

Research Article**Update on the signal crayfish, *Pacifastacus leniusculus* (Dana, 1852) range expansion in Croatia: a 10-year report**

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OPEN ACCESS**Abstract**

The signal crayfish (*Pacifastacus leniusculus*) is considered to be the most successful crayfish invader in Europe. It is present across the continental part of Croatia, with first records from the Mura-Drava river basin in 2008 and from the karstic Korana River in 2011. In both rivers, *P. leniusculus* presents an imminent threat to indigenous crayfish species (ICS). The aim of the study was to explore the range expansion of *P. leniusculus* 10 years after its first record in Croatia. Based on the data collected via an extensive literature search and our own fieldwork performed in 2018, we here demonstrated that *P. leniusculus* is the most successful non-indigenous crayfish species (NICS) in Croatia, with the invasion range covering the largest extent of Croatia compared to other NICS. Its dispersal rates in the rivers of the continental part of Croatia have remained among the highest in Europe. In the Drava River, recorded dispersal rate (21.3 km/yr) corresponded to the predictions made by the earlier study that estimated *P. leniusculus* dispersal over 10 years. However, due to the low number of caught individuals along the 128 km of the Drava River course, dispersal rates as well as invasion pathways (natural vs. human-mediated) need to be further explored. The predicted encounter of *P. leniusculus* with the invasive *Faxonius limosus* was not observed. In the Korana River, we observed a continued expansion of *P. leniusculus* invasion range in both upstream and downstream direction. Dispersal rates were higher in the upstream direction, potentially due to differences in competitive pressure by the native crayfish, *Pontastacus leptodactylus*, which abundances were 6 times higher at the downstream invasion front. In both rivers, a displacement of the native *P. leptodactylus* has been observed. Even though *P. leptodactylus* has been considered to be the most robust ICS, that successfully expands its range in water bodies of Croatia and Europe, it is also the species the most adversely affected by the range expansion of the *P. leniusculus* in the continental part of Croatia. Thus, the status of *P. leptodactylus* in Croatia should be monitored and re-examined.

Key words: non-indigenous crayfish species, dispersal, distribution, competitive pressure

Introduction

The introduction of non-indigenous crayfish species (NICS) is among the major causes of decline of indigenous crayfish species (ICS) in freshwater ecosystems in Europe (Holdich et al. 2009) and worldwide (Taylor 2002).

During the last two decades, three NICS have been recorded in Croatian freshwater ecosystems: the spiny-cheek crayfish *Faxonius limosus* (Rafinesque, 1817), the signal crayfish *Pacifastacus leniusculus* (Dana, 1852), and the marbled crayfish *Procambarus virginalis* Lyko, 2017 (Samardžić et al. 2014; Maguire et al. 2018). These species possess advantageous life history traits such as fast growth, early maturation, and high fecundity, as well as higher aggression in competitive interactions (Söderbäck 1991; Usio et al. 2001; Gherardi 2006; Pintor et al. 2008) and can outcompete ICS. More importantly, they are chronic carriers of the crayfish plague pathogen *Aphanomyces astaci* Schikora, 1906 (Holdich et al. 2009; Keller et al. 2014; Svoboda et al. 2017), which is listed among the 100 World's Worst Invasive Alien Species (Lowe et al. 2000). Crayfish plague is considered to be a major driver of the decline of the European ICS, although recent records suggest that some ICS populations can exhibit resistance to crayfish plague (e.g. *Astacus astacus* (Linnaeus, 1758): Jussila et al. 2011; Makkonen et al. 2012; *Austropotamobius pallipes* (Lereboullet, 1858): Martín-Torrijos et al. 2017; *Austropotamobius torrentium* (Schrank, 1803): Kušar et al. 2013; *Pontastacus leptodactylus* (Eschscholtz, 1823): Kokko et al. 2018), even to its most virulent genotypes (Martín-Torrijos et al. 2017; Kokko et al. 2018).

Pacifastacus leniusculus is currently the most widespread NICS in Europe and, according to the EU Regulation on invasive alien species No. 1143/ 2014, is on the list of species of EU Concern. It has been recorded in 29 European countries (Kouba et al. 2014) with the most recent records reported from EU candidate countries bordering with Croatia (Bosnia and Herzegovina; Trožić-Borovac et al. 2019). In Croatia, it is distributed across the continental part of the country, in the drainage system of the Sava and the Drava Rivers (Maguire et al. 2018). *Pacifastacus leniusculus* was first recorded in Croatia in 2008, in the Mura River (Maguire et al. 2008), where it spread as a result of the natural downstream dispersal of Slovenian and Austrian populations (Bertok et al. 2003; Govedič 2006; Govedič et al. 2007). It spread further downstream through the Mura to the Drava River at dispersal rate of 18–24.4 km/yr, which is among the highest recorded rates in Europe (Hudina et al. 2009). In 2011, it was recorded in the Korana River in the continental part of Croatia, where it was illegally introduced (Hudina et al. 2013). Here, it presents an immense threat to ICS diversity, since three out of four Croatian ICS inhabit Korana River and its tributaries (Hudina et al. 2017). In the Korana River *P. leniusculus* is expanding its range both upstream and downstream with the dispersal rate of 2.23–2.84 km/yr (Hudina et al. 2017) and gradually displaces the indigenous narrow-clawed crayfish *P. leptodactylus* (Hudina et al. 2013; Rebrina et al. 2015).

The aim of this study was to estimate *P. leniusculus* distribution and dispersal rates in Croatia, a decade after its first record (Maguire et al. 2008). In a study by Hudina et al. (2009) it was estimated that at the recorded

dispersal rate (18–24.4 km/yr), in 10 years *P. leniusculus* would come in contact with *F. limosus* in the lower section of the Drava River, 50 km upstream from the confluence with the Danube. Therefore, the additional aim was to examine whether predicted range expansion rates in the Drava River were accurate and whether contact with *F. limosus* has occurred as predicted by the study by Hudina et al. (2009). Finally, while there were recent studies of *F. limosus* range expansion in the Danube and Drava Rivers and its tributaries in Croatia (Maguire et al. 2018), such data for *P. leniusculus* downstream dispersal in the Drava River are lacking. The collected data provide an insight into the extent of the invasion, current distribution of *P. leniusculus* populations in Croatia and their distance from the native crayfish populations, as well as into potential management implications for both the invasive *P. leniusculus* and the native crayfish in the region.

Materials and methods

The field study was performed in the continental part of Croatia, in the Drava and the Korana Rivers. Both rivers belong to the Danube River basin.

The Korana River is a 134 km long karstic river belonging to the Sava River basin, with numerous natural and man-made cascades along the whole course of its length. Its springs are located at the end of a chain of sixteen barrage lakes in the Plitvice Lakes National Park. The river flows northward (Roglić 1974) to its confluence with the Kupa River in the town of Karlovac. Due to its karstic character and the man-made cascades, the discharge averages at approximately 29 m³/s (cf. Rebrina et al. 2015). Korana River and its tributaries are inhabited by populations of three ICS: *A. astacus*, *P. leptodactylus* and *A. torrentium* (Maguire and Gottstein-Matočec 2004; Maguire et al. 2011; Hudina et al. 2013). *Astacus astacus* (recorded in the Drava and Korana River and tributaries) and *A. torrentium* (recorded in the Korana River and its tributaries) are protected on both national (Nature Protection Act OG no. 80/13), and European level (listed in Appendix III of the Bern Convention).

The Drava River is a 719 km long tributary of the Danube River, with its source in Italy. It flows through Austria, Slovenia, Croatia and Hungary, and has a mouth into the Danube River in Croatia, near the city of Osijek. In the upper reaches of the river (up to the Donja Dubrava impoundment in Croatia, rkm 254), more than 20 dams have been constructed. The lower reaches of the Drava River have been considerably regulated with embankments and channels (Hudina et al. 2009). The discharge of the Drava River in Croatia averages around 500 m³/s (Rabi et al. 2015). Two ICS were recorded in the Drava River basin in Croatia: *A. astacus*, which was more numerous in the upper reaches of the Drava River in Croatia, and *P. leptodactylus*, which was more numerous in its lower reaches (Maguire and Gottstein-Matočec 2004).

For this study, data gathered via a comprehensive literature search and our own fieldwork were used. The literature search included studies examining the distribution of *P. leniusculus* in Croatia (Maguire et al. 2008, 2018; Hudina et al. 2009, 2012, 2013, 2017; Rebrina et al. 2015). This was followed by conducting a field study on the Korana and Drava Rivers. Throughout this study, invasion core refers to population established for some time now and with higher crayfish abundance, while invasion front refers to recently established populations from the very edge of the range with significantly lower relative crayfish abundance. In both the Korana and the Drava River, the fieldwork was conducted during the period of increased crayfish activity of both sexes (i.e. before mating period), in the early autumn of 2018. In the Korana River *P. leniusculus* distribution was analysed at a total of 8 sites distributed along 33 km of the watercourse: two invasion core sites, two invasion front sites from 2015 (upstream and downstream invasion front from a study by Hudina et al. 2017; hereon former invasion fronts) and four additional sites – one upstream and three downstream from these former invasion fronts. In the Drava River, range expansion was examined at a total of 17 sites downstream from the last invasion site recorded in the literature (Maguire et al. 2011). Sampling covered 128 km of the Drava River watercourse. Upstream dispersal of *P. leniusculus* through the Drava River was not monitored within this study, since recent research by Maguire et al. (2018) found no *P. leniusculus* records in this section of the river (upstream from the confluence with the Mura River). Smaller number of sites was investigated in the Korana River compared to the Drava River since *P. leniusculus* range expansion in the Korana River has been more frequently monitored (last monitoring: 2015 in the Korana River, 2011 in the Drava River) and since recorded dispersal rates are approximately 9 times lower in the Korana compared to the Drava River (Hudina et al. 2009, 2017).

Crayfish were captured using baited LiNi traps (Westman et al. 1978). At least five traps were exposed per 100 m of the watercourse (Maguire 2014) at each site and were left in the water overnight. All captured crayfish were identified to the species level. We counted the number of caught individuals per trap and determined their sex. Upon data collection, captured ICS were returned to the same location where they were caught, while NICS were taken to the laboratory for further analyses within the frame of the project STRIVE (<https://www.pmf.unizg.hr/strive/en>) which included the analyses of crayfish plague presence (Pavić et al. 2020). Based on the collected data, we calculated the catch per unit effort (CPUE, equal to the number of crayfish captured per LiNi trap per trapping night) for every trapping session for each site and each species. CPUE is a frequently used measure of relative crayfish abundance (Dana et al. 2010) and was used to compare the relative abundance of *P. leniusculus* between the sites and relative abundance of different crayfish species (ICS vs. NICS) within

the sites, in the case of mixed populations. After each fieldwork, the traps were washed in disinfectant solution using Chlormax (Genera, Croatia) in order to prevent potential cross-contamination and spreading of the crayfish plague between the sites.

Position of sampling sites was recorded using a Garmin GPS map 60CSx (projection WGS84). Collected data were analysed using descriptive statistic, and geographical presentations of crayfish distribution were performed by ArcGis 10.1 program package (ESRI Inc.).

Results

The Korana River

In the Korana River, a total of 523 crayfish were caught, belonging to two species: *P. leniusculus* (NICS: 415 individuals, 79.3% of all captured crayfish) and *P. leptodactylus* (ICS: 108 individuals, 20.7% of all captured crayfish). *Pacifastacus leniusculus* was recorded at 6 (75%) of the examined sites, while *P. leptodactylus* was found at 5 (62.5%) sites. At 3 sites (sites 1, 10 and 11; Figure 1) mixed populations of the invasive *P. leniusculus* and the native *P. leptodactylus* were recorded (Table 1). Since 2015, *P. leniusculus* range increased by the total of 5 km: 4 km in the upstream direction (dispersal rate: 1.3 km/yr) and 1 km in the downstream direction (dispersal rate: 0.3 km/yr) from the former invasion fronts (Figure 1). The invasion range of *P. leniusculus* now stretches along a total of 30 km of the lower course of the Korana River, covering approximately 22.4% of the entire watercourse.

Out of all captured *P. leniusculus* individuals, 362 individuals (87.2%) were captured at the invasion core (sites 4 and 8; Figure 1), while 23 individuals (5.5%) were captured at each of the former invasion fronts (sites 2 and 10; Table 1). At new upstream invasion front (site 1; Figure 1) 3 individuals (0.7% of all caught *P. leniusculus*) were captured, while 4 individuals (1%) were captured at new downstream invasion front (site 11; Figure 1). The new downstream invasion front is 1.8 km upstream from the confluence with the Mrežnica River (site 12; Figure 1). No NICS were recorded downstream from the confluence with the Mrežnica River (Table 1).

The native *P. leptodactylus* was recorded at both *P. leniusculus* invasion fronts (sites 1 and 11; Figure 1). In both cases, *P. leptodactylus* were more numerous than *P. leniusculus* (12.9 times higher CPUE at the downstream invasion front and 2.5 times higher CPUE at upstream invasion front; Table 1). Finally, *P. leptodactylus* abundance was 6 times higher at the downstream invasion front, compared to its abundance at the upstream invasion front of *P. leniusculus*. No *P. leptodactylus* were recorded at sites with very high *P. leniusculus* relative abundance (invasion core: sites 4 and 8; Figure 1).

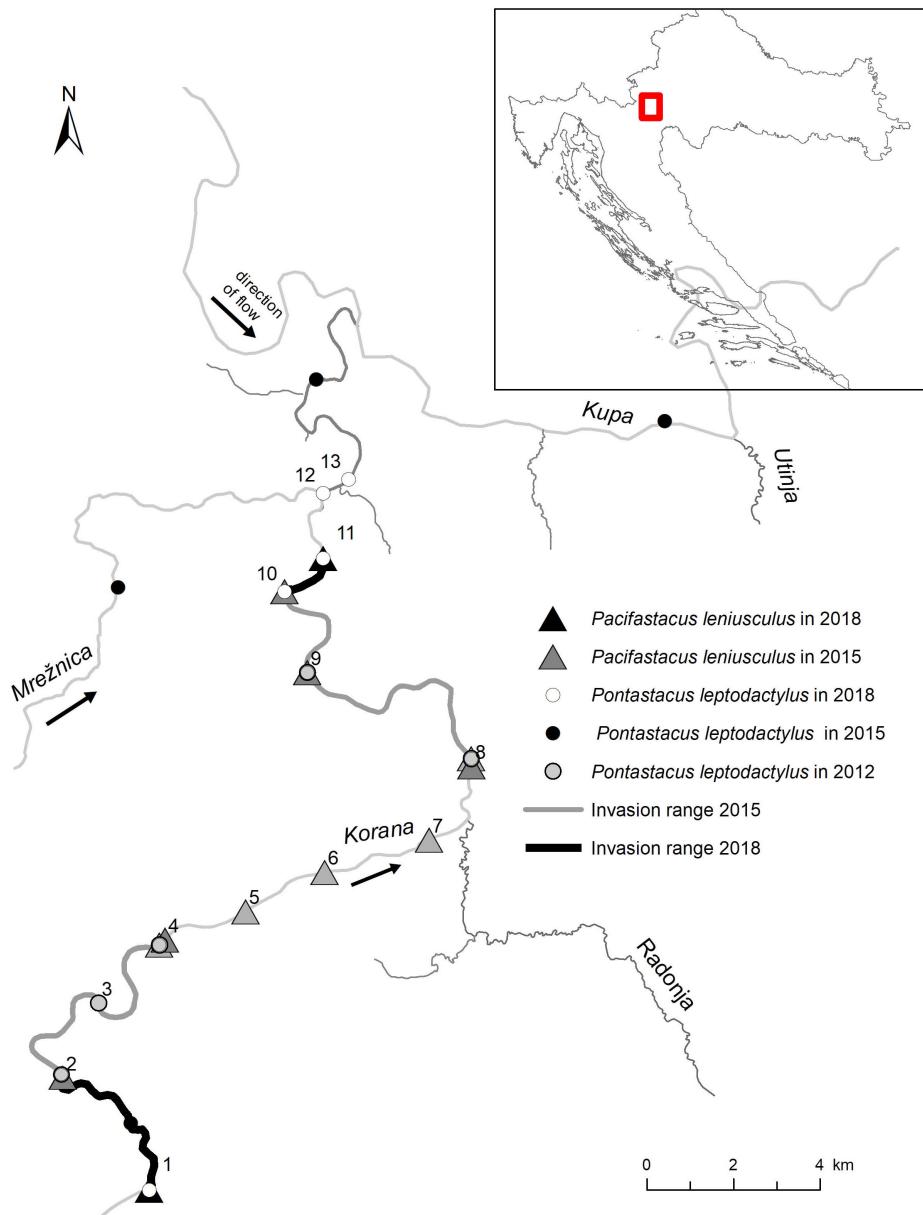


Figure 1. The distribution of *Pacifastacus leniusculus* in the Korana River, Croatia. The bold black line represents the increase in invasion range since 2015 (invasion range 2018), while the bold grey line represents the increase in invasion range from 2012–2015 (i.e. invasion range 2015). Site numbers are presented for both literature data and the fieldwork conducted within this study. Sites where *P. leniusculus* was recorded are labelled with triangles, while *P. leptodactylus* records are labelled with circles. Fieldwork in 2018 covered sites 4 and 8 (invasion core), 2 and 10 (former invasion fronts), 1 and 11 (new invasion fronts determined within the study), and sites 12 and 13 (no signal crayfish recorded).

The Drava River

During the study performed in the autumn of 2018, no ICS and only 4 NICS individuals were caught in the Drava River (Table S1): *P. leniusculus* (3 individuals; 75% of all captured crayfish) and *F. limosus* (1 individual, 25% of all captured crayfish). *Pacifastacus leniusculus* were captured at 3 sites, while *F. limosus* was recorded only at 1 site (Table 1; Table S1). In seven years, the invasion range of *P. leniusculus* has increased by approximately 148.9 km in the downstream direction from the former invasion front

Table 1. Number of captured crayfish individuals per site and catch per unit effort (CPUE; the number of crayfish captured per LiNi trap per trapping night) in the Drava and Korana Rivers during fieldwork in 2018. Crayfish numbers (No. Pl, Fl and Plept) and CPUE (CPUE Pl, Fl, Plept) are presented separately for each species of NICS: *P. leniusculus* (Pl) and *F. limosus* (Fl), and ICS *P. leptodactylus* (Plept). Site codes with associated GPS coordinates (X, Y) correspond to codes in Figures 1 and 2.

Water body	X (WGS84)	Y (WGS84)	Site code	No. Pl	No. Fl	No. Plept	CPUE Pl	CPUE Fl	CPUE Plept
Drava	45.920623	17.59068	2	1	0	0	0.33	0	0
Drava	45.858044	17.64762	3	1	0	0	0.2	0	0
Drava	45.699705	18.391038	8	1	0	0	0.2	0	0
Drava	45.60079	18.589261	12	0	1	0	0	0.2	0
Korana	45.319775	15.517625	1	3	0	8	0.043	/	0.107
Korana	45.343504	15.491309	2	23	0	0	1.1	/	0
Korana	45.371911	15.52147	4	134	0	0	8.93	/	0
Korana	45.408823	15.611404	8	228	0	0	12	/	0
Korana	45.445223	15.5578	10	23	0	13	1.577	/	1.39
Korana	45.451736	15.566728	11	4	0	75	0.106	/	1.366
Korana	45.465374	15.566272	12	0	0	11	0	/	2.2
Korana	45.468247	15.573795	13	0	0	1	0	/	0.25

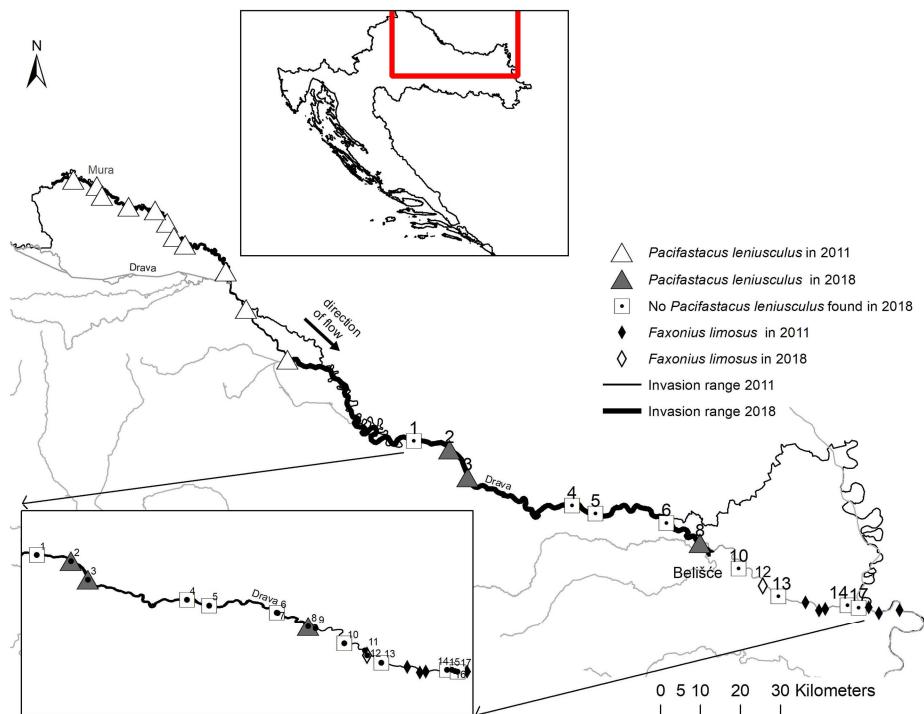


Figure 2. The invasion range of the signal crayfish in the Drava River, Croatia. The bold line along the river represents the invasion range recorded in 2018. Sites examined in 2018 are labelled by numbers (1–17). The figure shows both literature records of *P. leniusculus* (white triangles) and fieldwork records from 2018 (grey triangles). *Faxonius limosus* literature data for the Drava River (black diamond shapes) and 2018 fieldwork records (white diamond shapes) are also shown. The new *P. leniusculus* invasion front recorded in this study is located at site 8.

established in 2011 (Figure 2), which corresponds to dispersal rate of 21.3 km/yr. The new invasion front is located only 3.3 km upstream from the predicted point of contact between *P. leniusculus* and *F. limosus* by Hudina et al. (2009).

Only one individual of *F. limosus* was captured in the Drava River, at the Karašica River mouth (site 12, Figure 2), 15.3 km upstream from its former invasion front in the Drava (Hudina et al. 2009; Figure 2). This latest *F. limosus* record is located 25 km downstream from the current *P. leniusculus* invasion front.

Discussion

Range expansion constitutes a crucial element of invasion success and understanding its dynamics is a prerequisite for assessment of NICS regional and global impacts, as well as prioritization of sites and species for NICS management (Manfrin et al. 2019). While range expansion of one of the most successful NICS invaders in Europe, *P. leniusculus*, has been explored and monitored all over Europe (UK: Peay 1997; Peay and Rogers 1999; Bubb et al. 2004, 2005; Portugal: Bernardo et al. 2001, 2011; Croatia: Hudina et al. 2009, 2013, 2017; Maguire et al. 2011, 2018; Austria: Weinländer and Füreder 2009, 2012; Finland: Erkamo et al. 2010; Jussila et al. 2014; Ruokonen et al. 2018; Poland: Dobrzycka-Krahel et al. 2017) only several studies regularly monitored its long-term spread or prioritized sites for its potential management.

In this study, we present the results of a decade long monitoring effort of range expansion of *P. leniusculus*. The obtained results show that 10 years after its first record in Croatia, *P. leniusculus* continues to successfully expand its range in Croatian freshwater ecosystems. Out of all NICS currently recorded in Croatia, *P. leniusculus* is the most widespread due to its high dispersal rates and wide invasion range which covers a large portion of continental part of Croatia. Also, the proximity of its populations to endangered and protected ICS populations, as well as to protected areas (Plitvice Lakes National park), and the recorded presence of crayfish plague pathogen in both Drava and Korana populations (Maguire et al. 2016; Pavić et al. 2020) highlight its prominent threat to native Croatian astacofauna.

In the Korana River, the invasive range of *P. leniusculus* has increased by a total of 5 km in three years and now stretches along a total of 30 km of the river. *P. leniusculus* is expanding its range both upstream and downstream from the invasion core, but at approximately nine times slower rate than *P. leniusculus* populations in the Drava River. Korana River has much lower average discharge (29 m³/s) compared to the Drava (500 m³/s) and has numerous natural and man-made cascades along the whole course of its length (cf. Hudina et al. 2017), and both of these factors may influence both downstream and upstream invasion (Holdich et al. 2014). Thus, slower dispersal rates could be attributed to the river hydromorphology, but also to the differences in invasion pathways – natural dispersal in the Korana River versus undiscerned invasion pathway in the Drava (discussed in the later sections).

The recorded downstream dispersal rates of *P. leniusculus* in the Korana River (0.3 km/yr) are somewhat lower compared to other studies (1–7 km/yr: Peay 1997; Peay and Rogers 1999; Bubb et al. 2004, 2005; Weinländer and Füreder 2009; Bernardo et al. 2011), while upstream dispersal (1.3 km/yr) is similar to existing literature data (0.35–4 km/yr: Bubb et al. 2005; Weinländer and Füreder 2009; Bernardo et al. 2011). Since the last study in

2015 (Hudina et al. 2017), *P. leniusculus* dispersal rate has decreased in both downstream (6.5 times) and upstream (2 times) direction. Previous studies have reported that *P. leniusculus* dispersal rates are not constant (cf. Holdich et al. 2014) and that natural barriers can slow down both the upstream and the downstream invasion of *P. leniusculus* (Peay and Rogers 1999; Rosewarne et al. 2013; Bubb et al. 2004). In general, downstream dispersal is expected to be faster than movement upstream (Bubb et al. 2005), however recorded dispersal rates in the Korana River were higher in the upstream than in the downstream direction. Differences between upstream and downstream dispersal rates typically depend on the river characteristics (i.e. river gradient and the existence of barriers; Bubb et al. 2005; Bernardo et al. 2011) and in some cases are only weakly biased in downstream direction (Holdich et al. 1995; Guan and Wiles 1999). Also, high discharge events can facilitate downstream dispersal of juvenile crayfish (cf. Bubb et al. 2002; Bernardo et al. 2011), but factors other than river hydromorphology, such as limiting resources, predation and competitive pressure will also drive the dynamics range expansion (Bernardo et al. 2011).

Therefore, we believe that in the case of the Korana River, the observed lower downstream dispersal rates could potentially be due to high competitive pressure from the native *P. leptodactylus* at downstream invasion front. *Pontastacus leptodactylus* has been considered as the most robust ICS since it has better adaptive plasticity than the other native crayfish species (Lucić et al. 2012; Perdikaris and Georgiadis 2017), may exhibit partial resistance to the *A. astaci* infection (Svoboda et al. 2012; Kokko et al. 2012, 2018) and is the only ICS showing range expansion in water bodies of Croatia (Maguire et al. 2011, 2018) and other European countries (Kouba et al. 2014). Therefore, its high population abundance at the downstream invasion front (13 times higher CPUE than *P. leniusculus*) could be slowing down the downstream range expansion of *P. leniusculus*. The populations of the native *P. leptodactylus* at the downstream invasion front have much higher relative population abundance (6 times higher) than its populations at the upstream front due to its relatively recent spread to the Korana from the Mrežnica River (Maguire et al. 2011, 2018). Thus, the uneven competitive pressure exerted by the native ICS may be contributing to the observed differences in dispersal rates of *P. leniusculus* at two invasion fronts. Nevertheless, such dispersal rate reduction will probably be short term, since the invasive *P. leniusculus*, even in the absence of crayfish plague (disease transmission), is competitively advantageous over the native European crayfish. This was demonstrated in previous laboratory and field studies on other ICS (*A. astacus*: Söderbäck 1991, 1995; Westman et al. 2002), as well as for *P. leptodactylus* both experimentally (Hudina et al. 2016) and in the field (the Korana River; Hudina et al. 2017), where *P. leptodactylus* was gradually displaced from

the invasion core populations. At the invasion core, *P. leptodactylus* were present in 2012 (Hudina et al. 2013, 2017). Since then, the *P. leniusculus* populations abundances have increased over 20 times. Additionally, we have recently confirmed that the small proportion (6%) of the entire *P. leniusculus* population in the Korana River is *A. astaci*-positive (Pavić et al. 2020). Therefore, in addition to competitive advantage, crayfish plague transmission might be contributing to the observed decline of *P. leptodactylus* in the Korana River.

In the Drava River, based on the current study, it seems that from 2011 the invasion range of *P. leniusculus* has increased by approximately 148.9 km in the downstream direction with a dispersal rate of 21.3 km/yr. The dispersal rate matches the rates recorded in a study a decade ago (18–24.4 km/yr; Hudina et al. 2009). However, it is important to emphasize that dispersal rate calculations within this study are based on a low number of captured *P. leniusculus* individuals in the Drava River. Therefore, we cannot rule out the possibility that such fast dispersal rate in the Drava River is a consequence of human translocations, especially since voids in *P. leniusculus* distribution were recorded (no *P. leniusculus* recorded between sites 3 and 8). Currently, the evidence of human-mediated translocations of crayfish in Croatia is scarce (e.g. *A. astacus* in the Adriatic Sea drainage: Maguire et al. 2011, 2018; *A. astacus* in Plitvice Lakes region: Maguire et al. 2013; *P. leniusculus* in the Korana River: Hudina et al. 2013; Mijošek et al. 2017), most probably because crayfish are not commercially important species in Croatia (no crayfish farms exist in Croatia and crayfish are not sold in local markets nor used as baits). Also, recorded voids in distribution may be attributable to the river size (e.g. in this section the Drava is 200 m wide and crayfish distribution in the river is not uniform but patchy; Hudina et al. 2008). The high dispersal rate may potentially be attributed to hydrological conditions of the Drava River – high average discharges in combination with hydromorphological changes due to upstream hydropower plant constructions (cf. Hudina et al. 2009). Finally, the very low number of caught *P. leniusculus* indicates a low population density (which is expected at invasion fronts), and “standard” crayfish traps such as the ones used in this study (LiNi traps) are less effective compared to other trapping methods (i.e. baited stick catch – approximately 5 times more effective, artificial refuge traps – approximately 4 times more effective; Policar and Kozak 2005; Green et al. 2018). Therefore we hypothesize that, regardless of the invasion pathway (natural or human mediated), the low number of caught crayfish as well as voids in distribution are potentially a consequence of a patchy distribution in a large river and low population density in combination with lower trapping efficiency of “standard” crayfish traps. We used “standard” baited crayfish traps since: i) the Drava River is a large, deep and relatively turbid river and alternative trapping methods are not a viable option in this habitat and ii) their use remains commonplace and allows comparisons

with data from previous studies performed on this river (Hudina et al. 2009) as well as with other studies (Larson and Olden 2016; Green et al. 2018). Taking all above into consideration, the recorded dispersal rates as well as invasion pathways need to be further explored in order to discern whether the downstream spread in the Drava River is natural or human-mediated and to examine the effect of hydrological factors (e.g. the effects of high discharges and hydromorphological changes) on dispersal rates of *P. leniusculus*.

It was estimated that by 2018, *P. leniusculus* would encounter the invasive *F. limosus* in the Drava River and that the encounter area would be 50 km upstream from the confluence of the Drava and the Danube River (Hudina et al. 2009). While in this study *P. leniusculus* was recorded only 3.3 km upstream from the predicted encounter area by Hudina et al. (2009), *F. limosus* was absent from this newly established *P. leniusculus* invasion front. This might be due to the slower than expected upstream dispersal rate of *F. limosus*. However, due to low number of both captured NICS this cannot be discerned and further monitoring of this river section is required in order to determine population dynamics of the two invaders in this river stretch.

In the case of ICS, the lack of native *P. leptodactylus* records in the Drava River during our study and during the survey by Maguire et al. (2018) suggests its displacement by both *P. leniusculus* and *F. limosus*. The findings from both the Korana and the Drava Rivers and from previous studies (Hudina et al. 2009, 2017; Maguire et al. 2018) suggest that, even though currently robust, *P. leptodactylus* might in the long-term become completely displaced from large rivers and their tributaries in the continental part of Croatia (the Danube, the Drava and the Korana) due to the competitive pressure by NICS. Thus, the status of *P. leptodactylus* in Croatia should be monitored and re-examined – even though it is the only ICS undergoing range expansion in some water bodies, it is also currently the ICS species most adversely affected by the spread of the NICS in Croatia.

Other species threatened by *P. leniusculus* dispersal are the populations of the protected ICS (*A. astacus* and *A. torrentium*) in the Korana River and its tributaries. *A. torrentium* populations are located 46 km upstream of the invaded area in a tributary of the Korana River, while both *A. astacus* and *A. torrentium* populations are present 109 km upstream from the upstream invasion front, in the most well-known Croatian National Park, the Plitvice Lakes (Maguire et al. 2013; Hudina et al. 2013), where springs and upper course of the Korana River are located. Due to higher dispersal rates of *P. leniusculus* in the Korana River in upstream direction, as well as the existence of several populations of protected ICS upstream in the Korana and its tributaries, the dispersal rate of *P. leniusculus* in the upstream direction should be prioritized and carefully monitored, as well as any intentional or unintentional translocation of crayfish (Bohman et al.

2006; Diéguez-Uribeondo 2006; Ruokonen et al. 2018). Finally, due to recorded presence of crayfish plague pathogen *Aphanomyces astaci* in the invaded range of *P. leniusculus* in the Drava (Maguire et al. 2016) and the Korana (Pavić et al. 2020), disinfection protocols for fishing equipment should be put in place in order to prevent unintentional crayfish plague transmission to other parts of the rivers and their tributaries.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Records of native and non-native crayfish in Drava and Korana rivers.

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2020/Supplements/BIR_Dragicevic_etal_SupplementaryMaterial.xlsx