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The continuing spread of *Pacifastacus leniusculus* in Carinthia (Austria)

M. Weinländer[(1)], L. Füreder[(1)]

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ABSTRACT

Key-words: *invasion, signal crayfish, decline of native species,* Astacus astacus*,* Austropotamobius torrentium*, threats*

Crayfish plague and introductions of non-indigenous freshwater crayfish species (NICS) have had major consequences for the survival of autochthonous crayfish populations in Europe. Beside habitat loss, the invasive signal crayfish *Pacifastacus leniusculus* is currently responsible for the decline of indigenous crayfish species (ICS) in Carinthia (Austria). Here, we studied the distribution of *P. leniusculus* and native *Astacus astacus* and *Austropotamobius torrentium* in selected catchments to assess the ongoing colonisation with signal crayfish and to monitor the existence of ICS localities. Our results showed that *P. leniusculus* is widespread in Carinthia and many areas with native crayfish have disappeared within nine years. However, whereas populations of *A. astacus* became extinct in running waters, those of *A. torrentium* seemed to be more protected by occupying headwaters. In contrast to the ICS, *P. leniusculus* was found in a broad range of freshwater habitats and water quality conditions. We hypothesise that the fast expansion of *P. leniusculus* and the decline of ICS was caused by human-mediated stockings of NICS, followed by active signal crayfish invasions from established populations into new watercourses.

RÉSUMÉ

La propagation ininterrompue de *Pacifastacus leniusculus* en Carinthie (Autriche)

Mots-clés : *invasion, écrevisse signal, déclin des espèces indigènes,* Astacus astacus*,* Austropotamobius torrentium*, menace*

La peste de l'écrevisse et les introductions d'espèces d'écrevisses non indigènes d'eau douce (NICS) ont eu d'importantes conséquences sur la survie des populations d'écrevisses autochtones en Europe. Après les pertes d'habitat, l'écrevisse signal invasive *Pacifastacus leniusculus* est à présent responsable du déclin d'espèces d'écrevisses indigènes (ICS) en Carinthie (Autriche). Nous étudions ici la distribution de *P. leniusculus* et des ICS *Astacus astacus* et *Austropotamobius torrentium* dans 18 bassins versants choisis pour évaluer la colonisation en cours de l'écrevisse signal et pour suivre les localités où des ICS étaient présentes. Nos résultats montrent que *P. leniusculus* est largement répandue en Carinthie et que plusieurs localités où des écrevisses autochtones étaient présentes ont disparu en neuf ans. Toutefois, alors que des populations d'*A. astacus* disparaissent dans les eaux courantes, celles d'*A. torrentium* semblent plus protégées en occupant les têtes de bassin. En contraste avec les ICS, *P. leniusculus* a été trouvée dans une large gamme d'habitats d'eau douce et de qualité des eaux. Nous posons l'hypothèse que la rapide expansion de *P. leniusculus* et le déclin des ICS ont été causés par les déversements par l'Homme de NICS, suivis par l'invasion active de l'écrevisse signal depuis les populations établies dans les nouveaux cours d'eau.

(1) River Ecology and Invertebrate Biology, Institute of Ecology, University of Innsbruck, Technikerstrasse 25, 6020 Innsbruck, Austria, martin.weinlaender@student.uibk.ac.at

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INTRODUCTION

Biological invasions are a major threat to global biodiversity (Travis and Park, 2004) and especially alien freshwater crayfish are prominent for their negative effects on ecosystem integrity and indigenous crayfish (Hirsch, 2009). Therefore the Swedish introduction of signal crayfish *Pacifastacus leniusculus* (Dana) in the year 1959 had considerable consequences for many native crayfish populations in several European countries (Holdich *et al.*, 2006; Füreder, 2009). Today *P. leniusculus* is the most widely spread non-indigenous crayfish species in Europe (Holdich *et al.*, 2006) and apart from habitat loss caused by human activities currently the main threat to indigenous crayfish species in much of Europe (Füreder *et al.*, 2006; Füreder, 2009). *Pacifastacus leniusculus* is a carrier of the crayfish plague, caused by the fungus-like *Aphanomyces astaci* (Schikora), which is lethal for European crayfish (Oidtmann *et al.*, 2002). In Carinthia (Austria) this disease was recorded for the first time in the year 1880 (Hawlitschek, 1892) and together with later introductions of non-indigenous crayfish species (NICS) responsible for the decline of many native crayfish populations. Currently, Carinthian freshwaters harbour seven crayfish species, but only three of them are of autochthonous origin. The noble crayfish *Astacus astacus* (Linné), the stone crayfish *Austropotamobius torrentium* (Schrank) and the white-clawed crayfish *Austropotamobius pallipes* (Lereboullet) are indigenous, while the non-indigenous narrow-clawed crayfish *Astacus leptodactylus* (Eschscholz) and the three North American species, the signal crayfish *P. leniusculus*, the spiny cheek crayfish *Orconectes limosus* (Rafinesque) and the red swamp crayfish *Procambarus clarkii* (Girard) were introduced to Carinthia in the 20th century (Petutschnig, 2002; Petutschnig *et al.*, 2008).

Especially the introduction of *P. leniusculus* had wide impacts on indigenous crayfish species (ICS) in Carinthia. The invasion began in the early 1970s, when the signal crayfish was illegally introduced to boost stocks of native crayfish (Spitzy, 1973). In the following years signal crayfish stocks were established between 408 m and 1273 m above sea level to investigate its growth at different altitudes (Hofmann, 1971; Honsig-Erlenburg and Schulz, 1996). While the population at high altitude finally died due to unfavourable environmental conditions, the other sites were source for additional stockings and invasions into new watercourses. In particular the colonisation of the biggest river in Carinthia, the Drave, was mainly responsible for the further spread. In this 7th order stream the first dense signal crayfish populations were recognised by fishermen in some reservoirs of hydropower stations in the late 1980s. Subsequently signal crayfish spread into the nearby confluences of Drave-Gurk and Gurk-Glan. Once these big rivers were colonised, *P. leniusculus* was extending its range very fast. In the year 2000, *P. leniusculus* was finally occurring in wide stretches of the Drave and was already established in some parts of the Gurk and Glan catchment (Petutschnig, 2001). Finally also a beginning invasion of signal crayfish from the Drave into the Lavant catchment, near the border to Slovenia, was noticed (Petutschnig, 2002).

The present study followed the development of native and alien crayfish populations within an Austrian region. We assessed the current range of *P. leniusculus* and indigenous *A. astacus* and *A. torrentium* in selected catchments to monitor the spread of signal crayfish and the existence of ICS. Ecological water characteristics of these individual sites were analysed to evaluate preferred habitats and range of crayfish occurrence. This information on the existence of autochthonous *A. astacus* and *A. torrentium*, as well as potential causes for the continuing spread of *P. leniusculus*, are particularly needed to establish conservation measures in Carinthia.

MATERIALS AND METHODS

The study was carried out in Carinthia, which is a southern federal state of Austria near the border to Italy and Slovenia (Figure 1). Crayfish localities were investigated in the catchments of the Drave, Gurk, Glan and Lavant (Figure 1) based on available information of historical and recent Carinthian crayfish distribution (Wintersteiger, 1985; Honsig-Erlenburg and Schulz,

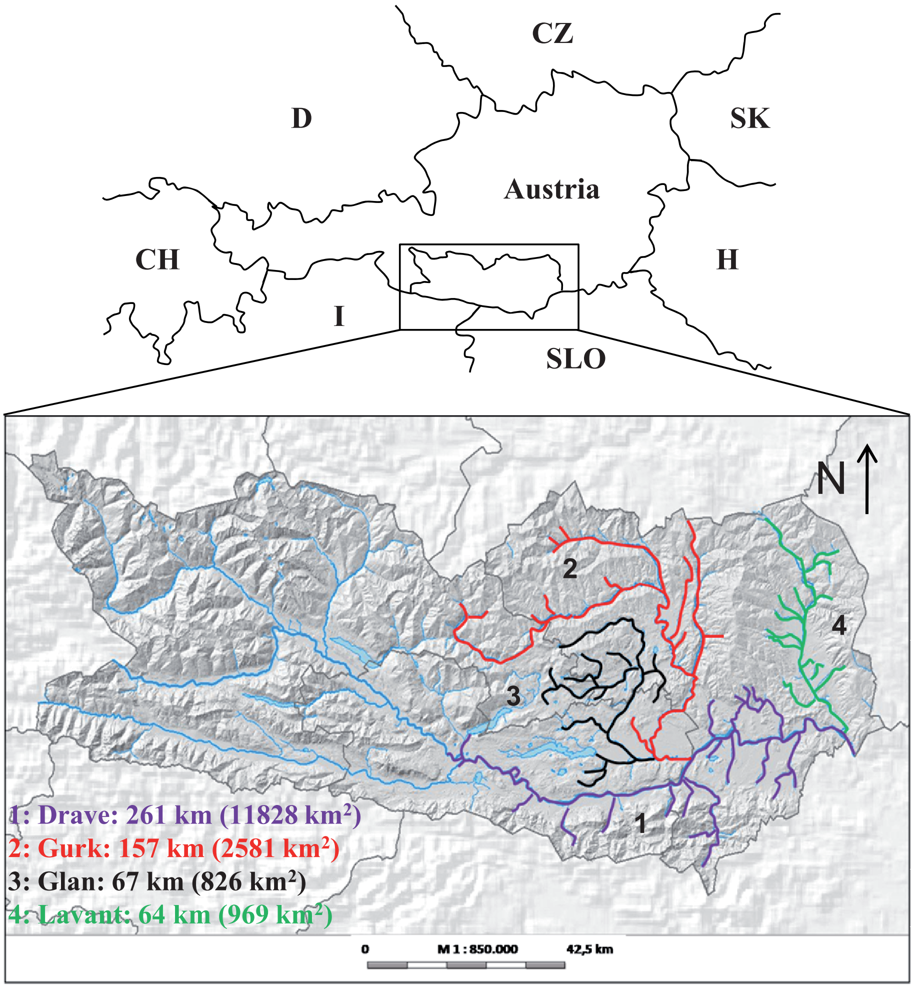

Figure 1
Investigation area with the Drave, Gurk, Glan and Lavant river systems. Number gives the position with length and catchment area of rivers. Map: www.kagis.ktn.gv.at.

Figure 1
Aire de l'étude avec les systèmes des rivières Drave, Gurk, Glan et Lavant. Les nombres indiquent la position avec la longueur du cours d'eau et l'aire de son bassin versant. Carte : www.kagis.ktn.gv.at.

1996; Petutschnig, 1997, 2001, 2002). These former mappings were compared with the current range of *P. leniusculus*, *A. astacus* and *A. torrentium* in the selected catchments. In the years 2008 and 2009 presence or absence of crayfish was detected in a total of 199 sites in running waters from July to November. In larger rivers crayfish were detected by traps, or by stone turning in smaller streams where the water level was shallow enough. The used traps were "pirate traps" (Bock-Ås Ky, Finland) with a length of 61 cm, a width of 31.5 cm, a height of 25 cm and a mesh sieve of 2.5 × 1 cm and were baited with a type of meat loaf popular in Austria. Three baited traps were set at every site in the afternoon and were retrieved the following morning after 14 h. In smaller streams observations were carried out at night with lamps (handcatch) on a 100 m stretch for about 20 min. When no indigenous crayfish were observed in stretches with good habitat suitability, but a historical existence of ICS was recorded in former studies, these sites were investigated several times to confirm the absence of ICS. Traps and boots were disinfected with 7% formaldehyde for 20 min and were dried for at least 24 h before setting into new watercourses. At every site presence/absence of crayfish, type of habitat and altitude was determined. In running waters, water temperature, stream order, width, depth and velocity were recorded. Statistical differences between habitat conditions

Table I
Number of crayfish populations found in the years 2000 and 2009 in the Drave, Gurk, Glan and Lavant catchment. ASA = A. astacus*, AUT =* A. torrentium*, PAL =* P. leniusculus*.*

Tableau I
Nombre de populations d'écrevisses trouvées en 2000 et 2009 dans les rivières Drave, Gurk, Glan et Lavant. ASA = *A. astacus*, AUT = *A. torrentium*, PAL = *P. leniusculus*.

	Drave		Gurk		Glan		Lavant		Total		Population difference
	2000	2009	2000	2009	2000	2009	2000	2009	2000	2009	
ASA	10	8	8	5	49	33	4	1	71	47	–24
AUT	19	12	9	7	18	9	19	16	65	44	–21
PAL	16	24	17	31	16	42	1	1	50	98	+48

of individual crayfish species were tested with one-way ANOVAs and Tukey's *post hoc* tests (level of significance at $P < 0.05$) in SigmaPlot 9.0.

RESULTS

Pacifastacus leniusculus was found to be the most frequent crayfish species in the investigation area, which was accompanied with a sharp decline of indigenous *A. astacus* and *A. torrentium* populations (Table I, Figure 2). Within nine years in a total of 24 former localities with *A. astacus* and in 21 with *A. torrentium* no existence of native crayfish was confirmed any longer, while *P. leniusculus* was detected in 48 additional sites (Table I, Figure 2). In this short time more than 30% of all known *A. astacus* and *A. torrentium* populations disappeared, while localities with *P. leniusculus* nearly doubled in the investigated catchments. In the year 2000 the noble crayfish *A. astacus* was the most common crayfish species by occurrence, followed by *A. torrentium* and *P. leniusculus*, while in the year 2009 *P. leniusculus* clearly dominated (Figures 2 and 3).

Pacifastacus leniusculus was mainly spreading in the Glan, Gurk and Drave catchment, while no further colonisation of the Lavant was detected (Table I, Figure 2). The estimated signal crayfish expansion rates per year were between 0.5 and 4 km upstream and between 1.9 and 7 km downstream.

The spread of *P. leniusculus* was also linked to a noticeable shift of occupied habitats in indigenous crayfish species. In the year 2000 *A. astacus* inhabited lotic as well as lentic water bodies, while in the present study this species was not found any longer in running waters (Figure 4). In both investigation years *A. torrentium* was only detected in lentic waters, especially in small mountain streams, where also a population decline was recognised (Figure 4). In contrary to indigenous crayfish species, *P. leniusculus* was occurring in a broad range of habitats from small ponds and brooks to large rivers and lakes, but especially in running waters stocks increased (Figure 4).

The habitat assessments in running waters showed significant differences in individual crayfish species occurrence (Table II). *Pacifastacus leniusculus* was found in higher stream orders ($F = 24.63$, $P < 0.001$), wider ($F = 3.2$, $P = 0.044$), and deeper channels ($F = 11.53$, $P < 0.001$), higher velocities ($F = 3.78$, $P = 0.025$) and water temperatures ($F = 8.54$, $P < 0.001$) than both or at least one of the indigenous crayfish species. The signal crayfish also existed in a wider range of habitat conditions in running waters than the two native crayfish species (Table II). On the contrary *Austropotamobius torrentium* occupied streams at higher altitudes (Tukey test, $P < 0.001$) than *P. leniusculus* and with lower water temperatures (Tukey test, $P < 0.001$) than the signal crayfish and *A. astacus* (Tukey test, $P = 0.008$).

DISCUSSION

The surveys and mappings carried out in the years 2008 and 2009 proved that the spread of *P. leniusculus* and the decrease of ICS had been extensive in Carinthia (Austria).

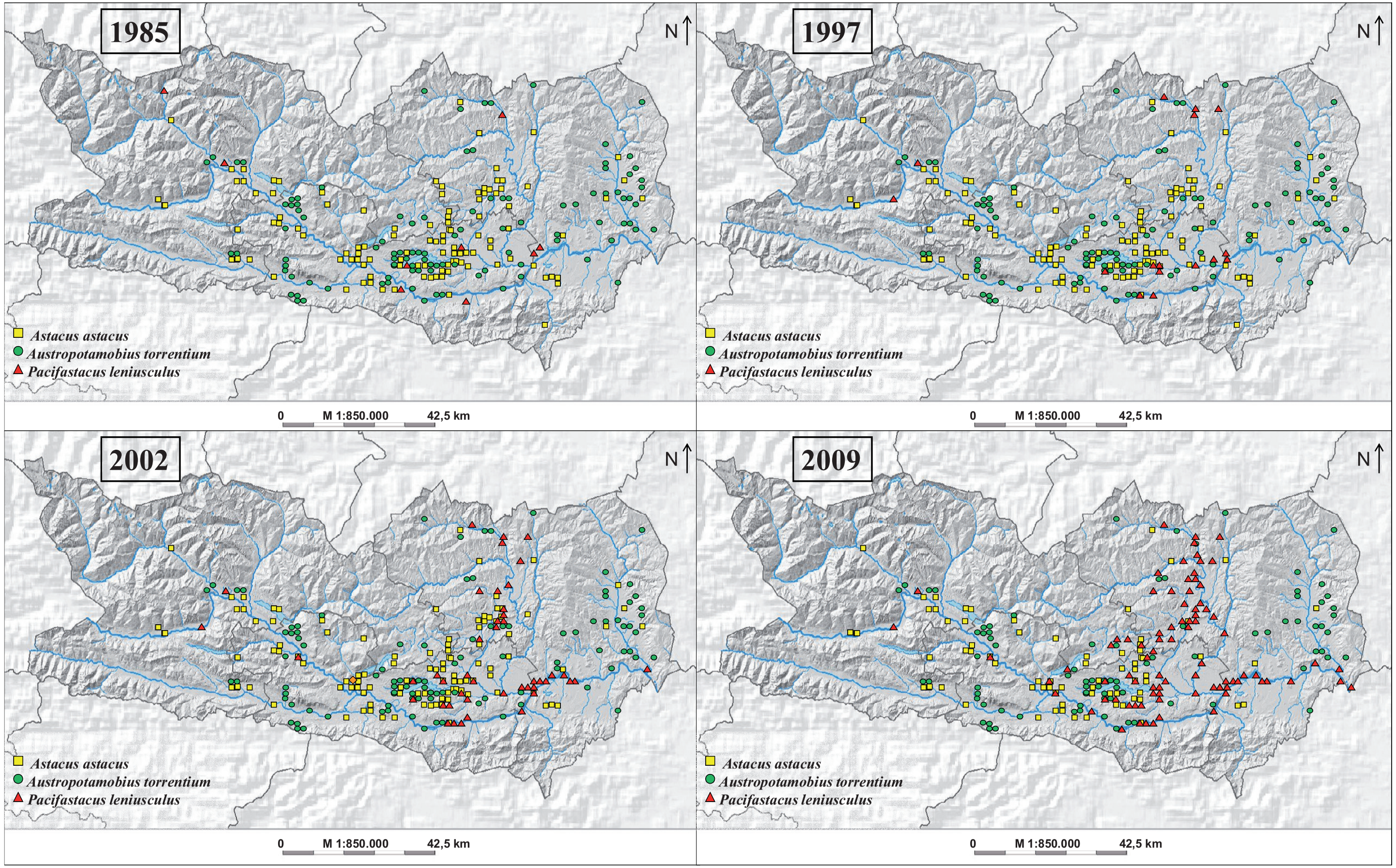

Figure 2
History of P. leniusculus, A. astacus *and* A. torrentium *stocks in Carinthia since the introduction of the signal crayfish, according to Wintersteiger (1985), Honsig-Erlenburg and Schulz (1996), Petutschnig (1997, 2002) and Weinländer and Füreder (2008). Map: www.kagis.ktn.gv.at.*

Figure 2
Évolution des populations de *P. leniusculus*, *A. astacus* et *A. torrentium* en Carinthie depuis l'introduction de l'écrevisse signal, selon Wintersteiger (1985), Honsig-Erlenburg et Schulz (1996), Petutschnig (1997, 2002) et Weinländer et Füreder (2008). Carte : www.kagis.ktn.gv.at.

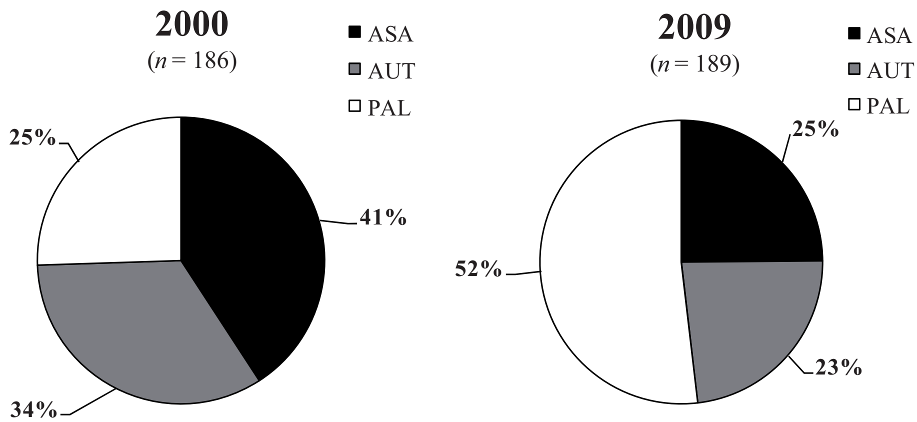

Figure 3
Frequency of crayfish species in the investigation area. ASA = A. astacus*, AUT* = A. torrentium*, PAL* = P. leniusculus*.*

Figure 3
Fréquence des espèces d'écrevisses dans les sites d'étude. ASA = *A. astacus*, AUT = *A. torrentium*, PAL = *P. leniusculus*.

Today *P. leniusculus* is the most common crayfish species by occurrence in most of the investigated catchments and especially widely distributed in the main rivers. There are numerous examples in other European countries, where the introduction of the signal crayfish had the same or similar impacts (Peay and Rogers, 1999; Savolainen *et al.*, 2003; Huber and Schubart, 2005; Bohman *et al.*, 2006; Bramard *et al.*, 2006; Diéguez-Uribeondo, 2006; Johnsen *et al.*, 2007). The estimated expansion rates of *P. leniusculus* were quite high compared to other studies (Guan and Wiles, 1997; Peay and Rogers, 1999; Bubb *et al.*, 2005; Huber and Schubart, 2005), although especially in the Glan catchment it was hard to follow, if the expansion was human-mediated or due to active migrations. In spite of not testing the infection rate of crayfish plague in *P. leniusculus* populations, it is most likely that many specimens are infected with *A. astaci*. No sympatric occurrence of NICS and ICS was found in the present study and previous invasions of signal crayfish were mostly accompanied with mass mortalities of ICS within a short time.

However, *P. leniusculus* did not invade all catchments to the same extent. Especially the Glan catchment was colonised, due to a low elevation, comparatively low velocities, moderate water temperatures and few migration barriers, which favoured active upstream and downstream invasions. Furthermore, signal crayfish were often stocked in former localities of *A. astacus* and finally escaped from these ponds and lakes. Hence, mainly *A. astacus* was concerned by extinction in the investigated catchments and its presence is currently limited to lentic waters. *Austropotamobius torrentium* seemed to be more protected by occupying small mountain streams at higher altitudes with steep gradients, as already observed within former studies (Weinländer and Füreder, 2008, 2010). Nevertheless, also these high altitude populations are threatened in future, because *P. leniusculus* already exists in a high gradient of altitudes (ponds up to 998 m a.s.l. in the Gurk catchment), but it might need longer time to reach these headwaters. In contrast to the native crayfish species, *P. leniusculus* was found in all habitat types from lentic to lotic waters of any sizes.

In Swedish streams Olsson *et al.* (2009) showed that *P. leniusculus* had twice the niche width of *A. astacus* and therefore greater efficiency in colonising new habitats. This is in support with our study, where the signal crayfish was found in a wider range of environmental conditions and habitats. Multivariate analyses also resulted in clear varieties of ICS and NICS locations in running waters (Weinländer and Füreder, unpublished data), where the environmental parameters of indigenous crayfish sites showed a limited variation. The presence of *P. leniusculus* was associated to ecological requirements very similar to that inhabited by indigenous

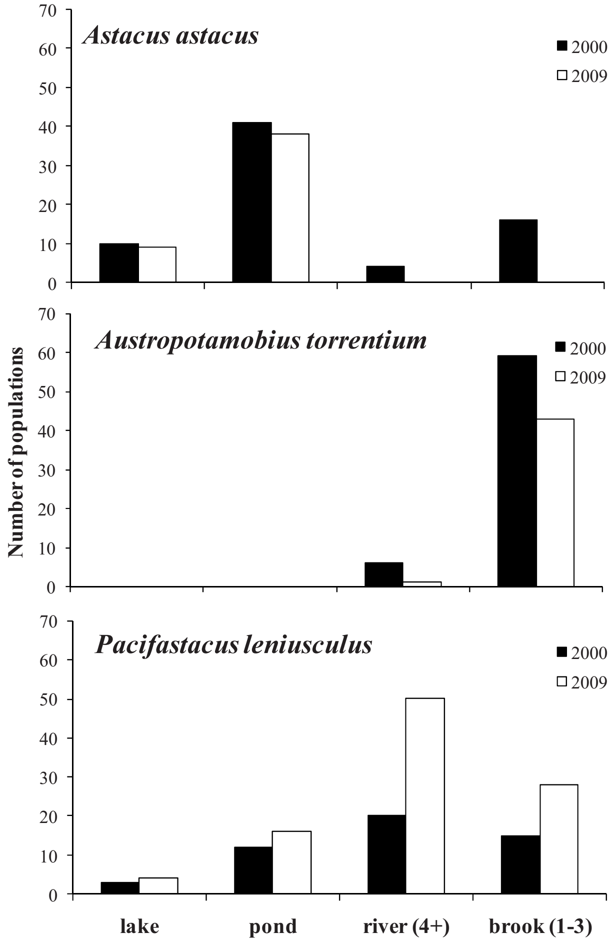

Figure 4
Habitat types where crayfish were found in the years 2000 and 2009. Number in brackets displays stream order.

Figure 4
Types d'habitat où des écrevisses ont été trouvées en 2000 et 2009. Les nombres entre parenthèses indiquent l'indice d'ordre du cours d'eau.

A. astacus and *A. torrentium*, but also to adverse conditions that would not be colonised by ICS. In two cases we even observed *P. leniusculus* in the canalisation system and in one case in an outlet of a wastewater treatment plant. This impressively proves that this species is more tolerant to adverse environmental conditions than ICS (Holdich *et al.*, 2006). The distribution of *P. leniusculus* is more closely linked to regulated streams with a stable hydrological regime than to those with a natural flow (Light, 2003), which was also observed in our study. The signal crayfish occurred in significantly higher stream orders, widths and depths than ICS. These conditions were found in reservoirs of hydropower stations in the obstructed main rivers, where also relatively high temperatures were detected. Water temperature seems to be important in predicting the distribution of *P. leniusculus* in streams (Usio *et al.*, 2006). The historical existence of *A. astacus* in running waters was associated to sites with moderate water temperatures, but these streams are now already occupied or in proximity of *P. leniusculus* and led to the extinction of these ICS populations. As the activity of *P. leniusculus* is at its peak at temperatures of about 20 °C (Rutledge and Pritchard, 1981), we would expect that the spread of this species will be slowed down in the significantly cooler environments of the *A. torrentium* streams. These populations are more protected from signal crayfish invasions due to their solely appearance in cooler and isolated headwaters.

Table II
One-way ANOVAs and Tukey's post hoc *tests (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$) on habitat assessments in running waters, measured in July and August 2009. ASA* = A. astacus*, AUT* = A. torrentium*, PAL* = P. leniusculus.

Tableau II
ANOVA simple et test Tukey *post hoc* (*** $P < 0,001$; ** $P < 0,01$; * $P < 0,05$) sur les évaluations d'habitat dans les eaux courantes, mesurées en juillet et août 2009. ASA = *A. astacus*, AUT = *A. torrentium*, PAL = *P. leniusculus.*

		ASA (n = 18)	AUT (n = 43)	PAL (n = 79)	P	Tukey test
Streamorder	mean ± SD range	2.01 ± 1.55 1–7	2.02 ± 0.97 1–4	3.97 ± 1.89 1–7	< 0.001	PAL *vs.* AUT*** PAL *vs.* ASA***
Altitude [m a.s.l.]	mean ± SD range	537.72 ± 115.96 347–775	573.7 ± 161.1 367–1095	485.35 ± 90.51 339–668	< 0.001	AUT *vs.* PAL***
Width [m]	mean ± SD range	8.39 ± 28.4 0.8–122.1	2.14 ± 2.17 0.6–11.3	31.74 ± 85.1 0.8–572.9	0.044	PAL *vs.* AUT*
Depth [cm]	mean ± SD range	37 ± 58.22 12–265	20.4 ± 10.4 7–56	76.75 ± 80.03 12–365	< 0.001	PAL *vs.* AUT*** PAL *vs.* ASA*
Velocity [m·s^{-1}]	mean ± SD range	0.3 ± 0.17 0.01–0.56	0.36 ± 0.16 0.02–0.63	0.43 ± 0.23 0–0.84	0.025	PAL *vs.* AUT*** PAL *vs.* ASA*
Water temp. [°C]	mean ± SD range	19.26 ± 3.36 14.3–24.2	16.33 ± 1.82 12.1–23.3	17.85 ± 2.91 13.1–26	< 0.001	ASA *vs.* AUT*** PAL *vs.* AUT**

CONCLUSIONS

The main threat for native crayfish species is still the spreading of *P. leniusculus* and the associated spread of the crayfish plague. Even so far uninfected specimen have ecological and biological advantages over ICS, like disease resistance, modesty concerning habitat and water quality, a larger dispersing range of adults, higher fecundity and faster growth (Evans and Edgerton, 2001; Huber and Schubart, 2005; Holdich *et al.*, 2006). The range of the non-indigenous crayfish *P. leniusculus* is now widely extended in most of the investigated Carinthian waters, resulting in the loss of many indigenous *A. astacus* and *A. torrentium* populations. The factors that potentially drive the invasiveness of *P. leniusculus* are human activities, which promote the spread of the signal crayfish in Carinthia. Escapes from lentic waters lead to the invasion of running waters of any size, where the expansion of the signal crayfish is currently going on. The main reasons for the decline of ICS are the presence and proximity of watercourses harbouring *P. leniusculus*, as well as habitat loss and degradation. Additionally ICS can hardly recover after physical and chemical alterations, due to low densities and low fecundity (Holdich *et al.*, 2006; Füreder, 2009). Our results suggest that the spread of *P. leniusculu*s will be continued in Carinthia and a further decline of *A. astacus* and *A. torrentium* populations can be expected. We predict that the spread of invasive *P. leniusculus* will be accelerated by moderate water temperatures, which are mostly found in the main rivers and outlets of lakes. Immediate information and education of fishery authorities, fishermen, politicians and the general public is needed to enlighten the threats, which are linked to this invasive species. Our results also underline the need for strict conservation measures to preserve the remaining indigenous crayfish populations in Carinthia.

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