

Understanding invasion success: life-history traits and feeding habits of the alien crayfish *Orconectes immunis* (Decapoda, Astacida, Cambaridae)

C. Chucholl^{(1,2)*}

Received September 9, 2011

Revised November 17, 2011

Accepted November 22, 2011

ABSTRACT

Key-words:
r-selected
species and life
history,
non-indigenous
crayfish,
polytrophic
omnivore

In the present study, the life history and diet of the highly successful North American invader *Orconectes immunis* was assessed for the first time in its introduced European range. In 2007, *O. immunis* population dynamics were monitored in a typical backwater habitat using unbaited funnel traps, and its life history was analysed using Von Bertalanffy's growth function. Juveniles hatched as early as March and may attain sexual maturity at the end of their first summer. The adult population moulted up to four times during the summer months, with the non-breeding form (II) lasting for a remarkably short time period. The high growth rate of *O. immunis* was combined with a short longevity, which was estimated at 2.5 years. The fecundity ranged from 119 to 495 pleopodal eggs. The stomach contents were dominated by detritus, followed by macroinvertebrates and macrophytes, and no ontogenetic shift in diet was observed. The ability to prey on a wide array of invertebrate taxa presumably supports the sustained high growth rate of *O. immunis*. The presented data provide evidence that *O. immunis* exhibits a strongly *r*-selected life history and omnivorous feeding habits. These ecological properties have often been linked to successful invaders and enhance the invasiveness of *O. immunis*.

RÉSUMÉ

Comprendre le succès d'invasions : traits d'histoire de vie et habitudes alimentaires de l'écrevisse non-indigène *Orconectes immunis* (Decapoda, Astacida, Cambaridae)

Mots-clés :
espèces à
stratégie *r* et
histoire de vie,
écrevisse
non-indigène,
omnivorie
polytrophique

Dans la présente étude, l'histoire de vie et le régime alimentaire d'*Orconectes immunis*, espèce fortement invasive d'Amérique du Nord ont été évalués pour la première fois dans la région européenne d'introduction. En 2007, la dynamique de la population d'*O. immunis* a été suivie dans un habitat typique de bras mort à l'aide de pièges en entonnoir non appâtés, et son histoire de vie a été analysée en utilisant la fonction de croissance de Von Bertalanffy. Les juvéniles éclosent dès mars et peuvent atteindre la maturité sexuelle à la fin de leur premier été. La population adulte mue jusqu'à quatre fois pendant les mois d'été, avec la forme de non-reproduction (II) d'une période de temps remarquablement courte. Le taux de croissance élevé d'*O. immunis* est associé à une longévité courte, estimée à

(1) Dept. Experimental Ecology (Bio 3), University of Ulm, Albert-Einstein-Allee 11, 89069 Ulm, Germany

(2) Fisheries Research Station BW, Lake Constance, Argenweg 50/1, 88085 Langenargen, Germany

* Corresponding author: Cchucholl@aol.com

2,5 ans. La fécondité varie de 119 à 495 œufs pléopodaux. Les contenus stomacaux sont dominés par des détritiques, suivis par les macroinvertébrés et les macrophytes, et aucun changement ontogénétique dans le régime alimentaire n'a été observé. La capacité à se nourrir sur un large éventail de taxons d'invertébrés soutient vraisemblablement le taux de croissance élevé d'*O. immunis*. Les données présentées démontrent que *O. immunis* présente une histoire de vie de stratège r et des habitudes alimentaires omnivores. Ces propriétés écologiques souvent liés aux espèces invasives soutiennent le caractère invasif d'*O. immunis*.

INTRODUCTION

Invasive alien species (IAS) are one of the greatest threats to global biodiversity (Clavero and García-Berthou, 2005; McGeoch *et al.*, 2010). IAS can perturb the functioning of indigenous ecosystems and compete with or displace indigenous species, resulting in a global homogenisation of biota (Lockwood *et al.*, 2007). Freshwater crayfish are important members of littoral food webs. They affect freshwater communities at different trophic levels, alter physical habitat characteristics and are considered to be keystone species (Momot, 1995; Nyström, 2002). Non-indigenous freshwater crayfish species (NICS) may out-compete indigenous crayfish species (ICS) and severely disturb indigenous ecosystem functioning. For instance, the invasive crayfish *Procambarus clarkii* degraded shallow, macrophyte-dominated lakes in Spain within a few years (Rodríguez *et al.*, 2005).

In Europe, only four to five species of crayfish are indigenous, whereas ten NICS have become established during the last 130 years (Souty-Grosset *et al.*, 2006; Holdich *et al.*, 2009; Chucholl and Pfeiffer, 2010). One of the 'new' NICS is the calico crayfish, *Orconectes immunis* Hagen, 1870, which was first reported in Europe in the mid-1990s from two locations in the Upper Rhine system (Dehus *et al.*, 1999; Gelmar *et al.*, 2006; cf. Figure 1). *Orconectes immunis* originates from north-eastern and central North America, where it is widely distributed in 26 US states and three Canadian provinces (Hobbs, 1989). The pathway of introduction into Europe remains unknown; it was probably introduced either as fishing bait by Canadian soldiers (Gelmar *et al.*, 2006) or as an ornamental pet (Dehus *et al.*, 1999). The calico crayfish is popular as fishing bait in North America and is cultivated in ponds to supply the bait market (Forney, 1957; Brown and Gunderson, 1997). It was introduced into the states of New York and Colorado and parts of Canada (summarised by Hobbs *et al.*, 1989; Jansen *et al.*, 2009), but there are no records of the calico crayfish outside of the American continent except for the present occurrence along the Upper Rhine River in Europe.

In the past fifteen years, the species has rapidly colonised the Upper Rhine system over a stretch of more than 98 km (Gelmar *et al.*, 2006; Chucholl and Dehus, 2011; Collas *et al.*, 2011; Figure 1). *Orconectes immunis* has successfully invaded several types of lentic and lotic habitats, including gravel pit lakes, small canals, temporary backwaters, small brooks and the main river channel. It has become abundant in the natural, slow-flowing or lentic backwaters and floodplains along the main river channel, of which most reaches are nature reserves and harbour a variety of rare plant and animal species (Chucholl, 2006; Gelmar *et al.*, 2006; Chucholl and Dehus, 2011). Unlike the indigenous European crayfish, *Orconectes immunis* digs deep burrows, which allows it to also inhabit shallow and temporary water bodies (Tack, 1941; Bovbjerg, 1970), a niche formerly not occupied by any ICS in central Europe (Souty-Grosset *et al.*, 2006).

Orconectes immunis is the second alien *Orconectes* species to invade the Rhine River; its predecessor *Orconectes limosus* Rafinesque, 1817, arrived approximately 50 years before but is now widely displaced by the newcomer where their range overlaps (Chucholl, 2006; Gelmar *et al.*, 2006; Chucholl *et al.*, 2008). *Orconectes immunis* was shown to be dominant in direct interactions and superior in competition for shelter. Furthermore, preliminary field observations have suggested that life-history differences between the two species may also contribute to the observed species displacement (Chucholl, 2006; Chucholl *et al.*, 2008),

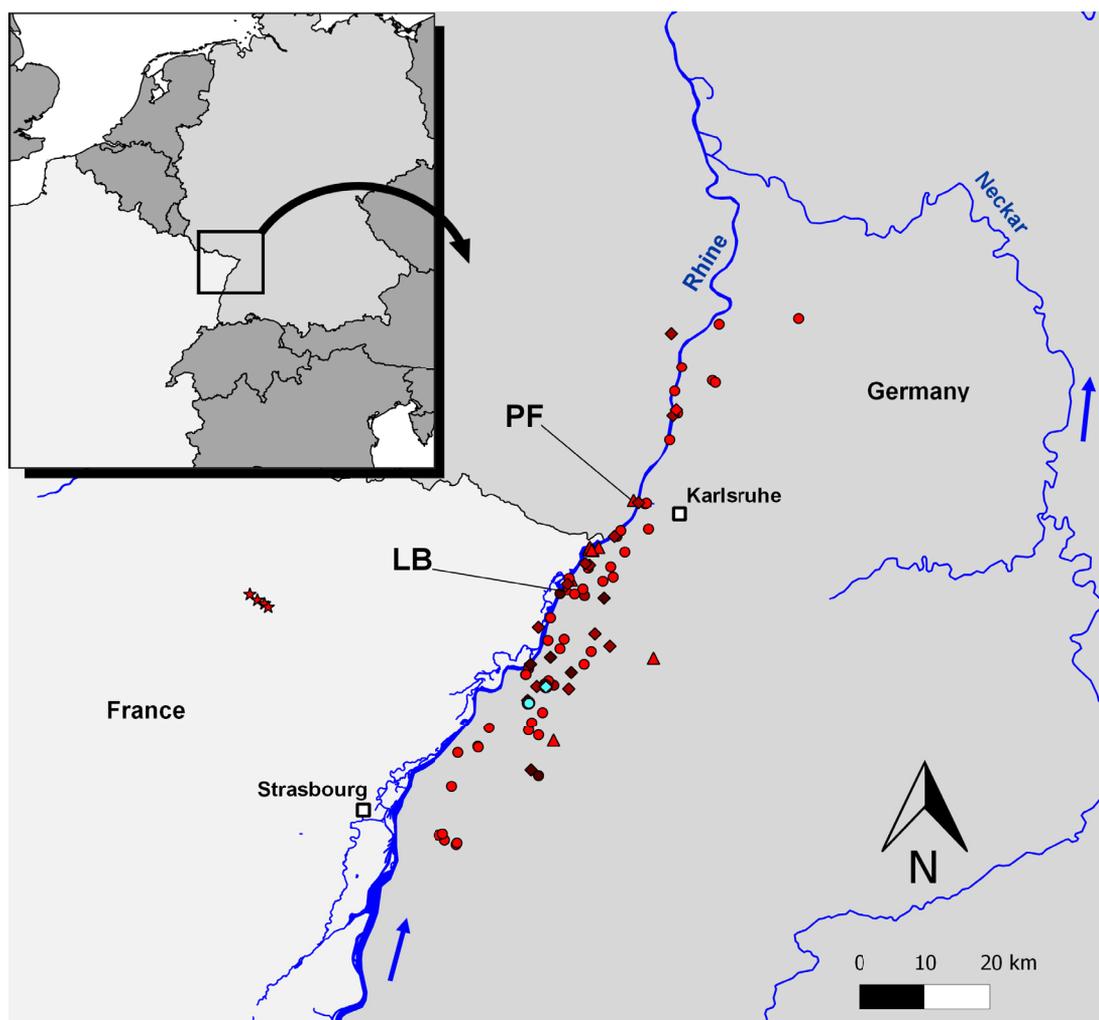


Figure 1

Currently known distribution of *O. immunis* in Europe. The symbol shape indicates the data source (circle: Chucholl and Dehus, 2011; diamond: Gelmar et al., 2006; triangle: Chucholl, unpubl. data; star: Collas et al., 2011), and the symbol colour indicates the year of the record (black: 1993–1999; dark red: 2000–2005; red: 2006–2010). Light blue symbols indicate the two sites where *O. immunis* was first discovered; PF and LB denote the two study populations.

whereas only minor differences have been found in the behavioural reaction to and learning of predatory cues (Schlenker, 2009).

To assess the risk that IAS represent for indigenous biota and ecosystems, it is important to understand their life history and feeding ecology. Furthermore, life-history data are crucial to develop population management or eradication strategies (cf. Scalici and Gherardi, 2007), especially when an IAS has become well established and early eradication has failed (Simberloff, 2003; Bufford and Daehler, 2011).

Filipová et al. (2011) recently demonstrated a considerable genetic divergence between European and North American cytochrome c oxidase subunit I (COI) gene fragment sequences of *O. immunis*. The authors suggested that *O. immunis* might represent a cryptic species complex, making the forecasting of ecological properties of European *O. immunis* populations based on data from populations in its indigenous North American range difficult because the latter might comprise different cryptic species. Moreover, the ecological properties of an IAS

can markedly differ between its indigenous and introduced range, as a result of genetic changes that accompany the founding process and different abiotic (e.g., climate) and biotic conditions (e.g., competitors, predators; Lockwood *et al.*, 2007; Chucholl, 2011).

The primary aim of the present study was to report the life-history data, population dynamics and feeding habits of a European *O. immunis* population in a representative backwater habitat near the Rhine River and, thus, to provide a better understanding of its invasion success. Specifically, the population dynamics were monitored using unbaited funnel traps, and the obtained length-frequency data were used to assess life-history parameters, such as growth performance, mean lifetime, longevity, asymptotic length, and mortality, using Von Bertalanffy's growth function. To assess the feeding habits of *O. immunis*, stomach contents of juvenile and adult crayfish were analysed and the prey electivity was calculated. With respect to the previously observed displacement of *O. limosus* (Chucholl *et al.*, 2008), fecundity and hatch data of both *O. limosus* and *O. immunis* were collected to assess whether those life-history traits may contribute to the species displacement.

METHODS

> STUDY SITE AND SAMPLING

To assess the population ecology and life history of *O. immunis*, an abundant population of calico crayfish was monitored in a typical backwater habitat, Lake Bärensee (LB; 15.7 ha, 48° 54' 4.72" N, 8° 9' 16.74" E). LB is a former branch of the Rhine River that has retained a shallow downstream connection to the main river channel and is part of the nature reserve 'Rastatter Rheinaue' and the special area of conservation 'Rheinniederung zwischen Wintersdorf und Karlsruhe' (SAC 7015-341). The lake is flooded during high-water events, usually several times per year. The lake water was turbid (Secchi depth < 1.25 m; Table I), and macrophytes were scarce (mostly represented by *Ceratophyllum demersum* and *Elodea nuttallii*). The bottom sediment was soft, and the water depth rarely exceeded 2 m. The lake had featured a large population of the endangered water chestnut (*Trapa natans*), but the species had recently disappeared from the lake, accompanied by a decline of other macrophyte species. The macro-zoobenthos was dominated by IAS, e.g., *Corbicula fluminea*, *Dreissena polymorpha*, *Gammarus tigrinus*, *Dikerogammarus villosus*, and *Chelicorophium curvispinum*. *Orconectes immunis* occurred syntopic with *O. limosus* in LB; however, the latter was very rare.

The crayfish were captured using unbaited, cylindrical funnel traps (0.4 m diameter opening, 3 m long, with 4- to 6-mm mesh). Two traps at a time were connected by a 2-m long net, with the openings facing towards each other. The pairs of traps were set along the shoreline at a depth of between 0.4 and 1.5 m and were exposed for seven days (one unit effort is equivalent to one trap set for seven days). On each sampling occasion, the surface water temperature, conductivity, and Secchi depth were measured at a distance from shore of approximately 20 m using a conductometer, LF 191, and a pH sensor, pH 197-S, from WTW (Weilheim, Germany).

The trapping lasted from early April to early August in 2007 (eight trapping occasions). Because of the high capture per unit effort (CPUE) in the late spring and summer (with a CPUE of up to 70 specimens in late July), only the contents of two randomly selected traps were sampled. The total number of traps varied between eight and 16. After a severe flooding event in August 2007, the CPUE decreased dramatically, and the trapping was ceased in October. An additional trapping occasion was performed in spring 2009 (four traps) to compare the reproductive pattern across years.

To assess juvenile growth, small crayfish were captured using manual net sampling on May 31, 2007. A hand net (with a mesh size of 1 mm) was pulled gently over the substrate perpendicular to the shoreline twelve times. Upon each pull, the net content was carefully searched for crayfish by hand.

Table 1

Orconectes immunis population dynamics, surface water temperature, Secchi depth and conductivity in LB. M means males and f females. The asterisks indicate significant differences from the previous sampling occasion based on Mann-Whitney rank sum tests (CL) or Chi-square tests with Yates correction (other parameters), except for the sex ratio, for which the asterisks show significant differences from 1:1. N.t. = not tested due to sample size < 10. The number of asterisks indicates the p-level: * ≤ 0.05, ** ≤ 0.01, and *** ≤ 0.001.

Sample date	N	CPUE	Mean CL m	Mean CL f	Prop. f	Sex ratio balanced	Prop. m II	Prop. f II	Prop. active glair glands	Prop. eggs	Prop. hatchlings	Prop. egg remains	T [°C]	Secchi depth (m)	Conductivity (µS·cm ⁻¹)
04.04.2007	158	10	37.4	38.6	0.17	no ***	0.03	0.0	0.04	0.12	0.19	0.31	13.6	0.7	416
10.04.2007	346	29	36.7	37.1	0.52 ***	yes	0.04	0.02	0.05	0.51 ***	0.08	0.30	17.9	0.6	402
24.04.2007	121	61	36.6	37.4	0.59	yes	0.90 ***	0.20 ***	0.01	0.0 ***	0.06	0.18	24.3	1.0	370
10.05.2007	133	67	37.2	39*	0.54	yes	0.36 ***	0.43 **	0.39 ***	0.02	0.0	0.02 **	19.0	0.5	379
08.06.2007	34	34	34.6	40 n.t.	0.26 n.t.	n.t.	0.24	0.11 n.t.	0.0 n.t.	0.0 n.t.	0.0 n.t.	0.0 n.t.	24.0	1.1	412
10.07.2007	72	36	36.7	37.9	0.39	yes	0.16	0.0	0.96	0.0	0.0	0.0	18.3	1.1	356
26.07.2007	139	70	32.5***	32.3***	0.42	yes	0.67 ***	0.50 ***	0.09 ***	0.0	0.0	0.0	21.5	1.3	405
01.08.2007	94	31	34.9***	36.7***	0.32	no *	0.23***	0.10 **	0.83 ***	0.0	0.0	0.0	21.6	1.1	401
03.04.2009	283	71	32.7***	34***	0.58 ***	yes	0.03	0.04	0.02	0.84 ***	0.07	0.01 ***	12.6	x	x

An additional crayfish population in a backwater downstream of LB ("Pforzer Altrhein", PF; 49° 1' 26.14" N, 8° 17' 31.45" E) was trapped on three occasions from April 10 to April 24, 2007. *Orconectes limosus* occurred in PF at a noticeably higher density than in LB, making it possible to compare the reproductive pattern of both of the species within the same habitat. The trapping method was the same as in LB, but the traps were only exposed for three to four days on each sampling occasion. The trapping at PF was ceased after all of the captured *O. immunis* females had released their offspring.

> MEASUREMENTS

The species identity (*O. immunis* or *O. limosus*), carapace length (CL; measured from the tip of the rostrum to the dorsal posterior margin of the cephalothorax with a digital slide calliper to the nearest 0.1 mm), sex and reproductive traits (*i.e.*, active glair glands, attached eggs, hatchlings or egg remains) were noted from all of the crayfish in the sampled traps. Mature cambarid crayfish show a cyclic dimorphism between a reproductively active (I) and a reproductively inactive form (II). The reproductive form, *i.e.*, form I or form II, was distinguished in both sexes and also noted. The form changes usually with every moult, *i.e.*, an individual in form I moults into form II and vice versa. The cyclic dimorphism (form alteration) occurs in mature males of all cambarid genera and was also reported from *Orconectes* spp. females (Wetzel, 2002; Buřič *et al.*, 2010). In *O. immunis* and *O. limosus*, form I males (hereafter m I) differ from form II (hereafter m II) in having distinctly larger chelae (Chucholl, 2006) and more slender and pronounced gonopod tips. The mesial gap between the terminal elements of the 1st gonopod is also conspicuously wider. Form I females (hereafter f I) have a distinctly wider pleon than form II females (hereafter f II; Wetzel, 2002; Buřič *et al.*, 2010) and usually show the above-mentioned reproductive traits. Moreover, form I individuals of *O. immunis* often have conspicuously purple-coloured chelae.

To assess the length-weight relationship, intact specimens (with no missing or regenerated chelae) of *O. immunis* ($N = 139$ and 98 for males and females, respectively) were transported to the laboratory and weighed to the nearest 0.01 g using a Kern balance (type 822-67). Prior to the weight measurement, the specimens were wiped with blotting paper and gently shaken ten times to remove adherent water drops.

> LIFE-HISTORY ANALYSIS

The obtained size-frequency data were analysed using the program FiSAT 2 (v. 1.2.2; Gayanilo and Pauly, 1997). The growth was described per sex using Von Bertalanffy's growth function (VBGF), adjusted for seasonal growth in summer and no growth in winter (Pauly and Morgan, 1987): $L(t) = L_{\infty} (1 - e^{-k(t-t_0)} + Ck/2\pi\{\sin 2\pi(t-t_s) - \sin 2\pi(t_0-t_s)\})$, where L is the CL at age t , L_{∞} is the asymptotic CL, k is the curvature parameter (*i.e.*, the rate at which L_{∞} is approached) and t_0 is the initial condition parameter (*i.e.*, the hypothesised age at which the CL is zero). t_s was substituted with WP , using the formula $WP = t_s + 0.5$, which represents the winter point at which the growth rate is slowest in the annual cycle. 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, as suggested by Tack (1941). L_{∞} and k were estimated within the ELEFAN module of FiSAT 2 (non parametric scoring), using the size frequencies obtained from the juvenile hand captures in late May 2007 as starting points, and t_0 was assessed using non-linear regression analysis.

Longevity (t_{\max}) was estimated using the equation $t_{\max} = (3/k) + t_0$, and mean lifetime ($t_{1/2}$) was estimated using the equation $t_{1/2} = \{\Sigma[n(t) \cdot t]\}/N$, where n is the number of individuals at time t and N the total number of individuals (Gayanilo and Pauly, 1997; Scalici and Gherardi, 2007; Chucholl, 2011). The growth performance index (ϕ') was derived from k and L_{∞} by applying the equation $\phi' = \log(k) + 2\log(L_{\infty})$ (Pauly and Munro, 1984).

The total mortality (Z) was estimated in FiSAT2 from the Powell-Wetherall plot equation, which allows for the calculation of L_{∞} and the ratio Z/k using length-frequency data. The natural

mortality (M) was computed by solving the equation $\log(M) = -0.0066 - 0.279\log(L_{\infty}) + 0.6543\log(k) - 0.463\log(T)$, where T is the mean environmental temperature during the study period (Pauly, 1980). Because Z is the sum of M and the fishing mortality (F), the fishing mortality was obtained by subtracting M from Z .

> FECUNDITY

The pleopodal fecundity was determined from 38 gravid *O. immunis* females captured from LB and 25 gravid *O. limosus* females captured from PF. Upon capture, the specimens were transported carefully to the laboratory, and all attached eggs were stripped off using forceps and counted.

> FEEDING ECOLOGY

Active crayfish were captured from the eastern littoral zone of LB on July 24 and August 6, 2007, beginning 30 min after sunset. The crayfish were captured with a hand net within a 10-m radius of the four transects used to assess the prey abundance (see below). Upon capture, the crayfish were immediately put on crushed ice to halt their digestion. The specimens were subsequently transported to the laboratory and dissected. The stomach was carefully removed and placed into 70% ethanol. To assess a possible ontogenetic shift in diet, the specimens were grouped into two size classes, roughly corresponding to juvenile and adult crayfish ($CL \leq 27$ mm and $CL > 27$ mm).

The stomach content was washed into a petri dish and analysed qualitatively and quantitatively under a binocular. Invertebrates were identified by characteristic hard parts (e.g., head capsule, legs, abdomen, and shell fragments) and counted. The relative volume proportion of the food categories (detritus, macroinvertebrates and macrophytes) was estimated on an ordinal scale (0–5). The percentage of the stomachs containing prey i (OcP_i) and the percentage of the total number of organisms representing prey i (AbP_i), and the percentage of the stomachs containing food category i (OcF_i) and the estimated volume proportion of food category i ($VolF_i$) were used to calculate a relative importance index (RI) for each prey item and food category using the following formula (modified from Pérez-Bote, 2005): $RI_i = AI_i \cdot 100 / \sum(AI_i = 1 - n)$, where $AI_i = OcP_i \cdot AbP_i$ or $AI_i = OcF_i \cdot VolF_i$ for prey items or food categories, respectively, and n is the number of prey items or food categories. The RI incorporates the information derived from two methods of stomach content analysis and thereby reduces the biases produced by using a single measure of stomach content (Windell, 1971; Pérez-Bote, 2005).

To assess the prey electivity, benthic macroinvertebrates were sampled in the eastern littoral zone of LB on July 19 and 30, 2007, and on August 3 and 6, 2007. A total of 12 samples were taken with a Birge-Ekman grab (15 x 15-cm opening) at 1, 5 and 10 m shore distance along four transects perpendicular to the shore line (with a maximum depth of 1.6 m). The samples were transported to the laboratory and searched for macroinvertebrates. The sediment fraction was rinsed two times through a 600- μ m sieve. The collected macroinvertebrates were identified as far as feasible and counted. The prey electivity of *O. immunis* was then assessed using Jacobs (1974) index, $D_{ji} = (RI_i - r_i) / (r_i + RI_i - 2r_i RI_i)$, where r_i is the relative abundance of prey item i in the environment. Values of D_j between 0 and 1 indicate positive prey selection, while values between 0 and -1 indicate negative selection.

> STATISTICS

All statistical analyses were performed using SigmaPlot 10.0 (with SigmaStat 3.5 Integration) except for the generalised linear models (GLMs; see below), which were run in the software package R 2.14 (R Development Core Team, 2011). The correlations between the abiotic factors and CPUE, CPUE and the proportion of form II individuals, and fecundity and CL were assessed using Pearson correlations. The mean CL was compared for each sex between consecutive sampling occasions using Mann-Whitney rank sum tests, and the proportions of

form II individuals and females with active glair glands, eggs, hatchlings or egg remains were compared using Chi-square tests with Yates correction. The sex ratio of the total catch and the sex ratio of the catch of each sampling occasion were tested for statistical differences from 1:1 using Chi-square tests with Yates correction.

The relationship between the *CL* and body weight (*W*) was described for each sex by means of the power equation $y = 10^a \cdot x^b$, with $x = CL$ (mm) and $y = W$ (g). The parameters *a* and *b* were estimated using a linear regression after log transformation of the data.

GLMs were used to assess whether sex had a significant effect on *W* and whether species (*O. immunis* or *O. limosus*) had a significant effect on the fecundity (cf. McCullagh and Nelder, 1989; Jones *et al.*, 2009). *W* and the number of pleopodal eggs were used as response variables, and *CL* was used as predictor variable. The sex and species were entered as factors. Both of the GLMs allowed for interactions between the factor and the *CL*.

To assess ontogenetic shifts in the diet of *O. immunis*, the *RI* values of prey items and food categories were compared between the two crayfish size classes using z-tests with Yates correction. Differences in the *RI* of prey items and food categories within each crayfish size class were also assessed using z-tests with Yates correction, followed by a Bonferroni adjustment of the *p* level. The AbP_i of prey items was compared within each crayfish size class using a Kruskal-Wallis one-way ANOVA on ranks, followed by Tukey's *post-hoc* test. A Chi-square test was used to assess significant differences between the *RI* of prey items and r_i .

RESULTS

> POPULATION DYNAMICS

In total, 1216 *O. immunis* specimens were captured and measured during the study period in 2007, and 283 additional crayfish were captured on April 3, 2009. The largest male had a *CL* of 49 mm, while the *CL* of the largest captured female measured 48 mm. The minimum size at maturity was 25.6 mm *CL* and 26.7 mm *CL* in males and females, respectively. The sex ratio of the total catch did not differ significantly from 1:1 (Chi-square-test with Yates correction: $p = 0.08$). The sex ratio was also balanced on each sampling occasion (Chi-square-tests with Yates correction: $p > 0.05$), except for April 4 and August 1, 2007, when it was significantly biased towards males (Chi-square-tests with Yates correction: $p < 0.001$ and $p < 0.05$, respectively; Table I).

The surface water temperature at LB ranged from 14 °C in early April to 27 °C in September and dropped below 10 °C in October (Table I). There was no significant correlation between the surface water temperature and CPUE (Pearson correlation: $p = 0.155$). The proportion of form II individuals within the catch tended to correlate with the CPUE in males (Pearson correlation: $R = 0.69$, $p = 0.058$; Figure 2) and correlated significantly with the CPUE in females (Pearson correlation: $R = 0.77$, $p = 0.025$; Figure 2). The highest proportion of m II occurred in late April, whereas the proportion of f II peaked later in mid-May (Table I, Figure 2). A second peak of form II individuals occurred simultaneously in both sexes in late July (Table I, Figure 2). Freshly moulted crayfish were abundant in the catch from mid-April to June and again from mid-July to August (Figure 2).

The mean size of the captured crayfish ranged between 32 mm *CL* in mid-July and 40 mm *CL* in early June, 2007. The mean *CL* decreased significantly in both sexes in mid-July, 2007 (Chi-square tests with Yates correction: $p < 0.001$; Table I), when the largest size classes mostly disappeared from the catch (Figure 3). By early August, 2007, the mean *CL* had significantly increased to values comparable to the previous months (Chi-square tests with Yates correction: $p < 0.001$; Table I, Figure 3).

> LIFE-HISTORY PARAMETERS

The length frequencies of the study population in *LR* and the resulting seasonal growth patterns are shown in Figure 3 for each sex. The obtained VBGF parameters (L_∞ , *k*, and t_0),

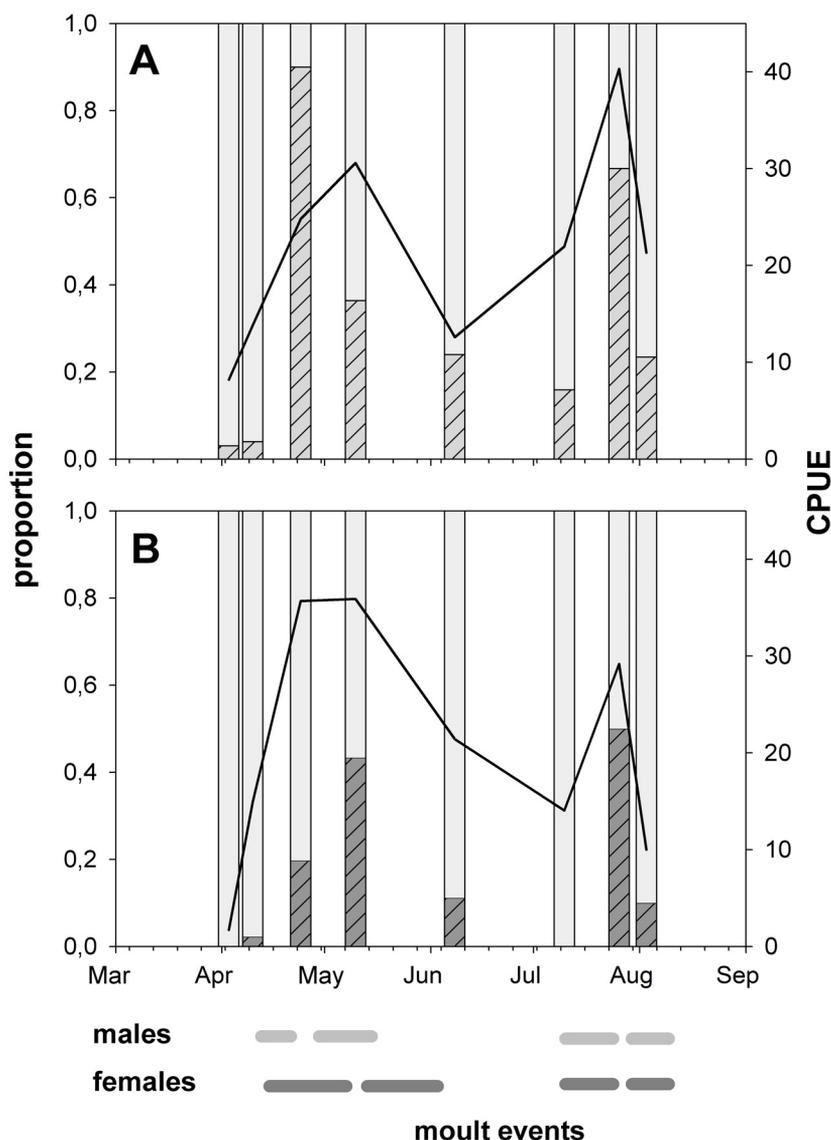


Figure 2

Proportion of form II individuals within the total catch (hatched bars), CPUE (solid line; right axis) and supposed moult events (bottom) of the *O. immunis* population in LB, according to sex (A, males; B, females).

their derivatives (longevity, t_{\max} , and the growth performance index, ϕ'), the calculated mean lifetime ($t_{1/2}$), and the mortality estimates (the total mortality, Z , the natural mortality, M , and the fishing mortality, F) are summarised according to sex in Table II.

> LENGTH-WEIGHT RELATIONSHIP

There was a significant positive relationship between CL and W in both sexes (Pearson correlation of log-transformed data: $p < 0.001$). The obtained parameters for the power equation are summarised per sex in Table III, and the relationship between CL and W is shown for each sex in Figure 4. The GLM analysis showed that sex had a significant effect on W (analysis of deviance: $F_{1,233} = 18.05$, $\eta^2 = 0.236$, $p < 0.001$). The GLM included also a

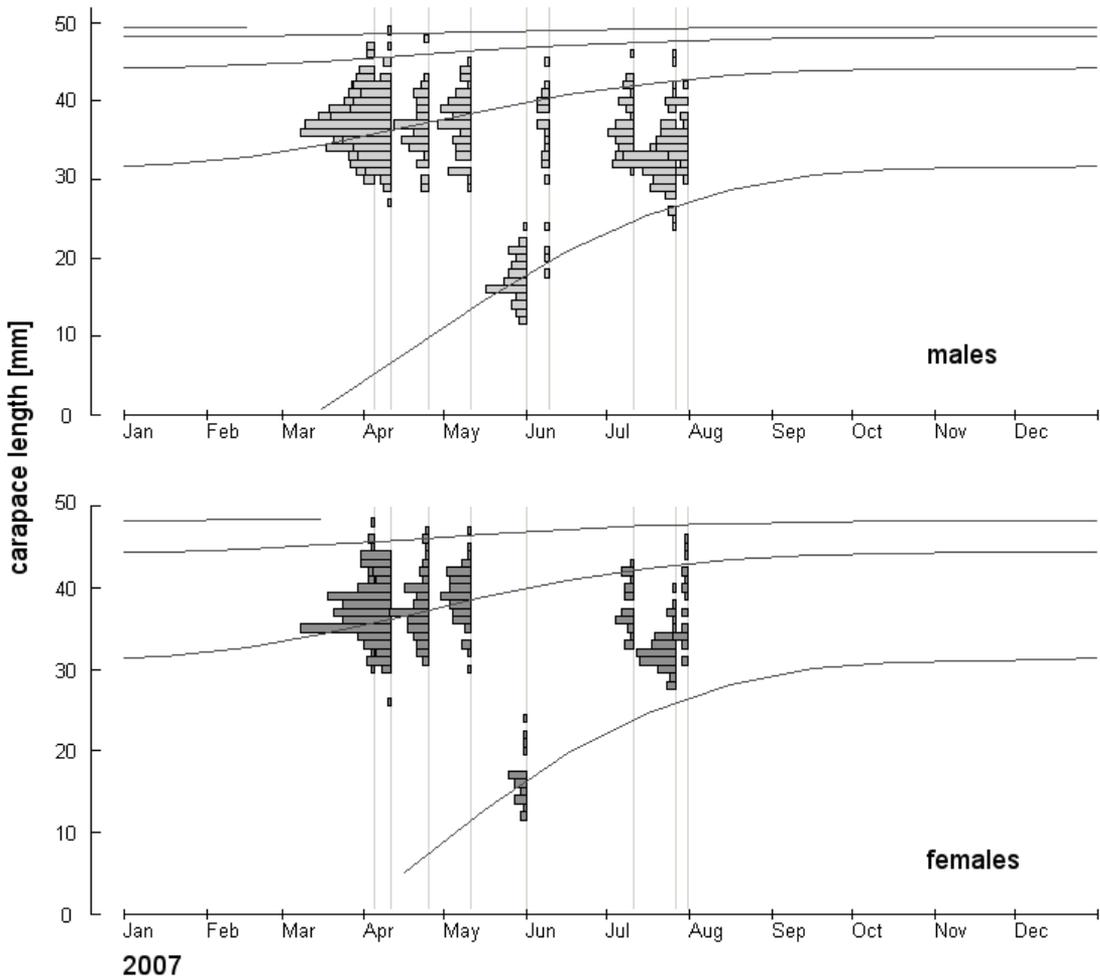


Figure 3
 Seasonal growth model for *O. immunis* males (light grey) and females (dark grey). YoY may attain sexual maturity within their first summer.

Table II
 VBGF parameters (L_{∞} , k , and t_0), their derivatives (longevity, t_{max} , and the growth performance index, ϕ'), mean lifetime ($t_{1/2}$), and mortality (the total mortality, Z , the natural mortality, M , and the fishing mortality, F) of the *O. immunis* population in LB, according to sex.

	L_{∞}	k	t_0	t_{max}	$t_{1/2}$	ϕ'	Z	M	F
Males	50.0	1.15	-0.09	2.52	2.09	3.46	3.68	1.30	2.38
Females	49.8	1.22	-0.09	2.37	2.06	3.48	3.95	1.36	2.59

significant interaction between sex and CL (analysis of deviance: $F_{1,233} = 58.40, p < 0.001$), indicating that W increased faster in males than in females (cf. Figure 4).

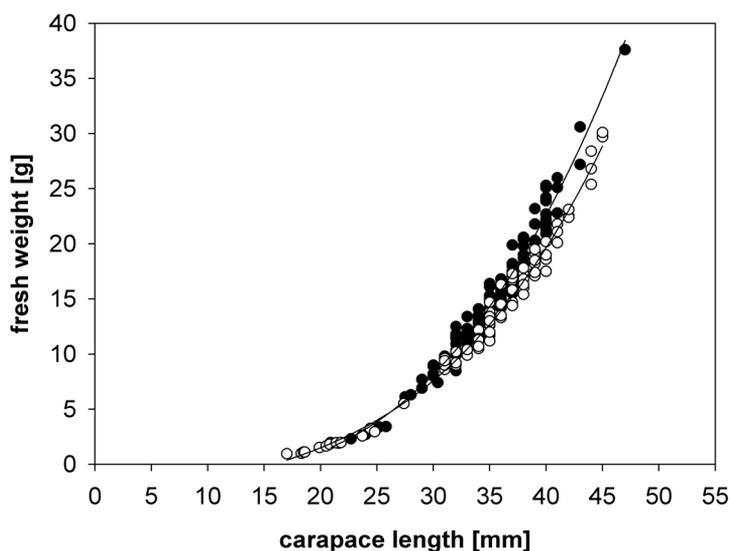
> REPRODUCTION

On April 10, 2007, approximately half of the captured *O. immunis* females from LB ($N = 181$) carried eggs, whereas eight per cent and 30 per cent already carried hatchlings and egg

Table III

Parameters of the length-weight relationship in *O. immunis* for each sex (form I in adults). R was determined using linear regression of the log-transformed data. The equation to derive the weight is as follows: $W \text{ (g)} = 10^a \text{ CL (mm)}^b$.

Sex	N	R	a	b
Males	133	0.98	-4.198	3.465
Females	85	0.98	-3.840	3.203

**Figure 4**

Length-weight relationship in *O. immunis*. Males are depicted as solid symbols, and females are depicted as open symbols. Adult crayfish were in form I. See Table III for the regression parameters.

remains, respectively (Table I). By late April 2007, none of the captured females ($N = 71$) carried eggs, and hatchlings were present on the pleopods of six per cent of the females. Egg remains were found on 18 per cent of the captured females (Table I). The last egg-bearing female was captured on May 10, 2007 (one out of 67 captured females), together with the last female with egg remains on the pleopods. The proportion of females with active glair glands increased significantly on the same sampling occasion (Chi-square test with Yates correction: $p < 0.001$; Table I), and by early August, 83 per cent of the sampled females had active glair glands (Table I). On April 3, 2009, 165 females were trapped from LB to compare reproductive the pattern across years: 84 per cent carried eggs, seven per cent carried hatchlings, and one per cent carried egg remains (Table I).

Orconectes immunis and *O. limosus* occurred together in PF, where reproductive patterns were analysed from April 10 to April 24, 2007, on three capture occasions (Figure 5). During this time period, the proportion of captured *O. immunis* females with attached eggs dropped from 44 to zero per cent, while the proportion of females with egg remains increased from eight to 100 per cent. Females with attached hatchlings were captured on the first two capture occasions (Figure 5). None of the captured *O. limosus* females carried hatchlings or egg remains, but up to 98 per cent of the females that were sampled carried eggs (Figure 5).

The pleopodal fecundity of the sampled *O. immunis* females ranged from 119 to 495 eggs and averaged 277.7 eggs (± 94.8 SD) per female, whereas the pleopodal fecundity of the

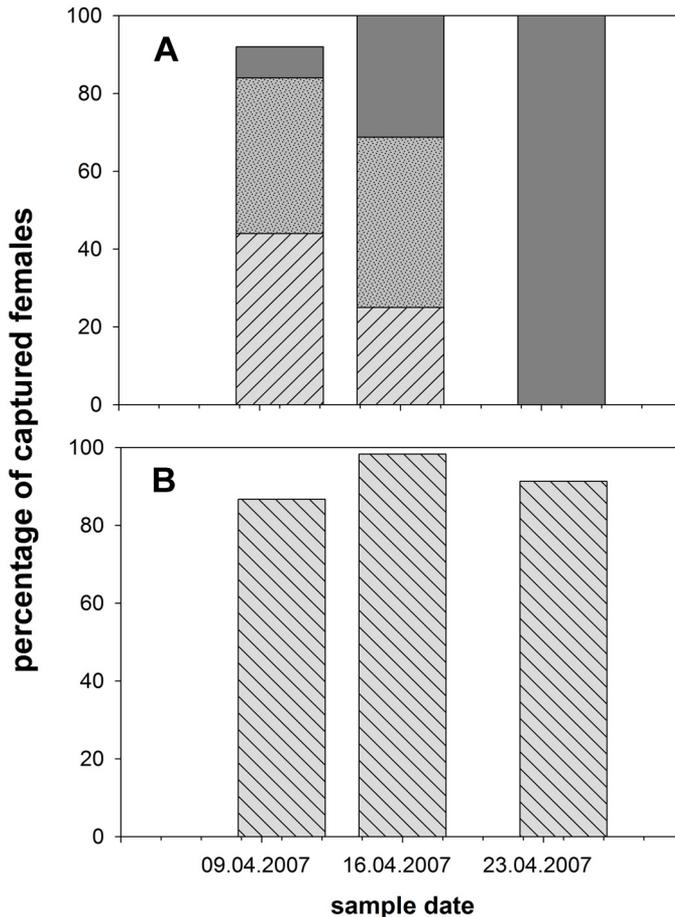


Figure 5

Reproductive pattern of *O. immunis* (A; top) and *O. limosus* (B; bottom) in PF in spring 2007. The hatched bars represent the proportion of females with attached eggs; dotted bars represent the proportion of females carrying hatchlings. The proportion of females with egg remains is depicted in dark grey. Note that *O. limosus* females did not carry hatchlings or egg remains within the study period, whereas all of the sampled *O. immunis* females had released their offspring by late April.

O. limosus females averaged 261.3 eggs (± 128.6 SD) per female. The number of pleopodal eggs and the female CL were significantly correlated in both of the species (Pearson correlation: $R = 0.62$, $p < 0.001$ and $R = 0.79$, $p < 0.001$, for *O. immunis* and *O. limosus*, respectively; Figure 6). The GLM analysis showed that there was no significant effect of species on the number of pleopodal eggs (analysis of deviance; main effect: $F_{1,58} = 2.222$, $p = 0.142$; interaction with CL: $F_{1,58} = 0.038$, $p = 0.847$), indicating that the fecundity did not differ between the two species (cf. Figure 6).

> FEEDING ECOLOGY

The stomach contents of 58 *O. immunis*, evenly grouped into two size classes, were analysed. The juvenile size class was made up of crayfish with a mean CL of 24.3 mm (± 2.3 mm SD), whereas the specimens of the adult size class averaged 32.3 mm CL (± 2.9 mm SD).

In both of the size classes, detritus was found to be the most important food category, followed by macroinvertebrates and macrophytes (Figure 7); however, the RI of the food

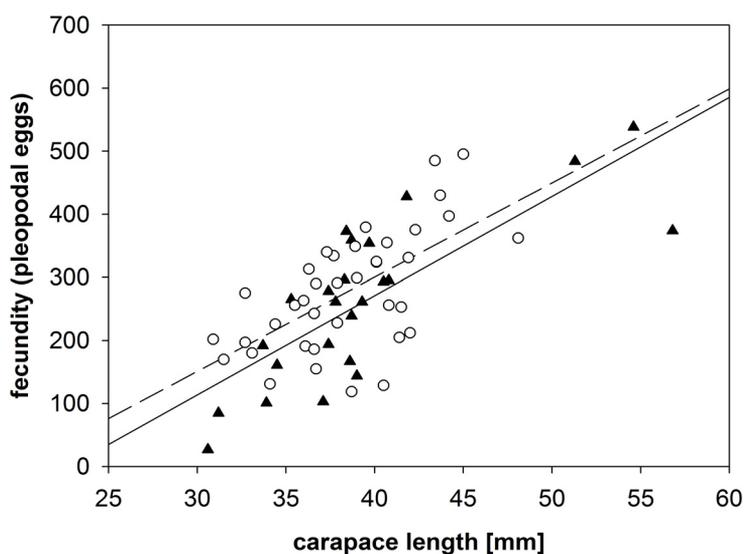


Figure 6

Fecundity of *O. immunis* (open circles) and *O. limosus* (solid triangles). The trend lines were determined using linear regression (*O. immunis*, dashed line; *O. limosus*, solid line; see the results section for the statistics).

categories did not significantly differ from each other (based on z-tests with Yates correction, followed by a Bonferroni adjustment of the p level). The consumed macroinvertebrate prey largely consisted of Chironomidae larvae and Cladocera, followed by unidentified insects and Ephemeroptera larvae (Figure 7). Chironomidae larvae and Cladocera attained significantly higher RI values than the other 15 prey items in both of the crayfish size classes (according to z-tests with Yates correction, followed by a Bonferroni adjustment of the p level) and were also consumed in significantly higher numbers than the other prey items (Kruskal-Wallis one-way ANOVA on ranks: $H_{11} = 221.0$, $p < 0.001$, and $H_{14} = 232.0$, $p < 0.001$, for the juvenile and adult size class, respectively; Figure 8). The RI of the prey items and food categories did not significantly differ between the two crayfish size classes (z-tests with Yates correction: $p > 0.05$; Figure 7).

To calculate the prey electivity, the stomach content data of the two crayfish size classes were pooled because they showed no significant statistical differences. D_J was found to be positive for Trichoptera larvae, Ephemeroptera larvae and *Dreissena polymorpha*, whereas D_J reached distinct negative values ($D_J < -0.5$) for Gammarida and Oligochaeta (Figure 9). The RI of *Dreissena polymorpha* and Oligochaeta differed significantly from r_i (Chi-square test: $p < 0.05$; Figure 9).

DISCUSSION

> LIFE HISTORY

The life-history analysis was based on an ample number of captured crayfish and was carried out in a typical *O. immunis* habitat. The traps used were not baited and produced, presumably, less bias in crayfish size and sex than baited traps, which typically show a bias towards more competitive and vagile individuals, *i.e.*, males and larger crayfish (France *et al.*, 1991; Olsen *et al.*, 1991; Chucholl, 2011). The sex ratio of the total catch was balanced, which is in accordance with the sex ratio suggested for other Cambaridae, including *Orconectes*

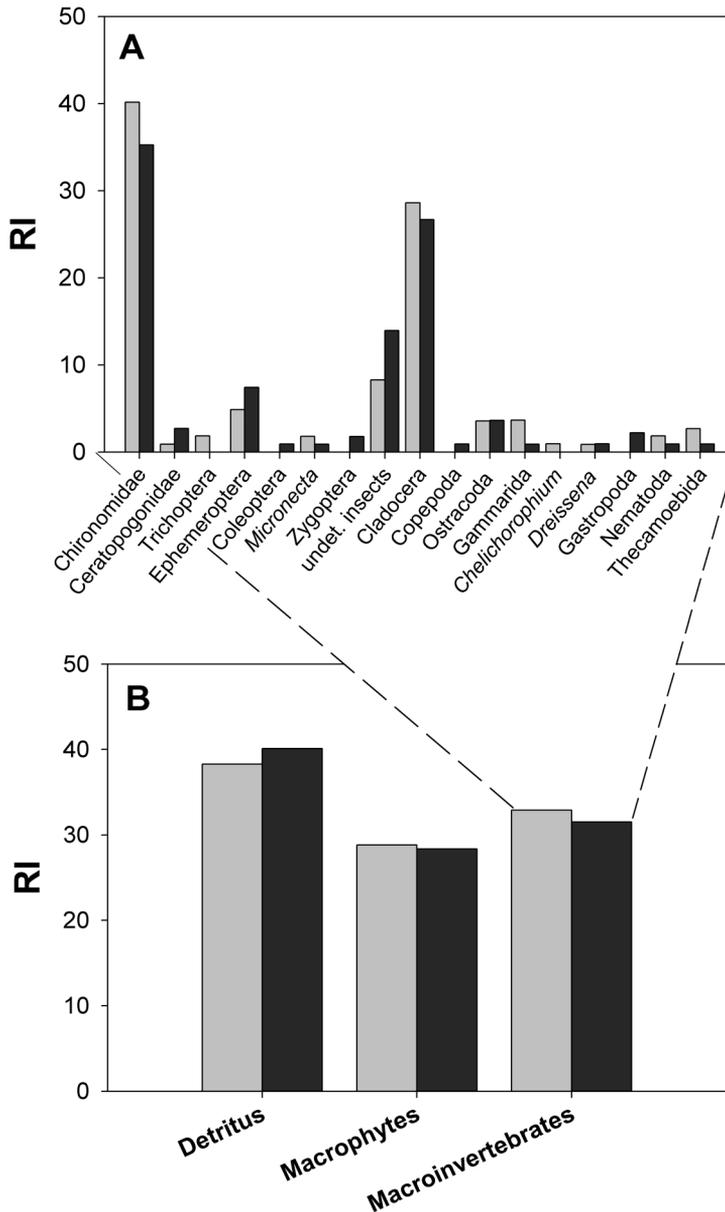


Figure 7

Relative importance (RI) of prey items (A; top) and food categories (B; bottom) in the diet of *O. immunis*. Crayfish shorter than 27 mm CL (juveniles) are depicted in light grey, crayfish longer than 27 mm CL (adults) are shown in dark grey.

spp. (Olsen *et al.*, 1991; Hamr, 2002 and citations therein). The trappable crayfish population was largely composed of crayfish larger than 27 mm CL and probably included individuals of the 0+ cohort in late summer and spring (*cf.* Figure 3). The observed total mortality resulted largely from fishing mortality, demonstrating the capture-effort to which the population was subjected in LB. In total, approximately 70 kg of crayfish were removed from LB during the 2007 study period, corresponding to approximately 3500 specimens (estimated from the obtained length-weight relationships and size-frequency distributions).

The growth rate (curvature parameter k) of *O. immunis* was estimated at 1.22 and 1.15, which indicates very rapid growth, especially when compared to the curvature parameters of ICS,

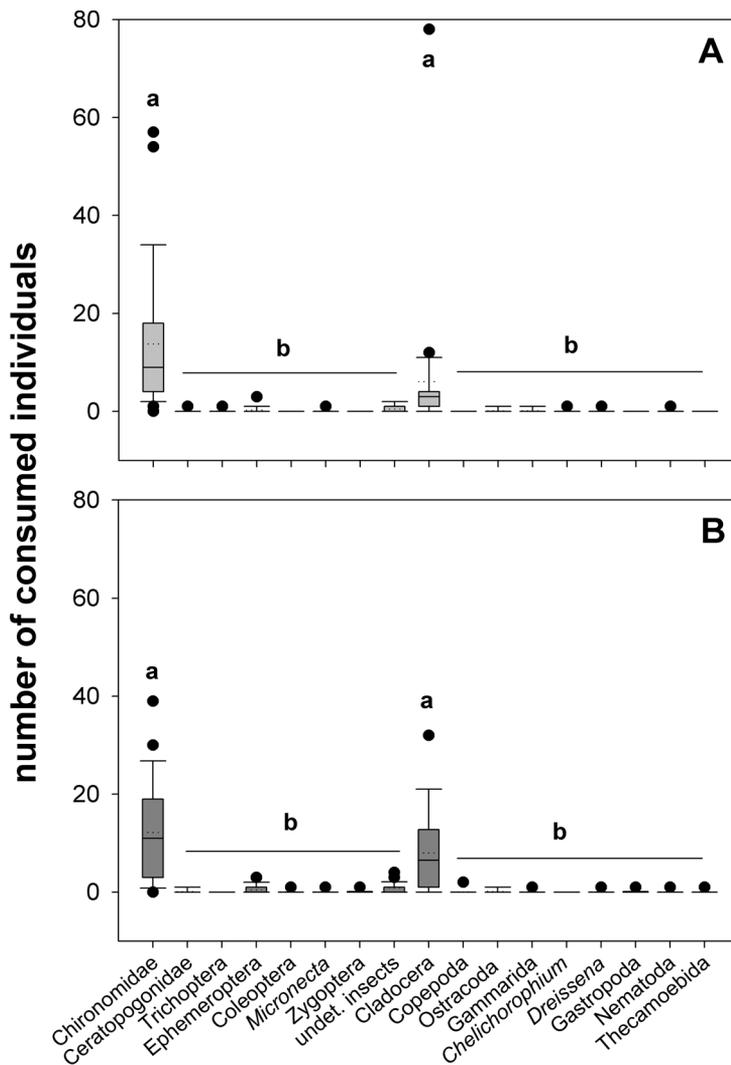


Figure 8

Number of consumed prey individuals per crayfish stomach. Juvenile crayfish are depicted on top (A; light grey); adult crayfish are shown below (B; dark grey). The dashed lines in the boxes indicate the mean value; the solid lines indicate the median. Different letters show significant differences, determined using a Kruskal-Wallis one-way ANOVA on ranks, followed by a Tukey's post-hoc test ($p < 0.05$).

which typically range between 0.25 and 0.50 (summarised by Scalici *et al.*, 2008). The obtained values of the growth performance index (ϕ') were also considerably higher than the ϕ' values reported for ICS (Scalici *et al.*, 2008) but were remarkably similar to values known from other fast-growing NICS, such as *P. clarkii* (Scalici *et al.*, 2009 and citations therein; Chucholl, 2011; Table IV). The k values of *O. immunis* obtained in the present study exceed those of *P. clarkii* (Scalici *et al.*, 2009 and citations therein), suggesting that *O. immunis* approaches its asymptotic length at a faster rate than *P. clarkii* and attains its sexual maturity earlier. In fact, young-of-the-year (YoY) *O. immunis* in LB may attain sexual maturity at the end of their first summer, a finding that coincides with data reported from permanent habitats in its indigenous range, where one third to three quarters of the YoY mature by autumn (Tack, 1941; Caldwell and Bovbjerg, 1969). This quick maturation probably represents a unique life-history trait because no other ICS or NICS in central Europe is known to mature within its first summer

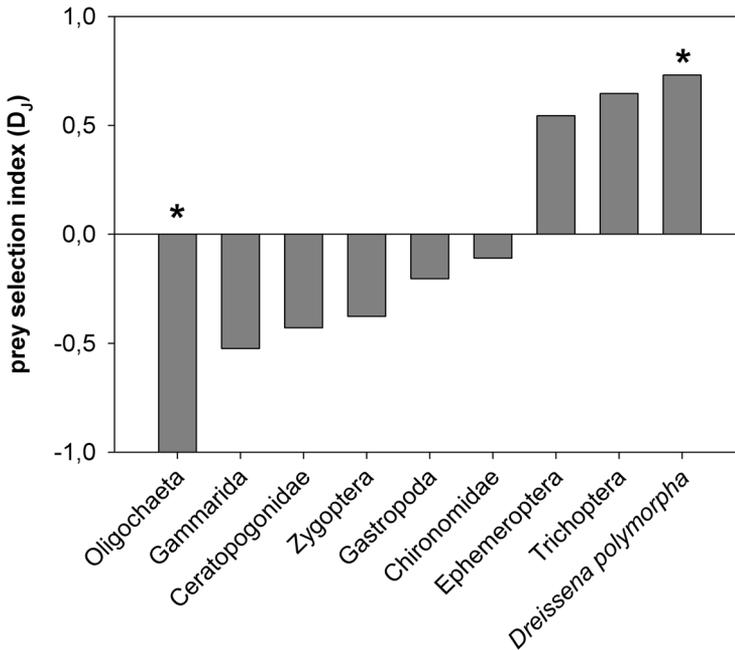


Figure 9

Prey electivity index ($D_{j,i}$) in *O. immunis*. Values between 0 and 1 indicate positive selection; values between 0 and -1 indicate avoidance relative to the abundance of prey taxa in the littoral zone of LB. The asterisks indicate significant differences between r_i and R_i , determined using Chi-square tests ($p < 0.05$).

(Stucki, 2002; Souty-Grosset *et al.*, 2006; Chucholl, 2011; Table IV), with the possible exception of *O. juvenilis*, for which no data are available (*cf.* Chucholl and Daudey, 2008). As a consequence of the high growth rate, adult *O. immunis* also moult more frequently than ICS. The observed occurrence of freshly moulted individuals in the traps and the temporal variation in the ratio of form I to form II individuals (Figure 2) suggest concordantly that the adult population probably moulted up to four times during the summer months. The form II condition prevailed only for a short time period, and high occurrences of form II individuals coincided with phases of great activity, resulting in a high CPUE. The form II condition may have lasted only a few weeks in individual crayfish, a finding that is supported by a casual aquarium observation: one form I male captured in May 2007 moulted into form II and back into form I within two weeks. A similar fast sequence of moults, resulting in a comparably short form II condition, was also recently reported for *O. limosus* (Buřič *et al.*, 2010). The fact that most adult *O. immunis* in LB had moulted back into form I by mid-June may reflect an adaptation to seasonally drying habitats, where mating in late summer and autumn may be hampered as a result of drying out (*cf.* Caldwell and Bovbjerg, 1969).

The fast growth rate of *O. immunis* was combined with a relatively small asymptotic *CL* and a short mean lifetime and longevity. ICS live markedly longer and attain larger sizes than *O. immunis*, with *Austropotamobius torrentium* being an exception concerning size (Souty-Grosset *et al.*, 2006; Scalici *et al.*, 2008; Table IV). Tack (1941) estimated the longevity of *O. immunis* in its indigenous range at 2–3 years, which is in good accordance with the estimates obtained in the present study. The mean lifetime of the study population in LB was close to the maximum lifespan, indicating a high mortality within the third year, possibly influenced by the high fishing mortality. Within the estimated mean lifetime, *O. immunis* individuals may reproduce two to three times, depending on whether they attain sexual maturity at the end of their first summer. For comparison, most ICS do not even attain sexual

Table IV
Comparison of the life-history traits of ICS and selected NICS in western and central Europe. NA = not available.

Species	Status	Maximum CL (mm)	Longevity (a)	Age at maturity (a)	ϕ'	Maximum fecundity	References
<i>Astacus astacus</i>	ICS	88	7.9–13.0	2+ (3+)	0.6–1.3	282	Stucki (2002); Scalici et al. (2008); Souty-Grosset et al. (2006)
<i>Austropotamobius pallipes</i>	ICS	55	7.7–14.3	2+ (1+)	0.4–1.1	200	Stucki (2002); Scalici et al. (2008); Souty-Grosset et al. (2006)
<i>Austropotamobius torrentium</i>	ICS	50	10.7–12.0	2+ (1+)	0.8	120	Stucki (2002); Scalici et al. (2008); Souty-Grosset et al. (2006)
<i>Pacifastacus leniusculus</i>	NICS	78	4–11	1+ (2+)	NA	242	Stucki (2002); Souty-Grosset et al. (2006); Füreder and Pöckl (2007)
<i>Procambarus clarkii</i>	NICS	76	6.1–6.6	1+ (2+)	3.4–3.5	597	Stucki (2002); Chucholl (2011)
<i>Orconectes limosus</i>	NICS	55	3–4	1+	NA	538	Hamr (2002); Stucki (2002); present study
<i>Orconectes immunis</i>	NICS	50	2.4–2.5	0+ (1+)	3.5	495	present study

maturity within the mean lifetime of *O. immunis* (Stucki, 2002; Souty-Grosset et al., 2006; Table IV).

The collected fecundity data of *O. immunis* are consistent with values reported from its indigenous range (Gunderson and Kapuscinski, 1992) and are remarkably close to the data collected for *O. limosus*. Both species are very fecund, especially when compared to ICS, which carry on average less than 200 eggs (Stucki, 2002; Table IV) in contrast to the 240 eggs carried on average by *O. immunis*. In 2007, *Orconectes immunis* eggs hatched in LB as early as March 17 (based on a preliminary net sampling prior to the main study period), and hatching continued throughout April until the first half of May. The early hatching time was confirmed in April 2009, when eight per cent of the sampled females were found to already carry hatchlings or egg remains, and is consistent with data from the native range of *O. immunis* (Tack, 1941; Caldwell and Bovbjerg, 1969). The early hatching time suggests that most *O. immunis* females in LB had laid their eggs in autumn and carried them throughout winter, as was reported by Caldwell and Bovbjerg (1969) for populations in permanent habitats. This autumnal egg-laying is a distinct difference to other *Orconectes* species, such as *O. limosus*, which typically lay their eggs in spring (Souty-Grosset et al., 2006). In PF, all of the captured *O. immunis* females had released their offspring by late April 2007, whereas *O. limosus* females were still breeding at this time. The egg incubation of *O. immunis* throughout the winter presumably favours the unusual early hatching period.

Overall, *O. immunis* is a strongly *r*-selected species, exhibiting typical *r*-selected life-history traits, such as rapid growth, a small asymptotic *CL*, a short life cycle, and high fecundity. The life history of *O. immunis* contrasts markedly with the life history of ICS, which are more *K*-selected, *i.e.*, live longer, grow slower but larger, and are less fecund (Stucki, 2002; Neveu, 2006; Souty-Grosset et al., 2006; Table IV). The strong *r*-selection of *O. immunis* probably represents an adaptation to its natural ecological niche; in its indigenous range, *O. immunis* often inhabits temporary backwaters or pools, where it is released from the competition pressure of other, larger *Orconectes* species, such as *O. virilis*, that prefer permanent habitats (Bovbjerg, 1970). The temporary habitats colonised by *O. immunis* feature seasonal dry-downs, during which crayfish retreat into burrows (Tack, 1941; Caldwell and Bovbjerg, 1969; Bovbjerg, 1970). While reproduction may take place in burrows, growth is most likely restricted to the flooding periods, favouring a fast growth rate and a short life cycle with an early sexual maturation.

> FEEDING ECOLOGY

Freshwater crayfish are generally considered to be omnivorous, but species-specific differences in feeding habits likely exist. Ontogenetic shifts in diet were reported for several larger species, suggesting interdependencies between growth rate, size and feeding preferences (Momot, 1995; Nyström, 2002; Alcorlo et al., 2004). A relatively small species like *O. immunis* may therefore exhibit other feeding preferences than larger NICS or ICS. The results of the present study clearly indicate that *O. immunis* is a polytrophic omnivore. It was found to feed on detritus and primary producers (algae and macrophytes) as well as on higher trophic levels, *e.g.*, predatory insect larvae (*cf.* Figure 7). Detritus was found to be the most important food category, followed by macroinvertebrates and macrophytes. A prevalence of detritus in the stomach content is a common phenomenon in crayfish and has been observed in many species (*cf.* Momot, 1995). No ontogenetic shift in the diet of *O. immunis* was observed in the present study, perhaps as a result of its rather small size and the sustained high growth rate throughout its life. Both a slower growth rate in adult crayfish and an incremental size difference between larger crayfish and their prey have been previously suggested as explanations for ontogenetic shifts in crayfish diets (Nyström, 2002; Alcorlo et al., 2004).

Orconectes immunis was found to prey on a wide spectrum of macroinvertebrates. The main prey taxa were Chironomidae larvae, Cladocera and Ephemeroptera larvae, of which the latter tended to be positively selected. A similar high importance of Chironomidae larvae in the diet of *Orconectes luteus* and *O. punctimanus* was reported by Whitley and Rabeni (1997),

and a preference for Chironomidae and Ephemeroptera larvae is also known for *P. clarkii* (Alcorlo *et al.*, 2004). *Orconectes immunis* positively selected for slow-moving or immobile prey that could be easily captured, such as *Dreissena polymorpha* and Trichoptera, whereas sediment-dwelling prey, such as Oligochaeta, were significantly underrepresented in the *O. immunis* stomachs. A similar under-representation of sediment-dwelling prey was reported in the diet of *P. clarkii* (Alcorlo *et al.*, 2004), suggesting that crayfish might generally select against sediment-dwelling taxa, probably because sediment dwellers are hard to capture and the handling is not profitable for crayfish. However, sediment-dwelling *Ephemera* sp. larvae were occasionally consumed by *O. immunis*, presumably because the larvae are fairly large and energy-rich.

The relatively high importance of zooplankton in the diet of *O. immunis* shown in the present study is in accordance with the results of Tack (1941), who found that *Daphnia* constituted up to 25 per cent of the stomach content of *O. immunis* in ponds in New York. Budd *et al.* (1978) provided evidence that *O. immunis* is able to filter feed on phytoplankton using a filter apparatus formed by the first maxillipeds and the maxillae. The authors concluded that juvenile *O. immunis* might be obligatory filter feeders, whereas adult *O. immunis* might be facultative filter feeders. However, it is unclear whether *O. immunis* is able to catch relatively large and mobile zooplankton (e.g., Cladocera) using this filter apparatus. During the present study, it was occasionally observed that *O. immunis* rapidly formed a 'trap basket', using the larger 2nd and 3rd maxillipeds and the subsequent pereopods, to catch smaller prey.

The relatively high importance of Cladocera in its diet, along with the positive selection of *Dreissena*, indicates that *O. immunis* is able to access the plankton pool as an energy resource, in addition to benthic macroinvertebrates, macrophytes and detritus. The relatively high importance of energy-rich macroinvertebrate prey in its diet probably supports the sustained high growth rate of *O. immunis* and underscores the importance of crayfish as functional predators, as suggested by Momot (1995) in his seminal paper.

CONCLUSION

An *r*-selected life history has often been linked to successful invaders, including many freshwater macroinvertebrates, such as *Dikerogammarus villosus* and *Corbicula fluminea* (Füreder and Pöckl, 2007 and citations therein), although it is not an exclusively predictive or consistent trait among IAS (Bufford and Daehler, 2011). Specifically, a fast life cycle and high reproductive output are beneficial throughout most stages of the invasion process, *i.e.*, initial introduction, establishment and spread. *Orconectes immunis* is no exception, in that it is a markedly *r*-selected species that has quickly become invasive. Moreover, its omnivorous feeding habits allow for a high flexibility in the allocation of nutrients needed for growth and reproduction. Both ecological properties, *i.e.*, the strongly *r*-selected life history and the omnivorous feeding habits, enhance its invasiveness and make *O. immunis* a perfect invader in the Upper Rhine plain. In contrast to other *r*-selected 'new' NICS in central Europe that originate from warmer, subtropical climates, such as *Procambarus clarkii* and Marmorcrebs (Souty-Grosset *et al.*, 2006; Chucholl and Pfeiffer, 2010; Chucholl, 2011), *Orconectes immunis* is perfectly adapted to cold habitats in temperate zones and will most likely continue to spread along the Rhine plain.

Within the invaded central European range, *Orconectes immunis* was observed to displace its invasive congener *O. limosus* from many habitats, probably as a result of niche overlap (Chucholl *et al.*, 2008). *Orconectes immunis* has been found to be dominant in direct aggressive interactions and competition for shelter (Chucholl *et al.*, 2008) and exhibits a faster life cycle and earlier hatching period than *O. limosus* (present study). Additionally, Chucholl (2006) found that the specific growth rate and relative moult increment of adult crayfish was significantly higher in *O. immunis* than in *O. limosus*, when held in the laboratory for 200 days. To date, *O. immunis* has not come into contact with ICS because ICS stocks have largely vanished from the upper Rhine plain during the last two centuries, as a result of habitat

degradation, water pollution, crayfish plague and the invasion by *O. limosus* (Souty-Grosset et al., 2006; Chucholl and Dehus, 2011). However, based on the observed displacement of *O. limosus*, the author anticipates that *O. immunis* has the potential to out-compete ICS. Additionally, *O. immunis* was recently shown to be a carrier of the crayfish plague (Maiwald et al., 2009). Any contact of *O. immunis* with ICS stocks will therefore most likely result in the loss of the latter. On the basis of its omnivorous feeding habits, extensive burrowing behaviour, and high abundance in many habitats, it is likely that *O. immunis* also has a pronounced ecological effect on indigenous biota and ecosystems. For instance, the decline of macrophyte species in LB coincided with the first observations of *O. immunis* in LB, suggesting that *O. immunis* might negatively affect macrophyte biomass, as was experimentally shown by Letson and Makarewicz (1994). However, explicit evidence for the ecological impact of *O. immunis* is currently lacking, and should be targeted in future research.

ACKNOWLEDGEMENTS

I am indebted to A. Martens, K. Grabow (both at the PH Karlsruhe), H.K. Schulz (University of Koblenz-Landau) and P. Dehus (FFS, Lake Constance) for providing information and kind support. I am also very grateful to A. Dannenmaier (Karlsruhe) for his invaluable support and assistance during the field work and to W. Grönitz (LUBW, Karlsruhe) and R. Treiber (RP Karlsruhe) for providing information and permits. The helpful comments and suggestions made by two reviewers are also gratefully acknowledged. This study was funded by the scholarship programme of the German Federal Environmental Foundation (DBU).

REFERENCES

- Alcorlo P., Geiger W. and Otero M., 2004. Feeding preferences and food selection of the red swamp crayfish, *Procambarus clarkii*, in habitats differing in food item diversity. *Crustaceana*, 77, 435–453.
- Bovbjerg R.V., 1970. Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). *Ecology*, 51, 225–236.
- Brown P. and Gunderson J. (eds.), 1997. Culture potential of selected crayfishes in the North Central region. *Tech. Bull. Ser.*, 112, 26.
- Budd T.W., Lewis J.C. and Tracey M.L., 1978. The filter-feeding apparatus in crayfish. *Can. J. Zool.*, 56, 695–707.
- Bufford J.L. and Daehler C.C., 2011. Life history strategies. In: Simberloff D. and Rejmánek M. (eds.), *Encyclopedia of Biological Invasions*, University of California Press, Los Angeles, 437–441.
- Buřič M., Kouba A. and Kozák P., 2010. Intra-sex dimorphism in crayfish females. *Zoology*, 113, 301–307.
- Caldwell M.J. and Bovbjerg R.V., 1969. Natural history of the two crayfish of northwestern Iowa, *Orconectes virilis* and *Orconectes immunis*. *Iowa Aca. Sci.*, 76, 463–472.
- Chucholl C., 2006. Konkurrenz zwischen zwei Neozoen: Verdrängungs-Mechanismen zwischen Kamberkrebs (*Orconectes limosus*, Crustacea: Decapoda) und Kalikokrebs (*O. immunis*), Diploma thesis, University of Ulm, Germany, 97 p.
- Chucholl C., 2011. Population ecology of an alien ‘warm water’ crayfish (*Procambarus clarkii*) in a new cold habitat. *Knowl. Managt. Aquatic Ecosyst.*, 401, 29.
- Chucholl C. and Daudey T., 2008. First record of *Orconectes juvenilis* (Hagen, 1870) in eastern France: update to the species identity of a recently introduced orconectid crayfish (Crustacea: Astacida). *Aquat. Invas.*, 3, 105–107.
- Chucholl C. and Dehus P., 2011. Flusskrebse in Baden-Württemberg, Fischereiforschungsstelle Baden-Württemberg (FFS), Langenargen, Germany, 92 p.
- Chucholl C. and Pfeiffer M., 2010. First evidence for an established Marmorokrebs (Decapoda, Astacida, Cambaridae) population in Southwestern Germany, in syntopic occurrence with *Orconectes limosus* (Rafinesque, 1817). *Aquat. Invas.*, 5, 405–412.

- Chucholl C., Stich H.B. and Maier G., 2008. Aggressive interactions and competition for shelter between a recently introduced and an established invasive crayfish: *Orconectes immunis* vs. *O. limosus*. *Fund. App. Lim./Arch. Hydrobiol.*, 172, 27–36.
- Clavero M. and García-Berthou E., 2005. Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.*, 20, 110.
- Collas M., Beinsteiner D., Fritsch S. and Morelle S., 2011. Première observation en France d'*Orconectes immunis* (Hagen, 1870) l' écrevisse calicot, Office National de l'Eau et des Milieux Aquatiques, La Petite Pierre, France, 22 p.
- Dehus P., Dussling U. and Hoffmann C., 1999. Notes on the occurrence of the calico crayfish (*Orconectes immunis*) in Germany. *Freshwater Crayfish*, 12, 786–790.
- Filipová L., Grandjean F., Chucholl C., Soes D.M. and Petrušek A., 2011. Identification of exotic North American crayfish in Europe by DNA barcoding. *Knowl. Managt. Aquatic Ecosyst.*, 401, 11.
- Forney J.L., 1957. Raising bait fish and crayfish in New York ponds. *Cornell Extension Bull.*, 986, 3–30.
- France R., Holmes J. and Lynch A., 1991. Use of size-frequency data to estimate the age composition of crayfish populations. *Can. J. Fish. Aquat. Sci.*, 48, 2324–2332.
- Füreder L. and Pöckl M., 2007. Ecological traits of aquatic NIS invading Austrian fresh waters. In: Gherardi F. (ed.), *Biological invaders in inland waters: profiles, distribution and threats*, Springer, Dordrecht, 233–257.
- Gayanilo F.C. Jr. and Pauly D., 1997. The FAO ICLARM stock assessment tools, FiSAT reference manual, FAO Computerized Information Series (Fisheries), Rome, FAO.
- Gelmar C., Pätzold F., Grabow K. and Martens A., 2006. Der Kalikokrebs *Orconectes immunis* am nördlichen Oberrhein: ein neuer amerikanischer Flusskrebis breitet sich rasch in Mitteleuropa aus (Crustacea: Cambaridae). *Lauterbornia*, 56, 15–25.
- Gunderson J.L. and Kapuscinski A., 1992. Crayfish Aquaculture Demonstration in Minnesota Rice Paddies, Legislative Commission on Minnesota Resources Report, 4 p.
- Hamr P., 2002. *Orconectes*. In: Holdich D.M. (ed.), *Biology of Freshwater Crayfish*, Blackwell Scientific Press, Oxford, 585–608.
- Hobbs H.H. Jr., 1989. An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae, and Parastacidae). *Smithson. Contrib. Zool.*, 480, 236 p.
- Hobbs H.H. Jr., Jass J.P. and Huner J.V., 1989. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). *Crustaceana*, 56, 299–316.
- Holdich D.M., Reynolds J.D., Souty-Grosset C. and Sibley P.J., 2009. A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. *Knowl. Managt. Aquatic Ecosyst.*, 394–395, 11.
- Jacobs J., 1974. Quantitative measurement of food selection. *Oecologia*, 14, 413–417.
- Jansen W., Geard N., Mosindy T., Olson G. and Turner M., 2009. Relative abundance and habitat association of three crayfish (*Orconectes virilis*, *O. rusticus*, and *O. immunis*) near an invasion front of *O. rusticus*, and long-term changes in their distribution in Lake of the Woods, Canada. *Aquat. Invas.*, 4, 627–649.
- Jones J.P.G., Rasamy J.R., Harvey A., Toon A., Oidtmann B., Randrianarison M.H., Raminosoa N. and Ravoahangimalala O.R., 2009. The perfect invader: a parthenogenic crayfish poses a new threat to Madagascar's freshwater biodiversity. *Biol. Invasions*, 11, 1475–1482.
- Letson M.A. and Makarewicz J.C., 1994. An Experimental test of the crayfish (*Orconectes immunis*) as a control mechanism for submersed aquatic macrophytes. *Lake Reservoir Management*, 10, 127–132.
- Lockwood J.L., Hoopes M.F. and Marchetti M.P., 2007. *Invasion Ecology*, Blackwell Publishing, Oxford, 304 p.
- Maiwald T., Vralstad T., Jaraus W., Schulz H.K., Smietana P. and Schulz R., 2009. Kamberkrebis und Edelkrebis zwischen Koexistenz und Krebspest, Abstracts volume 4, Internationales Flusskrebisforum, Gersfeld/ Röhn, Germany, 43–48.
- McCullagh P., and Nelder J.A., 1989. *Generalized Linear Models*, Chapman and Hall, London, 532 p.
- McGeoch M.A., Butchart S.H.M., Spear D., Marais E., Kleynhans E.J., Symes A., Chanson J. and Hoffmann M., 2010. Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Divers. Distrib.*, 16, 95–108.
- Momot W.T., 1995. Redefining the role of crayfish in aquatic ecosystems. *Rev. Fish. Sci.*, 3, 33–63.
- Neveu A., 2006. Les écrevisses étrangères sont elles invasives ? Quelles caractéristique expliquent leur développement ? *L'Astaculteur de France*, 86, 2–11.
- Nyström P., 2002. Ecology. In: Holdich D.M. (ed.), *Biology of Freshwater Crayfish*, Blackwell Scientific Press, Oxford, 192–224.

- Olsen T.M., Lodge D.M., Capelli G.M. and Houlihan R.J., 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails and macrophytes. *Can. J. Fish. Aquat. Sci.*, 48, 1853–1861.
- Pauly D., 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *J. Cons. CIEM*, 39, 175–192.
- Pauly D. and Morgan G.R., 1987. Length Based Methods in Fisheries Research, ICLARM, Manila, Philippines, and KIRSI, Safat, Kuwait, 468 p.
- Pauly D. and Munro J.L., 1984. Once more on growth comparison in fish and invertebrates. *Fishbyte, Newsletter Network of Tropical Fisheries Scientists*, 2, 21.
- Pérez-Bote J.L., 2005. Feeding Ecology of the exotic Red Swamp Crayfish, *Procambarus clarkii* Girard, 1852, in the Guadiana River (SW Iberian Peninsula). *Crustaceana*, 77, 1375–1387.
- R Development Core Team, 2011. R 2.14, available from: <http://www.r-project.org/> (accessed November 12, 2011).
- Rodríguez C.F., Bécares E., Fernández-Aláez M. and Fernández-Aláez C., 2005. Loss of diversity and degradation of wetlands as a result of introducing exotic crayfish. *Biol. Invasions*, 7, 75–85.
- Scalici M. and Gherardi F., 2007. Structure and dynamics of an invasive population of the red swamp crayfish (*Procambarus clarkii*) in a Mediterranean wetland. *Hydrobiologia*, 583, 309–319.
- Scalici M., Belluscio A. and Gibertini G., 2008. Understanding population structure and dynamics in threatened crayfish. *J. Zool.*, 275, 160–171.
- Scalici M., Chiesa S., Scuderi S., Celauro D. and Gibertini G., 2009. Population structure and dynamics of *Procambarus clarkii* Girard, 1852, in a Mediterranean brackish wetland (Central Italy). *Biol. Invasions*, 12, 1415–1425.
- Schlenker M.A., 2009. Verhaltensweisen der invasiven Flusskrebsarten *Orconectes immunitis* (Crustacea: Decapoda) und *O. limosus* bei Anwesenheit von Futter-, Artgenossen- und Räuberduftstoffen, Diploma thesis, University of Ulm, Germany, 31 p.
- Simberloff D., 2003. How much information on population biology is needed to manage introduced species? *Conserv. Biol.*, 17, 83–92.
- Souty-Grosset C., Holdich D.M., Noel P.Y., Reynolds J.D. and Haffner P. (eds.), 2006. Atlas of Crayfish in Europe, Museum national d'Histoire naturelle, Paris, Patrimoines naturels, 64, 187 p.
- Stucki T.P., 2002. Differences in life history of native and introduced crayfish species in Switzerland. *Freshwater Crayfish*, 13, 463–476.
- Tack I.P., 1941. The life history and ecology of the crayfish *Cambarus immunitis* Hagen. *Am. Midl. Nat.*, 25, 420–446.
- Wetzel J.E., 2002. Form alteration of adult female crayfishes of the genus *Orconectes* (Decapoda: Cambaridae). *Am. Midl. Nat.*, 147, 326–337.
- Whitledge G.W. and Rabeni C.F., 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analyses. *Can. J. Fish. Aquat. Sci.*, 54, 2555–2563.
- Windell J.T., 1971. Food analysis and rate of digestion. In: Ricker W.E. (ed.), *Methods for assessment of fish production in freshwaters*, Blackwell Scientific Press, Oxford, 197–203.