3). Between September and February and between November and December, CL did not differ (Tukey post hoc test; $p > 0.05$). In females, CL was 33.4 ± 4.4 mm (min-max: 18–45 mm), and in males, 33.6 ± 4.5 mm (min-max: 18–48 mm). Females and males reached largest CL in January (Sep=Feb<Oct<Nov=Dec<Jan, Kolmogorov-Smirnov post hoc test; $p < 0.05$). CL only differed between females and males in September, October, and January (Tukey post hoc test: $p < 0.05$).

Cephalothorax Length Distribution and Growth

In Figure 4, CL-distribution frequencies from monthly catches of the *P. acanthophorus* crayfish population are represented and that are associated with growth curves for each sex. Minimal CL was 18 mm for both sexes; this is illustrated in the February histogram, while the maximal CL value was 48 mm for males in October and 45 mm for females in December. The span of these frequency distributions registered 12 mm for females in November and 26 mm for males in February.

With the Bhattacharya method, the *P. acanthophorus* population was classified into 6 CL-classes for each sex, which were denoted with Arabic numerals. One alternating class was distinguished, which was denoted with Roman numeral III (Table 1). Histograms of CL-classes allowed visualization of the population structure succession of this crayfish throughout the monthly captures (Fig. 5). These CL-classes ranged from 2, 3, and 4 in September (both sexes) to 3, 4, 5, and 6 in January (both sexes); subsequently, there was a drop in February, a

month during which classes were 1, 2, 3, and 4 (both sexes). CL-classes of females and males in October were different in number and composition: while three CL-classes were presented in females, four were presented in males. In November, regardless of that the number of CL-classes in both sexes was the same, the composition was different: CL-classes 3, 4, and 5 were found in females, and 2, 4, and 5 CL-classes in males. December CL-classes were 3, 4, and 5 in both sexes. In February, both sexes showed class 1, females showed the broadest CL-classes (four classes, including 1, 2, 3, and 4) with the presence of alternating CL-class III; these features were not presented in other monthly catches. CL-class 4 was presented in all monthly captures of both sexes; class 5 appeared 1 month later, in October and remained for 4 months, until January, while CL-class 6 was found only in January. SI were always >2 , and no decomposition process was significant (χ^2 ; $p > 0.05$).

Parameters of the von Bertalanffy growth model for each sex are summarized in Table 2 and Fig. 4. Analysis of CL-frequency distribution for each sex presented in females as $CL_{\infty} = 57.43$ mm, $K = 0.39$ yr $^{-1}$, and $\phi' = 3.11$, and in males, as $CL_{\infty} = 58.20$ mm, $K = 0.40$ yr $^{-1}$, and $\phi' = 3.14$. Total mortality index (Z) was estimated at 2.37 ($r^2 = 0.97$) for females and at 2.56 ($r^2 = 0.97$) for males. Fishing mortality (F) was 1.65 for females and 1.83 for males. Estimated longevity ($t_{\max}$) for females was 6.73 years and for males, 6.59 years.

Physicochemical Analysis of Water

Regarding the physicochemical analysis of water, as depicted in Table 3, temperatures ranged from temperate to warm, and the pH was slightly acid. In general, the Dissolved Oxygen (DO) concentration was found at low levels (0.48–2.44 mg/L), although in October 2011, this was established at a higher concentration (4.26 mg/L). NH_4^+ concentrations ranged from 0.0–304.9 $\mu\text{g/L}$, PO_4^- from 27.7–334.7 $\mu\text{g/L}$, and water depth was shallow.

Discussion

Crayfish are poikilotherm and many traits in their life cycle are temperature-driven. In the temperate zones, variations in crayfish catches have been related with changes in water temperature and these changes have affected the species and the sexes differently. The results of Gottstein et al. (1999) showed that a positive correlation exists between the number of *Austropotamobius pallipes italicus* (Faxon, 1914) and water temperature. According to Olsson et al. (2010), winter temperature was one of the most important factors for annual fluctuations in catches of *Astacus astacus* L., 1758 and *Pacifastacus leniusculus* (Dana, 1852). In Lake Opeongo, Northeastern Ontario, Canada, a decrease in water temperature was associated with a reduction in *Cambarus bartoni* (Fabricius, 1789), catches, particularly females, but catches of *Orconectes virilis* (Hagen, 1870), did not change (Somers and Stechey 1986). In six south-central Ontario lakes in Canada,

catches of *C. bartoni* correlated with water temperature for both sexes (Somers and Green 1993), but male catches of *O. virilis* were less influenced than female catches (Somers and Green 1993). Hein et al. (2007) found that *Orconectes rusticus* (Girard, 1852) catch rates exhibited a seasonal peak, corresponding with the period of highest water temperature (20 and 25°C). In the La Mixtequilla tropical wetland, the highest water temperature was at September but, unlike the northern species, the catch peak of *P. acanthophorus* rose when the temperature decreased to $27.5 \pm 0.1^\circ\text{C}$. After that, a reduction in catches was associated with a decrease in water temperature and catches again increased when the temperature rose to $25.3 \pm 1.5^\circ\text{C}$, this near the temperature (15–20°C) of the catch peak of *O. virilis* and 5°C above (10–15°C) of that found in *Orconectes propinquus* (Girard, 1852) (Richards et al. 1996). All of these indicate that *P. acanthophorus* have a different temperature threshold from that of the temperate *Orconectes* and that the threshold is possibly negatively related with latitude. Regardless of that crayfish are poikilothermal and that many features of their physiology and behavior are temperature-driven, other factors can affect the number of individuals that can be captured (Somers and Stechey 1986; Araujo and Romaine 1989; Hein et al. 2007; Olsson et al. 2010). It is noteworthy that, in the current study, the largest catch of *P. acanthophorus* in October coincided with greatest water depth, highest concentrations of ammonium and DO, and lowest concentration of phosphate.

Variations in sex ratio have been observed among crayfish species, both in samples as a whole and in partial samples. Some of these variations were

statistically far from the 1:1, such as the equilibrium sex ratio (cf. Fisher 1930; Hamilton 1967). The similarity of the sex ratio in complete samples of the present study (0.86) and calculated at the same population (0.89) by Signoret-Poillon et al. (2008) some years ago, as well as the differences in sex ratios in the monthly samples, may be indicative of the suitability of the method. In *Fallicambarus fodiens* (Cottle, 1863), another secondary burrower crayfish that also lives in a floodplain, the sex ratio of total captures was 1.22 (Norrocky 1991)². Between the two previously mentioned values of *P. acanthophorus*, there is a 0.88 sex ratio, determined by Noro and Buckup (2008) for the fossorial crayfish, *Parastacus defossus* Faxon, 1898. Adult sex ratio variations exhibited by the *P. acanthophorus* population throughout the monthly captures could be settled by three complementary outlooks: its relationship with temperature (Abrahamsson 1966; Grandjean et al. 2000); breeding behavior (Abrahamsson 1966, 1971; Dörr et al. 2006; Larson and Magoulick 2008; Noro and Buckup 2008; Rogowski et al. 2013), and the mating system. In the current study, results showed that lowest proportion of *P. acanthophorus* females occurred with lowest water temperature, while highest proportion coincided with highest water temperature. The high proportion of *P. acanthophorus* females at the beginning of the flood period could be explained by that they emerge in synchrony, bearing newly hatched crayfish. Without doubt, the testing of this hypothesis for this *P. acanthophorus* population requires another method and other capture equipment, different from those used in this study. However, there is disagreement surrounding the existence of synchronous

²This was calculated from Table 1 of Norrocky (1991: 77).

reproduction in populations of nearctic crayfish (Ortmann 1906; McManus 1960; Williams et al. 1974; Somers and Green 1993; Fidalgo et al. 2001). Because in other monthly catches of *P. acanthophorus* the sex ratio ranges from 0.63–0.94, it is likely to be that an individual can have access to more than one mate in a polygamous mating system (cf. Emlen and Oring 1977). Studies on other crayfish support this hypothesis. In accordance with Andrews (1904), in *Orconectes limosus* (Rafinesque, 1817), one male unites with several females. Tack (1941) described the mating behavior of *Orconectes immunis* (Hagen, 1870) as promiscuous because either the male or the female may mate again with the same or other individuals. With microsatellite analyses, there was genetic confirmation of multiple paternities in broods, and no single paternity clutches of crayfish (Walker et al. 2002; Yue et al. 2010; Kahrl et al. 2014). Within this context, it is striking that the lowest proportion of females was found in a population of introduced *O. limosus* (Đuriš et al. 2006), and the highest, in a population of protected species *Austropotamobius pallipes* (Lereboullet, 1858), in which female fertility was low (Grandjean et al. 2000). Consequently, with the aim of predicting mating systems in crayfish, as in other crustaceans (Jossart et al. 2014), the sex ratio requires more attention.

With a clearly defined 6 CL-class for females and males, CL-frequency analysis confirmed a stable structure of *P. acanthophorus* population. In other populations of crayfish species the number of length classes can vary from three to seven (Rodríguez-Almaraz 1992; Anastácio and Marques 1995; Gutiérrez-Yurrita and Latournerié-Cervera 1999; Benabid et al. 2003; Chiesa et al. 2006; Ligas 2008;

Scalici et al. 2008; Ibarra and Arana 2012). From the class structure succession of the *P. acanthophorus* throughout the months of its capture, during which they spend time in open water, some issues can be raised. It is likely to be classes 2–4 that were present in September, at the start of the flood period, representing cohorts of previous seasons. Because class 4 remained throughout this period, crayfish that left classes 2 and 3 could have been incorporated into class 4, and this class could have incorporated individuals that included 5 or 6 classes. Since class 6 was only present in the January capture and class 5 was not localized in February, the crayfish reached CL_{∞} in January. Considering the growth lines obtained and the $t_{\max}$ values, it is plausible that the oldest age class included specimens aged 6 years. Only classes 1–4 are present in February, the last month of capture. It is likely that the survivors of these classes are the individuals returning to burrows, and that class 1 represents the young of the current year and smaller crayfish from the previous year. All of these suggest that in a flood period, there are CL-classes from at least three previous seasons; in other words, a cohort passes through at least three periods, meaning that in two periods, it returns into its burrows. This adaptive mechanism of secondary burrower *P. acanthophorus* is consistent with the utilization of a 'stable' environment, a climate that is 'fairly constant and/or predictable', slow growth rate, large asymptotic CL , and relatively longevity when compared with crayfish that have been classified as r-selected species (Price and Payne 1984; Beatty et al. 2004, 2005; Dörr et al. 2006; Scalici and Gherardi 2007; Scalici et al. 2008; Chucholl 2012; Huang et al. 2012; Dörr and Scalici 2013). The previously mentioned traits of *P. acanthophorus* resemble, to a

greater degree, some correlates of a *K*-selected life-history, as noted by Pianka (1970). Other relatively *K*-selected crayfish included three threatened species (Gherardi et al. 1997; Lindqvist and Huner 1999; Brusconi et al. 2008).

The CL-class dynamic in the population of *P. acanthophorus* may reflect life-history adaptations to seasonal changes in the animals' habitat. The following represent some possibilities: growth is most likely restricted to the flooding period; juveniles and adults that were active during this period can fall into a state of aestivation inside their burrows in the dry season and, as in other crayfish, there could be changes in their physiology and behavior (Tack 1941; Thomas and Ingle 1971; Pratten 1980; Hobbs 1981; Swain et al. 1987; McMahon 2002; Payette and McGaw 2003). This may be a mechanism by which *P. acanthophorus* maintains its efficiency with respect to utilization of environmental resources, in accordance with *K*-selection (cf. Pianka 1970).

From analysis of the CL-frequency distributions of *P. acanthophorus*, six growth lines were observed in both sexes (Fig. 4); because each line corresponded to 1 year of age, there are agreements with regard to the $t_{\max}$ of both sexes. The growth parameters for females ($K = 0.39$ and $CL_{\infty} = 57.43$) and males ($K = 0.40$ and $CL_{\infty} = 58.99$) of this population fall within the range of values calculated for other crayfish, such as the two endemic species of Mexico: $K = 0.45$, $TL_{\infty} = 77.40$, and $K = 0.64$, $TL_{\infty} = 88.40$, for *P. bouvieri* and *P. digueti*, respectively (Gutiérrez-Yurrita and Latournerié-Cervera 1999). Scalici et al. (2008) found that the relationship between latitude and the *K* of *A. pallipes* populations exhibits a negative correlation for both sexes. This correlation was also found by Chucholl (2011) for the populations of *P.*

clarkii introduced into Europe. The small $K = 0.21$ (calculated from Pratten 1980 by Scalici et al. 2008) applies to the northernmost population of *A. pallipes*.

Regardless of whether these are different species and whether the difference in latitude is very large, the similarities that exist between the K of the southernmost population of *A. pallipes* (Scalici et al. 2008) and the K of the population of the Neotropical *P. acanthophorus* should be highlighted. Contrary to the negative correlation of K with the latitude of the introduced *P. clarkii*, the CL_{∞} had a direct correlation (Chucholl 2011). As expected, the $CL_{\infty} = 56.00$ of the southernmost population of *P. clarkii* living in Portugal (Anastácio and Marques 1995) is most similar to that of *P. acanthophorus*. Due to the analyzed data derived from the artisanal capture, total mortality ($Z = 2.37$ for females and $Z = 2.56$ for males) of *P. acanthophorus* was high. Fishing mortality ($F = 1.65$ for females and $F = 1.83$ for males) is primarily caused by commercial catch; thus, natural mortality ($M = 0.72$ for females and $M = 0.73$ for males) is the lesser cause of the death of crayfish in the La Mixtequilla. This mortality may be due to maximal development reached and/or to predation.

As is known, some birds are predators of crayfish (Correia 2001; Huner et al. 2002; Marion 2013; Boyle et al. 2014). In tropical wetland La Mixtequilla, some bird pellets were discovered on the local roads and trails in sampling months; these pellets contained some crayfish claws. One of the birds that could have regurgitated these is the Black-Crowned Night-Heron (*Nycticorax nycticorax*); this species presents high average consumption of *P. clarkii* (Correia 2001). Also, there

are evidences that traces of crayfish dominated in the pellets (boluses) of White Ibis (*Eudocimus albus*) (Dorn et al. 2008; Boyle et al. 2014).

Regardless of that current research findings described the presence of a still, well established population of the endemic *P. acanthophorus* in the tropical wetland La Mixtequilla, there are environmental risks derived from the fragmentation and homogenization of this already widely transformed ecosystem and from the possible overexploitation of that crayfish, both products of the globalization of markets. Therefore, it is necessary to test the assumptions made about the life-history of this secondary burrower crayfish and to improve knowledge on the landscape of La Mixtequilla.

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Figure legends:

Figure 1. Study site for a population of the crayfish *Procambarus acanthophorus* Villalobos, 1948 at La Mixtequilla, Veracruz, Mexico.

Figure 2. Monthly catches of the crayfish *Procambarus acanthophorus* Villalobos, 1948. Numbers on the bars depict the female/male ratio.

Figure 3. Cephalothorax length of the crayfish *Procambarus acanthophorus* Villalobos, 1948 in monthly catches.

Figure 4. Cephalothorax Length (CL) distributions of females and males of the crayfish *Procambarus acanthophorus* Villalobos, 1948 among monthly catches. Each growth curve is 1 year of age.

Figure 5. CL-classes (1–6 and III) of crayfish *Procambarus acanthophorus* Villalobos, 1948 analyzed by the Bhattacharya method.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Table 1. Monthly Samples (MS) and Class Numbers (CN) of cephalothorax length by sex-Means of CL (MCL), Standard Deviation (SD), Separation Index values (SI), and Regression index (R^2), for a population of crayfish *Procambarus acanthophorus* Villalobos, 1948; not applicable (n. a.).

MS	CN	Females				MS	CN	Males			
		MCL	SD	SI	R^2			MCL	SD	SI	R^2
Sep	2	26.37	0.93	n. a.	0.83	Sep	2	25.91	0.77	n. a.	0.99
	3	30.19	0.71	4.66	1.00		3	30.00	0.74	5.42	1.00
	4	35.19	1.30	4.98	1.00		4	34.82	0.83	6.14	1.00
Oct	2	27.85	0.66	n. a.	1.00	Oct	2	27.47	1.23	n. a.	0.74
							3	32.30	1.70	2.13	1.00
	4	33.60	2.82	2.10	1.00		4	36.03	1.23	2.05	0.58
	5	38.71	0.67	2.09	0.85		5	38.50	0.98	2.01	1.00
Nov						Nov	2	27.92	1.35	n. a.	0.93
	3	32.73	1.17	n. a.	1.00						
	4	35.90	0.87	3.11	0.90		4	35.24	1.59	2.30	0.63
	5	39.88	0.78	4.82	1.00		5	40.40	0.36	2.17	1.00
Dec	3	31.06	0.93	n. a.	0.95	Dec	3	32.00	0.77	n. a.	1.00
	4	35.20	0.77	2.50	1.00		4	35.57	0.94	4.18	0.90
	5	40.29	0.95	2.19	0.69		5	40.15	0.64	5.80	1.00
Jan	3	33.00	0.85	n. a.	1.00	Jan	3	32.12	1.31	n. a.	1.00
	4	36.92	1.26	3.72	0.92		4	36.72	1.34	2.12	0.61
	5	39.50	0.69	2.65	1.00		5	39.50	1.10	2.02	1.00
	6	41.50	0.72	2.84	1.00		6	43.05	0.96	2.07	1.00
Feb	1	23.00	0.85	n. a.	1.00	Feb	1	21.93	0.85	n. a.	1.00
	2	26.83	1.03	4.07	0.66		2	25.98	1.28	3.80	0.42
	3	29.50	1.06	2.56	1.00		3	32.04	0.88	5.61	1.00
	III	31.50	0.89	2.05	1.00						
	4	36.38	1.08	4.95	0.71		4	35.57	0.77	4.28	0.87

Table 2. Von Bertalanffy growth parameters for a population of crayfish *Procambarus acanthophorus* Villalobos, 1948. CL_{∞} : asymptotic Cephalothorax Length (mm); K : curvature parameter (year^{-1}); t_0 : age at zero length (years); $t_{\max}$: expected longevity (years); $t_{1/2}$: expected mean lifetime (years); Z : total mortality index (year^{-1}); M : natural mortality (year^{-1}); F : mortality due to catching (year^{-1}); $F\%$: fishing mortality percentage; ϕ' : growth performance index.

	CL_{∞} (mm)	K (year^{-1})	t_0 (years)	$t_{\max}$ (years)	$t_{1/2}$ (year)
Females	57.43	0.39	-0.96	6.73	2.12
Males	58.99	0.40	-0.91	6.59	2.06
	Z (year^{-1})	M (year^{-1})	F (year^{-1})	$F\%$	ϕ'
Females	2.37	0.72	1.65	69.62	3.11
Males	2.56	0.73	1.83	71.48	3.14

Table 3. Parameters (means $\pm$ Standard Deviations [SD]) recorded in the water column from September 2011 to February 2012, at La Mixtequilla, Veracruz, Mexico. Water Temperature (WaTe), Dissolved Oxygen concentration (DO).

Parameter	Months					
	Sep	Oct	Nov	Dec	Jan	Feb
WaTe ($^{\circ}\text{C}$)	30.1 $\pm$ 0.4	27.5 $\pm$ 0.1	28.0 $\pm$ 0.6	24.7 $\pm$ 0.3	21.4 $\pm$ 0.2	25.3 $\pm$ 1.5
pH	5.79 $\pm$ 0.03	6.05 $\pm$ 0.01	6.42 $\pm$ 0.06	6.14 $\pm$ 0.05	6.27 $\pm$ 0.04	6.46 $\pm$ 0.05
DO (mg/L)	0.48 $\pm$ 0.1	4.26 $\pm$ 0.3	2.44 $\pm$ 0.6	1.67 $\pm$ 0.3	1.22 $\pm$ 0.4	0.85 $\pm$ 0.4
NH_4^+ ($\mu\text{g/L}$)	44.9 $\pm$ 39	304.9 $\pm$ 40	74.6 $\pm$ 42	0.0 $\pm$ 0.0	214.1 $\pm$ 79	240.8 $\pm$ 105
PO_4^- ($\mu\text{g/L}$)	196.0 $\pm$ 99	27.7 $\pm$ 22	49.7 $\pm$ 26	334.7 $\pm$ 289	43.9 $\pm$ 41	42.4 $\pm$ 33
Water depth (cm)	22.0	31.7	29.0	27.2	26.0	2.0