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Factors influencing crayfish occurrence, distribution and movement activity of crayfish population

Faktory ovlivňující výskyt raků, distribuce a migrační aktivita račí populace

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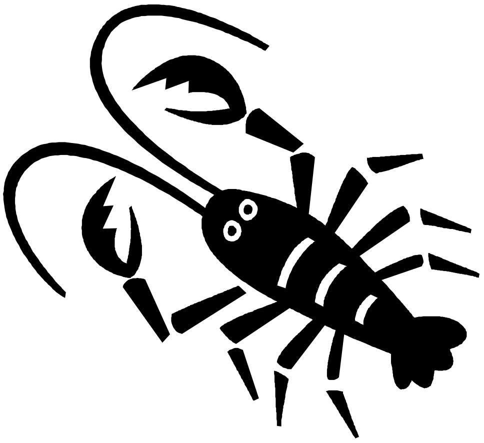

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Kateřina Římalová

In Praha, …………………………….

Content

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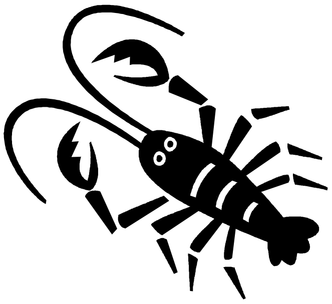

Czech Summary

Předložená disertační práce je zaměřena na raky, největší sladkovodní bezobratlé živočichy, kteří jsou také často považováni za tzv. „vlajkové druhy“ vodních ekosystémů. Disertační práce prohlubuje znalosti v oblasti pohybu raků, popisuje rozdíly mezi pohybovými schopnostmi a tendencemi raka říčního (*Astacus astacus*) a raka kamenáče (*Austropotamobius torrentium*) a zkoumá schopnost těchto dvou druhů raků překonávat příčné bariéry v toku. V rámci práce byla objevena nová mramorovaná barevná forma raka kamenáče v oblasti chráněné krajinné oblasti Křivoklátsko. Součástí disertační práce je vyhodnocení databáze z celorepublikového mapování raků v České Republice ve spojení s ukazateli degradace vodních toků.

English Summary

This dissertation is focused on crayfish, the largest and highly mobile water macroinvertebrates which are also often called “flagship species” of the water ecosystems. The thesis deepens knowledge in the area of movement patterns of Noble crayfish (*Astacus astacus*) and Stone crayfish (*Austropotamobius torrentium*) in the case when they co-occur in one stream and investigates movement abilities of Noble and Stone crayfish to cross transverse movement barriers in stream. New marble colour morph of Stone crayfish was observed in Křivoklátsko Protected Landscape Area and described within this thesis. Also analyses of crayfish occurrence database collected by Nature Conservation Agency of the Czech Republic in connection with other environmental characteristics indicating habitat degradation of running waters were performed.

Chapter 1: Aims of the dissertation

1) The dissertation is focused on movement patterns of Noble crayfish (*Astacus astacus*) and Stone crayfish (*Austropotamobius torrentium*) observed during mark-recapture experiment. Their movement patterns were monitored in two streams in Křivoklátsko Protected Landscape Area for five years 2007-2011. During monitoring movement patterns also coloration of crayfish was registered and a new colour morph of *A. torrentium* was discovered.

Specific aims:

- Comparison of sex-related movement directions and distances covered during 3-year mark-recapture experiment of two crayfish species *A. astacus* and *A. torrentium.*
- Evaluation of two stony steps 60 and 110 cm high as movement barriers for *A. astacus* and *A. torrentium* for an active upstream movement.
- Identification of newly observed colour morph of *A. torrentium* in Bzovský stream.

2) This dissertation analyzes complexly biotic and abiotic characteristics indicating habitat degradation of the running waters in the Czech Republic in connection with crayfish occurrence database. The database was collected by Nature Conservation Agency of the Czech Republic in 2004-2008.

Specific aim:

- Habitat specification of each crayfish species occurring in the Czech Republic.

Chapter 2: Introduction

2.1 General Introduction

Among the phylum Arthropoda, the subphylum Crustacea constitutes a large and morphologically diverse taxon, with members inhabiting all major habitats except the air (Schram, 1986). Crustacea are the most diverse group of present-day marine animals (Chen et al., 2001) from which the order Decapoda stands as one of the most morphologically diverse orders of Crustacea in terms of expressed variations on its body plan (Schram, 2009). The taxonomy of Decapoda is an active field with productive researchers constantly making new discoveries. Till 2009 the order Decapoda contained 13,335 species from which some are known as exclusivelly fossil (2,979 species) or next to alive specimens they are also known as fossils (321 species) (De Grave et al., 2009).

This dissertation is concentrated on crayfish, the biggest and most mobile water macro-invertebrates (Holdich, 2003). They are often referred as an ecosystems flagship species because of their size, longevity and reliance on aquatic systems throughout life (Reynolds and Souty-Grosset, 2012) and are even considered as indicators of the ecological status of water bodies (Water Framework Directive 2000/60/EC).

Crayfish are mainly connected with freshwaters; however there are 14 terrestrial crayfish species of the genera *Engaeus* and *Geocharax* which live in burrows in marshes, river banks or hilltop areas in Australia (Suter and Richardson, 1977). The freshwater crayfish belong to the monophyletic suborder Reptantia within Decapoda. Freshwater crayfish are taxonomically ranged into two superfamilies, the Astacoidea (northern Hemisphere crayfish with two families Astacidae and Cambaridae) and the Parastacoidea (Southern Hemisphere crayfish with one family Parastacidae) (Martin and Davis, 2001). In recent period there are more than 640 recognised species of crayfish, with diversity being highest in North America and Australia (Crandall and Buhay, 2008; Holdich et al., 2002), the main centre of crayfish diversity is located in the southeastern United States where 80% of the cambarid species can be found. They occur naturally on all of the continents except Africa and Antarctica, and the Indian subcontinent (Grandjean, 2006).

The biological diversity of freshwater ecosystems is nowadays experiencing much greater declines than are seen in the majority of terrestrial ecosystems (Sala et al., 2000; Dudgeon et al., 2006). Most declines have multiple causes, but physical habitat modification, invasive species and water quality degradation are thought to be the most important (Allan and Castillo, 2009).

Crayfish inhabit a wide range of habitats including streams, lakes, wetlands, ditches, caves and sloughs (Bouchard, 1978). Many studies showed that the abundance of crayfish depends on stream morphology (Bohl, 1987; Eversole and Foltz, 1993; Streissl and Hödl, 2002, Wienländer and Füreder, 2012), shelter availability (Lodge and Hill, 1994; Nystrøm et al., 2006; Johnsen and Taugbøl, 2008) and water quality (Demers and Reynolds, 2002; Holdich and Reeve, 2006b; Svobodová et al., 2012).

Indigenous crayfish species (ICS) in Europe are considered to be endangered by several changes, such as habitat loss, deteriorating water quality, overfishing and climate change as well as competition with non-indigenous crayfish species (NICS) and crayfish plague (Holdich et al., 2009). One of the most significant threats is the continued spread of NICS with their capacity to directly outcompete indigenous crayfish species (Söderbäck, 1995; Westman, 2000; Schulz et al., 2006) and, even more importantly, to transmit diseases that are detrimental to the native crayfish species (Lozán, 2000; Füreder et al., 2006; Kozubíková et al., 2008).

In the Czech Republic, there are currently three crayfish species considered as ICS: *Astacus astacus* (Linnaeus 1758), *Austropotamobius torrentium* (Schrank 1803) and *Astacus leptodactylus* Eschscholtz 1823, which are protected under Czech or international legislation (Czech regulation no. 395/1992 of the law no. 114/1992 and *A. astacus* and *A. torrentium* also by international conventions: Convention on the conservation of European Wildlife and Natural Habitats, Habitats Directive 92/43/EEC) and listed in IUCN Red list as vulnerable species. *Astacus leptodactylus* is not indigenous in entire Europe. It was introduced to Germany, Lithuania, Latvia, Austria, Italy, Great Britain, France, Denmark and most probably also to the Czech Republic from the Ponto-Caspian basin. There are also two NICS present: *Orconectes limosus* (Rafinesque 1817) and *Pacifastacus leniusculus* (Dana 1852), both native in North America. The introduction of crayfish from the North America causes a continuous decrease in the population sizes of *A. astacus* (Westman et al., 2002) and *A. leptodactylus* in Europe (Bohl, 1996). *Austropotamobius torrentium* might be less affected by crayfish plague due to its demands for water quality and morphological characteristics of streams (Renz and Breithaupt, 2000).

2.2 Movement patterns, movement barriers

Movement patterns of all species are important in contributing to an understanding of their habitat requirements, patterns of resource utilisation, and potential for interspecific interactions (Sutherland, 1996). Movement ability of crayfish is quite high, and a better knowledge of their movement tendencies and movement abilities could influence conservation management and also the numbers of crayfish plague outbreaks.

Generally, it is known that some crayfish remain in the same place for a time and then move (Merkle, 1969; Hazzlet et al., 1974). Crayfish movements can be caused by microhabitat conditions, flooding (Momot, 1966), or density of the crayfish population (Bovbjerg, 1959), but individuals can also move in a reaction to a special disturbance, such as being captured by humans (Bohl, 1999; Robinson et al., 2000, Bubb et al., 2002). Crayfish are also known to exhibit seasonal movements (Hazlett et al., 1974; Smejtek, 2010).

The movement patterns of indigenous and stocked *A. astacus* were investigated in Germany using radio-telemetry. Whereas indigenous crayfish moved within a small-scale dimension of only a few metres in four weeks (Bohl, 1999), stocked *A. astacus* tended to move downstream in a 14-day experiment, whereas crayfish moved between 50 m to more than 1 000 m (Bohl, 1999; Schütze et al., 1999). Sint and Füreder (2004) noted that individuals of both *A. astacus* and *A. torrentium* move until they find shelter; in general, males moved longer distances than females. The maximum observed travelled distance by *A. astacus* was 73.1 m in four nights (Hudina et al., 2008) whereas mean home range of *A. astacus* calculated by Hudina et al. (2008) is 63.94 m^2 of the water surface area.

Unlike *A. astacus,* little is known about the movement patterns of *A. torrentium*. Pöckl and Streissel (2005) observed that the majority of *A. torrentium* changed their location by 4 meters in median. Only a few crayfish moved more than 55 m within 24 hours. Pöckl and Streissel (2005) found no significant relationship between the body size or sex and the total distance covered; moreover, distances moved against the current were not significantly different between the sexes. A larger number of males moved upstream rather than downstream, whereas females did not exhibit a preferred direction of movement. **Chapter 2** contributes to this topic with results of movement patterns of *A. astacus* and *A. torrentium* in syntopy. It appears that *A. torrentium* moves similar maximal distances as *A. astacus* in native environment but in general shows a tendency to be more sedentary than *A. astacus* and thus it seems that *A. torrentium* is more vulnerable to natural or human-made disturbances.

Much more is known about the movement of NICS. The migration and movement activities of the signal crayfish, *P. leniusculus* have been investigated by several authors (Holdich et al., 1995; Guan and Wiles, 1999; Light, 2003; Bubb et al., 2004; Moorhouse and MacDonald, 2011) in experiments with different time durations. Crayfish in these studies tend to remain a few metres from the place where they were first observed or exhibited a weak tendency towards downstream colonisation. Moreover, Moorhouse and MacDonald (2011) revealed no significant effect of sex on recapture probability of signal crayfish in mark-recapture experiments. On the other hand the red swamp crayfish, *Procambarus clarkii* (Girard 1852), is known to be able to move out of the water and thus to go around a barrier, such as a waterfall or ditch, or to travel up to 50 m overland between two water canals. In the stream, there was no difference in the probability of *P. clarkii* travelling downstream or upstream (Gherardi et al., 2000; Kerby et al., 2005).

Specific information about the tendency of crayfish species to move across particular types of barriers can influence conservation management and can help to explain the prevalence of crayfish plague outbreaks (Söderhäll et al., 1977; Peay, 2001). Information about these abilities appears to be important for the conservation of indigenous crayfish species at a time when we are trying to minimise contact between these indigenous crayfish species and non-indigenous (and especially invasive) crayfish species which are often acting as a carriers of crayfish plague.

In general, movement barriers are considered to represent a solution to the problem of artificially dividing the biotopes of two crayfish species to protect the populations of the endangered species (Gill-Sanchez and Alba-Tercedor, 2006; Dana et al., 2011; Peay et al., 2011). Previous publications have addressed the abilities of *A. torrentium* and *A. astacus* to move across particular types of barriers (Schütze et al., 1999; Renz and Breithaupt, 2000). Prior to 2001, no fence-like barriers designed for crayfish eradication had been evaluated (Peay, 2001). However, artificial steps in streams could also represent undesirable barriers hindering the movement of other freshwater species (Joy and Death, 2001; Kerby et al., 2005). **Chapter 3** discusses two particular stony steps 60 and 110 cm high as potential movement barriers for *A. astacus* and *A. torrentium* during 3-year monitoring of crayfish movements by mark-recapture method.

2.3 Crayfish coloration

Pigmentary components responsible for coloration in Crustacea are two carotenoids astaxanthin and canthaxanthin. Carapax surface coloration or pigmentation is in the subphylum Crustacea determined by amounts of both pigments in the exoskeletal material (Fox, 1953; Castillo et al., 1982) and long has been studied in crayfish (Kent, 1901). Many crayfish species exhibit a variety of colours that are determined genetically (Fox, 1953; Volpe and Penn, 1957; Walker et al., 2000). However, crayfish coloration can be also environmentally induced and strongly correlated with habitat background colour, water depth or sunshine intensity (Kent, 1901; Thacker et al., 1993; Finlay et al., 2006). The level of pigmentation can be negatively influenced by poor crayfish diet (Wolfe and Cornwall, 1964; Sommer et al., 1991). Beingesser and Copp (1985) noted that, among other factors, crayfish colour change depends upon the animals' age and size. Crayfish cannot alter their coloration as quickly as can some shrimp species, for which rapid colour change occurs typically within seconds, minutes or hours. Rather, crayfish display colour change over periods of several weeks or months (Vogt et al., 2008).

Occurrences of rare crayfish colour morphs, as described by numerous authors, have long been well known (Lereboullet 1851; Holdich et al., 2006a) and have been recorded in a variety of genera, such as *Astacus*, *Cambarellus*, *Cambarus*, *Cherax*, *Orconectes*, *Pacifastacus* and *Procambarus* (Hand, 1954; Volpe and Penn, 1957; Momot and Gall, 1971; Walker et al., 2000). Although great variation in crayfish coloration is well documented, many species determination keys are based upon, among other things, exoskeletal coloration (Goddard and Hogger, 1986), as noted by Füreder and Machino (2002). The most frequent coloration of adult *A. torrentium* varies from pale to dark brown and to olive green, occasionally being beige or orange (Holdich et al., 2006). In contrast to the sister species White-clawed crayfish (*Austropotamobius pallipes*, Lereboullet 1858), blue individuals among Stone crayfish have never been found (Holdich et al., 2006). **Chapter 4** describes newly discovered marble colour morph of *A. torrentium* in the Křivoklátsko Protected

Landscape Area and emphasizes that the coloration of crayfish is not always the best feature to determine crayfish species.

2.4 Habitat degradation

The degradation of water courses can be caused by eutrophication, acidification, income of toxicants, habitat alterations, non-suitable land-use or fragmentation of the landscape (Holland et al., 1995; Nedeau et al., 2003; Brönmark and Hansson, 2005; Allan and Castillo, 2009). All these mainly anthropogenic processes change the biotic and abiotic character of water courses and lead to changes in the distribution of aquatic biota. The physical habitat niche of particular species determines its potential geographical spread and biotic interactions (Guisan and Zimmermann, 2000; Pulliam, 2000; Dyer et al, 2013). Also competition and dispersal abilities together with niche size and the distribution of environmental conditions in space and time all play role in determining species distributions in relationship to the presence of suitable habitat (Pulliam, 2000).

Literature resources imply considerable differences in physical habitat requirements between particular crayfish genera occurring in the Central Europe. The genera *Astacus* and *Pacifastacus* may exploit a wide variety of habitats (Lewis, 2000; Skurdal and Taugbøl, 2002), nevertheless generally prefer areas with available hiding places or they may make small and simple burrows (Holdich, 2002; Souty-Grosset et al., 2006). *Astacus astacus* should be rather sensitive to pollution and physical damage of the environment (Holdich, 2002). The species of the genus *Austropotamobius* are variable in their habitat preferences, whereas *A. torrentium* seem to typically inhabit high gradient small brooks; *A. pallipes* (Lereboullet 1858) is not habitat specific. Similarly to *A. astacus*, they are referred to be susceptible for the indication of pollution such as ammonia, nitrite and nitrate (Füreder et al., 2006). The habitat requirements and preferences of invasive *O. limosus* in Europe have not been thoroughly studied and its spatial distribution with connection to habitat morphology and ecological state of the environment remains unknown. **Chapter 5** presents results from our analyses where more degradated habitats of running waters appeared to be more often occupied by *O. limosus* than by *A. astacus* or *A. torrentium* within the area of the Czech Republic.

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Chapter 3: Movement patterns of the co-occurring species *Astacus astacus* (noble crayfish) and *Austropotamobius torrentium* (stone crayfish)

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Article

Movement patterns of the co-occurring species *Astacus astacus* (noble crayfish) and *Austropotamobius torrentium* (stone crayfish)

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With 5 figures and 4 tables

Abstract: Crayfish are the largest and most mobile invertebrate animals in streams, and their movement potential is quite high. Thus, detailed knowledge about their movement patterns can influence conservation management and thus the number of crayfish plague outbreaks. The movement patterns of two crayfish species, *Austropotamobius torrentium* (Schrank 1803) and *Astacus astacus* (Linnaeus 1758), were investigated in streams of Central Bohemia in the Czech Republic where these two crayfish species co-occur. The observed sections of the streams were divided into segments along which the movement of crayfish was observed. On 11 separate sampling occasions, crayfish were captured by hand and individually marked using a visible implanted elastomer. From 2008 to 2010, a total of 1,079 specimens of *A. torrentium* and 402 specimens of *A. astacus* were marked. One hundred and twenty-nine specimens of *A. torrentium* and 26 specimens of *A. astacus* were later recaptured. *Astacus astacus* exhibited a significantly greater tendency to move upstream than *A. torrentium*. We found no relationship between the length of a crayfish's body and the distance and direction of its movement. We also did not find any significant difference between the movement directions of males and females in either crayfish species. The longest distances recorded for crayfish movement were 133 m downstream in 55 days (female of *A. torrentium*) and 151 m upstream in 36 days (female of *A. astacus*). Due to the significantly greater tendency of upstream movement of *A. astacus* (compared to *A. torrentium*), we can assume *A. astacus* to have a generally higher colonising and moving ability than *A. torrentium*, which tends to be sedentary. The protection of existing localities of *A. torrentium* appears to be crucial for the conservation and management of the species based on its sedentary behaviour in the stream.

Key words: invertebrate, sympatry, mark-recapture, Europe, Czech Republic.

Introduction

Crayfish are the largest and most mobile invertebrate animals in streams (Holdich 2003). Their movement patterns are important in contributing to an understanding of their habitat requirements, patterns of resource utilisation, and potential for interspecific interactions (Sutherland 1996). *Astacus astacus* (Linnaeus 1758) (Crustacea: family Astacidae) and *Austropotamobius torrentium* (Schrank 1803) (Crustacea: family Astacidae) are native to Central European waters, both are protected under Czech law (Public notice Czech Republic 1992), and susceptible to crayfish plague. Their potential movement ability is quite high, and a better knowledge of their tendencies to move upstream or downstream could influence

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conservation management and the number of crayfish plague outbreaks.

The movement patterns of indigenous and stocked *A. astacus* were investigated in Germany using radiotelemetry. Whereas indigenous crayfish moved within a small-scale dimension of only a few metres in four weeks (Bohl 1999), stocked *A. astacus* tended to move downstream in a 55-day experiment (Bohl 1999, Schütze et al. 1999). Sint & Füreder (2004) noted that individuals of both *A. astacus* and *A. torrentium* move until they find shelter; in general, males moved longer distances than females.

Little is known about the movement patterns of *A. torrentium*. Pöckl & Streissel (2005) observed that the majority of *A. torrentium* changed their location by only a few metres (median 4 m). Only a few crayfish moved more than 55 m within 24 hours. Pöckl & Streissel (2005) found no significant relationship between the body size or sex and the distance covered; moreover, distances moved against the current were not significantly different between the sexes. A larger number of males moved upstream rather than downstream, whereas females did not exhibit a preferred direction of movement.

Much more is known about the movement of non-indigenous crayfish species (NICS). The migration and movement activities of the signal crayfish, *Pacifastacus leniusculus* (Dana 1852) (Crustacea: family Astacidae), a native of North America, have been investigated by several authors (Holdich et al. 1995, Guan & Wiles 1999, Light 2003, Bubb et al. 2004, Moorhouse & MacDonald 2011) in experiments with different time durations. Crayfish in these studies tend to remain a few metres from the place where they were first observed or exhibited a weak tendency towards downstream colonisation. Moreover, Moorhouse & MacDonald (2011) revealed no significant effect of sex on recapture probability of signal crayfish in mark-recapture experiments.

The red swamp crayfish, *Procambarus clarkii* (Girard 1852) (Crustacea: family Cambaridae), a native of North America (Kerby et al. 2005), is known to be able to move out of the water and thus to go around a barrier, such as a waterfall or ditch, or to travel up to 50 m overland between two water canals. In the stream, there was no difference in the probability of *Procambarus clarkii* travelling downstream or upstream (Gherardi et al. 2000, Kerby et al. 2005).

Generally, it is known that some crayfish remain in the same place for a time and then move (Merkle 1969, Hazzlet et al. 1974). Crayfish movements, in general, could be caused by microhabitat conditions (Momot 1966), flooding (Momot 1966), or the density of the crayfish population (Bovbjerg 1959), but individuals can also move as a reaction to a special disturbance, such as being captured by humans (Bohl 1999, Robinson et al. 2000, Bubb et al. 2002). Crayfish are also known to exhibit seasonal movements (Hazlett et al. 1974, Smejtek 2010).

Because there are very few papers comparing the movement patterns of crayfish species that co-occur within one stream, the aim of this study is to focus on the population characteristics of *A. astacus* and *A. torrentiu,* and to determine their movement patterns in syntopy. In our research, we focused on the population characteristics of both crayfish species in the observed streams. The following questions were asked:

1. Is there a difference in the direction of movement (downstream, upstream, or no movement) between species or between sexes? Is there an interseasonal variability in the direction of movement?
2. Is the distance that a crayfish individual covers and its movement direction dependent on the crayfish's body size or species?
3. Is the recapture rate of males and females in each crayfish species the same?
4. Do both crayfish species move regularly between the observed streams?

Material and methods

Study site

The study site (Stroupinský stream) is situated in the Křivoklátsko Unesco Biosphere Reserve (Elbe drainage basin, Central Europe, 49° 53′ N, 13° 53′ E; Fig. 1) 50 km west of Prague, Czech Republic. The two crayfish species occurred in sympatry and syntopy over a 9-km stretch of the Stroupinský stream and its tributaries. The Stroupinský stream is a fourth-order stream (its tributaries are second-order streams) and is 20.9 km long from its headwaters to its mouth (Kadlecová 2008). The geological strata are predominately comprised of slate and greywacke and flows at 283–471 m above sea level. The Stroupinský stream primarily flows through agricultural land with many fields, meadows, and pastures and very little forest. The stream passes through six villages, within which the stream is usually tiled, whereas outside the villages the stream meanders freely across the land. The average width of the streambed in the studied area was 4 m, and its average depth was 12.6 cm. Water quality in the study area was influenced by both point and non-point sources of anthropogenic pollution. We measured the chemical characteristics of the water, which are provided in Table 1 and Table 2, in March, June and September of each year during the research; the water temperature was measured continually during our field work.

We focused on a 161-m-long section of the Stroupinský stream (71 m long, 4.05 m mean width) along with part of its

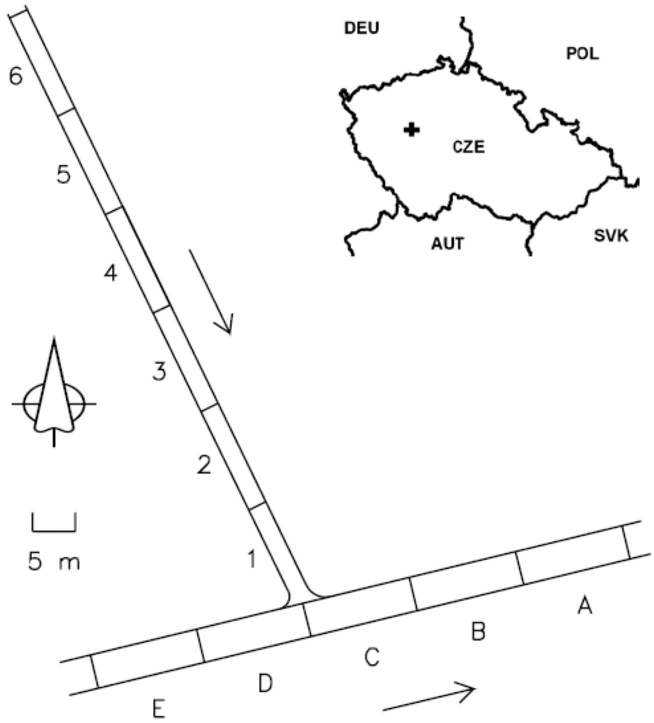

Fig. 1. The section of interest of the stream, drawn to scale with designations for the researched areas within the Czech Republic; A–E: segments of the Stroupinský stream (main stream), 1–6: segments of the Bzovský stream (tributary). The arrows indicate the direction of the current.

Table 1. Mean (minimum and maximum) values of the chemical parameters for the researched streams calculated from 5–11 measurements. Hydrogen ion concentration, dissolved oxygen, ammonium, conductivity, nitrate, total phosphorus, calcium cation and chloride content were measured.

	pH	O_2 (mg l^{-1})	NH_4^+ (mg l^{-1})	γ (μS cm^{-1})	BOD (mg l^{-1})	NO_3^- (mg l^{-1})	TP (mg l^{-1})	Ca^{2+} (mg l^{-1})	Cl^- (mg l^{-1})
Stroupinský stream	7.9 (7.3–8.9)	9.2 (7.5–12.1)	0.093 (0.006–0.369)	699 (543–851)	3.9 (1.4–7)	26 (11.5–39.8)	0.5 (0.21–0.91)	67.2 (50.6–76.3)	70.9 (46.1–93.2)
Bzovský stream	7.7 (7.4–8)	9.6 (7.9–11.8)	0.057 (0.019–0.16)	495 (387–614)	2.2 (1–4.8)	17.2 (13.8–21.6)	0.09 (0.05–0.19)	50.5 (37.7–74.3)	19.1 (12.8–26.7)

Table 2. Average temperatures, t, within specified time intervals during 2008–2010.

	t (°C)			
	1–15 Aug	16–31 Aug	1–15 Sep	16–30 Sep
Stroupinský stream	17.8	16.8	13.5	12.5
Bzovský stream	15.9	15.1	12.9	12

tributary, the Bzovský stream (90 m long, 2.34 m mean width) (Fig. 1), where the sympatric occurrence of *A. astacus* and *A. torrentium* was observed. We divided the area of the monitored streams into 11 segments, each approximately 13 m long, along which the movement of crayfish was observed.

Field work

We conducted 11 mark-recapture sessions over three years: 2008, 2009, and 2010. There were two mark-recapture sessions in August and two in September of each year, and the time interval between sessions within the same year was 14 days. In 2010, floods made it impossible to do the mark-recapture session scheduled for the end of August. The time intervals between mark-recapture sessions and number of sessions were designed according to Nowicki et al. (2008). Crayfish were sought in all available shelters and captured by hand by two people in each segment for 30 minutes in the Stroupinský stream and by one person for 15 minutes in its tributary, with far fewer available shelters for crayfish and a smaller area of the streambed to inspect in the tributary. The sex, the length of the cephalothorax and the total body length (from the apex of the rostrum to the posterior margin of the telson) of each crayfish were recorded. The captured crayfish were checked for the presence of a tag from previous sessions, and when we did not find a tag, the crayfish were individually marked on the ventral side of the abdomen using a visible implanted elastomer (Northwest Marine Technology 2010), which was injected using a needle. Marked crayfish were returned to the segment where they had been captured immediately after marking. Only tags of no more than 3 punctures were used; an example of the mark is provided in Fig. 2. A different colour of elastomer was

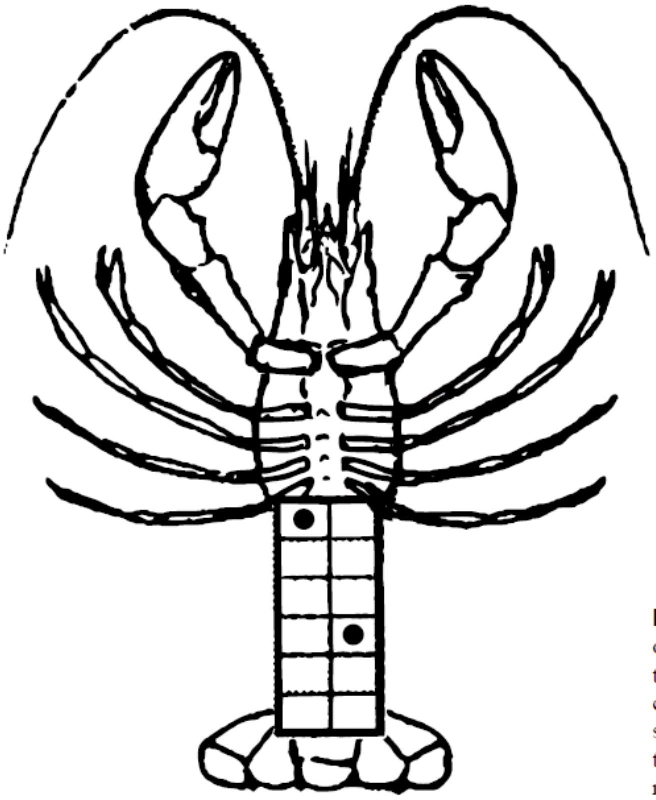

Fig. 2. Example of a mark that was injected into the abdomen of the ventral side of a crayfish; the mark was made by making two punctures by injecting an elastomer by a needle into the crayfish's abdomen. The crayfish's abdomen from the ventral side was theoretically divided into 12 spots (using pleopods as the basis), where an elastomer can be injected. This mark is readable as first on the left and fourth on the right.

used for each marking session. Only crayfish of at least 35 mm in total length were marked (according to recommendations in the elastomer manual), but some crayfish smaller than 35 mm were also captured to assess the distribution of crayfish sizes in the population. Field work was generally performed at the time when crayfish had just released their hatchlings but had not yet started mating.

Statistical approaches

To determine whether the direction of movement and distance covered observed during our experiment were dependent on crayfish species, sex or body size, generalised linear modelling framework (GLM) was applied under two different model assumptions: modelling a multinomial probability distribution for different movement directions and modelling the Poisson counts for the number of segments covered. A stepwise forward procedure was used to obtain the final model. Regarding the movement directions, two definitions for movement were used, and the model outcomes from the two definitions were compared. Movements downstream were interpreted either as active movements or as natural drifts, where drifts were specified as passive movements caused by water flow. To distinguish between the different movement patterns, two models were used as follows:

1. "Active model" – three movement categories were specified: 0 – crayfish were recaptured in the same segment in which they had been marked, 1 – crayfish moved to another segment downstream from the one which they had been marked, and 2 – crayfish moved to another segment upstream from the one which they had been marked. A generalised logit link was used for the three nominal categories.
2. "Passive model" – only two movement categories were specified: 0 – crayfish were recaptured in the same segment in which they had been marked or in a segment downstream from the one in which they had been marked, and 1 – crayfish were recaptured in a segment upstream from the one in which they had been marked. A model with a binomial distribution and a logit link function for the two nominal categories was used.

The distance covered by a crayfish was represented as the number of segments that the crayfish had traversed, which was analysed using a GLM with a Poisson distribution and logarithm link function.

Potential differences in recapture rates between the sexes of each crayfish species and the tendencies of the crayfish to move between streams were evaluated using simple chi-squared tests. The numbers of marked and not recaptured versus those marked and recaptured males and females in the three observation years together were arranged into a contingency table to test the possible differences in recapture rates. Counts of crayfish individuals remaining in the same stream where they were marked versus those who changed streams between marking and recapture were arranged into another contingency table (i.e., *A.astacus* marked and also recaptured in the same stream in contrast with *A.astacus* marked and recaptured in different streams) and used to conduct a chi-squared test of independency regarding the regularity of crayfish movements between streams.

In order to correct problems with multiple testing within the same dataset, the Bonferroni correction was applied.

To estimate the population size, we used the Schnabel mark-recapture techniques recommended by Krebs (1999).

We used the Ecological Methodology 6.1.1 (Krebs 1999) and R software (R Development Core Team 2010) statistical programs.

Results

From 2008 to 2010, a total of 1,079 specimens of *A. torrentium* and 406 specimens of *A. astacus* were marked. One hundred and twenty-nine specimens of *A. torrentium* and 26 *A. astacus* were recaptured. It was not possible to recognise the marks on 14 recaptured crayfish (eight specimens of *A. torrentium* and six of *A. astacus*) due to alterations of the mark in the crayfish body. The size and density of the population of each crayfish species for each stream was estimated via Schnabel's method for crayfish equal or larger than 35 mm in total length (equals a cephalothorax length of approximately 17.5 mm) (Table 3). The densities of both crayfish species were higher in the Stroupinský stream (main stream) than in the Bzovský stream (tributary). The estimated population sizes of *A. astacus* (3,300 specimens) and *A. torrentium* (4,800 specimens) in the entire monitored area were calculated (Table 3). For the estimation of population sizes, we used techniques that presume a closed population because nearly half of the recaptured crayfish (see Table 4) were captured in a year other than the one in which they were marked. The proportion of crayfish recaptured in a different year from when they were marked indicates that the population is stable and does not exhibit large interseasonal movements.

The minimum and maximum cephalothorax lengths of the captured crayfish were 9 mm and 68 mm for *A. torrentium* and 8 mm and 60 mm for *A. astacus*. *Austropotamobius torrentium* individuals in the main (Stroupinský) stream were not statistically different than those in the tributary (total length: $t = -0.0037$, $p = 0.9970$; cephalothorax length: $t = -0.7585$, $p = 0.4484$). The size structures of both crayfish populations are represented in Figure 3. The lowest number of crayfish marked within one mark-recapture session was 34 specimens of *A. torrentium* and 4 specimens of *A. astacus*; the greatest number was 172 specimens of *A. torrentium* and 81 specimens of *A. astacus*. The longest distance of a crayfish movement was 133 m downstream in 55 days (female of *A. torrentium*) and 151 m upstream in 36 days (female of *A. astacus*). The recapture rates for the three study years as a whole were 12.0 % and 6.4 % for the species *A. torrentium* and *A. astacus*, respectively.

Table 3. Estimated population sizes, *n*, confidence limits of estimates, *c.i.*, and density of crayfish populations, ρ in 2008–2010 are provided. Str – Stroupinský stream, Bz – Bzovský stream.

species	stream	2008 n (95 % c.i.)	2009 n (95 % c.i.)	2010 n (95 % c.i.)	average n (95 % c.i.)	crayfish density ρ / m^{-2}
A. astacus	Str	2174 (1326–3756)	4385 (1387–8344)	NA	3280 (1357–6050)	11
	Bz	21 (6–118)	NA	NA	21 (6–118)	0.1
A. torrentium	Str	2331 (1641–3426)	2020 (1376–3227)	7782 (2462–14809)	4044 (1826–7154)	14
	Bz	606 (370–1046)	1505 (808–3036)	174 (55–331)	762 (411–1471)	3.6

Table 4. The numbers of crayfish that were recaptured in the same year as marked and the numbers that were recaptured in a subsequent year of the mark-recapture study and the numbers of crayfish recaptured in the same stream where they were marked during 2008–2010.

	A. astacus		*A. torrentium*	
	marked in Stroupinský stream	marked in Bzovský stream	marked in Stroupinský stream	marked in Bzovský stream
Total recaptured	23	3	87	42
Recaptured in Stroupinský stream	23	3	85	3
– in the same year	13	1	49	2
– in a subsequent year after marking	10	2	36	1
Recaptured in Bzovský stream	10	0	2	38
– in the same year	0	0	2	21
– in a subsequent year after marking	0	0	0	17

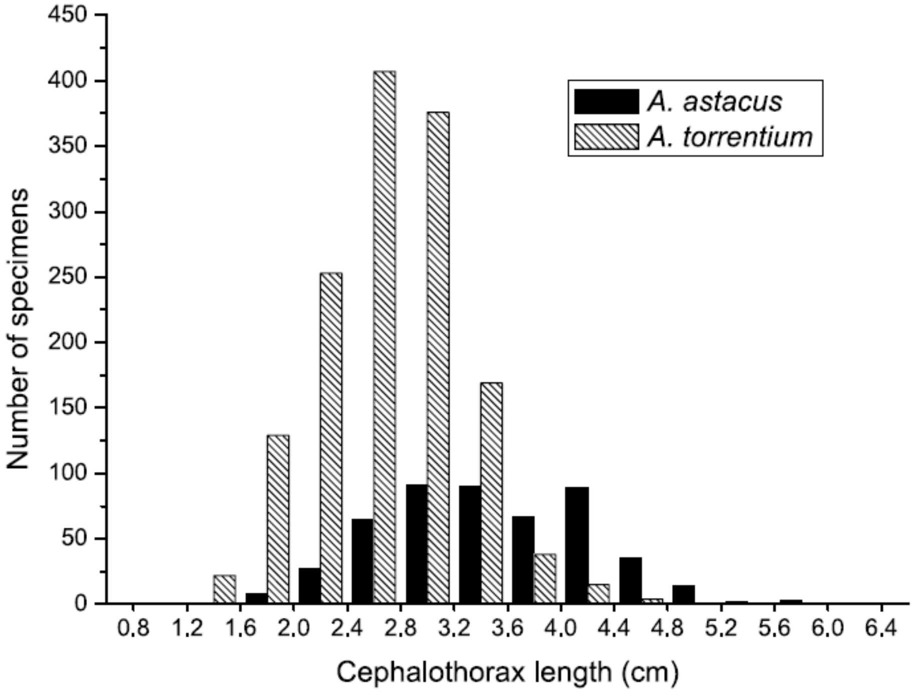

Fig. 3. Cephalothorax lengths (cm) of *A. torrentium* and *A. astacus* captured during 2008–2010 in the Stroupinský stream and the Bzovský stream.

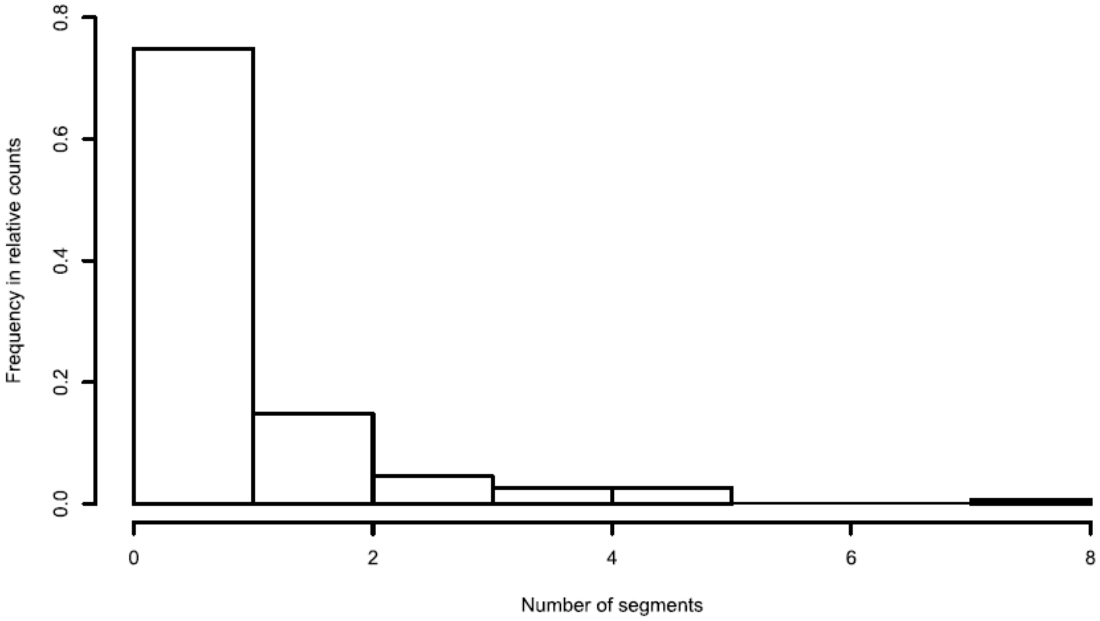

Fig. 4. Frequency of movement directions (%) (no movement, upstream or downstream) of both crayfish species recaptured during 2008–2010 in both the Stroupinský and Bzovský streams.

There was a significant difference in the movement directions between the two considered species *A. torrentium* and *A. astacus*, where *A. astacus* revealed a significantly higher tendency to move upstream (Fig. 4). The same pattern was observed using both movement definitions (the "Active" and "Passive" models). Both models were significant when tested at a level of 90 %. However, the "Passive" model with two categories only had slightly more power and therefore, it also showed slightly higher significance (significance for a species factor in the "Active" three-category movement model $p = 0.0770$, and significance for a species factor in the "Passive" two-category movement model $p = 0.0277$). In general, the results from both models are in agreement with each other. We did not find any significant differences in the crayfish movement pat-

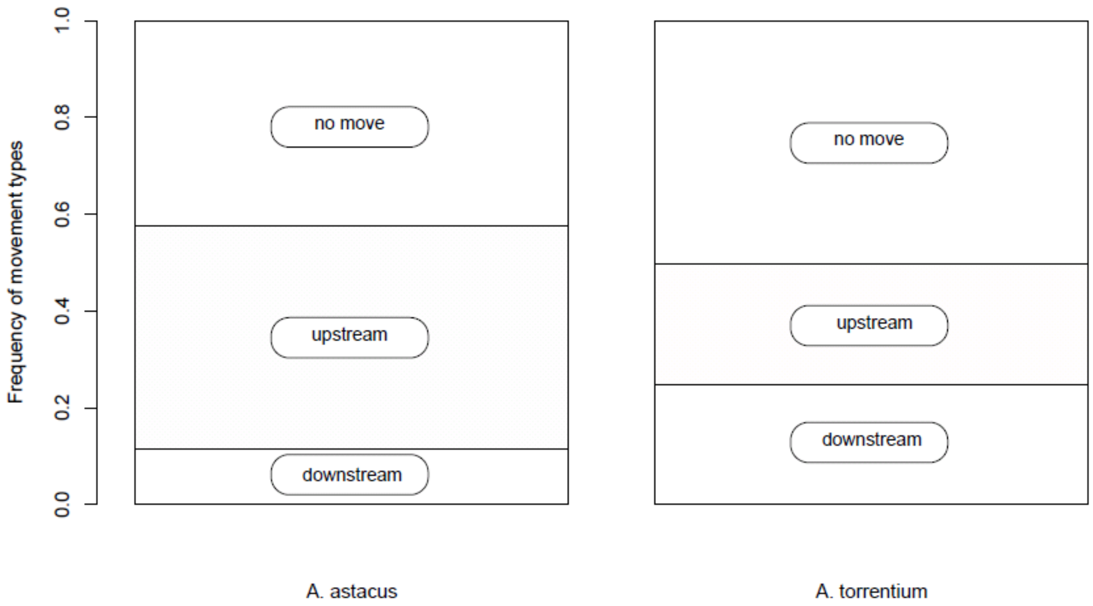

Fig. 5. Frequency of crayfish movement among segments for *A. astacus* and *A. torrentium*. One segment of the stream is, on average, 13 m long.

terns among the three observed years, which could indicate that the observed movement tendencies of crayfish did not differ according to particular biotic and abiotic conditions during 2008–2010. The final GLM takes the form:

Movement direction odds ratio ~ f (species),

where the *Movement direction odds ratio* represented the corresponding probability ratio of upstream movement over no movement or downstream movement over no movement in the three-category "Active" model and upstream movement over downstream or no movement in the two-category "Passive" model. Function *f ()* stayed for an inverse of the corresponding link function and *species* is a two-level variable distinguishing the two different crayfish species.

The distance covered by crayfish was not species-dependent ($p = 0.6690$) or dependent on the crayfish's cephalothorax length ($p = 0.6360$). With respect to a histogram of movement distances (Fig. 5), it is evident that the highest probability was assigned to moving within only one segment, which corresponds with an approximate length of 0–13 m.

The recapture probabilities of both crayfish species were not sex-dependent. A two-way contingency table was constructed, and a simple chi-squared independence test was performed ($\chi^2 = 1.3283$, $p = 0.2491$ for *A.astacus* and $\chi^2 = 0.0046$, $p = 0.9459$ for *A. torrentium*).

A. torrentium appeared to be very sedentary and remained in the stream where it was marked (3 out of 129 specimens changed stream locations between mark and recapture; see Table 4); however, *A. astacus* appeared to have a stronger tendency to move between streams, as 3 out of 26 recaptured specimens changed streams between mark and recapture (see Table 4). Based on chi-squared tests, it was also shown that the probability of the movement activity between streams was not species-dependent (Fischer's test $p = 0.0596$). To the extent that the relative counts in contingency tables are consistent estimations of unknown probabilities, it is evident that the probability that *A. torrentium* remains in the same stream between mark and recapture is higher than for *A. astacus*.

Discussion

Population size

Originally, we calculated the population size and density of both crayfish species for each stream. The density of both crayfish species was higher in the Stroupinský stream (see Table 3). The estimated density, based on a closed population size estimate, could be overestimated due to the immigration and emigration of crayfish, which were not included in the population size estimate. The neglected migration patterns should be more evident in the population estimate of

A. astacus, which, according to our results, tended to move more than *A. torrentium*. The population sizes were underestimated because the estimations were made for crayfish equal to or larger than 35 mm and smaller-sized crayfish were not captured in equivalent numbers. We performed our experiment during August and September, which could be a time of seasonal movements (Hazlett et al. 1974, Bubb et al. 2002), but interseasonally recaptured crayfish (that were marked in previous years) indicate that large movements do not take place there.

Abiotic factors, density

Austropotamobius torrentium occurred in the Stroupinský stream as well as in the Bzovský tributary, whereas *A. astacus* occurred primarily in the Stroupinský stream and very rarely in its tributary; the described crayfish distribution was observed constantly during the three years of observations. Our locality was situated 1.1 km downstream from the end of the section of Stroupinský stream where both crayfish species co-occurred. Both crayfish species occurred together during the entire stretch of the stream, and thus, both crayfish species theoretically had the same potential to move upstream or downstream. The question of why *A. astacus* did not move more into the tributary has several possible answers.

One answer could be a possible difference in water quality parameters between the two streams in question (see Table 1). Comparing the observed values with the values given in the literature (Kivivuori 1980, Bohl 1987, Troschel & Dehus 1993, Jensen 1996, Rukke 2002, Demers et al. 2006, Štambergová et al. 2009), we can conclude that water quality differences did not appear to be a factor that determined the distribution of crayfish in the studied area. Both crayfish species are able to tolerate the water quality conditions of both streams.

Another answer could be the density of crayfish. It appeared that a relatively high density of crayfish in the main stream did not force *A. astacus* to migrate into the tributary. In terms of interspecific competition, *A. torrentium* was smaller-sized than *A. astacus* (average cephalothorax lengths in our dataset are 2.8 and 3.5, respectively), which should play an important role in the competitive balance (Vorburger & Ribi 1999). *Austropotamobius torrentium* is more successful in fights with equal-sized *P. leniusculus* than *A. astacus* (Söderbäck 1991). The fact that *A. torrentium* wins some of the fights with *A. astacus* (when it is larger or equal-sized), in connection with the large number of shelters and rich trophic status of the stream, can explain the sympatric occurrence of two crayfish species, a possibility that has also been mentioned by Corkum & Cronin (2004). The trophic status of the stream can be characterised by the average value of total phosphorus measured (Carlson 1977; see Table 1), which, at our site, exceeded the average value calculated from localities with occurrences of *A. astacus* ($0.135\ \mathrm{mg\ l^{-1}}$) and *A. torrentium* ($0.327\ \mathrm{mg\ l^{-1}}$) in the Czech republic (Štambergová et al. 2009).

Crayfish are known to be able to adapt to available refuge sizes (Streissl & Hödl 2002). *Austropotamobius torrentium* in the main (Stroupinský) stream were not larger than those in the tributary; however, stones (as a primary type of shelter at our locality) are generally larger in the main stream than in the tributary (authors' personal observation).

It appeared that *A. astacus* was the dominant species at our site according to its size; *A. torrentium* was limited to the tributary, although it had the potential to prosper in the main stream. The reason why *A. astacus* did not penetrate far into the Bzovský stream is likely related to a factor that was not included in our work, such as a preference for a specific habitat parameter, stream morphology or other interspecific interactions. The density of crayfish (see Table 3), with a maximum of 14 individuals of *A. torrentium* per square metre in the tributary, which was similar to the density of approximately 13 individuals per square metre reported by Vlach et al. (2009), appeared to be very high. No comparable results for observed densities of *A. astacus* were found in the literature due to the different methodologies used by other authors.

Movement

The *Astacus astacus* specimens in our study generally tended to move upstream. The highest probability of *A. astacus* movement was within one segment (maximum distance of 13 m), which agrees with the results of Bohl (1999) where *A. astacus*, which were indigenous to that locality, tended to move only a few metres in four weeks. In contrast, our results were inconsistent with the studies of *A. astacus* taken from a hatchery (Bohl 1999, Schütze et al. 1999), where a large downstream movement of crayfish was observed. Both of these studies were conducted using telemetry, where only larger crayfish were observed. We have tested whether there was a difference in movement direction in our dataset according to the length of the cephalothorax or if the distance that crayfish moved was size-dependent. We found no relationship between the length of a crayfish's body and the direction of its movement; larger crayfish in our study did not exhibit a significant tendency to move downstream.

Concerning *A. torrentium*, we achieved results very similar to Pöckl & Streissel (2005). As with the earlier study, we also found a tendency for *A. torrentium* to remain within a few metres over several weeks (in some cases also over multiple years). In our case, crayfish moved within 13 m, which was the average length of one segment. Moreover, similarly to Pöckl & Streissel (2005), we did not find a significant relationship between the distance covered and crayfish body size; however, Pöckl & Streissel (2005) found different movement directions between the sexes, which we cannot confirm. The direction and distances travelled by *A. torrentium* in our study were very close to the movement characteristics of *P. leniusculus,* as described by Bubb et al. (2004). The only difference was that we found no tendency of *A. torrentium* towards downstream movement.

Recapture rates, distances covered

The recapture rates of both *A. astacus* and *A. torrentium* were not different between the sexes, which is a result comparable to the study performed on *P. leniusculus* by Moorhouse & MacDonald (2011). The recapture rate of *P. leniusculus* was higher (15.3 %) than those in our study (maximum value 12.0 %), which was most likely due to the length of experiment. *Pacifastacus leniusculus* were captured within 6 months in one season, and thus, the crayfish had less time to move into another section of the stream. However, the different results were most likely also influenced by the different trapping methods employed, as Moorhouse & MacDonald (2011) used baited traps. The maximum distance covered in our study by *A. astacus* (151 m upstream in 36 days; female of *A. astacus*) was less than that given by Schütze et al. (1999) for stocked *A. astacus* and also less than the distance travelled by *P. leniusculus*, which moved a maximum distance of 277 m in the upstream direction over 8 weeks from July to September (Light 2003) or 790 m in 74 days in the summer (Bubb et al. 2004). *Orconectes limosus* (Rafinesque 1817) (native of North America) has been recorded as travelling 273 m in the upstream direction per day (Smejtek 2010). Unfortunately, we could not register moves longer than 161 m, which provides us no opportunity to compare the movement abilities of ICS and NICS.

We can summarise that the two studied crayfish species moved similarly, both when alone and when in syntopy. According to the density and behavioural structure of the crayfish populations, it appeared that the spread of *A. torrentium* is dependent on the occurrence of *A. astacus*, which is, in the long term, able to outcompete *A. torrentium* primarily due to its larger average size. We are aware of the limits of the relatively short section of the stream that we observed, but we can assume that *A. astacus* has a generally high colonising and moving ability along with stronger tendencies towards upstream movement and movement between streams compared with *A. torrentium*. Concerning *A. torrentium*, we found that this species has a tendency to remain in the same location and thus has lower colonising and moving abilities; however, the maximum travelled distance (133 m downstream in 55 days; female) was very close to the maximum distances moved by *A. astacus*. In terms of conservation management, our results suggest that it is necessary to robustly protect existing occurrence localities for *A. torrentium* because this species has a tendency to be sedentary and is more directly related to the conditions of its biotope than *A. astacus*.

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Chapter 4: The movement patterns of *Austropotamobius torrentium* and *Astacus astacus*: Is a stony step a barrier?

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The Movement Patterns of *Austropotamobius torrentium* and *Astacus astacus*: Is a Stony Step a Barrier?

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Abstract.— *Austropotamobius torrentium* (Schrank) and *Astacus astacus* (Linnaeus) are endangered crayfish species in Europe. They are currently being excluded from their original localities by non-native crayfish species, which are often causal agents of the spread of crayfish plague and also competitors with native crayfish species. Artificial barriers represent one option for halting the spread of non-native crayfish species. In Bzovský Stream (Czech Republic, Central Bohemia) the streambed contains stony steps placed to decrease the flow of water. Two stony steps (60 cm and 110 cm high) were evaluated as a movement barrier for crayfish. At the area of confluence of Bzovský and Stroupinský streams, 1887 crayfish were marked with a visible implanted elastomer, whereas 56 recaptured crayfish were marked in Bzovský Stream. In a four-year mark-recapture study, we showed that *A. torrentium* was able to cross a step 60 cm high and that both *A. torrentium* and *A. astacus* were able to cross a perpendicular stony step 110 cm high. These results show that these stony steps do not act as strong movement barriers for crayfish in streams. However, the ability of crayfish to move across a concrete barrier appears to depend on the design of the barrier. [*Keywords*.— central Europe; crayfish; mark-recapture; movement; obstacle].

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INTRODUCTION

Crayfish are the largest active macroinvertebrates in freshwaters (Souty-Grosset et al. 2006). Knowledge of a species' movement patterns can represent an important contribution to the understanding of habitat requirements, patterns of resource utilisation, and the potential for interspecific interaction (Sutherland 1996). The noble crayfish, *Astacus astacus* (Linnaeus, 1758), and the stone crayfish, *Austropotamobius torrentium* (Schrank, 1803) (both Crustacea: Decapoda: Astacidae), are native to Central European waters. Both are protected under Czech law by act No. 114/1992 Sb., and both are susceptible to crayfish plague. They are both highly capable of movement (Gherardi 2002). *Astacus astacus* in its natural environment moves most frequently within the range of a few meters, as suggested by a four week search using radiotelemetry (Bohl 1999) and by mark-recapture techniques used over four nights (Hudina et al., 2008) or from two weeks to three years (Kadlecová et al. 2012). The maximum observed travelled distance was 73.1 m in four nights (Hudina et al. 2008) whereas mean home range of *A. astacus* calculated by Hudina et al. (2008) is 63.94 m^2 of the water surface area. *Austropotamobius torrentium* moves similar distances to *A. astacus* in its native environment (Kadlecová et al. 2012). Specific information about the tendency of crayfish species to move across particular types of barriers can influence conservation management and can help to explain the prevalence of crayfish plague outbreaks (Söderhäll et al. 1977, Peay 2001). Information about these abilities would appear to be important for the conservation of indigenous crayfish species at a time when we are trying to minimise contact between these indigenous crayfish species and other non-indigenous (and especially invasive) crayfish species, which are often acting as a carriers of crayfish plaque. The need to minimise such contact is critical because *A. torrentium* and *A. astacus* are endangered in Europe by several other threats, such as interspecific competition, destruction of habitat or other diseases (Füreder et al. 2006). Nowadays, the abundance of *A. astacus* and *A. torrentium* is declining throughout their range (Kozák et al. 2002; Füreder et al. 2006).

In general, movement barriers are considered to represent a solution to the problem of artificially dividing the biotopes of two crayfish species to protect the populations of the endangered species (Gill-Sanchez and Alba-Tercedor 2006; Dana et al. 2011; Peay et al. 2011). Few previous publications have addressed the abilities of *A. torrentium* and *A. astacus* to move across particular types of barriers (Schütze et al. 1999; Renz and Breithaupt 2000). Prior to 2001, no fence-like barriers designed for crayfish eradication had been evaluated (Peay 2001). However, artificial steps in streams could represent undesirable barriers hindering the movement of freshwater species (Joy and Death 2001; Kerby et al. 2005). In view of the lack of knowledge about the movement abilities of Europe's indigenous crayfish species, this study was conducted to determine whether the stony steps in a selected

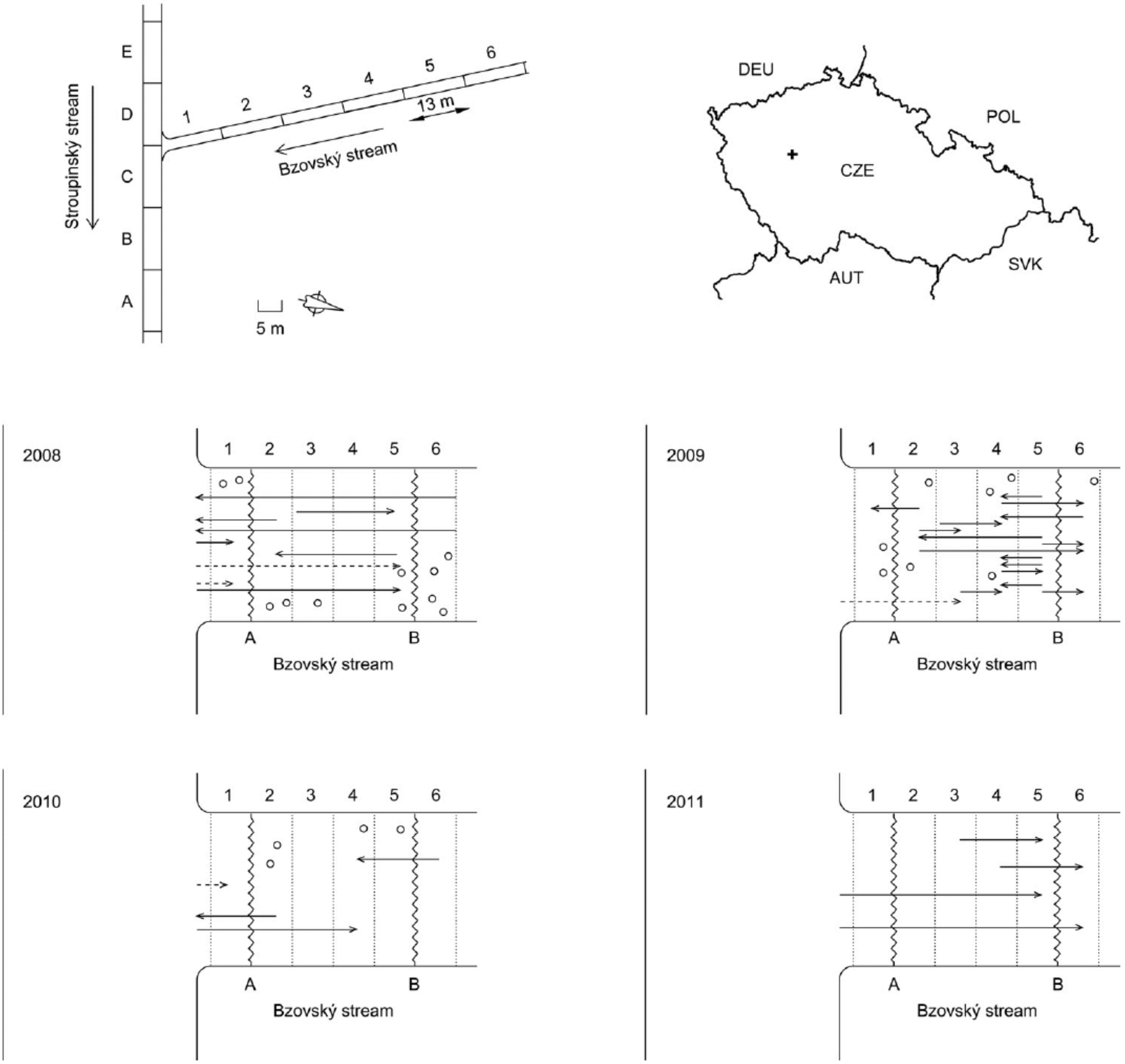

Figure 1. Scheme of the area inspected, orientation within the Czech Republic (both from Kadlecová et al. 2012) and observed crayfish movements in Bzovský stream in 2008 – 2011 based on mark-recapture data. Solid line represents a specimen of *Austropotamobius torrentium*, dashed line a specimen of *Astacus astacus*. Wavelike lines represent stony steps; step A is 110 cm high, step B is 60 cm high. Circles represent specimens of *A. torrentium* that did not move between mark and recapture. The schematic drawings for each year 2008 – 2011 are not to scale.

stream represented strong movement barriers and whether crayfish could move upstream across these barriers.

MATERIALS AND METHODS

Study Area

This study was conducted at the confluence of the Bzovský and Stroupinský streams, where on the Bzovský two potential migration barriers are present. This site is located in the Křivoklátsko UNESCO Biosphere Reserve (Elbe drainage basin, Central Europe, GPS coordinates: 49.895231, 13.888309, WGS-84, S-JTSK_Krovak_East_North, see Figure 1), 50 km west of Prague, Czech Republic. The crayfish species *A. astacus* and *A. torrentium* occur sympatrically on a 9 km stretch of these streams. The estimated density of *A. torrentium* and *A. astacus* were 14 and 11 specimens m^{-2}, respectively, in the Stroupinský and 3.6 and 0.1 specimens m^{-2}, respectively, in the Bzovský (Kadlecová et al. 2012). The Bzovský is a second-order stream (Strahler), 5.4 km in length from its source (a spring) to its mouth. The geological strata along the stream consist primarily of slate and greywacke. The stream descends from 471 m down to 283 m. It flows primarily through agricultural land with fields, meadows, pastures and forests. The stream passes through one village, Bzová. Outside the village, the stream meanders freely across the land. The average width of the riverbed in the area studied is 2.3 m, and the average depth is 12.2 cm. During the experiment, water temperature and selected water quality parameters were measured in the Bzovský from March to October, 2008 – 2011. The pH ranged from 7.4 – 8.0, dissolved oxygen from 7.9 – 11.8 mg L^{-1}, conductivity from 387 – 614 µS cm^{-1}, NH_4^+ from 0.01 – 0.13 mg L^{-1}, temperature from 4.5 – 18.8°C and nitrate ions from 10.5 – 22.5 mg L^{-1}. The average flow during July – September was 0.02 m^3 s^{-1}. The detailed hydrochemical characteristics of the Stroupinský in 2008 – 2010 are given in Kadlecová et al. (2012).

Our area of interest included a 90 m long section of the Bzovský and a 71 m long section of the Stroupinský at their confluence. We divided this area into 11 segments, each approximately 13 m long (Figure 1). The movement of crayfish between these segments was monitored. Stony steps, potential barriers to movement, were located between the first and second segments and between the fifth and sixth segments of the Bzovský. Also, crayfish in Stroupinský stream were observed to obtain information about crayfish moving into or out of Bzovský stream. The steps were designated A and B. Measured from the bottom of the riverbed, step A was 110 cm high, step B 60 cm high. Both steps were originally constructed in 1925, and were built to slow down the flow of water (see Figure 2 and 3).

The water depth immediately downstream from step A was 10 cm, whereas the average depth immediately upstream from step A was 8.5 cm; the average water depth immediately downstream from step B was 29 cm, whereas the depth immediately upstream from step B was 8 cm. The steps were constructed of large quadrate stones and partially covered with a layer of moss or other organic material (see Figures 2 and 3). The steps were cracked between the quadrate stones, especially at places where the water flow was fastest. Step A had five large cracks. These cracks were 2.5 – 4 cm wide; their maximum depth was 15 cm down from the top of the step. These cracks appeared impassable for upstream crayfish movement because they were narrow and were not deep enough to reach the water surface under the step. One crack between stones at the edge of the step formed a bypass around the step. The crack was 10 cm wide and allowed a flow of 0.3 L s^{-1} at a water velocity of 0.2 m s^{-1}. The bypass lead partly under stones thus it was not possible to perform a thorough inspection to locate crayfish in the throughput area. The angle of the step was 90°.

Step B had two large cracks. These cracks were 3 cm wide and 10 cm deep from the top of the step. It is probable that they could not be used by crayfish in case of upstream movement because the water flow here was very rapid (4 L s^{-1}; water velocity 1.3 m s^{-1}). Moreover, the cracks were not deep enough to reach water surface under the step. The angle of the step was 50° – 90°. Ninety percent of step A and all of step B were covered by the moss *Platyhypnidium riparioides* (Hedw.) Dixon, a species of moss typically found in flooded areas.

Because both steps were deeply embedded in the stream, the crayfish could not dig underneath them. The banks were composed of soil and covered with vegetation. The gradual slope of the banks in certain places allowed human access. The water level at the study site was found to change dramatically in response to rainfall.

Figure 2. Stony step A in Bzovský stream. The step is 110 cm high. (Photo: K. Římalová-Kadlecová).

Figure 3. Stony step B in Bzovský stream. The step is 60 cm high. (Photo: K. Římalová-Kadlecová).

Field Work

All of the available shelters in the study streams (e.g., rocks, vegetation, banks and roots) were examined to locate crayfish. One person collected crayfish for 15 min in each segment of the Bzovský, and two people collected crayfish for 30 min in each segment of the Stroupinský, with far fewer available shelters for crayfish and a smaller area of streambed to inspect in the Bzovský. Also, the Stroupinský was searched for crayfish for the entire duration of our field study, however, there were no movement barriers present. Some crayfish moved from the Stroupinský to the Bzovský, and on the basis of data from the Stroupinský, we could determine the starting and final positions of crayfish crossing the potential movement barriers.

Table 1. Observations of relative positions for mark and recapture of crayfish in Bzovský stream in different years according to sex and species; *m* means male, *f* means female.

	year	sex	movement direction			crossed stony step	
			upstream	no move	downstream	A	B
A. torrentium	2008	m (f)	2 (1)	8 (3)	1 (3)	1 (0)	0 (0)
	2009	m (f)	6 (2)	4 (4)	4 (3)	0 (0)	4 (0)
	2010	m (f)	0 (1)	1 (3)	1 (1)	0 (1)	0 (0)
	2011	m (f)	1 (3)	0 (0)	0 (0)	0 (2)	1 (1)
A. astacus	2008	m (f)	1 (1)	0 (0)	0 (0)	0 (1)	0 (0)
	2009	m (f)	1 (0)	0 (0)	0 (0)	1 (0)	0 (0)
	2010	m (f)	0 (1)	0 (0)	0 (0)	0 (0)	0 (0)
	2011	m (f)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Table 2. Crayfish recaptured separated by species, year of recapture and year of marking.

year of recapture	2008	2009		2010			2011				
year of mark	2008	2008	2009	2008	2009	2010	2008	2009	2010	2011	Σ
A. torrentium	18	14	9	5	1	1	0	2	2	0	52
A. astacus	2	1	0	0	1	0	0	0	0	0	4

All crayfish were caught by hand. The crayfish caught were examined for marks from previous years. If no marks were found, the individual was then marked on the ventral side of the abdomen with a visible implanted elastomer tag (VIE) (Northwest Marine Technology 2010). The elastomer was injected into predetermined locations on the abdomen of the crayfish. No more than three punctures were used to mark an individual specimen. For marking purposes, the ventral side of the crayfish was schematically divided into 12 sites (according to the bases of pleopods and distinguishing the left and right sides), where an elastomer could be injected. An example of the mark is provided in Kadlecová et al. (2012). A different colour of elastomer was used for each marking exercise. Only crayfish that were 3.5 cm or greater in total length (measured from the apex of the rostrum to the posterior margin of the telson) were marked. The sex, the length of the cephalothorax and the total body length were recorded. The marked crayfish were then returned to the stream segment in which they had been caught. We completed 15 mark-recapture sessions from 2008 through 2011. In each year, two mark-recapture sessions were completed in August and two in September. The time interval between the sampling periods in a given year was 14 days. In 2010, floods prevented us from conducting the mark-recapture session scheduled for the end of August. The field work was generally performed when the crayfish had just released their young and had not yet started to mate.

To test possible impact of time between mark and recapture on the distance moved we used the following regression model: distance moved ≈ log (time between mark and recapture), performed in R version 2.12.0 (R Development Core Team 2010).

RESULTS

A total of 1,403 specimens of *A. torrentium* and 484 of *A. astacus* were marked in the study area. In all, 143 specimens of *A. torrentium* and 30 specimens of *A. astacus* were recaptured, whereas 52 specimens of *A. torrentium* and four specimens of *A. astacus* were marked and recaptured (or just recaptured) within the six segments of the Bzovský. These crayfish were included in our analyses. *Austropotamobius torrentium* was found to move upstream across both potential barriers. Of the 52 specimens recaptured, 16 were found upstream from the segment in which they were marked, 23 remained in the segment in which they were marked and 13 moved downstream from the segment in which they were marked. Four of the crayfish that moved upstream had moved across step A. One of these crayfish was a male, and three were females. The total lengths of these four specimens ranged from 6.4 to 7.5 cm. Six specimens (one female and five males, ranging in total length from 6.4 to 8.2 cm) had moved upstream across step B (Figure 1, Table 1). Twenty-eight *A. torrentium* moved within 0 – 10 m, maximum distance moved was 133 m downstream (female *A. torrentium* marked and recaptured in 2008) and 91 m upstream (female *A. torrentium* marked in 2010 and recaptured in 2011). *Astacus astacus* moved between 41 – 106 m, in any case they were not found in the same segment in which they were marked. All four recaptured *A. astacus* moved upstream between marking and recapture. Of these crayfish, one 6.6 cm male and one 8.3 cm female had moved across step A (Figure 1, Table 1). Possible differences in movement abilities between the sexes were not analysed because of the small number of specimens observed to cross the barriers in an upstream direction (see Table 1). The time between marking and recapture did not influence the observed distance moved ($t = -0.711$; $P = 0.48$).

In all, 29 crayfish specimens were marked and recaptured during the same year, whereas 24 were recaptured during the year after marking and three during the second year after marking. For details see Table 2.

Our results show that the steps in the Bzovský stream did not hinder the movements of either crayfish species. In all, 19% of the *A. torrentium* specimens travelling upstream moved across the 110 cm high barrier. Moreover, 38% moved across the 60 cm high barrier. Two of the four *A. astacus* specimens that moved upstream moved across the 110 cm high barrier.

DISCUSSION

Visible implanted elastomer tags are used in a wide range of species in mark-recapture experiments. Crustaceans, including juvenile lobsters (*Homarus gammarus* (Linnaeus)), crayfish (*Cherax destructor* Clark) and spiny lobsters (*Jasus edwardsii* (Hutton)) were marked with VIE tags with little impact on survival and successful moulting, with 92% surviving in case of *Homarus gammarus* (Northwest Marine Technology 2010). Also, we did not observe large scale movements of crayfish after marking, although we know crayfish move long distances after some disturbance (Schütze et al. 1999). Moreover, we recaptured crayfish at the same locality after three years, thus we presume this marking method works correctly.

It is known that crayfish can live in sympatry. There are studies observing *A. astacus* and *Pacifastacus leniusculus* (Dana) for 29 years in Finland (Westman and Savolainen 2001), *P. clarkii* and *Procambarus zonangulus* (Hobbs and Hobbs 1990) (Blank and Figler 1996) in Louisiana in the USA, or even five crayfish species occurring together in one stream in Australia (Johnston and Robson 2009). In the Czech Republic, we know of nine streams where *A. astacus* occurs with *A. torrentium,* and one stream where *A. torrentium* occurs together with *Astacus leptodactylus* (Eschscholtz) (Vlach et al. 2010). Crayfish living in sympatry are competitive, using similar and potentially limited resources, while their ecological niches are overlapping (Blank and Figler 1996). As discussed in Kadlecová et al. (2012), *A. astacus* is generally larger than *A. torrentium*, but in equal-sized encounters, *A. torrentium* is more successful in defending its shelter (Vorburger and Ribi 1999). Streams with a sufficient supply of shelters could be a reason why mixed populations of these two crayfish species can survive.

It is known that crayfish can move longer distances after some disturbance, but in natural environments with no disturbances, they tend to move only a few meters over the course of several weeks (Bohl 1999), or until they find a shelter (Sint and Füreder 2004).

The angle of step A was perpendicular to the water surface. The moss covering the step was typically short-grown, thus it is probable that the movements of crayfish were not influenced by the presence of this moss. Moreover, the crayfish could not use the cracks in the steps, and the water flow through the actual bypass around step A was not sufficiently rapid to enable the crayfish to move through the bypass. These observations support the hypothesis that the crayfish used a bypass partly hidden in the rock to move around the step, however, this bypass could not be inspected.

Step B was smaller than step A, and thus could be more easily overcome by both crayfish species. The step does not extend far above the water level (its height above the water is only 31 cm). In our opinion, the crayfish were able to move upstream due to the moderate slope of this step (only 50° in places), the covering of moss on the entire step, or they simply went overland. Because *A. torrentium* is generally smaller than *A. astacus* (Holdich in Souty-Grosset et al. 2006), we hypothesise that *A. astacus* could move across the smaller step B. However, we did not find support for this suggestion. During a pilot mark-recapture study at the same stream site in 2007, located further upstream, we found specimens of *A. torrentium* crossing stony steps 57 and 62 cm high.

The downstream movement of crayfish can be considered non-deliberate to a certain extent because crayfish are flushed downstream by high water (Light 2003; Kozák et al. 2004). For this reason, the results section above emphasised upstream movement.

In California (USA), *P. leniusculus* has been observed crossing a fence-like barrier 3 m in height. These crayfish were seen to ascend the algae-covered sloping face of the barrier (Kerby et al. 2005). At our study site, it is possible that the crayfish can climb on step B due to the moderate slope of the step. It is also possible that the crayfish at our study site could leave the water and move around the barrier along the banks, which are partly covered by vegetation. Such behaviour has been reported in *Procambarus clarkii* (Girard, 1852) (Kerby et al. 2005). However, we have never observed this type of terrestrial movement in crayfish in the field at our locality.

In general, non-indigenous crayfish species have a broader environmental tolerance and are able to spread rapidly (Puky and Schád 2006; Peay and Füreder 2011). For this reason, the introduction of non-indigenous crayfish species, followed by crayfish plague outbreaks, is considered the most important threat to indigenous crayfish species (Souty-Grosset et al. 2004). To prevent the invasive signal crayfish *P. leniusculus* from invading new localities, Peay et al. (2011) recommend a barrier that is vertical, smooth and higher than two meters. This recommendation appears consistent with our results. The design features of a concrete barrier for controlling the movements of invasive crayfish appear to be very important (Ellis 2005, Peay 2001). A barrier that cannot be traversed (no vegetation, no gradually sloping banks) or bypassed appears to be the most effective option.

The two steps examined in this study did not act as barriers to movement for the native crayfish species *A. torrentium* and *A. astacus* and we can infer that they will not be a barrier to non-indigenous crayfish species as well. Cracks in the steps, vegetation covering steps, and banks enabled crayfish to cross these potential barriers in an upstream direction. Further field work using cameras, or other kinds of monitoring equipment, is needed in order to reveal the means by which crayfish cross these stony steps.

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Chapter 5: Frequency of new marble-colored morph in wild population of *Austropotamobius torrentium* (Schrank, 1803) (Decapoda, Astacidae)

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Frequency of new marble-colored morph in wild population of *Austropotamobius torrentium* (Schrank, 1803) (Decapoda, Astacidae)

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Running title: New color morph of stone crayfish

Abstract

In contrast with the usual coloration of stone crayfish (*Austropotamobius torrentium*), we newly discovered a rare marble morph in a brook in the Czech Republic (Central Europe). During mark-recapture sessions, we captured by hand 1082 individuals over the 3 years 2008–2010 from which only 5 were marble-colored. This color morph's frequency of occurrence was thus less than 1% within the estimated subadult and adult stone crayfish population. Although many biological papers and determination keys regarding crayfish are based upon analysis of exoskeletal coloration, recent studies have asserted that this characteristic provides unreliable guidance when determining species inasmuch as it easily results in errors because many crayfish species exhibit an extensive variety of color morphs.

Key words: stone crayfish; coloration; mark-recapture; estimated population

Introduction

Stone crayfish (*Austropotamobius torrentium*, Schrank 1803) is an indigenous European crayfish with wide distribution in central and south-eastern European countries (Machino & Füreder 2005; Vlach et al. 2009). The species is protected under Czech law, and in connection with European protection it has been added to the species list under Natura 2000 (Holdich et al. 2006). Stone crayfish prefers small streams with higher altitude gradient but with lower water velocity and plentiful refuges (Streissl & Hödl 2002; Holdich et al. 2006).

Pigmentary components responsible for coloration in crustaceans are the two carotenoids astaxanthin and canthaxanthin. Carapace surface coloration, or pigmentation, in crustaceans is determined by a combination as to the type and amount of pigment in the exoskeletal material (Fox 1953; Castillo et al. 1982) and long has been studied in crayfish (Kent 1901). Many crayfish species exhibit a variety of colors that is influenced by genetics (Fox 1953; Volpe & Penn 1957; Walker et al. 2000). Moreover, crayfish coloration can be environmentally induced and strongly correlated with habitat background color, water depth, and sunshine intensity (Kent 1901; Thacker et al. 1993; Finlay et al. 2006). The level of pigmentation also can be negatively influenced by poor crayfish diet (Wolfe & Cornwall 1964; Sommer et al. 1991). Beingesser & Copp (1985) had noted that, among other factors, crayfish color change depends upon the animals' age and size. Crayfish cannot alter their coloration as quickly as can some shrimp species, for which rapid color change is typically within seconds, minutes or hours. Rather, crayfish display color change over periods of several weeks or months (Vogt et al. 2008). Occurrences of rare crayfish color morphs, as described by numerous authors, have long been well known and have been recorded in a variety of genera, such as *Astacus*, *Cambarellus*, *Cambarus*, *Cherax*, *Orconectes*, *Pacifastacus* and *Procambarus* (Holdich et al. 2006). Although great variation in crayfish coloration is well documented, many species determination keys are based upon, among other things, exoskeletal coloration (Goddard & Hogger 1986; Pöckl et al. 2003), as noted by Füreder & Machino (2002). The most frequent coloration of adult stone crayfish varies from pale to dark brown and to olive green, occasionally being beige or orange (Holdich et al. 2006). In contrast to the sister species white-clawed crayfish (*Austropotamobius pallipes,* Lereboullet 1858), blue individuals among stone crayfish have never been found (Holdich et al. 2006).

The objective of this paper is to provide information about a rare color morph in stone crayfish and to report the frequency of its occurrence in a wild population.

Material and methods

Study area

A mark–recapture study was conducted at Stroupínský brook and its tributary Bzovský brook, situated in the Křivoklátsko UNESCO Biosphere Reserve (Elbe drainage basin, Central Europe, 49°53'N, 13°53'E), Czech Republic (Fig. 1). This protected area has one of the most abundant populations of this species in the Czech Republic (Kozák et al. 2002). While the stretches of stream selected for this study are located between a small road and meadows with trees and scrub growth along the stream banks, they are relatively safe due to their protected area status and ensuing special protection and management. Sympatric and syntopic occurrence of stone crayfish (*A. torrentium*) and noble crayfish (*Astacus astacus*, L. 1758) is known over a 9 km stretch of the Stroupínský brook and its tributaries (Kadlecová et al. 2012). This mixed population has been relatively stable for many years, as is documented by data from Natura 2000 monitoring (Vlach et al. 2009). The Stroupínský brook that flows into the Červený brook is a fourth-order stream and its tributaries are second-order streams. Stroupínský brook has a length of 20.9 km from the headwaters to its mouth, a catchment area of 109 km^2, and flows at the altitude range of 283–471 m a.s.l. Water depth is 0.1–0.7 m and average riverbed width is 4 m. The substrate consists mostly of slate and greywacke with sand deposits. The stream passes through six villages, in most of which it is straightened and tiled, while outside the villages it flows freely and meanders across the landscape. Bzovský brook is a tributary of Stroupínský brook and has a length of 4.0 km from its headwaters to its mouth. Water depth is 0.1–0.5 m and average riverbed width is 2 m. The substrate is mostly stony with boulders and with sand deposits. The higher gradient is reduced by two old stony weirs with heights of 1.1 and 0.6 m. The study area has a length of 71 m (beginning at the 7 river-kilometer point) on Stroupínský brook and 106 m (beginning at the 1 river-kilometer point) on Bzovský brook. The part of the study area on Stroupínský brook is bordered at the upstream end by a stretch that is silted with sand deposits and detritus.

Data collection

Stone crayfish were captured by hand continually along the brooks in the study area as described by Bubb et al. (2002) and Kadlecová et al. (2012). Eleven mark-recapture sessions were conducted from August to September in the years 2008-2010 at 14-day intervals. Stone crayfish had just released their hatchlings and had not yet begun mating during this period (Streissl & Hödl 2002). One capture session was canceled due to a flood in August 2010. We divided the observed stream transects into 12 segments of equal length. Crayfish in each segment were captured for 30 min by two persons on Stroupínský brook and for 15 min by one person on its Bzovský brook tributary during each session. Captured individuals were held in containers. They were sexed, measured (for total length and cephalothorax length), individually tagged, and their coloration type determined. Subsequent to this procedure, each crayfish was released back into that segment from which it had been captured. In accordance with Pârvulescu (2010), total body length (TL) was measured along the median line of the body, from the anterior end of the rostrum to the posterior end of the telson (tail fin), and cephalothorax (shell) length (CTL) from the anterior end of the rostrum to the posterior median edge of the carapace. Individuals were tagged using visible implant elastomer marks (VIE) (Northwest Marine Technology, Shaw Island, WA, USA) injected into tissue close to the swimmeret (abdominal leg) bases on the ventral side of the crayfish abdomen as an aid to recapture identification. Unique codes were based upon two or three color points and a swimmeret sequence for each specific individual. The captured crayfish were checked for the presence of a tag from previous sessions. In accordance with recommendations in the VIE manual, only subadult and adult individuals with TL greater than or equal to 3.5 cm were tagged.

Data analysis

For estimating population sizes, we used techniques that presume a closed population because nearly half of the recaptured crayfish were captured in a year other than that in which they were marked (Kadlecová et al. 2012). The proportion of crayfish recaptured in a different year from that in which they were marked indicates that the population is stable and does not make large interseasonal movements. Although the occurrence of stone crayfish is known to be greater in the Stroupínský brook basin, the observed population can be considered as closed for purposes of the presented study. That is as suggested by Kadlecová et al. (2012) and is in accordance with Pöckl & Streissel (2005), who noted sedentary behavior of stone crayfish, and with Vorburger & Ribi (1999), who described a strong tendency for stone crayfish to defend occupied shelters. The Modified Schnabel Method (Schnabel 1938) within Ecological Methodology 2003 software was used to estimate the crayfish population based on the multiple sampling. An estimate of the total population and density of usual- and marble-colored crayfish was made for each year, and on that basis 3-year averages were calculated. The percentage of marble coloration in the total catch was then determined from the catch record, and subsequently the frequency of occurrence and abundance in the estimated population were calculated.

Results

A total of 1103 subadult and adult stone crayfish individuals were captured and tagged within the years 2008–2010. Recaptures totaled 142 individuals. It was not possible to recognize the tags of 8 recaptured crayfish due to VIE tag shift in their abdominal tissue. Within mark-recapture sessions an average 98 individuals were marked (range 33–172 individuals) and an average 13 individuals were recaptured (range 0–29 individuals). Most of the captured stone crayfish were uniformly colored brownish or greenish on the entire carapace surface (Fig. 2). One male and four females were colored atypically with enormously contrasting dark marmoration on a light brown background that completely covered the cephalothorax, abdomen and chelae (Fig. 3). These individuals measured 4.0–6.5 cm by TL and 1.9–2.9 cm by CTL. All of them were tagged and recaptured in the tributary of the main stream. As shown in Table 1, one individual was recaptured later in the same year in which it had been tagged, two were recaptured in subsequent years, and the other two were never recaptured. One marble-colored individual moved in a longitudinal profile 15.5 m upstream. The marble coloration was persistent in all recaptured individuals, and no usual-colored crayfish were recorded as converting to marble coloration between marking and recapture. The estimated population and density of subadult and adult stone crayfish with total body length ≥ 3.5 cm based on 11 mark-recapture sessions over 3 years is shown in Table 2. The 3-year averages were as follow: estimated population 1243 individuals and density 2.5 individuals per m^2. The frequency of marble coloration’s occurrence in the captured crayfish was 0.45%. The abundance of marbled crayfish within the estimated population was deduced to be 6 individuals with total body length ≥ 3.5 cm.

Discussion

The frequency of marble coloration's occurrence was less than 1% in the entire estimated population of subadult and adult animals with total body length ≥ 3.5 cm, which is much less than the generally recorded occurrence of blue crayfish morphs (Momot & Gall 1971). Recaptures of tagged marbled individuals suggest persistence of this rare coloration for at least 3 years without noticeable change, which is in accordance with the report of Beingesser & Copp (1985), who had noted morphologically fixed coloration in subadult and adult crayfish. Marble-colored individuals probably lived in the same stony habitat type and depth and with the same food scale as did the usual-colored crayfish. Moreover, they arguably were similarly dispersed in the stream. Part of the marble-colored individuals was not strictly sedentary, and longitudinal movement was recorded. It follows that although environmental effects on crayfish coloration including substrate color, absence of sunshine and water depth have been noted in a number of previous studies (Kent 1901; Thacker et al. 1993; Finlay et al. 2006), and while many authors have described an influence of diet on crayfish coloration, such as green plant material or carotenoid deficiency (Wolfe & Cornwall 1964; Sommer et al. 1991), similar resources at the observed locality were probably regularly available for both usual- and marble-colored individuals as they lived under comparable abiotic conditions. These facts suggest that marble coloration of stone crayfish is probably not related to habitat variety or disparity in diet and its occurrence is most probably affected by genetics, as corresponds with the views of numerous authors (Fox 1953; Volpe & Penn 1957; Walker et al. 2000). This view is consistent with the persistence of marble coloration in the recaptured individuals. Although all the marble-colored individuals were captured in a tributary of the main stream, usual-colored crayfish clearly dominated in both observed streams and it follows that marble coloration is not caused by isolation, as reported by Hand (1954) in local populations of blue *Cambarus carolinus* (Erichson 1846) and *Procambarus advena* (LeConte 1856). Nevertheless, the marmoration pattern could be not inherited but rather formed due to natural variability of this species as described by Vogt et al. (2008), who had compared marmoration variability of *Procambarus fallax* f. *virginalis* (Hagen 1870), among others, with that of leopard spots or human fingerprints. Both a marbled male and females were recorded. Thus the occurrence of this coloration morph is not sex-related, as reported also by Momot & Gall (1971) in blue

Orconectes virilis (Hagen 1870). Future research should concentrate on answering whether marble-colored individuals are better camouflaged from predators and have less need of shelters than usual-colored crayfish. This fact could result in higher probability of survival. Due to the small number of marble-colored individuals, we are not able to state more precise conclusions about the importance of capturing marble-colored individuals only in a tributary, which differs from the main stream in some characteristics.

Finding a marble-coloration morph in stone crayfish reinforces the view of Füreder & Machino (2002), who had suggested that exoskeletal color in crayfish is well known for its great variability and that determination of species based on coloration analysis is a typical source of false identification in many papers and determination keys cited in biological publications. They had documented false identification of stone crayfish found at a museum in France and by a specialist in Austria.

Although marble coloration is represented only very rarely in the population, capture of such an individual can easily result in an error of crayfish determination. Hence, in agreement with the assertions from recent studies, we emphasize that crayfish determination based on exoskeletal coloration analysis is not appropriate.

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Tab. 1: Tagged marble-colored stone crayfish, their sex (F – female, M – male), total body length (TL), cephalothorax length (CTL), and year of recapture.

Year of tagging	Sex	TL (cm)	CTL (cm)	Year of recapture
2008	F	6.5	2.8	2009
2008	F	6.1	2.9	2010
2009	F	6.2	2.9	2009
2010	M	5.2	2.5	no recapture
2010	F	4.0	1.9	no recapture

Tab. 2: Sums of tagged and recaptured individuals, estimated populations, confidence intervals, and density of stone crayfish for each year.

Year	Tagged individuals	Recaptured individuals	Estimated population	Confidence intervals	Density (per m^2)
2008	408	42	1671	1264–2338	3.4
2009	438	81	1100	812–1701	2.3
2010	257	19	957	628–1627	2.0

Fig. 1: Map of the Czech Republic. Study area is indicated by black dot.

Fig. 2: Usual-colored stone crayfish. (Photo: Jiří Patoka)

Fig. 3: Marble-colored stone crayfish. (Photo: Jiří Patoka)

Chapter 6: Habitat degradation relates to crayfish distribution within a river network: implications for conservation

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Habitat degradation relates to crayfish distribution within a river network: implications for conservation

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Abstract

1. Degradation of aquatic habitats has increasingly become one of the most important factors influencing the distribution of freshwater species worldwide.

2. We analysed the occurrence of three crayfish species, *Astacus astacus* (Linnaeus 1758), *Austropotamobius torrentium* (Schrank 1803) and *Orconectes limosus* (Rafinesque 1817), in relation to indices of habitat degradation status (based on Water Framework Directive 2000/60/ES), stream morphology, geographical characteristics and the surroundings of the investigated streams. In total, we analysed 6,768 sites in the vicinity of the Czech Republic (Central Europe), of which 6,187 sites lacked crayfish; among the remainder, A. astacus was present in 507 sites, O. limosus occurred in 44 sites and A. torrentium was present in 30 sites.

3. The analysis revealed that *A. astacus* preferred streams of better water quality that were not surrounded by agricultural land or settlements. This species also preferentially occurred in smaller streams with stony bottom substrata that were located at higher altitudes. *Austropotamobius torrentium* occurrence was associated with the natural character of the water body (according to the Water Framework Directive) and the presence of protected areas at higher altitudes. Conversely, the non-indigenous crayfish species *O. limosus* was typically

recorded at lower altitudes in downstream reaches surrounded by agricultural land and with deteriorated water quality.

4. Collectively, the indigenous crayfish species are distributed in areas with lower pressure from human activities relative to the non-indigenous *O. limosus*. This fact may be of general importance for conservation strategies related to central European crayfish species, mainly because the habitat-driven co-occurrence pattern (and its possible changes in the future) may strongly influence interspecific relationships, such as direct competition and spreading of infectious diseases between species.

Keywords: ecological status, monitoring, protected species, invertebrates, alien species, pollution

Introduction

Water courses can be degraded by eutrophication, acidification, influx of toxicants, habitat alterations, non-suitable land use or fragmentation of the landscape (Holland *et al.*, 1995; Nedeau *et al.*, 2003; Brönmark and Hansson, 2005; Allan and Castillo, 2009). All of these primarily anthropogenic processes change the biotic and abiotic character of water courses and lead to shifts in the distributions of aquatic biota. The physical habitat niche of a particular species determines its potential geographical spread and biotic interactions (Guisan and Zimmermann, 2000; Pulliam, 2000; Dyer *et al*, 2013). In addition, competition and dispersal abilities, together with niche size and the distribution of environmental conditions in space and time, all play roles in determining species distributions with respect to the presence of suitable habitat (Pulliam, 2000).

Freshwater ecosystems are currently experiencing much greater declines in biological diversity than observed in the majority of terrestrial ecosystems (Sala *et al.*, 2000; Dudgeon *et al.*, 2006). Most declines have multiple causes, but physical habitat modification, invasive species and water quality degradation are thought to be most important (Allan and Castillo, 2009). Our study focuses on crayfish, the largest mobile water macro-invertebrates. Crayfish are often referred to as ecosystem flagship species because of their size, longevity and reliance on aquatic systems throughout life (Reynolds and Souty-Grosset, 2012); they are even considered indicators of the ecological status of water bodies (Water Framework Directive 2000/60/EC).

Crayfish inhabit a wide range of habitats, including streams, lakes, wetlands, ditches, caves and sloughs (Bouchard, 1978). Many studies have shown that the abundance of crayfish depends on stream morphology (Bohl, 1987; Eversole and Foltz, 1993; Streissl and Hödl, 2002; Wienländer and Füreder, 2012), shelter availability (Lodge and Hill, 1994; Nystrøm *et al.*, 2006; Johnsen and Taugbøl, 2008) and water quality (Demers and Reynolds, 2002; Holdich and Reeve, 2006b; Svobodová *et al.*, 2012). However, the role of environmental degradation on crayfish species distribution patterns and the interactions between native and invasive species are still rather understudied.

Indigenous crayfish species (ICS) in Europe are considered to be endangered by several factors, including habitat loss, deteriorating water quality, overfishing and climate change, as well as competition with non-indigenous crayfish species (NICS) and crayfish plague (Holdich *et al.*, 2009). One of the most significant threats is the continued spread of NICS, with their capacity to directly outcompete indigenous crayfish species (Söderbäck, 1995; Westman, 2000; Schulz *et al*., 2006) and, even more importantly, to transmit diseases that are detrimental to native crayfish species (Lozán, 2000; Füreder *et al*., 2006; Kozubíková *et al*., 2008).

In our study area (the Czech Republic, Central Europe), there are currently three ICS: *Astacus astacus* (Linnaeus, 1758), *Austropotamobius torrentium* (Schrank, 1803) and *Astacus leptodactylus* (Eschscholtz, 1823), which are protected under Czech law No. 114/1992. There are also two NICS present: *Orconectes limosus* (Rafinesque, 1817) and *Pacifastacus leniusculus* (Dana, 1852), both native to North America. The introduction of crayfish from North America has caused a continuous decrease in the population sizes of *A. astacus* (Westman *et al*., 2002) and *A. leptodactylus* in Europe (Bohl, 1996). *Austropotamobius torrentium* might be less affected by crayfish plague due to its demands for water quality and particular morphological stream characteristics (Renz and Breithaupt, 2000).

Literature resources imply considerable differences in physical habitat requirements between particular crayfish genera occurring in Central Europe. The genera *Astacus* and *Pacifastacus* may exploit a wide variety of habitats (Lewis, 2000; Skurdal and Taugbøl, 2002) but nevertheless generally prefer areas with available hiding places or substrates that can be converted into small and simple burrows (Holdich, 2002; Souty-Grosset *et al*., 2006). *Astacus astacus* is thought to be rather sensitive to pollution and physical damage to the environment (Holdich, 2002). Species of the genus *Austropotamobius* show variable habitat preferences: whereas *A. torrentium* seems to typically inhabit high gradient small brooks, *A. pallipes* (Lereboullet 1858) is not habitat specific. Similarly to *A. astacus*, they are thought to be susceptible to indicators of pollution, such as ammonia, nitrite and nitrate (Füreder *et al*., 2006). The habitat requirements and preferences of invasive *O. limosus* in Europe have not been thoroughly studied, and its spatial distribution with respect to habitat morphology and the ecological state of the environment remains unknown.

The aim of this paper was to determine the relationship between the level of degradation of the water body and the occurrence of three crayfish species, *A. torrentium*, *A. astacus* and *O. limosus*, throughout the entire Czech Republic. The identification of habitat requirements and limitations will help in the evaluation of the possible spread of invasive species and assessments of the vulnerability of threatened crayfish species.

Materials and Methods

Data collection

We performed detailed monitoring of crayfish occurrence in running waters in the Czech Republic between 2004 and 2008 (see Svobodová *et al*. 2012 for details). Localities throughout the entire Czech Republic were examined for crayfish occurrence and for biotope characteristics. The localities were defined on a map base 1: 50 000, with the first site on a given stream set at the confluence with a larger stream and subsequent sites extending 3 – 3.5 km upstream. The last site was 1 km from the source of the spring. At each site, crayfish were sought in all available shelters (a minimum of 50 shelters searched per site, e.g., stones, banks, roots or other organic material in the stream) and caught by hand in a 100 m section of stream. For larger rivers (6^{th}-8^{th} – order streams), baited traps were used. In addition, environmental characteristics related to stream morphology and stream surroundings were observed as indicators of habitat degradation. These characteristics included the width of the stream, stone coverage of the bottom, mud at the bottom, modification of the stream channel, settlements as surroundings or fields as surroundings. Information on the catchment area, sea drainage affiliation, altitude and protected areas were obtained from the T.G.M. Water Research Institute hydroecological information system as well as from data from Water Framework Directive 2000/60/EC (hereafter “Water Framework Directive”) on the character of the water body, the chemical state of the water body, fish zone (salmonid or cyprinid waters) and vulnerable areas.

Statistics

Redundancy analysis (RDA) was used to relate the species occurrence data to the 11 habitat variables (altitude, modification of stream channel, mud at the bottom, stone coverage at the bottom, stream width, fields as surroundings, settlements as surroundings, vulnerable areas, character of the water body, chemical state of the water body and protected areas). Sea drainage affiliation was used as a covariable in the analysis. Inclusion of particular variables in the final model was tested using a Monte Carlo permutation procedure with 500 permutations. The analysis was performed using CANOCO 4.5 (Ter Braak and Šmilauer, 2002).

We used multiple logistic regression models (Jongman *et al*., 1995) to examine the relationship between the presence/absence of particular crayfish species and the 11 habitat variables. We used stepwise backward selection for the choice of final models for each of the studied species. The significance of model variables was tested by comparing the deviance reduction (chi-square, $P<0.05$). These analyses were also performed on a more detailed scale, using the presence of *A. torrentium* in the Berounka River catchment and *O. limosus* in Elbe River catchment (i.e., sites with concentrated abundances of *A. torrentium* and *O. limosus*) (see Fig. 1) to address possible spatial effects.

Pairwise Wilcoxon rank sum tests (with adjusted *p* values determined using the Bonferroni method) were used to test differences in environmental characteristics at those sampling sites at which particular species occurred. A nonparametric method was used because normality and variance homogeneity assumptions were not satisfied (using the Shapiro-Wilk normality test and the Bartlett test for homogeneity of variances). These tests were performed in R software (R Development Core Team, 2010). To describe the differences between species for each specific parameter, we performed individual Wilcoxon tests at the scale of the entire Czech Republic and at the scale of the Berounka River catchment. To provide information on the effect of catchment area, sea drainage area and fish zones on crayfish distributions, simple contingency tables and chi-square tests, which accommodated the categorical character of the variables, were used.

Results

The final statistical analysis of crayfish distribution in streams of the Czech Republic entered 6,187 sites without crayfish, 507 sites with *A. astacus*, 44 sites with *O. limosus* and 30 sites with *A. torrentium*. Five sites with *P. leniusculus* and 4 sites with *A. leptodactylus* were considered very rare occurrences, and these species were thus not included in the analyses. The spatial distribution of sites of interest is depicted in Fig. 1.

The RDA multivariate analysis distinguished the biotope characteristics of NICS and ICS by the effects of altitude, stream width and affiliation with protected areas. In this analysis, the NICS *O. limosus* showed a strong affiliation with downstream reaches ($P<0.05$; Monte Carlo permutation test). Figure 2 shows an ordination diagram in which species, samples and significant variables (with sea drainage affiliation considered a covariate) are plotted on the first two RDA axes. The first axis explained 19.2%, and the second axis 1.0% of the variability in the species data. Occurrence of *A. astacus* was associated with higher altitude, good chemical state of the water body, the presence of stones in the substrata and the presence of vulnerable areas. The biotope characteristics of *A. torrentium* were not clearly revealed in this analysis, but it was significantly affiliated with protected areas and negatively correlated with vulnerable areas, as revealed by Nitrate Directive 91/676/EEC (see Fig. 2).

More detailed information on the habitat preferences of each crayfish species was obtained from multiple logistic regressions. The presence of *A. astacus* was best predicted by the following parameters: altitude, stones covering the stream bottom, stream width, fields as surroundings, settlements as surroundings, vulnerable areas and chemical state of the water body. The presence of *A. torrentium* was best characterised by the following parameters: altitude, character of the water body and presence of protected areas. The subsequent analysis for *A. torrentium* restricted to the Berounka River catchment did not provide significant results due to the small amount of data. The presence of *O. limosus* was best predicted by the following parameters: altitude, stream width, fields as surroundings and chemical state of the water body, with similar results in the Elbe River catchment. More detailed results and the respective significance levels are given in Tab. 2.

The environmental characteristics of sites of occurrence of particular species and associated significant differences are listed in Tab. 1 and Tab. 3. Parameters related to the chemical state of the water body revealed that sites with *O. limosus* had worse water quality than sites with *A. astacus, A. torrentium* or no crayfish (Tab. 1). An analysis of the parameter ‘character of the water body’ revealed that *A. torrentium* occurred in more natural streams than *O. limosus* and *A. astacus* (Tab. 1).

Four variables related to stream morphology were different between native and invasive crayfish species (see Tab. 1), though no such parameters differed between the native crayfish species *A. astacus* and *A. torrentium*. The occurrence of *A. torrentium* within the Berounka River catchment was associated with higher coverage of stones at the bottom and narrower streams compared to sites lacking *A. torrentium* (Tab. 3). Spatial features, such as sea drainage affiliation, catchment affiliation and fish zones, were also found to influence crayfish distribution in the Czech Republic (Tab. 4).

Discussion

Our study corroborates the profound differences in habitat characteristics and degree of environmental pressure at sites inhabited by native and invasive crayfish species in the Czech Republic. Conversely, only slight differences in habitat quality were observed between sites inhabited by the two endangered native crayfish species.

Habitat degradation

Water quality status, defined according to the Water Framework Directive approach (a joint categorical parameter based on temperature, oxygenation conditions, water transparency, nutrient concentrations and contents of specific synthetic and non-synthetic pollutants), was not significantly different between sites inhabited by native crayfish species. This finding is in accord with Svobodová *et al.* (2012), who did not find differences in water quality parameters from detailed water quality datasets between sites in the Czech Republic inhabited by native crayfish. However, the authors did detect differences between sites with native and invasive crayfish species. *Orconectes limosus* most likely originates from Pennsylvania, USA, where it inhabits soft-bottomed, silty, turbid waters, such as large rivers, but it is also known to inhabit small brooks and rivulets in New Brunswick, Canada (Souty-Grosset *et al.*, 2006). In Europe, *O. limosus* is considered common in eutrophic or polluted waters (Lindquist and Huner, 1999) and is known to primarily inhabit large rivers in Germany (Troschel and Dehus, 1993; Dehus *et al.*, 1999), Hungary (Puky and Schád, 2006), France (Vigneux, 1997; Arrignon *et al.*, 1999), Lithuania (Burba, 2010) and Switzerland (Mickasch, 1999; Hefti and Stucki, 2006). This NICS is found in all types of fresh waters in more than 75% of Poland (Grabowski *et al.*, 2005; Souty-Grosset *et al.*, 2006). In the Czech Republic, its distribution is also concentrated in large rivers – particularly the Elbe and Vltava River catchments and their major tributaries – but it is also found in distant, smaller brooks. Our results corroborate the finding that *O. limosus* can tolerate a wide range of water quality parameters, which enables this species to inhabit more degraded habitats and further facilitates its spread (Holdich *et al.*, 2006a; Svobodová *et al.*, 2012).

Parameters indicating the level of human impact on the streams and thus the degradation status of the study sites (i.e., the character of the water body and presence of protected areas) revealed that *A. torrentium* is generally found in relatively pristine localities with natural stream characteristics. This finding confirms the hypothesis that this crayfish species prefers stream headwaters (Souty-Grosset *et al*., 2006; Weinländer and Füreder, 2012).

Morphological parameters linked to the order of the stream (i.e., stream width, altitude and mud in the bottom substrate) clearly distinguished NICS and ICS positions along the river continuum in the Czech Republic. The altitude and width of the stream are the most important variables explaining the distributions of *O. limosus* and *A. astacus* in the Czech Republic. *Astacus astacus* inhabits narrower streams at higher altitudes, and *O. limosus* prefers wider streams in lowlands. This result is in agreement with the current distribution of *O. limosus* in Central Europe, where it is concentrated in lowland rivers. Moreover, having fields in the surroundings was found to be an important factor explaining the distributions of *A. astacus* and *O. limosus* in the final models created for each species. This result can be explained by the preference of *O. limosus* for lowland areas, particularly along the Elbe River, where most fertile muck soils in the Czech Republic are located. From our results, we can conclude that the typical stream inhabited by *O. limosus* is a slow-flowing, large, deep stream with a muddy bottom. Nevertheless, it is evident that this species is also able to penetrate into smaller brooks. Such infiltration may be caused by other factors, such as the presence of competitors (Souty-Grosset *et al*., 2006).

We found no differences in the stream morphological parameters of sites inhabited by the native crayfish species *A. astacus* and *A. torrentium*; we can thus consider their morphological demands to be quite similar. This result is in accord with Weinländer and Füreder (2012), who reported that, relative to *P. leniusculus*, *A. astacus* and *A. torrentium* were confined to smaller streams either at higher altitudes with specific physical habitat conditions (*A. torrentium*) or moderate water temperatures (*A. astacus*) in the area of Carinthia (Austria). In the final model predicting the occurrence of *A. astacus*, we observed a strong influence of stony substrate in the stream bottom. The importance of stones in streams for *A. astacus* was emphasised by Huolila *et al*. (1997), Sint and Füreder (2004) and Johnsen and Taugbøl (2008), who used stones as crayfish shelter prototypes in field experiments. In general, *A. astacus* is known to inhabit a great variety of running waters, avoiding sites with muddy substrata and preferring streams with stony banks and bottoms (Troschel, 1997; Westman *et al*., 2002). This species often uses alder roots and large woody debris as shelter (Bohl, 1999a). As stones are the most common type of shelter in streams, our results show the importance of all types of shelters in streams for *A. astacus*, as opposed to *O. limosus*, which is supposed to be able to build extensive burrows in soft substrates (Holdich, 2002). Stones of different sizes create shelters for all size classes of crayfish (Huolila *et. al*., 1997) and therefore seem to be one of the most important factors for the occurrence of *A. astacus*.

In the literature, a preference for stones in the stream bottom substrate is also attributed to *A. torrentium* (Vorburger and Ribi, 1992; Maquire *et al*., 2002). This association was supported by our independent tests in the Berounka River catchment. The occurrence of *A. torrentium* is reported to be positively dependent on coarse-grained substrata, which it uses for shelter. This species is also known to avoid fine-grained substrata and high water velocities (Bohl, 1987; Streissl and Hödl, 2002; Vlach *et al*., 2010a; Vlach *et al*., 2010b). We can presume that *A. torrentium* is not as profiled in its habitat preferences as *O. limosus*, although the two species occurred at almost the same number of sites in our source database. In the more detailed assessment of the Berounka River catchment, we observed only slight differences in the morphology of streams with and without *A. torrentium*, where the most significant features were narrower streams with more stones in the bottom substrata. In the final model for *A. torrentium* (where the character of the water body and the presence of protected areas were also found to be significant factors), it appears that in the Czech Republic, *A. torrentium* typically inhabits naturally formed, smaller streams situated at sites of low human impact. Similar biotopes have been reported for *A. torrentium* in other European countries (Bohl, 1999b; Renz and Brithaupt, 2000; Pârvulescu and Zaharia, 2012; Weinländer and Füreder, 2012).

Conservation implications

We observed that the distribution of protected natural areas fit well with the distribution of *A. torrentium*, which is an endangered species under Czech and international legislation (Czech regulation No. 395/1992 of law No. 114/1992; Convention on the conservation of European Wildlife and Natural Habitats, Habitats Directive 92/43/EEC; vulnerable species in the IUCN Red list). This congruence suggests that future conservation actions have good potential, as it seems to be very important to protect *A. torrentium* catchments against increased human impact in the future. By contrast, Dresser and Swanson (2012) recommended strong preventive legislation to protect native crayfish populations against crayfish invaders, and Gherardi *et al*. (2011) emphasised quick action after the establishment of NICS to prevent their spread. The presence of vulnerable areas, as defined by the Nitrate directive 91/676/EEC, appeared to be negatively correlated with the occurrence of *A. astacus*, which may also indicate the vulnerability of this crayfish species to intensive agricultural activities. This vulnerability should be taken into account when adopting conservation measures for this species.

The distribution of crayfish species within the study area is most likely also affected by a range of factors besides degradation status, stream morphology and water quality, with the presence of predators, competitors and diseases each having a potentially important influence. The most widespread competitor for native crayfish species in the Czech Republic is *O. limosus.* This species was accidentally introduced into Central Europe in 1890 and was first observed in the Czech Republic in 1989 in the Elbe River, approximately 40 km from the German border (Petrusek *et al*., 2006). In general, crayfish are the most mobile invertebrates in streams. Puky and Schád (2006) calculated the velocity of *O. limosus* spread as more than 13 km per year, and we infer that the 24 years since the first report were sufficient for *O. limosus* to become established in streams of the Czech Republic. No indigenous crayfish of Central Europe is competitively stronger than *O. limosus*, even when free of crayfish plague. The preference of *O. limosus* for lowland running waters observed in our distributional data allows us to conclude that headwaters are less threatened by crayfish plague and host more indigenous crayfish communities. High growth rates, early maturity, large amounts of offspring and high tolerance to habitat conditions (Lindquist and Huner, 1999) make *O. limosus* a frequent winner in competition with ICS. The differences in habitat characteristics and the degree of environmental pressure at sites with native and invasive crayfish species may therefore be of general importance for conservation strategies aimed at central European native crayfish species, primarily because the habitat-driven co-occurrence pattern (and its possible changes in the future) may strongly influence interspecific relationships, such as direct competition and spreading of infectious diseases between crayfish species.

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Fig. 1: A distributional map of all observed localities by Nature Conservation Agency of the Czech Republic, where sites with *O. limosus* (□), *A. torrentium* (▲), *A. astacus* (●) and without crayfish (˙) are distinguished.

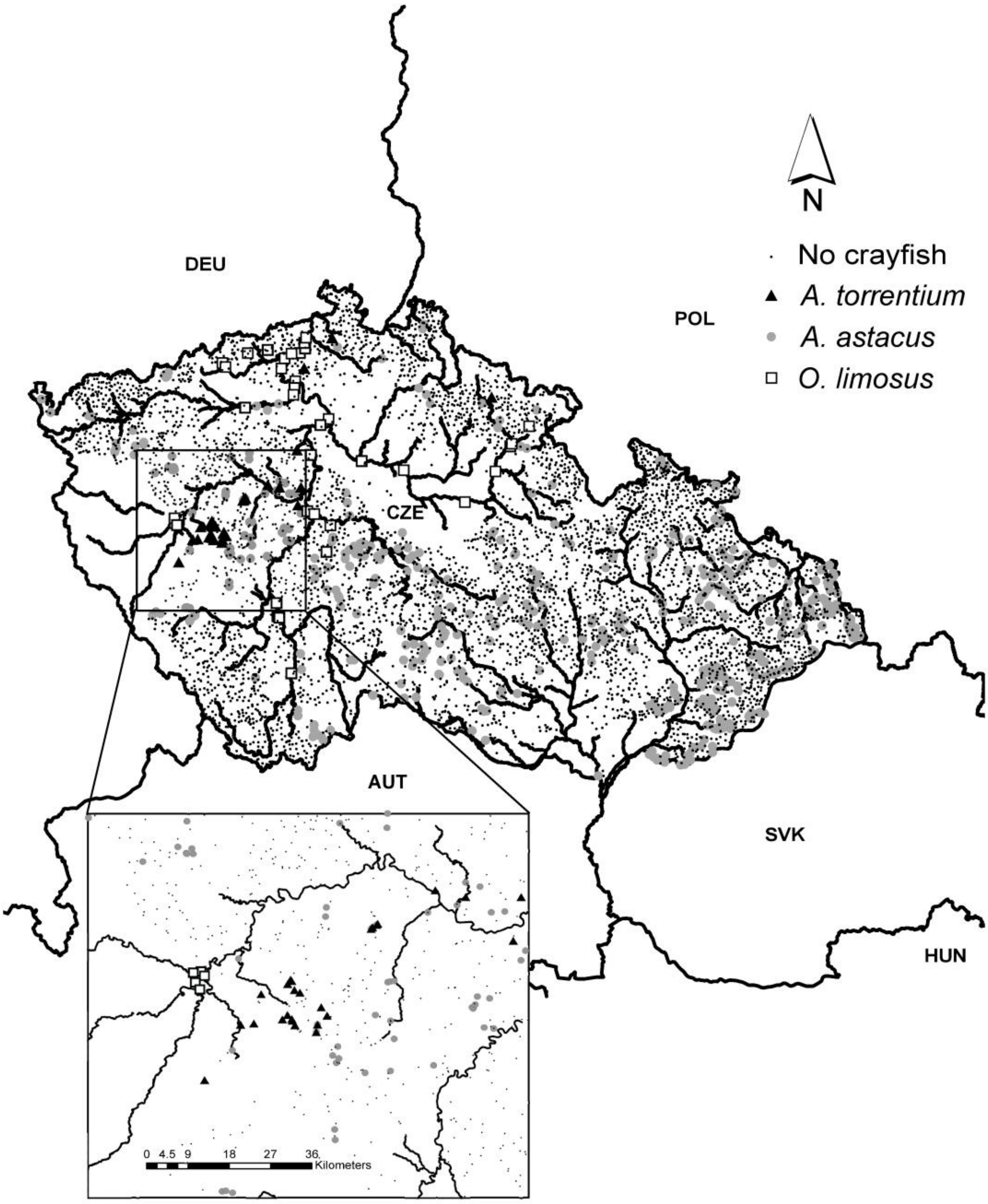
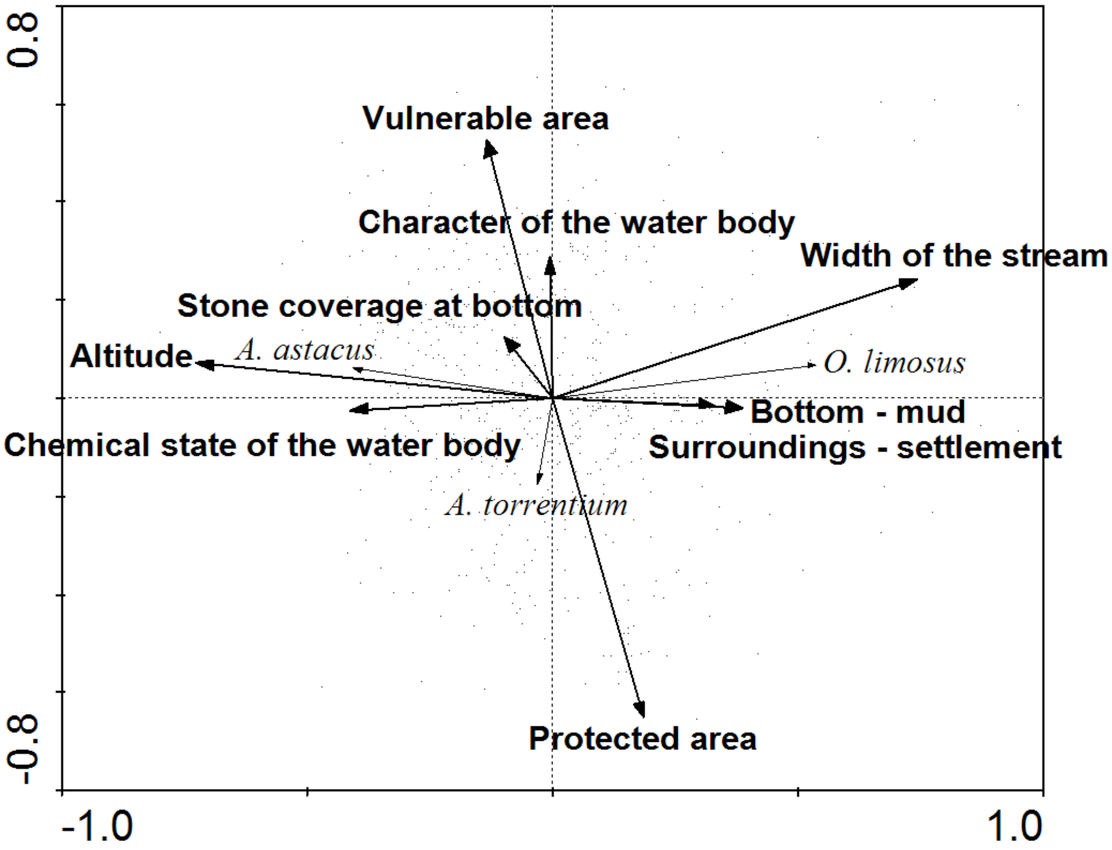


Fig. 2: Ordination diagram displaying crayfish species (*A. astacus*, *A. torrentium*, and *O. limosus*), environmental variables related to habitat degradation and study sites (dots), produced by redundancy analysis (RDA) in CANOCO 4.5. The first axis explained 19.2%, and the second axis 1.0% of the variability in the species data.



Tab. 1: Mean (*sd*) environmental characteristics of sites with or without crayfish across the entire Czech Republic. Different superscripted letters indicate significant differences between species (pairwise Wilcoxon rank sum tests with adjusted P values from the Bonferroni method, P<0.05); *n* - number of sites, * - insufficient data.

Environmental characteristic	*A. astacus*			*A. torrentium*			*O. limosus*			no crayfish		
Entire CR	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n
altitude (m a.s.l.)	407.9 ^{A}	117.9	507	407.8 ^{AB}	105.1	30	233.58 ^{C}	86.1	42	434.8 ^{B}	162.31	6186
stone coverage of the stream bottom (%)	46.8 ^{A}	32.36	507	39.53 ^{AB}	28.07	30	37.26 ^{AB}	33.6	42	33.1 ^{B}	29.74	6186
stream width (cm)	452.8 ^{A}	503.2	507	308.3 ^{AC}	143.67	30	2722.7 ^{B}	2447	42	371.5 ^{C}	485.26	6186
mud on the stream bottom (%)	0.19 ^{A}	0.18	507	0.17 ^{A}	0.16	30	0.31 ^{B}	0.2	42	0.19 ^{A}	0.19	6186
modified stream (%)	0.2 ^{A}	0.37	507	0.14 ^{A}	0.28	30	0.44 ^{B}	0.38	42	0.21 ^{A}	0.36	6186
surroundings - settlements (%)	0.16 ^{A}	0.32	507	0.15 ^{A}	0.31	30	0.37 ^{B}	0.35	42	0.19 ^{A}	0.34	6186
surroundings - fields (%)	0.07 ^{A}	0.22	507	0.12 ^{AB}	0.28	30	0.08 ^{AB}	0.23	42	0.12 ^{B}	0.28	6186
character of the water body (natural, modified, artificial)	1.2 ^{A}	0.4	471	1 ^{B}	0	28	1.36 ^{AC}	0.48	33	1.17 ^{AB}	0.37	5608
chemical state of the water body (good, not good)	0.73 ^{A}	0.44	471	0.64 ^{A}	0.48	28	0.18 ^{B}	0.39	33	0.72 ^{A}	0.45	5608
vulnerable area (yes, no)	0.27 ^{A}	0.44	507	0.2 ^{A}	0.4	30	0.31 ^{A}	0.46	42	0.32 ^{A}	0.47	6186
protected area (yes, no)	0.24 ^{A}	0.43	507	0.4 ^{A}	0.49	30	0.29 ^{A}	0.45	42	0.23 ^{A}	0.42	6186

Tab. 2: Significant environmental variables (with units or categories) for each crayfish species of interest, detected from multiple logistic regression and stepwise backward selection in the entire Czech Republic and for *O. limosus* within the Elbe River catchment. Parameter estimate (*SE*), test parameter (*z-value*) and significance (*P*) are given for each significant variable.

	Estimate	SE	z-value	*P*
A. astacus				
intercept	-3.331	0.408	-8.155	<0.001
altitude (m a.s.l.)	-0.002	<0.001	-4.734	<0.001
stone coverage of the stream bottom (%)	0.012	0.001	8.103	<0.001
stream width (cm)	0.466	0.13	3.575	<0.001
surroundings - fields (%)	-0.979	0.227	-4.311	<0.001
surroundings - settlements (%)	-0.611	0.153	-3.992	<0.001
vulnerable area (yes, no)	-0.245	0.107	-2.28	0.023
chemical state of the water body (good, not good)	0.283	0.112	2.522	0.012
A. torrentium				
intercept	-5.662	0.236	-23.981	<0.001
character of the water body (natural, modified, artificial)	-2.53	1.188	-2.131	0.033
protected area (yes, no)	0.875	0.379	2.311	0.021
O. limosus				
intercept	-7.201	1.49	-4.832	<0.001
altitude (m a.s.l.)	-0.013	0.002	-5.514	<0.001
stream width (cm)	2.544	0.385	6.604	<0.001
surroundings - field (%)	-1.552	0.726	-2.138	0.032
chemical state of the water body (good, not good)	-1.139	0.414	-2.753	0.006
O. limosus in the Elbe River catchment				
intercept	-9.459	1.552	-6.094	<0.001

altitude (m a.s.l.)	-0.012	0.002	-5.488	<0.001
stream width (cm)	2.84	0.384	7.387	<0.001
vulnerable area (yes, no)	-0.983	0.401	-2.451	0.014
character of the water body (natural, modified, artificial)	1.176	0.407	2.888	0.004

Tab. 3: Mean (*sd*) environmental characteristics of sites where *A. torrentium* was present or absent in the Berounka River catchment. Different superscripted letters indicate significant differences between species (pairwise Wilcoxon rank sum tests with adjusted *P* values from the Bonferroni method, P<0.05); *n* - number of sites, * - insufficient data.

Environmental characteristic	No *A. torrentium*			*A. torrentium* present			
	mean	sd	n	mean	sd	n	p-value
altitude (m a.s.l.)	412.000	111	420	423	102	26	0.490
stone coverage of the stream bottom (%)	28.971	27.71	420	38.31	28.57	26	0.040
stream width (cm)	418.410	682.4	420	322.31	143.24	26	0.045
mud on the stream bottom (%)	0.193	0.19	420	0.15	0.16	26	0.330
modified stream (%)	0.160	0.32	420	0.12	0.25	26	0.840
surroundings - settlements (%)	0.143	0.28	420	0.16	0.33	26	0.850
surroundings - fields (%)	0.110	0.24	420	0.08	0.22	26	0.480
character of the water body (natural, modified, artificial)	1.000	0.07	397	1	0	24	0.999
chemical state of the water body (good, not good)	0.675	0.48	397	0.67	0.47	24	0.930
vulnerable area (yes, no)	0.314	0.47	420	0.15	0.36	26	0.085
protected area (yes, no)	0.205	0.41	420	0.38	0.49	26	0.031

Tab. 4: Distribution of study sites across the entire Czech Republic according to fish zone, sea drainage area and catchment affiliation. The results of chi-square tests (*significance*) are provided for each category.

Environmental characteristic		*A. astacus*	*A. torrentium*	*O. limosus*	no crayfish	significance
fish zone	cyprinid waters	151	17	35	283	$\chi^2 = 52.3763$, df = 3, p = 2.49e-11
	salmonid waters	341	13	7	3642	
	data unavailable	15	0	0	283	
sea drainage affiliation	North sea	177	30	42	3406	$\chi^2 = 143.4315$, df = 6, p < 2.2e-16
	Black sea	201	0	0	1839	
	Baltic sea	129	0	0	941	
river catchment affiliation	Danube	0	0	0	13	$\chi^2 = 486.8789$, df = 27, p < 2.2e-16
	lower Vltava	59	1	7	646	
	Thaya	71	0	0	712	
	upper Odra	127	0	0	788	
	upper and middle Elbe	21	1	7	736	
	upper Vltava	41	0	5	822	
	Nisa and other Odra tributaries	2	0	0	153	
	river Morava and its tributaries	130	0	0	1114	
	Ohře, lower Elbe and other tributaries of Elbe	20	2	18	782	
	Berounka	36	26	5	420	

Chapter 7: Conclusions

This thesis deepens knowledge in the field of movement patterns of sympatrically living populations of indigenous crayfish species in Europe: Noble crayfish *Astacus astacus* (Linnaeus 1758) and Stone crayfish *Austropotamobius torrentium* (Schrank 1803). *Austropotamobius torrentium* was found to be more sedentary than *A. astacus* and thus *A. torrentium* seems more vulnerable to natural or human-made disturbances. This observation should be respected by conservation management of these species. Stony steps situated in the stream and forming potential movement barriers for crayfish in their active upstream movement were evaluated. The particular design of barriers (slope, vegetation cover, holes) was found to be the most important factor determining a possibility for crayfish to overcome these stony steps. Third result is an identification of a new marble colour morph of *A. torrentium* which was found in Křivoklátsko Protected Landscape Area during field works. Part of this dissertation forms analyses of crayfish occurrence database collected during the crayfish mapping by Nature Conservation Agency of the Czech Republic in the area of entire Czech Republic in 2004 – 2008 in connection with other biotic and abiotic characteristics indicating habitat degradation. Non indigenous crayfish species *Orconectes limosus* (Rafinesque 1817) was found to occur more often on more degradated (artificially modified) sites than *A. astacus* and *A. torrentium,* whereas *A. torrentium* occupied more pristine sites than *A. astacus*. Dissertation comprises of three accepted papers (two in journals with impact factor and one peer reviewed) and one manuscript submitted into a journal with impact factor. Results of the thesis are published (or are accepted for publishing) in journals Fundamental and Applied Limnology, Biologia and Freshwater Crayfish.