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Research Article

The clones are coming – strong increase in Marmorkrebs [*Procambarus fallax* (Hagen, 1870) f. *virginalis*] records from Europe

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Abstract

We describe a new occurrence of parthenogenetic Marmorkrebs in southwestern Germany and give a synopsis of recent records of this species in Europe. Including the most recent records, 15 Marmorkrebs records are currently known, most of which are from Germany. At least six records represent established populations, which is an alarming increase beyond the one Marmorkrebs population known prior to 2010. Most established populations occur in lentic habitats near conurbations, typically in highly frequented secondary habitats, such as gravel pit lakes. In three instances, Marmorkrebs migrated over land, demonstrating their potential for active spread, and two invasive populations endanger indigenous crayfish populations. Most Marmorkrebs populations are large and are most likely several years old, suggesting a considerable lag between introduction and detection. Marmorkrebs populations in Europe are most likely the result of deliberate releases from aquaria, although secondary introductions may have occurred in one instance. Because Marmorkrebs are still widespread in the European pet trade, which most likely generates substantial propagule pressure, it is likely that the number of established populations will further increase over time. To mitigate the risk of further harmful crayfish releases, we suggest the prohibition of trading live high-risk crayfish species, including Marmorkrebs.

Key words: aquarium introductions; marbled crayfish; invasiveness

Introduction

The Marmorkrebs is an enigmatic crayfish species of North American origin. It was first discovered in the German pet trade in the mid 1990s, when aquarium enthusiasts reported an all-female crayfish species that reproduces without males (Lukhaup 2001). Due to their characteristic and conspicuous color pattern, these crayfish quickly became known as `Marmorkrebs´ (German, which translates into English as `marbled crayfish´). Scientists have puzzled for almost a decade about their phylogenetic position and status. Using genetic and morphological comparisons, Martin et al. (2010a) recently showed that Marmorkrebs are the parthenogenetic form of *Procambarus fallax* (Hagen, 1870) and proposed the tentative scientific name *Procambarus fallax* f. *virginalis*. The Marmorkrebs is unique because it is the only known decapod crustacean that obligatory reproduces by apomictic parthenogenesis: only females exist, which lay unfertilized eggs that develop into genetically identical offspring (Scholtz et al. 2003; Martin et al. 2007; Vogt et al. 2008). No males have been found in the laboratory or in introduced, wild populations (Seitz et al. 2005; Jones et al. 2009; Janský and Mutkovič 2010).

Marmorkrebs had circulated in the European pet trade for several years before the first free-living individuals were captured in Europe and Madagascar in 2003 (Soes and van Eekelen 2006; Jones et al. 2009). The major pathway for Marmorkrebs introduction is the deliberate release of aquarium specimens (Soes and van Eekelen 2006; Souty-Grosset et al. 2006; Chucholl 2011). Their appealing coloration, undemanding nature and exceptional mode of reproduction make Marmorkrebs attractive to aquarium hobbyists. However, parthenogenesis permits a high reproductive potential, and Marmorkrebs can overpopulate an aquarium quickly. Aquarium hobbyists will likely offload

their excess stock to either other aquarium hobbyists or natural habitats (Souty-Grosset et al. 2006; Chucholl 2011). Because Marmorkrebs reproduce by parthenogenesis, the risk that released Marmorkrebs may seed viable populations in the wild is considerably greater than that for sexually reproducing crayfish species – a single Marmorkrebs is sufficient to create a new population.

Marmorkrebs quickly became established in Madagascar and are considered to be `perfect invaders´ there (Jones et al. 2009). On the contrary, in Europe, almost all published Marmorkrebs records between 2004 and 2009 are accounts of single individuals, suggesting that Marmorkrebs might fail to establish self-sustaining populations in temperate zones (Marten et al. 2004; Souty-Grosset et al. 2006; Nonnis Marzano et al. 2009; Martin et al. 2010b). In 2010, the situation dramatically changed when the first informal evidence for an established Marmorkrebs population in Germany was published by newspapers (Privenau 2010): the local media repeatedly reported on Marmorkrebs emerging from a small pond in a village near Halle (Saxony-Anhalt; Wendt 2011). Shortly afterward, a research paper provided evidence that Marmorkrebs had established another stable, reproducing population in a small lake near the city of Freiburg (Baden-Württemberg; Chucholl and Pfeiffer 2010). Since then, numerous additional Marmorkrebs records from Europe were reported, including more reproducing populations.

The purpose of the present article is twofold: (1) to describe a new occurrence of Marmorkrebs in southwestern Germany that was discovered in 2011, and (2) to give a synopsis of the recent records of this species in Europe, including newly discovered populations in other parts of Germany and Slovakia. We then use the available information to discuss the introduction history, population trend, and invasiveness of Marmorkrebs in Europe. Because Marmorkrebs are primarily introduced from aquaria (Souty-Grosset et al. 2006; Chucholl 2011), we focus on the risks associated with aquarium introductions, a newly emerging introduction pathway of non-indigenous crayfish species (NICS) that may add yet another chapter to the notorious history of NICS introductions in Europe (cf. Holdich et al. 2009; Chucholl 2010). Our findings may therefore help with invasive species risk assessment and the prioritization of introduction pathway management.

New occurrence of established Marmorkrebs in southwestern Germany

On September 14, 2011, one of the authors (KM) discovered a live Marmorkrebs at a pedestrian underpass, 130 m from a gravel pit lake (Lake Epplesee; Figure 1A, B; Table 1, Nr. 13). Lake Epplesee is a shallow, eutrophic lake with a surface area of 26.6 ha and a maximum depth of 5 m. It lies 302 m above sea level, in close proximity to the River Neckar. The lake is popular for several recreational activities, including swimming, sunbathing, and angling, and is highly frequented because of its easy accessibility from a nearby highway. Lake Epplesee is situated in the vicinity of Tübingen but also attracts people from Reutlingen and Stuttgart.

To verify the sighting, the northern lake margin was sampled using a hand-held net on September 30, 2011. Within five minutes, two Marmorkrebs were captured within an area of approximately 2 m^2, and a third individual was spotted, but escaped. One of the captured females carried hatchlings, while the other female exhibited active glair glands on the ventral side of the pleon, indicating breeding condition. In addition, two dead individuals were found at the pedestrian underpass, which is separated from the northern lake margin by a 100 m stretch of sunbathing area (Figure 1C, D). The Marmorkrebs captured from the lake measured 29.6 and 50.2 mm in carapace length (*CL*: measured from the tip of the rostrum to the dorsal posterior margin of the cephalothorax with a digital slide caliper), and the two dead individuals measured 47.1 and 44.5 mm *CL*.

The occurrence of a `new crayfish´ in Lake Epplesee has been known to recreational fishermen since at least 2010, when the species was reportedly already very abundant. Close to Lake Epplesee is the brook Schlierbach (*cf.* Figure 1C), which is inhabited by indigenous stone crayfish [*Austropotamobius torrentium* (Schrank, 1803)], an endangered species in the federal state of Baden-Württemberg (Chucholl and Dehus 2011). The environmental and fisheries agencies currently attempt to control and to contain the Marmorkrebs population, *e.g.*, through stocking and managing of predatory fish and discouraging the public from transplanting and fostering Marmorkrebs (M. Konrad, pers. comm. 2011).

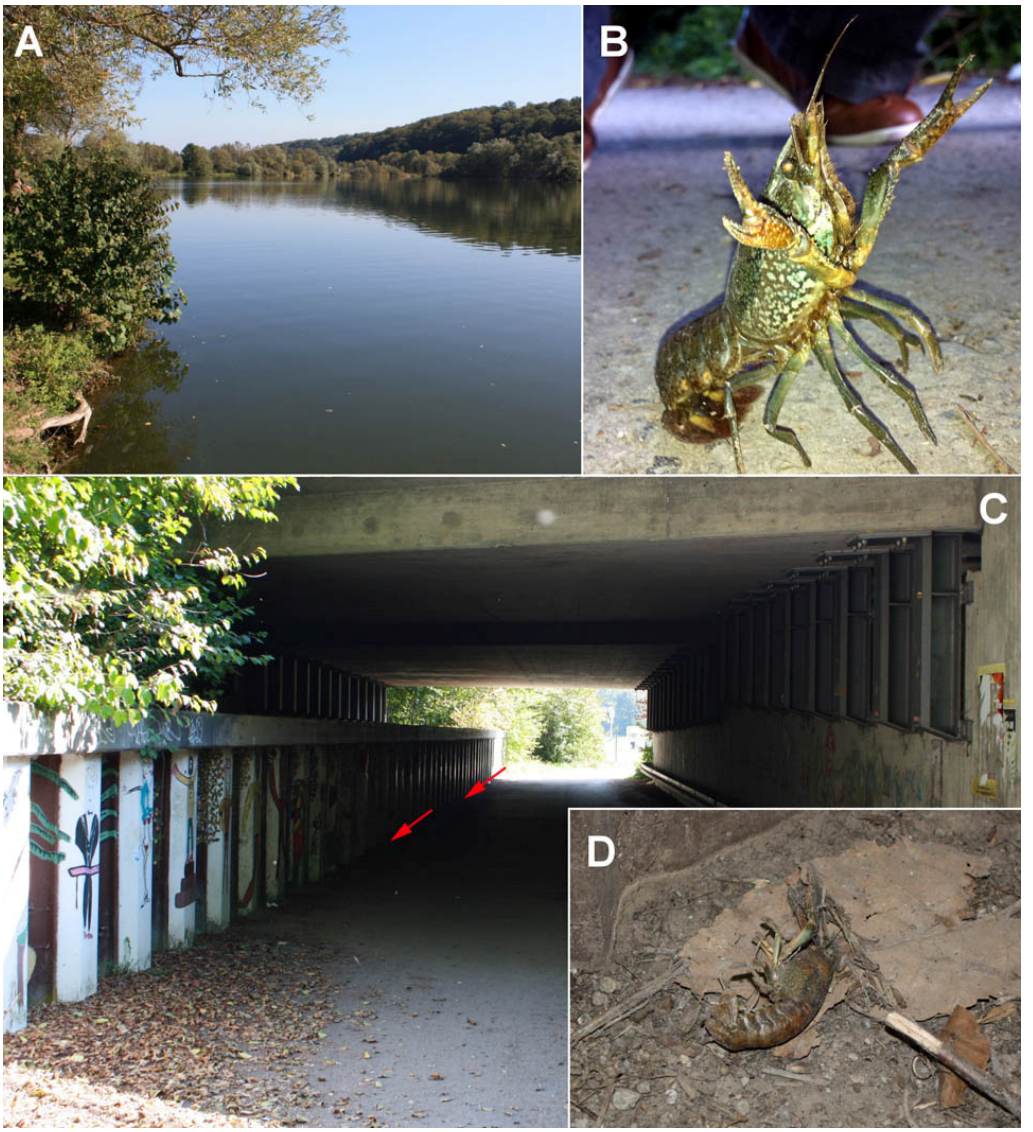

Figure 1. Lake Epplesee (**A**) and the pedestrian underpass (**C**), where Marmorkrebs were first found (**B**: live individual on September 14, and **D**: dead individual on September 30, 2011; red arrows mark the locations where the two dead Marmorkrebs were found). The pedestrian underpass is located 130 m northeast of Lake Epplesee, and it is separated from the lake by a 100 m stretch of sunbathing area (visible in the background of **C**). Behind the metal boarding on the left side of the walkway is the brook Schlierbach, which is inhabited by the endangered stone crayfish (*Austropotamobius torrentium*). Photographs **A**, **C**, and **D** by CC, photograph **B** courtesy of KM.

Synopsis of Marmorkrebs records from Europe

The year of the initial recording, country, location, habitat, population status, collection method, and additional comments are summarized for each of the known Marmorkrebs records from Europe in Table 1, and the present European distribution of Marmorkrebs is shown in Figure 2.

In total, 15 Marmorkrebs records are currently known in Europe, excluding putative records that could not be verified by voucher specimens or photos. Most of the records were initially discovered after 2005, and 13 of the 15 records were only discovered within the past four years (Figure 3). The vast majority of the records were reported in Germany (12), while one record each was reported from the Netherlands, Italy and

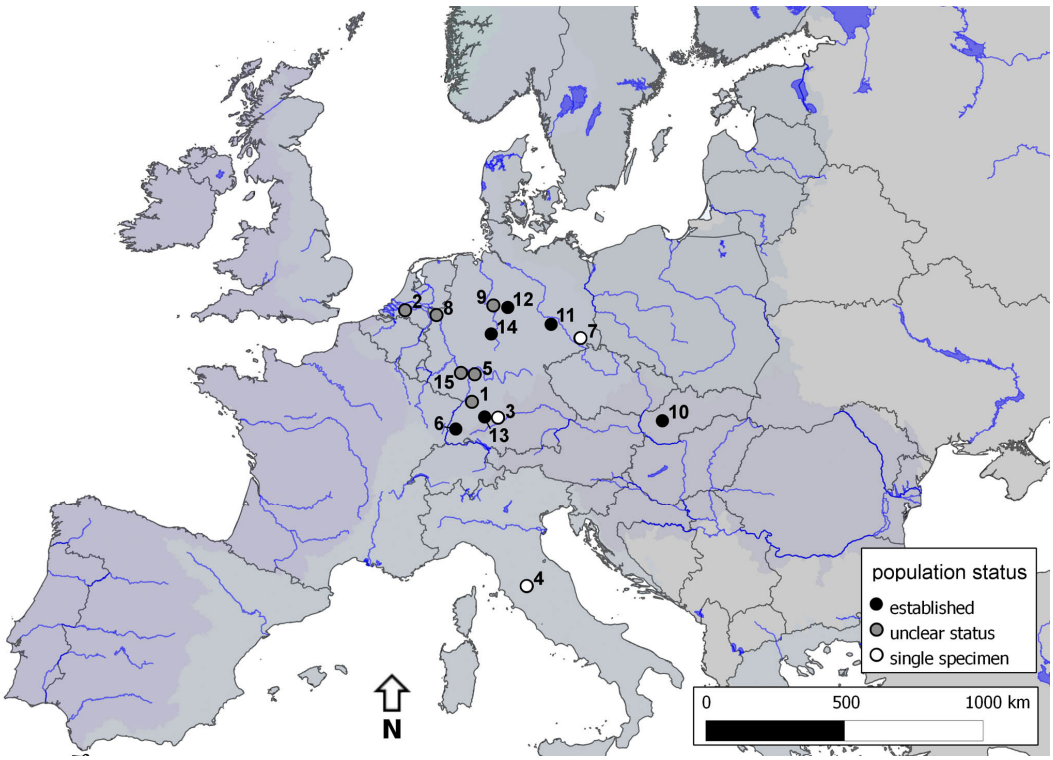

Figure 2. Current distribution of Marmorkrebs in Europe, shown as presence in CGRS grid squares. Numbers refer to the records summarized in Table 1.

Slovakia (Figure 2). Marmorkrebs were found in both lotic and lentic freshwater habitats, including brooks, rivers, canals, natural and artificial lakes, and ponds; however, established populations have only been found in lentic habitats (*cf.* Table 1). Out of the 15 records, six clearly represent established populations, and on the basis of the collection of several individuals, five additional records might also represent established populations. Single individuals that most likely failed to propagate, *i.e.*, failed introductions, were reported in three cases, of which two involved captures from small brooks (Table 1, Nr. 3 and 7). The methods used to detect Marmorkrebs varied considerably and included accidental by-catch, observations/ captures of individuals crawling on land, electrofishing, trapping, manual search, and observations made by snorkeling/diving. In at least four cases, Marmorkrebs occurred in sympatry with *Orconectes limosus* (Rafinesque, 1817) or *Procambarus clarkii* (Girard, 1852) (Table 1, Nr. 1, 4, 6, and 15).

Apart from the records summarized above, at least four additional putative records of Marmorkrebs in Germany have been reported and cover three federal states; however, these records have not been verified yet (Chucholl and Dehus 2011; H. Groß, unpublished data). In Slovakia, Marmorkrebs apparently also formed breeding populations in garden ponds (Stloukal 2009). Dead Marmorkrebs found on the land were repeatedly reported from North Rhine-Westphalia (Germany; H. Groß unpublished data), suggesting that the estimated number of unreported Marmorkrebs occurrences is still high (*cf.* Chucholl and Pfeiffer 2010).

Discussion

The Marmorkrebs is an extraordinarily successful crayfish species. It was first discovered in the German pet trade in the mid-1990s (*cf.* Werner 1998; Figure 3) and was first mentioned in a scientific publication in 2002 (Scholtz et al. 2002). By this time, it was already

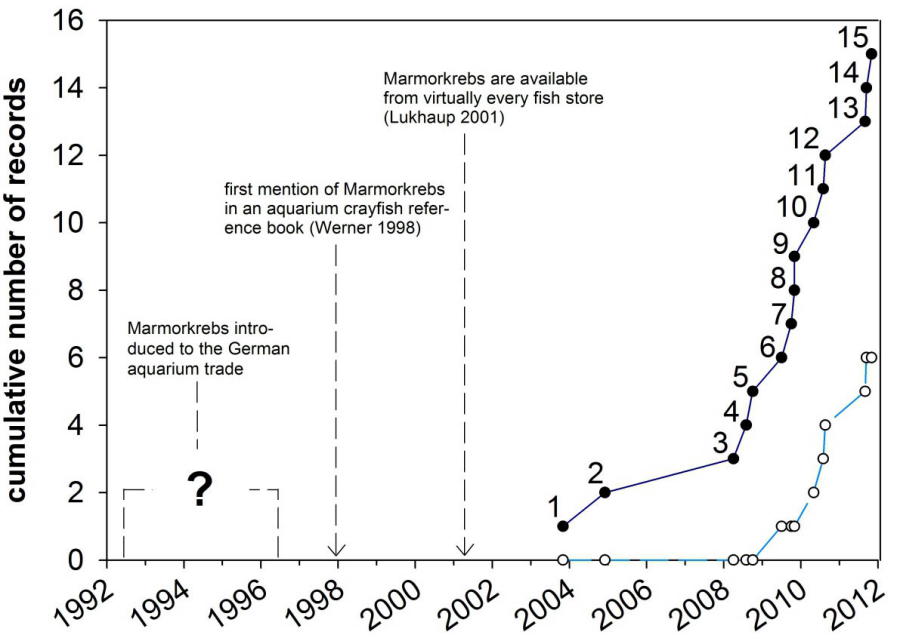

Figure 3. Important events and cumulative number of Marmorkrebs records in Europe in relation to time. The total number of records is depicted as a solid line with solid symbols, and the number of established populations is depicted as a broken line with open symbols. Numbers refer to the records summarized in Table 1.

very popular as an aquarium pet (Lukhaup 2001; Figure 3). Only 10 years later, it has become a highly invasive species in Madagascar (Jones et al. 2009), was introduced into freshwater habitats in Japan (Kawai and Takahata 2010), and is well established in various parts of Europe (summarized in Table 1; Figures 2 and 3). Including the new occurrence described here, at least six established Marmorkrebs populations are currently known in Europe, representing an alarming increase beyond the one population known prior to 2010 (*cf.* Figure 3). Most populations are large and are most likely several years old, suggesting a considerable lag between introduction and detection. Given this probable lag between introduction and detection, it is likely that the currently observed trend of increasing population numbers is a result of introductions that occurred several years ago, presumably around the time that Marmorkrebs became popular in home aquaria (*cf.* Figure 3). This interpretation is in accordance with the propagule pressure hypothesis, which states that a major determinant of the invasion success of a non-indigenous species is the number of independent release events (propagule number) plus the number of individuals released in any one event (propagule size), that is, introduction effort or propagule pressure (Lockwood et al. 2005; Lockwood et al. 2007).

The proliferation of Marmorkrebs as aquarium pets likely increased propagule pressure, and thereby the likelihood of establishment in nature (Lockwood et al. 2005; Duggan et al. 2006; Lockwood et al. 2007). Specifically, the great popularity of Marmorkrebs as aquarium pets probably results in many independent release events, *i.e.,* a high propagule number, which serves to overcome negative forces that are spatially structured, such as an unsuitable habitat at the site of introduction (Lockwood et al. 2005; Duggan et al. 2006). For instance, Marmorkrebs apparently failed to establish in cool, rapid-flowing brooks but eventually invaded lentic habitats. Marmorkrebs propagule pressure and, thus, the likelihood of establishment in nature, is probably highest in countries where (1) Marmorkrebs are popular aquarium pets and (2) human population density is high (*cf.* Lockwood et al. 2005; Perdikaris et al. 2012). Both of the criteria apply to Germany (Lukhaup 2001; Perdikaris et al. 2012), where five out of the six currently known Marmorkrebs populations in Europe are located (Figure 2).

Table 1. Current records of Marmorkrebs in Europe. Only records verified by voucher specimens or photos are included. *NA* means not available.

Nr	Year of record	Country, region	Location	Habitat	Population status	Collection method	Comments	References
1	2003	Germany, Baden-Württemberg	49°5'19"N, 8°22'17"E	gravel pitlake	unclear; single specimen	by-catch during *Lymnomysis* sampling	the specimen was first taken to be *Orconectes limosus*, but was later identified as Marmorkrebs; current status unclear	Marten et al. 2004
2	2004	Holland, Dordrecht, Vlij	51°48′49"N, 04°41′36"E	canal	unclear; established from 2004-2008	capture of crayfish crawling on the land	the current status is unclear (Soes and Koese 2010)	Soes and van Eekelen 2006
3	2008	Germany, Bavaria	48°26'46"N, 10°09'28"E	brook	single specimen	electrofishing	nocturnal manual search yielded no further specimens	C. Chucholl, unpublished data
4	2008	Italy, Tuscany	43°16'51"N, 11°50'12"E	canal	single specimen	electrofishing, trapping	single Marmorkrebs in sympatry with a large *Procambarus clarkii* population	Nonnis Marzano et al. 2009
5	2008	Germany, Hesse	49°58'43"N, 08°36'59"E	shallow ditch	unclear; three individuals were captured	trapping	the ditch was almost dry, and the Marmorkrebs were captured from a pool	R. Hennings, pers. com. 2012
6	2009	Germany, Bden-Württemberg	48°01'53"N, 07°48'18"E	lake	established population	observation (snorkeling), manual search	in sympatry with *O. limosus*; a few Marmorkrebs were later observed in the lake outflow	Chucholl and Pfeiffer 2010
7	2009	Germany, Saxony	51°20'17"N, 13°33'33"E	brook	single specimen	electrofishing	subsequent trapping yielded no further specimens	Martin et al. 2010
8	2009	Germany, North Rhine-Westphalia	51°27'36"N, 06°43'24"E	Rhine harbor	unclear; several specimens were collected	NA	the harbor was later subject to construction works, possibly destroying the potential population	H. Groß, unpublished data
9	2009	Germany, Lower Saxony	52°10'14"N, 09°05'48"E	river	unclear; several specimens were collected	NA	no further information available	H. Groß, unpublished data
10	2010	Slovakia, Western Slovakia	48°28' N, 17°49' E	gravel pit lake	established population	electrofishing	more than 150 Marmorkrebs were captured	Jansky and Mutkovic 2010
11	2010	Germany, Saxony-Anhalt	51°28'58"N, 12°07'13"E	pond	established population	observation of crayfish crawling on the land	people collected Marmorkrebs migrating over land and probably transplanted them to garden ponds	Privenau 2010; Wendt 2011
12	2010	Germany, Lower Saxony	52°12'55"N, 09°49'33"E	pond	established population	observation made by divers, netting	Divers took a picture of a Marmorkrebs in 2010; an unconfirmed record dates back to 2007	Pyka 2010
13	2011	Germany, Baden-Württemberg	48°32'36"N, 09°09'14"E	gravel pit lake	established population	observation of crayfish crawling on the land, manual search	Marmorkrebs were observed to migrate over land; probably a large population	present study
14	2011	Germany, Hesse	51°03'33"N, 09°18'22"E	pit mine lake	established population	observation, dip netting	Marmorkrebs were first observed by a recreational angler; probably a large population	Dümpelmann and Bonacker (in press); Hessenfischer 2011
15	2011	Germany, Rhineland-Palatinate/ Hesse	49°58' N, 07°53' E	Rhine River	unclear; one reproducing individual was captured	NA	one Marmorkrebs with attached hatchlings and six *O. limosus* were collected from the Rhine River	H. Groß, unpublished data

Because Marmorkrebs are still abundant in the European pet trade (Stloukal 2009; Chucholl 2010; Soes and Koese 2010) and there is potentially a lag between introduction and detection, it is likely that the number of records of established populations will further increase with time. Marmorkrebs are acquired through retail pet shops, various online sources, and personal contacts between aquarium hobbyists (Stloukal 2009; Faulkes 2010; Soes and Koese 2010). Retail stores offer Marmorkrebs at approximately €5 per animal, whereas aquarium hobbyists often give their excess stock away for free (*cf.* Chucholl 2011). For instance, a search for `Marmorkrebs´ at a German online marketplace (http://www.kleinanzeigen.ebay.de) on January 12,

2012 resulted in 36 hits, and most of these vendors offered the animals for free or at prices below €5 per crayfish. In recent years, Marmorkrebs have also become popular as live food for predatory aquarium fish and ornamental turtles owing to their undemanding nature and high reproductive potential. Because ornamental turtles are frequently kept in outdoor ponds, using Marmorkrebs as a food source may facilitate accidental introductions. It is an even greater concern that Marmorkrebs are deliberately released into garden ponds (Stloukal 2009), from which they can easily escape to nearby freshwater habitats.

Introduced Marmorkrebs have been found in both lentic and lotic freshwater habitats (e.g., Marten et al. 2004; Martin et al. 2010b). However, established populations in Europe have been found in lentic habitats only (cf. Table 1), which agrees with Chucholl's and Pfeiffer's (2010) suggestion that Marmorkrebs are most likely able to colonize summer-warm, lentic habitats in most parts of Europe. In Madagascar, Marmorkrebs were reported from a great variety of habitats, including rice paddies, rivers, lakes and swamps (Heimer 2010), as well as brick pits, drainage ditches and fish ponds (Jones et al. 2009). Most established populations in Europe occur in habitats near conurbations, typically in highly frequented secondary habitats, such as gravel pit lakes. Introductions from aquaria are more likely to occur in highly frequented habitats than in remote habitats because the latter are usually more easily accessible and may already be known to the potential pet releaser. However, the probability of detection is presumably also higher in highly frequented habitats, which may confound this effect.

In at least three instances, Marmorkrebs were observed to migrate over land (Table 1, Nr. 2, 11, and 13; Figure 1), and single dead Marmorkrebs found on the land were repeatedly reported from North Rhine-Westphalia (H. Groß, unpublished data). The frequent observation of Marmorkrebs migrating over land suggests that this behavior is most likely an inherent dispersal mechanism for this species, rather than an escape mechanism in response to adverse environmental conditions. Established Marmorkrebs populations may therefore act as latent `bridgeheads´ for a further active range expansion both *via* waterways and land. Any attempts to contain local populations should take both pathways into account. A further potential pathway for spreading is translocation by humans, *i.e.,* secondary introductions. This mechanism of spreading most likely occurred in Saxony-Anhalt (Table 1, Nr. 11), where people collected Marmorkrebs migrating over land and most likely transplanted them to garden ponds (Wendt 2011).

During the last decade, Marmorkrebs were primarily known as aquarium pets. Most research on these organisms was carried out in the laboratory and was concerned with their exceptional mode of reproduction or use as a model organism for development, epigenetics and toxicology (*e.g.*, Seitz et al. 2005; Martin et al. 2007; Vogt 2008). It is only more recently that Marmorkrebs have been considered as an invasive species, and in fact their life history and trophic ecology in nature are almost unknown. For instance, nothing is known about the trophic position and ecological impact of Marmorkrebs. Given the major impacts of the related species *P. clarkii* on recipient ecosystems (Souty-Grosset et al. 2006, and citations therein), Marmorkrebs may have a profound impact on the species richness, functioning and integrity of ecosystems.

Marmorkrebs most likely pose a serious threat to the indigenous European crayfish species because they may compete with other species for food and space, and they may transmit crayfish plague (Jones et al. 2009; Chucholl and Pfeiffer 2010). Jimenez and Faulkes (2011) studied direct aggressive interactions between Marmorkrebs and *P. clarkii* and concluded that Marmorkrebs have the potential to compete with other crayfish species. Furthermore, Marmorkrebs differ ecologically from the more *K*-selected indigenous European crayfish because Marmorkrebs have a fast growth rate, very high fecundity and an extended breeding period (Seitz et al. 2005; Jones et al. 2009; Chucholl and Pfeiffer 2010), all of which might give an additional competitive advantage to Marmorkrebs. The risk of devastating consequences for indigenous crayfish would dramatically increase if Marmorkrebs were infected with the causative agent of crayfish plague, *Aphanomyces astaci* Schikora, 1903: any contact between Marmorkrebs and the susceptible European crayfish would almost certainly result in mass mortalities among the susceptible species. This potential threat to indigenous crayfish is alarming, especially because at least two of the six established Marmorkrebs populations already endanger indigenous crayfish populations (Table 1, Nr. 6 and 13).

Conclusion

Without much doubt, all Marmorkrebs introductions trace back to this species' first occurrence in the German pet trade in the mid-1990s. It circulated in the European pet trade for several years before the first free-living individuals were captured in Germany and the Netherlands (*cf.* Table 1 and Figure 3). The currently observed and alarming increase in established populations is likely to continue over time, unless Marmorkrebs propagule pressure from the pet trade decreases. The introductions occurred despite public education efforts, explicitly advising to not release Marmorkrebs into nature (*e.g.*, Lukhaup 2001; Lukhaup and Pekny 2005; Lukhaup and Pekny 2007; Edelkrebsprojekt NRW 2009). In fact, one of the first articles on Marmorkrebs in a popular German aquarium magazine (Lukhaup 2001) and the first scientific mention of Marmorkrebs, published in *Nature* (Scholtz et al. 2002), both implied warning that Marmorkrebs may become a pest if released from captivity. Unfortunately, there is no magic "silver bullet" to eradicate established NICS populations (Gherardi et al. 2011) and Marmorkrebs do not need to maintain a minimum viable population size. Their resilience against small population size renders eradication of established Marmorkrebs populations even more difficult or even impossible. The prevention of new introductions is therefore imperative. Given the apparent ineffectiveness of public education efforts to halt exotic crayfish releases, we suggest the prohibition of trading live high-risk crayfish species, including Marmorkrebs.

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References

Chucholl C (2010) Invaders for sale: Does the ornamental freshwater crayfish trade constitute an actual and overlooked risk? In: Souty-Grosset C, Grandjean F, Mirebeau C (eds) (2010) Proceedings of the European crayfish, food, flagship and ecosystem services conference, Poitiers, France, October 26-29, 2010. Imprimerie Copy-Media, p 108

Chucholl C (2011) Der Handel mit exotischen Flusskrebsen. *Forum Flusskrebse* 15: 33–39

Chucholl C, Pfeiffer M (2010) First evidence for an established Marmorkrebs (Decapoda, Astacida, Cambaridae) population in Southwestern Germany, in syntopic occurrence with *Orconectes limosus* (Rafinesque, 1817). *Aquatic Invasions* 5: 405–412, http://dx.doi.org/10.3391/ai.2010.5.4.10

Chucholl C, Dehus P (2011) Flusskrebse in Baden-Württemberg. Fischereiforschungsstelle Baden-Württemberg (FFS), Langenargen, Germany, 92 pp

Duggan I, Rixon CAM, MacIsaac HJ (2006) Popularity and propagule pressure: determinants of introduction and establishment of aquarium fish. *Biological Invasions* 8: 377–382, http://dx.doi.org/10.1007/s10530-004-2310-2

Dümpelmann C, Bonacker F (in press) Erstnachweis des Marmorkrebses *Procambarus fallax f. virginalis* (Decapoda: Cambaridae) in Hessen. *Forum Flusskrebse*

Edelkrebsprojekt NRW (2009) Flusskrebse im Aquarium und Gartenteich. Edelkrebsprojekt NRW, Bad Münstereifel-Schönau, Germany, 6 pp

Faulkes Z (2010) The spread of the parthenogenetic marbled crayfish, Marmorkrebs (*Procambarus* sp.), in the North American pet trade. *Aquatic Invasions* 5: 447–450, http://dx.doi.org/10.3391/ai.2010.5.4.16

Gherardi F, Aquiloni L, Diéguez-Uribeondo J, Tricarico E (2011) Managing invasive crayfish: is there a hope? *Aquatic Sciences* 73: 185–200, http://dx.doi.org/10.1007/s00027-011-0181-z

Heimer K (2010) Invasion of self-cloning crayfish alarms Madagascar. Deutsche Presse-Agentur wire story. http://www.earthtimes.org/articles/news/339974,alarms-madagascar-feature.html (Accessed 12 January 2011)

Hessenfischer (2011) Vorkommen des invasiven Marmorkrebses (*Procambarus fallax* f. *virginalis*) im Singliser See. http://www.hessenfischer.net/natur/natur_18.htm (Accessed 9 January 2012)

Holdich DM, Reynolds JD, Souty-Grosset C, Sibley PJ (2009) A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. *Knowledge and Management of Aquatic Ecosystems* 11: 394–395. http://dx.doi.org/10.1051/kmae/2009025

Janský V, Mutkovič A (2010) Rak *Procambarus* sp. (Crustacea: Decapoda: Cambaridae) – Prvý Nález na Slovensku. *Zbornik Slovenského Národneho Múzea (Acta rerum naturalium Musei Nationalis Slovaci Bratislava*) 56: 64–67

Jimenez SA, Faulkes Z (2011) Can the parthenogenetic marbled crayfish Marmorkrebs compete with other crayfish species in fights? *Journal of Ethology* 29: 115–120, http://dx.doi.org/10.1007/s10164-010-0232-2

Jones JPG, Rasamy JR, Harvey A, Toon A, Oidtmann B, Randrianarison MH, Raminosoa N, Ravoahangimalala OR (2009) The perfect invader: a parthenogenic crayfish poses a new threat to Madagascar's freshwater biodiversity. *Biological Invasions* 11: 1475–1482, http://dx.doi.org/10.1007/s10530-008-9334-y

Kawai T, Takahata M (eds) (2010) Biology of Crayfish. Sapporo, Japan: Hokkaido University Press, Japan, 556 pp

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20: 223–228, http://dx.doi.org/10.1016/j.tree.2005.02.004

Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion Ecology. Blackwell Publishing, Oxford, UK, 304 pp

Lukhaup C (2001) *Procambarus* sp. - Der Marmorkrebs. *Aquaristik Aktuell* 7-8: 48–51

Lukhaup C, Pekny R (2005) Krebse im Aquarium. Dähne Verlag, Ettlingen, Germany, 160 pp

Lukhaup C, Pekny R (2007) Marmorkrebs bedroht madagassische Flusskrebsarten. http://www.crusta10.de (Accessed 30 May 2007)

Marten M, Werth C, Marten D (2004) Der Marmorkrebs (Cambaridae, Decapoda) in Deutschland - ein weiteres Neozoon im Einzugsgebiet des Rheins. *Lauterbornia* 50: 17–23

Martin P, Kohlmann K, Scholtz G (2007) The parthenogenetic Marmorkrebs (marbled crayfish) produces genetically uniform offspring. *Naturwissenschaften* 94: 843–846, http://dx.doi.org/10.1007/s00114-007-0260-0

Martin P, Dorn N, Kawai T, van der Heiden C, Scholtz G (2010a) The enigmatic Marmorkrebs (marbled crayfish) is the parthenogenetic form of *Procambarus fallax* (Hagen, 1870). *Contributions to Zoology* 79: 107–118

Martin P, Shen H, Füller G, Scholtz G (2010b) 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. *Aquatic Invasions* 5: 397–403, http://dx.doi.org/10.3391/ai.2010.5.4.09

Nonnis Marzano F, Scalici M, Chiesa S, Gherardi F, Piccinini A, Gibertini G (2009) The first record of the marbled crayfish adds further threats to fresh waters in Italy. *Aquatic Invasions* 4: 401–404, http://dx.doi.org/10.3391/ai.2009.4.2.19

Perdikaris C, Kozák P, Kouba A, Konstantinidis E, Paschos I (2012) Socio-economic drivers and non-indigenous freshwater crayfish species in Europe. *Knowledge and Management of Aquatic Ecosystems* 402, http://dx.doi.org/10.1051/kmae/2011077

Privenau K (2010) Marmorkrebs bringt Pest. Mitteldeutsche Zeitung news story. http://www.mz-web.de/servlet/ContentServer?pagename=ksta/page&atype=ksArtikel&aid=1286541132341&calledPageId=987490165154 (Accessed 2 December 2010)

Pyka H (2010) Marmorkrebs im Giftener Teich. http://www.fvhannover.de/joomla/index.php/neuigkeiten/469-Marmorkrebs-im-giftener-teich.html (Accessed 6 March 2012)

Scholtz G, Braband A, Tolley L, Reimann A, Mittmann B, Lukhaup C, Steuerwald F, Vogt G (2002) Parthenogenesis in an outsider crayfish. *Nature* 421: 806–806, http://dx.doi.org/10.1038/421806a

Seitz R, Vilpoux K, Hopp U, Harzsch S, Maier G (2005) Ontogeny of the Marmorkrebs (marbled crayfish): a parthenogenetic crayfish with unknown origin and phylogenetic position. *Journal of Experimental Zoology* 303: 393–405, http://dx.doi.org/10.1002/jez.a.143

Soes M, van Eekelen R (2006) Rivierkreeften, een oprukkend probleem? *De Levende Natuur* 107: 56–59

Soes M, Koese B (2010) Invasive crayfish in the Netherlands: a preliminary risk analysis. Interim report, Bureau Waardenburg bv, Stichting EIS-Nederland, Invasive Alien Species Team, Waardenburg, The Netherlands, 69 pp

Souty-Grosset C, Holdich DM, Noel PY, Reynolds JD, Haffner P, (eds), (2006) Atlas of crayfish in Europe. Muséum national d´Histoire naturelle, Paris, France, 187 pp

Stloukal E (2009) Recent distribution of non-indigenuous (sic) crayfish species in Slovakia. *Folia faunistica Slovaca* 14: 119–122

Vogt G (2008) The marbled crayfish: a new model organism for research on development, epigenetics and evolutionary biology. *Journal of Zoology* 276: 1–13, http://dx.doi.org/10.1111/j.1469-7998.2008.00473.x

Vogt G, Huber M, Thiemann M, van den Boogaart G, Schmitz OJ, Schubart CD (2008) Production of different phenotypes from the same genotype in the same environment by developmental variation. *The Journal of Experimental Biology* 211: 510–523, http://dx.doi.org/10.1242/jeb.008755

Wendt W (2011) Erstnachweis des invasiven Marmorkrebses, *Procambarus fallax* (HAGEN, 1870) f. *virginalis*, für Sachsen. *Forum Flusskrebse* 15: 39–42

Werner U (1998) Garnelen, Krebse und Krabben im Süßwasseraquarium, Aqualog Spezial, A.C.S., Mörfelden-Walldorf, Germany, 48 pp