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Characteristics and movement patterns of a recently established invasive *Pacifastacus leniusculus* population in the river Mura, Croatia

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ABSTRACT

Key-words: *year cycle, population characteristics, movement, crayfish, freshwater invasion*

The presence of the signal crayfish, *Pacifastacus leniusculus*, in waterbodies of Europe is of high concern due to its potentially major ecological impact on invaded ecosystems and native crayfish. In this study, we examined population characteristics and spatial dynamics of a recently established signal crayfish population near the edge of its invasive range in the Mura river (Croatia), by analyzing population density, fecundity, and sex and size structure, as well as movement patterns. The obtained results revealed that the examined population is characterized by relatively low population density, balanced sex and size structure of adult crayfish, and high spatial activity of examined individuals, with an average daily movement of 28 m/day. Pleopodal fecundity was in a similar range to other signal crayfish populations in Europe. The large minimal size of caught mature females (85 mm total length), coupled with the estimated low population density (0.8–1.2 crayfish·m^{-2}), suggested that the examined population has not reached its maximum density yet. Obtained results represent baseline information for the development of monitoring procedures and management strategies aimed at signal crayfish control within the Mura and Drava catchments and also highlight the importance of understanding local factors controlling invasive species' population dynamics and productivity.

RÉSUMÉ

Caractéristiques et schéma de déplacement d'une population invasive de *Pacifastacus leniusculus* récemment installée dans la rivière Mura, Croatie

Mots-clés : cycle de vie, caractéristiques de population, déplacement, écrevisse, invasion en eau douce

La présence de l'écrevisse signal, *Pacifastacus leniusculus*, dans les plans d'eau de l'Europe est très préoccupante en raison de ses impacts écologiques majeurs potentiels sur les écosystèmes envahis et les écrevisses indigènes. Dans cette étude, nous avons examiné les caractéristiques démographiques et la dynamique spatiale d'une population d'écrevisses signal récemment établie près de la limite de son aire d'invasion dans la rivière Mura (Croatie), en analysant la densité de population, la fécondité, le sexe et la structure en taille ainsi que les modes de déplacement. Les résultats obtenus ont révélé que la population examinée se caractérise par une densité de population relativement faible, un sexe ratio et une structure en taille des écrevisses adultes équilibrés et une forte activité spatiale

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des individus examinés, avec un déplacement journalier moyen de 28 m/jour. La fécondité a été dans des gammes similaires à celles d'autres populations d'écrevisses signal en Europe. La grande taille minimale des femelles matures captures (85 mm de longueur totale), couplée avec une basse densité de population estimée (0,8 à 1,2 crayfish.m^{-2}), a suggéré que la population examinée n'a pas encore atteint sa densité maximale. Les résultats obtenus représentent l'information de base pour le développement de procédures de surveillance et des stratégies de gestion visant à contrôler les écrevisses signal dans les bassins de la Mura et de la Drava et soulignent également l'importance de la compréhension des facteurs locaux contrôlant la dynamique et la productivité de populations d'espèces invasives.

INTRODUCTION

Biological invasions are considered a major component of human-induced environmental change (Sala *et al.*, 2000), with invasive alien species (IAS) recognized as the second leading factor of biodiversity loss after habitat destruction (Lodge *et al.*, 2000). With the harmful effects of biological invasions and the complexity of the problem being widely recognized, management of invasive species is a growing and persistent problem facing conservation managers around the world (Pyšek and Richardson, 2010). Invasive species management efforts will depend on the stage of invasion being managed (*e.g.* Hulme, 2006), with each stage requiring knowledge of key traits that facilitate invasion success (Kolar and Lodge, 2002), as well as knowledge of population characteristics affecting invaders' population and spatial dynamics. Moreover, since the rate of invasive species spread is determined by key population characteristics such as population growth and dispersal coupled with density dependence (Burton *et al.*, 2010), acquiring information on invaders' population characteristics is essential in attempts to understand the exceptional speed at which invasive species are able to expand their range.

Crayfish are among the most frequently introduced non-indigenous aquatic invertebrates (Holdich *et al.*, 2009; Moorhouse and MacDonald, 2011). In Europe, non-indigenous crayfish species (NICS) are currently twice as numerous as native crayfish species (Holdich *et al.*, 2009). Due to their relatively large body size, potentially very high population densities, long life span and omnivorous feeding habits (Usio and Townsend, 2002), NICS can dramatically alter aquatic community composition and ecosystem functioning. The signal crayfish (*Pacifastacus leniusculus*, Dana), currently present in 27 European countries, is the most widespread NICS in Europe (Holdich *et al.*, 2009). Along with habitat loss, it represents the main threat to native European crayfish species (Weinländer and Füreder, 2009), which are displaced through competition with more aggressive (Söderbäck, 1991), faster-growing and more fecund signal crayfish (*cf.* Souty-Grosset *et al.*, 2006). Besides competition, native crayfish displacement also occurs through transmission of diseases such as crayfish plague (*e.g.* Diéguez-Uribeondo, 2006). In addition, signal crayfish exhibits adverse impacts on other biota (*e.g.* macroinvertebrates and fish: Griffiths *et al.*, 2004; Crawford *et al.*, 2006; Reynolds, 2011) and on the physical environment of streams and rivers (Johnson *et al.*, 2010). The efforts to control the population growth and spread of signal crayfish have so far elicited only limited success (Peay *et al.*, 2006; Freeman *et al.*, 2009, but see also Dana *et al.*, 2010) on a small scale.

The range expansion of signal crayfish in some European waterbodies has been very fast, especially in a downstream direction, reaching up to 18–24.4 km·yr in the lower section of the Mura river (Hudina *et al.,* 2009). Reported downstream dispersal rates in this area are over 3 times higher than those recorded in Austria (up to 7 km·yr in Austria; Weinländer and Füreder, 2009), from where the signal crayfish in the Mura river originated after its illegal introductions into Austria in the 1970s (Pöckl, 1999; Holdich *et al.*, 2009). Within only a few years, *P. leniusculus* has expanded its range throughout the whole lower section of the Mura and has almost reached the confluence with the Drava river (Hudina *et al.*, 2009).

Despite its prevalence in the region and high recorded rates of downstream range expansion, little information is available on population characteristics and spatial dynamics of the signal crayfish in the lower section of the Mura River, where the edge of the expanding signal crayfish population occurs (Hudina *et al.*, 2009). As data on population characteristics represent baseline information for the development of targeted signal crayfish control strategies, and for understanding the dynamics of its range expansion, our aim was to acquire such information for the examined signal crayfish population in the Mura River. We compare our results on population density, fecundity, sex structure, year cycle and spatial dynamics with other signal crayfish populations in Europe, and discuss our findings in relation to the potential effects of population density on the recorded population parameters, as well as in relation to potential management implications.

METHODS

> STUDY AREA

The Mura river is the largest tributary of the Drava river. More than a half of its length of 444 km and catchment area of 14 304 km^2 belongs to Austria, while the rest is situated in Slovenia, Croatia and Hungary. The lower part of the Mura river (the last 83 km) forms a border between Croatia and Hungary (Figure 1). A mild-continental (Legrad mouth, Croatia 132 m a.s.l.) and partly humid climate (average annual temperature 10.9 °C and an average rainfall of 600–750 mm/year) dominates the catchment (Sommerwerk *et al.*, 2009). The hydrological regime is dependent upon the snow-melting season in Austria, with usually higher discharge during spring (March–May) and lower discharge in winter (Globevnik and Kaligarič, 2005).

The Mura River has been severely impacted by hydromorphological changes due to river regulation, sand and gravel excavation, and bank stabilization activities (Schneider-Jacoby, 2005). Despite such changes, natural habitats along the river have been well preserved and host numerous rare and endemic species, which led to the recent establishment of a Mura – Drava regional park in all countries sharing the basin (Slovenia, Hungary and Croatia).

Signal crayfish population characteristics and spatial dynamics were studied at site M1 in an approximately 500-m-long stretch of the lower section of the Mura river in Croatia (rkm 80–81; Figure 1). At this site, the signal crayfish population has been established for over 5 years (*cf.* Hudina *et al.*, 2009), with the first record of the established population originating from 2008 (Maguire *et al.*, 2008). The river width in the examined stretch varied between 68–103 m, while the average annual water temperature in the period of the fieldwork performed was 10.9 °C (range 3.1–19 °C). The examined site is characterized by sparsely developed riparian vegetation, with dominating willows (*Salix* sp.) and steep banks with revetments. Stone blocks of up to 40 cm along with gravel and sand dominated in the substrate composition of the examined river stretch.

> ANALYSES OF POPULATION CHARACTERISTICS

Population characteristics of the signal crayfish such as year cycle, sex ratio, fecundity, size structure and frequency of injuries were examined monthly by exposure of a similar number (6–8) of baited LiNi traps (Westman *et al.*, 1978) along the Croatian bank of the Mura river over a period of one year (April 2009–March 2010). During each sampling occasion, LiNi traps were set at approximately the same position within the examined stretch. The LiNi traps, similar to other baited traps, are biased towards capturing larger size classes (Hogger, 1988; Dorn *et al.*, 2005), since their construction and mesh size allows the escape of smaller individuals (usually smaller than 6 cm total length). As size at maturity in signal crayfish varies between 6 and 9 cm total length (*cf.* Souty-Grosset *et al.*, 2006; Westman *et al.*, 1999), we were able to sample the adult and sub-adult part of the signal crayfish population.

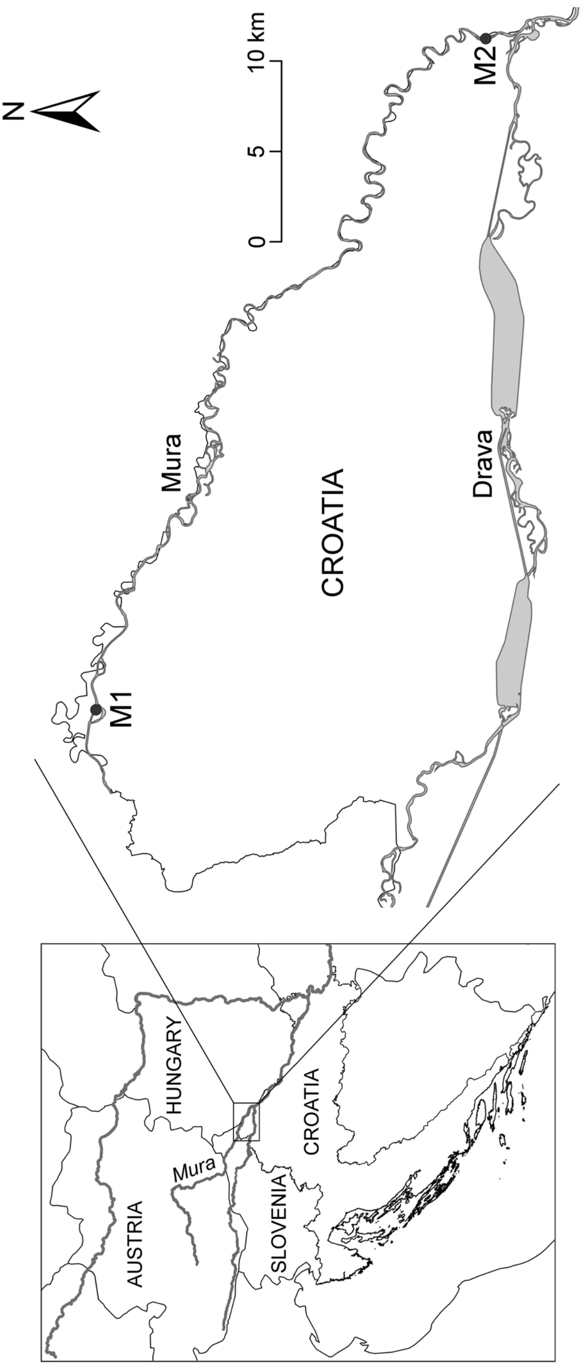

Figure 1
The position of the examined site (M1) in the lower section of the Mura River, Croatia. The examined site is situated 80 km from the recorded signal crayfish invasion front (M2).

For every trapping session we recorded water temperature using a digital thermometer (DT-131 Trotec) and calculated the catch per unit effort (CPUE; equal to the number of crayfish caught per trap per night). Since passive sampling methods depend on animal abundance and activity levels (Dorn *et al.*, 2005), CPUE was used to estimate crayfish activity and relative abundance within a year cycle. For each crayfish caught we recorded sex, weight (*W*) and 5 morphometric parameters: total length (*TL*), carapace length (*CL*), chela length (*CLL*), abdomen length (*AL*) and abdomen width (*AW*). Pleopodal fecundity was measured as the number of pleopodal eggs for each berried female, while juvenile survival up to independence was examined as the number of attached 2nd stage juvenile crayfish (just before juvenile independence). Females with very low numbers of pleopodal eggs were not included in analyses, as high egg loss is frequently the result of poor egg attachment, disturbance, fungal infections and aggressive interactions with other crayfish (*cf.* Reynolds, 2002; Maguire *et al.*, 2005), rather than an indication of low pleopodal fecundity. Additional year cycle characteristics such as the molting and mating periods and reproductive readiness of females (females with visible cement glands; Westman *et al.,* 1999) were recorded as well. The size of reproductively active females was used to determine the minimal size of mature females (Westman *et al.,* 1999). Lastly, all animals were inspected for the presence of injuries. Upon recording all parameters, all crayfish caught were removed from the population to prevent recaptures.

> *ANALYSES OF POPULATION DENSITY AND MOVEMENT PATTERNS*

Population density and movement patterns were examined in the period of increased crayfish activity, identified by the increase in CPUE during the research into population characteristics described in the previous section. Both density and movement patterns were examined by mark-recapture studies, performed intensively during seven consecutive trapping nights in August 2010. Altogether, 20 baited LiNi traps were exposed continuously at the same distance within a stretch of 150 m (distance between each trap was 7.5 m) and were checked daily for crayfish presence. Each caught crayfish was weighed (*W*), measured (*CL*, *TL*), marked by piercing a hole in the telson and/or uropodes (Guan, 1997) and released back into the watercourse at the exact point of capture. Population size was estimated using mark-recapture-based models (Jolly-Seber, Schnabel and Schumacher-Eschmeyer models; summarized by Krebs, 1989). As previous research demonstrated that the attraction of baited traps decreases with distance, and identified the distance of 6 m from the trap as an effective sampling distance (Acosta and Perry, 2000), we used this value (as the attraction segment width) and the length of the analyzed segment to calculate crayfish density (number of crayfish per square meter) from the obtained population size estimates.

Crayfish movement was analyzed under the assumption that animals were moving linearly, thus passing the minimal possible distance between traps. We recorded the minimum and maximum cumulative distance moved by any crayfish (*cf.* Light, 2003; Bubb *et al.*, 2002, 2004, 2006a, 2006b) and mean daily movement (the cumulative distance between the first and the last capture divided by the number of days between these events; *e.g.* Robinson *et al.*, 2000; Hudina *et al.*, 2008). Also, we distinguished crayfish caught each time in the same trap as animals exhibiting minimal movements (stationary individuals), and crayfish caught in different traps (moving individuals). Recorded parameters were analyzed in order to identify whether differences in movement patterns exist between animals of different gender or size.

> *STATISTICAL ANALYSES*

When the assumptions of normality of data and homogeneity of variance were met on either raw or transformed data, parametric tests (*t*-test for independent samples, Pearson correlation) were applied. The relationship between the total body length (*TL*) and the number of eggs per female was determined using regression analysis and Pearson's correlation coefficient. When assumptions necessary to use parametric analyses were not met on transformed data, their nonparametric analogues (Mann-Whitney *U* test, Spearman Rank

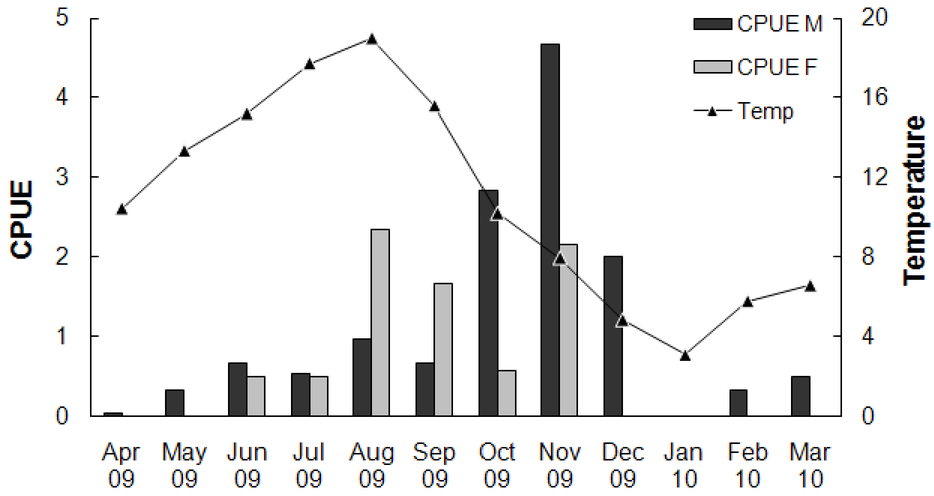

Figure 2
Activity of signal crayfish males and females (measured as CPUE) in a year cycle, coupled with water temperature data recorded during every sampling occasion.

correlation) were used instead (*cf.* Zar, 1996). The level of significance for all statistical tests performed was set at $p < 0.05$.

RESULTS

> *ANALYSES OF POPULATION CHARACTERISTICS*

The year cycle of *P. leniusculus* in the lower section of the Mura river is represented in Figure 2 and Table I. During the one-year trapping period altogether 342 crayfish were caught. The sex ratio for the composite sample of all 12 months was 1: 1.17 (M: F), although it varied significantly on a monthly basis (Figure 2). A period of increased female activity was observed in August, September and November, while male activity peaked in October and November (Figure 2). A positive, but non-significant correlation was recorded between CPUE and water temperature (Spearman rank order correlation: $r = 0.37$).

Both sexes molted in late summer, while an additional molting period of males was observed in October (Table I). In September, the majority of females caught (80%) were preparing for mating (activated glair glands), which occurred in October (Table I). The smallest reproductively active female with activated glair glands was 85 mm *TL*, while the average *TL* of reproductively active females was 112.3 mm (Figure 3c). The smallest berried female caught was 90.5 mm *TL*, with the average *TL* of berried females recorded at 109.8 mm (Figure 3d). Smaller-sized reproductively inactive females (<85 mm *TL*) comprised a small proportion of the examined population (Figure 3b). The average recorded pleopodal fecundity was 261 eggs and only two females were found with 103 and 147 2nd stage juveniles, respectively. The relationship between *CL* and pleopodal fecundity was explained slightly better by the power model than the linear model ($R^2_{power} = 0.18$, $R^2_{linear} = 0.17$), but high variation in fecundity caused poor representation of those data by all models tested. In comparison with average fecundity obtained from the power model (Figure 4) for corresponding CL, estimated juvenile survival up to independence of these two females was 39% and 56%. Egg number was positively correlated with female body size, weight and abdomen size (Pearson correlation: $r_{CL} = 0.41$; $r_W = 0.33$; $r_{AL} = 0.50$; $r_{AW} = 0.38$; Figure 4), while no statistically significant correlation was observed between egg diameter and the measured parameters of female morphology and weight.

Table I

Year cycle parameters of examined signal crayfish population measured within a 12 month period. Recorded parameters are presented in the table as either percentage of individuals in the population or presence/absence data. Data in parentheses represent life cycle parameters which were not observed in respective months but are assumed to be present.

	Apr 09	May 09	Jun 09	Jul 09	Aug 09	Sep 09	Oct 09	Nov 09	Dec 09	Jan 10	Feb 10	Mar 10
Molting M / F				+/+	+/+		+/-					
Mating							+					
Glair glands %F					35	80						
External eggs	(+)	(+)						+	+	+	(+)	(+)
2nd stage juveniles			+									
% Damage			14	48	51	14	34	32	25		50	33
% Claw damage				24	20	14	27	25	25			

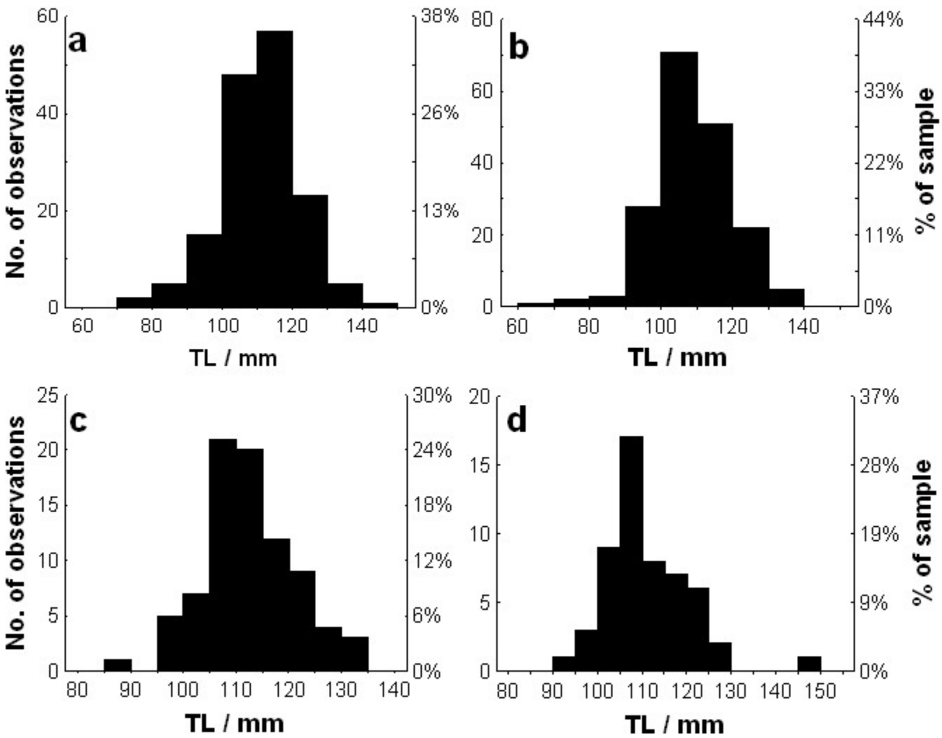

Figure 3

The distribution of body size (total length) of captured males (a) and females (b) in the examined population for the composite sample of 12 months. Distribution of reproductively active (c) and ovigerous (d) signal crayfish females in the examined population is also presented.

The crayfish size distribution pattern was similar for both males and females, with the majority of animals caught of both sexes ranging between 100–120 mm *TL* (Figures 3a and 3b). Males and females differed significantly in all measured morphometric parameters and weight (*t*-test: t_{CL} = 4.8, $p \ll 0.001$; t_W = 7.5, $p \ll 0.001$; t_{CLL} = 9.48, $p \ll 0.001$; t_{AL} = –2.25, $p \ll 0.025$; t_{AW} = –7.83, $p \ll 0.001$). Males were on average larger and heavier than females and had larger claws, while females had a larger and wider abdomen. The highest percentage of injured

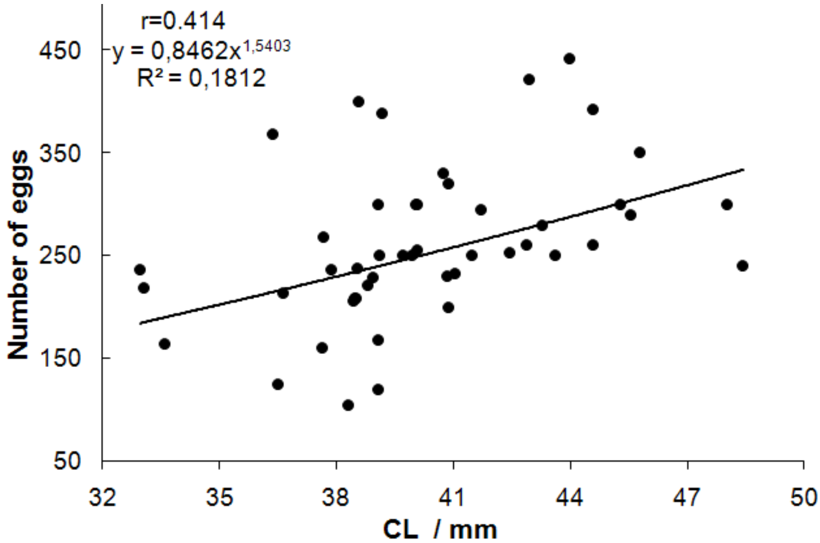

Figure 4
Relationship between berried female carapace length (CL) and number of eggs (pleopodal fecundity). Pleopodal fecundity was positively correlated with crayfish body size (r-Pearson correlation coefficient, R^2-coefficient of determination).

animals was recorded in August; however, the highest percentage of claw injuries was observed in October (Table I). There was no significant difference in proportion of injured males and females in each examined month or for the composite sample of all 12 months ($p > 0.05$ for all χ^2 tests). Also, no significant difference between males and females in proportion of claw injury was observed for each examined month or for the composite sample of all 12 months ($p > 0.05$ for all χ^2 tests). In both cases, the proportion of all injuries and claw injuries was always slightly higher for males than females (38% males with all injuries *vs.* 35% females with all injuries; 29% males with claw injuries *vs.* 22% females with claw injuries in the composite sample).

> DENSITY AND MOVEMENT PATTERNS

In mark-recapture experiments a total of 474 crayfish were captured and marked. A total of 246 individuals (51.9%) were recaptured, of which 171 (69.5%) were recaptured more than once. The estimated number of crayfish per meter of the examined segment length ranged between 4.7–7.2 crayfish/m (Table II), which corresponded to a density of 0.78–1.2 crayfish·m^2, when the effective sampling distance obtained from the literature data (see methods section) was taken into account. The calculated mean daily movement averaged 28.2 m·day (Table III)

Table II
Signal crayfish population size estimated by three models on the basis of mark recapture experiments. Population size per meter was calculated by dividing obtained population size estimates with the analyzed segment length.

Method	Estimated population size	95% confidence limits	Population size / m	95% confidence limits
Schnabel	701.96	596.20–853.30	4.68	3.97–5.69
Schumacher-Eschmeyer	704.00	656.00–759.00	4.69	4.37–5.06
Jolly-Seber	1073.38	780.00–1961.00	7.15	5.20–13.07

Table III
Mean daily movement and cumulative distance moved (range in parentheses) by signal crayfish individuals in the lower section of the Mura river.

Parameter	Both sexes	Males	Females
Mean daily movement / m	28.2 (0–225)	22.1 (0–135)	32.1 (0–225)
Cumulative distance moved / m	34.4 (0–270)	26.16 (0–112.5)	39.56 (7.5–270)

and there was no statistically significant difference in mean daily movement between the sexes (Mann Whitney *U* test: $U = 3160$, $p = 0.35$), although females on average moved higher cumulative distances and exhibited higher mean daily movement (Table III). There was no significant correlation between crayfish size (*CL*) or weight (*W*) and mean daily movement.

Only 5.3% of consecutively recaptured individuals displayed larger-scale movements over 80 m. The maximum cumulative distance moved by any crayfish was 270 m, while the minimum distance moved by any crayfish was 7.5 m (Table III). Animals making minimal movements (stationary individuals; caught each time in the same trap) comprised 24% of all recaptures. No statistically significant difference in body size (*CL*), weight (*W*) or gender was observed between stationary individuals and moving individuals (caught in different traps; Mann Whitney *U* test: $p >> 0.05$).

DISCUSSION

The results obtained on population characteristics and spatial dynamics of a recently established signal crayfish population near the edge of its invasive range in the Mura River suggest that the examined population is characterized by relatively low population density, balanced sex and size structure of adult individuals, and that it exhibits high spatial activity. The activity pattern of the signal crayfish population in the lower section of the Mura River, measured as monthly CPUE, showed a clear seasonal variation. Similar to other signal crayfish populations in Europe (*e.g.* Guan, 2000; Capurro *et al.*, 2007; Dana *et al.*, 2010), minimum crayfish yields were recorded from early winter to early spring, while maximum yields were observed in fall. Activity of males and females fluctuated within a year, but the overall yearly sex ratio was close to the natural equilibrium reported for *P. leniusculus* populations (1:1; Lewis, 2002). Since the sex structure of newly established populations demonstrates a significant male bias (Hudina *et al.*, unpubl. data), balanced sex ratios suggest that the examined population has been established for a longer period. The observed activity pattern of both sexes reflects crayfish behavior related to reproduction (increased activity of both sexes during mating season, lower activity of egg-bearing females in fall, followed by an increase in female activity after hatching in spring) and molting (lower activity of both sexes during molting). Although temperature influences crayfish activity by increasing crayfish metabolic rates and movement (Ackefors, 1999; Bubb *et al.*, 2004), it was not a direct driver of crayfish activity, since activity in spring did not increase proportionally to the increase in water temperature, and the activity pattern in fall (September to November) showed a reverse trend to that of water temperature.

The reproductive cycle corresponded to that of other signal crayfish populations in Europe, with mating occurring in October, the egg incubation period lasting from November to May (approximately 212 days) and egg hatching occurring in June (Souty-Grosset *et al.*, 2006; Lewis, 2002). The size of the smallest reproductively active female caught (*i.e.* female with activated cement glands) was close to the upper limit of size at maturity for signal crayfish recorded in the literature (from 6 to 9 cm *TL*; Souty-Grosset *et al.*, 2006; Westman *et al.*, 1999), while the average *TL* of both reproductively active and ovigerous females were well above these values (112.3 mm *TL* and 109.8 mm *TL*, respectively). The average size of reproductively active females caught in this study might have been affected by the applied trapping methodology, since LiNi traps are biased towards capturing larger specimens and since proportions of captured smaller-sized adult females (<100 mm *TL*) were relatively low. Nevertheless, since reproductively inactive females smaller than 85 mm *TL* were caught within the study (the smallest female caught was 63 mm *TL*), we assume that such bias did not significantly influence the average size of mature females recorded in this study. As crayfish growth is density-dependent (Guan and Wiles, 1999; Westman and Savolainen, 2002), and stress caused by high population density may promote earlier maturation (*i.e.* maturation at smaller size; *cf.* Westman *et al.*, 1999), it is likely that the minimal size of mature females recorded in this study was mostly affected by local conditions primarily related to population density, which was in the lower range of signal crayfish densities observed in other European populations (<1–21.7 crayfish·m^2; Guan, 2000; Gherardi, 2007). As exceptionally high growth rates of crayfish in newly established populations have been reported in the literature (*cf.* Guan, 2000), based on the relatively low population density in comparison with other European populations and relatively young population age (slightly over 5 years since population establishment), coupled with the observed large minimal size of mature females, we assume that the examined population has not reached its maximum density yet.

The recorded number of pleopodal eggs was in a similar range to other European populations (up to 400 eggs, Souty-Grosset *et al.*, 2006), although the maximum recorded egg number in our study was slightly higher (442 eggs for a female of 44 mm CL). As in other crayfish species (*e.g.* Stucki, 2002; Maguire *et al.*, 2005) and other signal crayfish populations (*e.g.* Westman *et al.*, 1999; Nakata *et al.*, 2004), the number of eggs was positively correlated with crayfish size. Therefore, even though the proportion of reproductively active females decreases with increasing female size (*cf.* Kirjavainen and Westman, 1995; Westman *et al.*, 1999; Figure 3c this study), large females still represent the most productive portion of a population, due to the observed increase in the number of eggs with female size and their abdomen size; the latter being frequently used as a measure of egg-carrying capacity and reproductive fitness in crayfish (Grandjean *et al.*, 1997). We were able to estimate, albeit on a very small sample, a 39–56% survival up to juvenile independence. Although pleopod egg counts are informative when determining recruitment to the population (Lewis, 2002), as is the juvenile survival up to independence; future studies are needed to assess the survival of young-of-the-year (YOY) within the examined population in order to examine juvenile recruitment more thoroughly.

Analyses of injuries revealed no significant difference between sexes in the frequency of all injuries and claw injuries, although the proportion of all injuries and claw injuries was always slightly higher for males than females. We expected to observe a significantly higher frequency of injuries in male crayfish, since males are considered to be more aggressive than females (*e.g.* Berry and Breithaupt, 2010). The increase in proportion of overall injuries observed in July and August might be associated with molting. Finally, as claws represent a valuable and frequently damaged tool in aggressive interactions between crayfish (Schroeder and Huber, 2001) and proportion of claw injuries is frequently used as an indirect measure of competition intensity (Söderbäck, 1991; Hudina *et al.*, 2011), the observed increase in the proportion of claw injuries in October is assumed to be the result of intensified competition during mating season.

In analyses of signal crayfish movement patterns, the recorded values of cumulative distance moved by crayfish were in line with data obtained from other studies of signal crayfish spatial behavior (Bubb *et al.*, 2002, 2004, 2006a, 2006b; Light, 2003), while mean daily movement was substantially higher than in other analyzed populations (Bubb *et al.*, 2004, 2006a). Similar ranges of cumulative distances moved by crayfish suggest that the same type of movement was recorded by our study and other studies analyzing crayfish movement patterns, probably as a reflection of the bias of the applied methodologies (mark-recapture and telemetry) towards a specific movement pattern (explorative, routine movements on a small scale; *cf.* Van Dyck and Baguette, 2005). On the other hand, higher mean daily movement of 28 m/day suggested higher spatial activity of the examined population in comparison with other signal crayfish populations studied within a similar trapping period (summer; Bubb *et al.*, 2004, 2006a). However, since there were methodological differences between our study (mark-recapture study) and studies by other authors (telemetry; Bubb *et al.*, 2004, 2006a), the observed differences should be treated with caution and examined more thoroughly by application of the same methodology as in respective studies (*i.e.* telemetry). Similar to research on signal crayfish movements in rivers in the UK (Bubb *et al.*, 2002, 2004, 2006a) but contrary to research in a US catchment (Light, 2003), we recorded no sex or size bias in the amount of movement, and no sex or size bias between stationary and moving individuals. The lack of differentiation might again stem from the bias of the methodologies applied (mark-recapture and telemetry) towards small-scale routine movements in which all animals, regardless of the sex or size, engage (*cf.* Van Dyck and Baguette, 2005). This limits the application of mark-recapture and telemetry methodology in invasive species range expansion studies, since long-distance movements as well as movements of juvenile crayfish remain underestimated (Van Dyck and Baguette, 2005). However, data on routine movements remain useful for analyzing the interspecific and inter-population variability in crayfish movement patterns and their relation to other population or ecological parameters such as population density, density of predators, effects of barriers and flows, etc.

This research represents the first study of population characteristics and movement patterns in a recently established signal crayfish population near the edge of its invasive range in the Mura River and forms a baseline for future monitoring activities and research into drivers of signal crayfish spread along its invasive range within the region. Based upon the obtained results, we suggest that standardized yearly monitoring of population density and size structure is required in order to discriminate local factors controlling signal crayfish population growth and productivity. As juvenile recruitment represents one of the crucial demographic parameters affecting population dynamics, future monitoring activities will need to examine this parameter and its fluctuations with changes in population density. Therefore, the optimal combination of trapping methodologies will need to be identified (*e.g.* LiNi traps in combination with hand nets or electrofishing), which will enable monitoring of changes in both juvenile and adult signal crayfish population structure in a relatively large river such as the Mura. Data collected from the described monitoring activities can then be used to develop site-specific population models, through which different management scenarios aimed at signal crayfish population control can be compared, and the most suitable management option identified and tested (*cf.* Galić and Hudina, 2010). Since invasive signal crayfish represents a high priority for population control efforts worldwide (*e.g.* Light, 2003; Holdich *et al.*, 2009; Usio *et al.*, 2009), such a targeted approach to its management is urgently required.

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