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Research article

The first record of the parthenogenetic Marmorkrebs (Decapoda, Astacida, Cambaridae) in the wild in Saxony (Germany) raises the question of its actual threat to European freshwater ecosystems

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Abstract

A cambarid specimen was collected in a brook in Saxony (south-east Germany). Preliminary morphological inspection identified it as the parthenogenetic Marmorkrebs (Decapoda, Astacida, Cambaridae). However, this individual showed some striking morphological differences compared to specimens of our laboratory Marmorkrebs culture. Hence, we conducted a molecular analysis based on two mitochondrial genes, COI and 12S, to check its identity. The results of the genetic study verified the initial assumption of a Marmorkrebs identity for the Saxon specimen. Thus, in addition to the two indigenous species, the new find is the fourth recorded introduced crayfish species in this area. However, a search for further Marmorkrebs specimens at the same site was not successful. Most published records of Marmorkrebs in European waters concern just single individuals and an established population has so far not been observed. This stands in contrast to other recently introduced cambarid species. Thus, we critically discuss the potential of the Marmorkrebs to spread within Europe. The major obstacle may be that the temperature necessary for optimal development and reproduction of the Marmorkrebs is significantly higher than that found in most European waters. However, given globally increasing temperatures, this might change in the future.

Key words: intraspecific variability, developmental noise, genetic identification, potential invader, conservation of species diversity, thermal adaption, global warming

Introduction

It is common knowledge that invasive species can impose serious consequences on native ecosystems (Sala et al. 2000; Wittenberg and Cock 2001; Hulme et al. 2008). Rarely, however, has this effect being as dramatic as in the case of the anthropogenic introduction of North American freshwater crayfish species into Europe (Lodge et al. 2000; Pöckl and Pekny 2002). Since their first release into the lower course of the Oder River during the end of the 19th century, as well as further introductions, these non-indigenous crustaceans have spread across almost the entire continent, extensively displacing the few indigenous species (Holdich 2002; Souty-Grosset et al. 2006; Holdich et al. 2009). The crayfish plague, *Aphanomyces astaci* Schikora 1906, which is a highly contagious disease, plays a decisive role in this ongoing process. It is mainly transmitted by the largely resistant introduced North American crayfish species, which act as a carrier, and causes mass mortalities in indigenous crayfish populations (Oidtmann et al. 1999). In the past, fishery exploitation was the primary reason for introducing new crayfish species to Europe. Today, however, the aquarium trade is increasingly becoming a critical factor (Schulz et al. 2009). Cultivating exotic crayfish has come into fashion during recent years. This increases the risk that North American species are released into the wild where they sometimes encounter similar living conditions to those in their original distribution area. Hence, the number of recorded non-indigenous, and apparently released, North

American species in the wild has grown to eight to date and is continuing to rise (Pöckl and Souty-Grosset 2009). These invasive species include the Marmorkrebs (marbled crayfish), a cambarid freshwater crayfish of unknown geographic origin and taxonomic identity, which has become quite famous as the only example of parthenogenesis known to date in any species within the large decapod group (Scholtz et al. 2003). The Marmorkrebs appeared in the German aquarium trade in the middle of the 1990s (Lukhaup 2001). It is regarded as especially dangerous because even a single individual is capable of establishing a new population due to its asexual reproduction mode (Marten et al. 2004; Jones et al. 2008; Jimenez and Faulkes 2010). Up to now four incidences of the Marmorkrebs in Europe have been verified: in Lower Saxony (north Germany), in Baden-Württemberg (south-west Germany), in Tuscany (central Italy), and in the Netherlands (Blanke and Schulz 2003; Marten et al. 2004; Koese and Vletter 2008; Marzano et al. 2009). Two further records in Baden-Württemberg and Rhineland-Palatinate (south-west Germany) require confirmation (Pfeiffer, M; Marten, M; personal communication). However, in most of these cases just a single individual was found and it appears that a proper European population in the wild has not yet been established.

Here, we report the detection of a cambarid crayfish in Saxony (south-east Germany) that was initially identified as a Marmorkrebs. However, uncertainties concerning its identity remained for two reasons. One was that we noticed some morphological differences between the specimen found in Saxony and the Marmorkrebs from our laboratory culture at the Humboldt-Universität zu Berlin. The other doubt was based on the fact that Marmorkrebs are quite similar to two North American species, *Procambarus fallax* (Hagen, 1870) and *P. alleni* (Faxon, 1884) (Braband et al. 2007; Vogt 2008) that are commonly sold in the German aquarium trade. To dispel doubts about the identity of the cambarid specimen collected in Saxony, we analyzed and compared the sequences of two mitochondrial genes (see Braband et al. 2007).

Despite this new record of a Marmorkrebs in the wild, an established population of this North American crayfish is still lacking in Europe. We discuss possible reasons for this in terms of adaptations to climatic conditions.

Materials and methods

Study site and sampling

The presumptive Marmorkrebs was discovered on 11th October 2009 in the lowland brook Elligastbach (13°33'33"E, 51°20'17"N) near the small village of Zabeltitz-Uebigau situated about 30 km north-west of the Saxon capital of Dresden, Germany (Figure 1). The stream belongs to the Elbe River watershed and flows mainly through an agriculturally used area. At this locality the water has an average width of 1.5 m and its depth varies between 25 and 50 cm. Its flow pattern is characterized by alternating sections of extensive glide and riffle and in spite of previous high-impact hydro-engineering alterations to this brook, its stony streambed and tree-bordered banks provide much shelter for freshwater crayfish. During the study period in

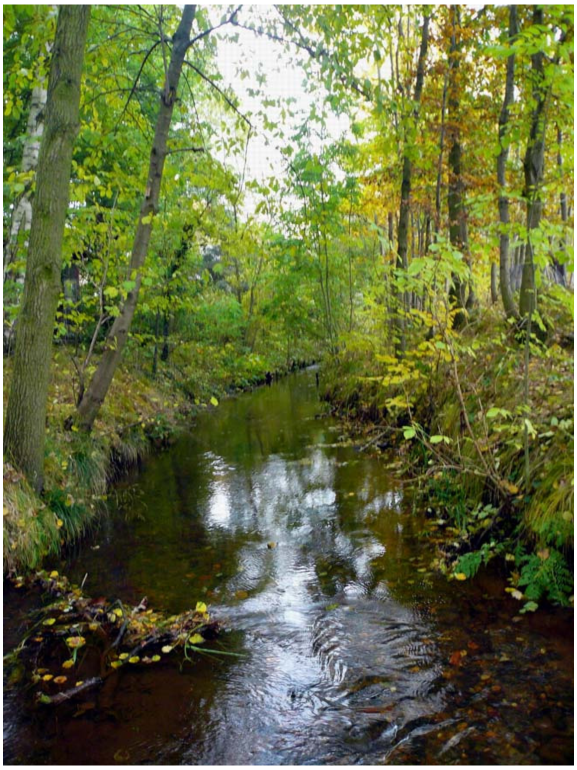

Figure 1. Location of the Marmorkrebs in Saxony.

autumn 2009, the measured water parameters were a temperature of 10.5°C, an oxygen content of 5.14 mg l^{-1}, a pH of 6.82, and an electrical conductivity of 550 µS. The above mentioned crayfish was coincidentally caught during a survey of freshwater fish fauna required by the EU Water Framework Directive, using hand-held electrofishing equipment (EFGI 650, Brett-schneider Spezialelektronik & Co., Germany). The specimen was transferred into an aquarium for further investigations. A follow-up examination at the location was carried out on 28th October 2009 by setting 45 "Pirate" traps (Bock-Ås Ltd., Finland) baited with pelleted fish food in a brook section, approximately 200 m above and below a small weir and in an adjacent fish pond. The traps remained there overnight and were checked the next morning.

Molecular analysis

For the molecular genetic analysis we used partial sequences of the mitochondrial protein coding cytochrome oxidase subunit I gene (COI) and the mitochondrial 12S ribosomal RNA gene, two well established markers for identifying species (Hebert et al. 2003; Balitzki-Korte et al. 2005; Braband et al. 2007; Melton and Holland 2007; Ferri et al. 2009). These sequences were obtained from tissues samples of the cambarid found in Saxony, from one specimen belonging to our Marmorkrebs laboratory culture at the Humboldt-Universität zu Berlin, and from specimens of the two morphologically similar cambarid species, *Procambarus fallax* and *P. alleni*, both bought in the Berlin aquarium trade. Total DNA was extracted using a DNA extraction kit (DNeasy® Blood & Tissue Kit, Qiagen). For amplifying the COI fragment we used the universal primer pair LCO1490/HCO2198 designed by Folmer et al. (1994) following the slightly modified protocol described by the same authors. PCR was performed in a final volume of 25 µl with 10 to 100 ng of total DNA, $1\times(NH_4)_2SO_4$ buffer, 3 mM $MgCl_2$, 0.2 mM of each dNTP, 0.2 µM of each forward and reverse primer, and 0.6 U Taq DNA polymerase. Amplification commenced with 94°C for 2 min followed by five cycles of 1 min at 96°C, 1.5 min at 45°C and 1.5 min at 72°C, afterwards succeeded by 35 cycles of 93°C for 1 min, 50°C for 1.5 min, 72°C for 1.5 min, and finished finally with a 5-min extension at 72°C. 12S rRNA was amplified using the primers CF12FOR (5'-AMATGARAGCGACGGGCGAT) and CF12REV(5'-AWCAAYTAGGATTAGATACC) designed by Braband et al. (2007) according a standard PCR protocol with 40 cycles of 94°C for 30 s, 40°C for 30 s, and 72°C for 40s, and with a final extension of 72°C for 5 min. All PCR products were purified by the QIAquick® PCR Purification Kit (Qiagen) and sense and antisense strand of the fragments were sequenced by the sequencing service company AGOWA genomics. The received sequences of the analyzed crayfish were aligned using the computer program BioEdit vers. 7.0.9.0. for Windows (Ibis Biosciences, USA; Hall 1999).

Results

The specimen caught by electrofishing in Saxony was a female with a total length (tip of rostrum to end of telson) of 6.8 cm and a weight of 5.7 g. Thus far, it is the only individual found at the collection site. The later trap sampling campaign in the area did not lead to the collection of any additional crayfish specimens. In spite of its overall similarity, the Marmorkrebs from Saxony shows distinct morphological differences to the specimens in our laboratory culture in Berlin. These differences concern the marbled pattern, the rostrum shape, and the presence of several spines at the margin of the rostrum (Figure 2). In particular, the rostrum variations led to uncertainties because shape and other features of this body part are important characters for species identification within cambarids (Hobbs 1942). The collected specimen was placed separately into a tank and kept isolated under the conditions of our laboratory Marmorkrebs culture as per Jimenez and Faulkes (2010). After about one month in captivity it laid eggs on the 16th November that developed normally. The absence of any sign of a previous fertilisation (i.e. no spermatophores) indicates that the individual reproduced parthenogenetically.

Multiple sequence alignment of identically long COI and 12S sequences revealed that the specimen from Saxony showed a 100% sequence identity in both genes to the Marmorkrebs in our laboratory culture. In contrast to this, there were some differences to *Procambarus fallax* in the COI gene and distinct differences to *P. alleni* in both genes (Table 1). In addition, a pairwise sequence alignment of combined longer COI and 12S sequences from the crayfish collected in Saxony and the Marmorkrebs revealed concurrence in 1057 nucleotide positions.

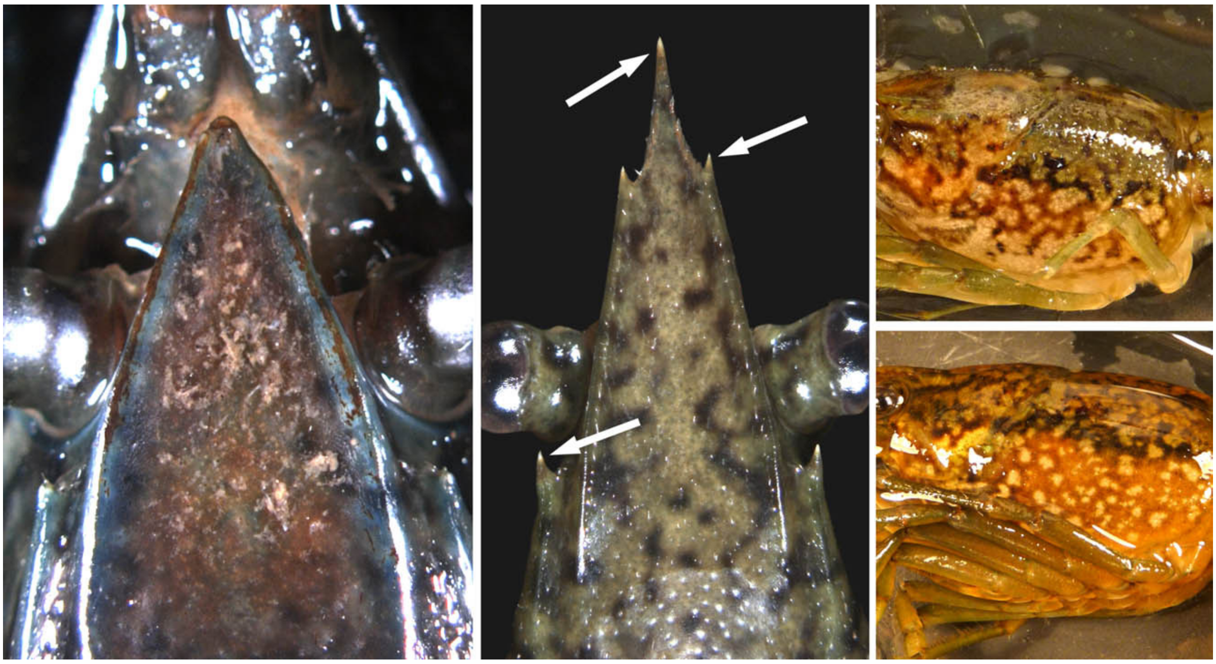

Figure 2. Dorsal view of the rostrum of a Marmorkrebs from the laboratory culture at the Humboldt-Universität zu Berlin (left) and that of the specimen collected in Saxony (centre). Lateral aspect of the carapace of the same specimens of the Humboldt-Universität zu Berlin (top right) and from Saxony (bottom right). Arrows point to the differences between the Saxon specimen and the animals from the Berlin laboratory culture (see text for details).

Table 1. Alignments of the COI and 12S sequences of the Marmorkrebs from Saxony (GenBank® accession numbers: HM358011 and HM358015), of one specimen from our laboratory culture at the Humboldt-Universität zu Berlin, and of two other crayfish species having a similar appearance. The values beside the gene name indicate the total lengths of the sequences.

Species	GenBank® accession number, nucleotide substitutions and percentage similarity					
	COI (678 bp)			12S (366 bp)		
Marmorkrebs (HU)	HM358010	0	100%	HM358014	0	100%
Procambarus fallax	HM358012	4	99.4%	HM358016	0	100%
Procambarus alleni	HM358013	46	93.2%	HM358017	11	97.0%

Discussion

The molecular genetic analysis strongly suggests that the specimen collected in Saxony is a Marmorkrebs. This result is supported by the fact that this animal reproduces parthenogenetically. In contrast to this, the individual from Saxony shows some striking morphological differences to the Marmorkrebs in our laboratory culture. This initially seems surprising bearing in mind the fact that the parthenogenetic Marmorkrebs propagates apomictically (i.e. eggs do not undergo meiosis); a reproduction mode which leads to genetically identical offspring (Martin et al. 2007). Nevertheless, this observation corroborates the results of Vogt et al. (2008) who described a high variability concerning coloration, growth, life-span, reproduction, behaviour and number of sense organs within Marmorkrebs maintained under standardised conditions. As a reason for this unexpected variability the authors suggested "developmental noise" (Vogt et al. 2008). The term developmental noise comprises all internal and randomly occurring non-genetic or environmentally induced changes during ontogenesis (Scheiner et al. 1991). On the other hand, the formation of several spines in the free-living Saxon specimen could also be a sign of predator-induced plasticity (Krueger and Dodson 1981; Bollache et al. 2005) or caused by strong water currents, but these are speculations and explicit evidence is currently lacking.

With the new record of a Marmorkrebs, the number of freshwater crayfish species in Saxony increases to six (in addition to the Marmorkrebs, the indigenous species: *Astacus astacus* (Linnaeus, 1758), *Austropotamobius torrentium* (Schrank, 1803), and the introduced species: *Astacus leptodactylus* (Eschscholtz, 1823), *Orconectes limosus* (Rafinesque, 1817), *Pacifastacus leniusculus* (Dana, 1852)) (Martin et al. 2008). However, despite some efforts we could not find further specimens at the Saxon collection site. Thus, the existence of a stable free living Marmorkrebs population in Europe has yet to be demonstrated. As in Saxony, all previous records of Marmorkrebs (Blanke and Schulz 2003; Marten et al. 2004; Koese and Vletter 2008; Marzano et al. 2009) were based solely on the collection of single individuals (except for the Dutch instance where, according to www.marmorkrebs.org, the species is said to still be present four years after its first detection; however, this needs confirmation). Furthermore, the small number of detected wild Marmorkrebs in Europe is somewhat surprising. The Marmorkrebs is known for its undemanding nature and its high fertility, and is thus common and widespread among aquarium hobbyists (Lukhaup and Pekny 2009). This raises the general question of whether the Marmorkrebs really has the potential for considerable expansion in Europe.

Other examples of crayfish introductions into Europe might shed some light on this problem. The most successful invasive cambarid crayfish species in Europe over the last hundred years or more is the spiny-cheek crayfish *Orconectes limosus* which originates from the colder parts of North America (Hamr 2002). The same is true for the North American astacid, *Pacifastacus leniusculus*, which has also established stable populations in central and northern Europe over the last fifty years (Holdich 2002; Souty-Grosset et al. 2006; Holdich et al. 2009). The most interesting case in this context, however, is the papershell crayfish, *Orconectes immunis* (Hagen, 1870), an American cambarid species of similar size and behavior to the Marmorkrebs which like the latter appeared in south-west Germany in the mid-1990s. Within just six years, this species spread along the northern Upper Rhine spanning a length of more than 90 km and reaching abundances of up to two individuals per square metre (Bernauer and Jansen 2006; Gelmar et al. 2006). The natural distribution of *O. immunis* is the northeastern United States and southeastern Canada (Hobbs 1989). Hence the central European climate offers ideal living conditions for this species

The origin and natural habitats of the Marmorkrebs are still unknown. Nevertheless, it is reasonable to assume that the natural distribution of the Marmorkrebs lies in the south-eastern USA. This assumption is based on the fact that the two species considered the closest relatives to the Marmorkrebs, *Procambarus fallax* and *P. alleni* (Scholtz et al. 2003; Vogt 2008), occur in Florida. Hence, the key to understanding the relatively poor success of the Marmorkrebs in establishing populations in central Europe might lie in its requirement for higher water temperatures. It is known that Marmorkrebs are able to survive the European winter (Pfeiffer 2005). Nevertheless, their optimum water temperature with respect to growth, reproduction, and mortality ranges between 20–25°C (Seitz et al. 2004). On the other hand, at temperatures lower than 15°C, the individual growth rate of Marmorkrebs decreases significantly and reproduction stops (Seitz et al. 2004). Florida waters reach this optimal temperature for, on average, seven to ten months (from North to South) (Beaver et al. 1981), while in Central Europe the water temperature barely exceeds 20°C over a period of only three months (according mean values of the Wannsee Lake in Berlin recorded by the Institute of Meteorology, Freie Universität Berlin, 2010). In northern Florida the period with water temperatures less than 15°C is only three months or one month in southern Florida respectively (Beaver et al. 1981). In contrast to this, Central European water bodies exhibit such unfavourable temperatures over seven months. This means, therefore, that Marmorkrebs may find unfavourable environmental conditions in the largest part of Europe, under which they can neither grow well nor reproduce, during most of the year. Furthermore, if one considers that the brooding period of the Marmorkrebs is on average one month, and that the time after release of the young to the next spawn is on average two months at a temperature of 20 to 25°C (Seitz et al. 2004), it seems unlikely that they are able to propagate in the wild more than once a year. In addition, because of the reduced growth rate at lower temperatures Marmorkrebs would be expected to mature later and their body size to remain small for a longer period, which also means fewer eggs (Seitz et al. 2004). Last but not least, the Marmorkrebs is an all female population that is thought as less aggressive than gonochoristic species with their combative males (Vogt 2008). Thus, it could be suggested that the Marmorkrebs, in spite of all previous expectations, does not have the potential for wide expansion within Europe.

However, with this tentative conclusion we do not want to downplay the risks of a Marmorkrebs introduction. For instance, in Madagascar, which has regionally a subtropical climate similar to Florida, large populations of Marmorkrebs have recently become established at several sites and now threaten the vulnerable endemic crayfish fauna (Jones et al. 2008; Kawai et al. 2009). Whether such a scenario is also possible in parts of Europe with a milder climate can only be speculated. Nevertheless, given that the world is currently in a phase of "global warming" there is an increasing possibility for a successful invasion of Europe by the Marmorkrebs. In summary, we think there is no reason for panic. Nevertheless we strongly recommend extreme caution in dealing with Marmorkrebs, not the least because of the risk of spreading the crayfish plague to the already threatened indigenous species (Culas 2003).

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