# Marmorkrebs (*Procambarus virginalis*)
## Ecological Risk Screening Summary

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Photo: C. Chucholl. Licensed under Creative Commons B-SA 3.0 Unported. Available: https://commons.wikimedia.org/wiki/File:Marmorkrebs_Procambarus_fallax_forma_virginalis.JPG. (February 15, 2018).

# 1 Native Range and Status in the United States

## Native Range

From Faulkes (2015a):

"There are no known indigenous populations of *P. fallax* f. *virginalis* (Martin et al., 2010a)."

According to Gutekunst et al. (2018), *Procambarus virginalis* arose recently during breeding of *P. fallax* in captivity and therefore there is no native range for *P. virginalis*.

## Status in the United States

No records of wild populations of *Procambarus virginalis* in the United States were found.

From Faulkes (2015b):

"Three species account for most (83.7%) of the online crayfish trade in North America: Marmorkrebs (*Procambarus fallax* f. *virginalis*), the Cajun dwarf crayfish (*Cambarellus shufeldtii*), and the Mexican dwarf crayfish (*Cambarellus patzcuarensis*)."

"By every measure, Marmorkrebs are the most common crayfish species in the North American pet trade. They are the most commonly offered at auction. They are the most commonly bought, as measured by number of individuals sold and number of unique buyers. They are tied with *C. patzcuarensis* as the cheapest crayfish on the market. […] This unusual method of reproduction probably also contributes to their spread in the pet trade. Parthenogenesis has a novelty value, increasing their attractiveness to buy. Parthenogenesis also makes it a virtual guarantee that a Marmorkrebs owner will have to decide what to do with tens to hundreds of crayfish offspring."

"Marmorkrebs has not been reported in natural habitats in North America (Faulkes, 2010), although the sexually reproducing form, *P. fallax,* is a North American native."

"There are several reports of Marmorkrebs being sold in local pet stores in North America (Faulkes, 2013), but there are no available reports of Marmorkrebs being distributed by larger business franchises (i.e., national or multinational businesses)."

CABI (2018) reports *Procambarus virginalis* as present in the pet trade in the United States under the name *P. fallax* f. *virginalis*.

From CABI (2018):

"Currently, Marmorkrebs is a specifically prohibited species in Missouri (USA) (according to http://www.marmorkrebs.org) […]"

## Means of Introductions in the United States

No records of wild populations of *Procambarus virginalis* in the United States were found.

## Remarks

Previously known as *Procambarus fallax* forma *virginalis*, this species is now considered distinct under the name *Procambarus virginalis* (Lyko 2017; Gutekunst et al. 2018). This assessment considered information published under the names *P. fallax* f. *virginalis* or *P. virginalis* to be relevant to this species. The species *P. fallax* was considered distinct from the evaluated species and information pertaining strictly to *P. fallax*, including its native range and known distribution were not used for the analysis or the climate match.

Marbled crayfish is the English translation of Marmorkreb, and both names are commonly used.

From CABI (2018):

“The proliferation of Marmorkrebs as aquarium pet increases the propagule pressure and thereby the probability and risk of establishment in the wild. For instance, there is concern that its arrival and spread in the North American pet trade will inevitably also result in releases from captivity there (Faulkes, 2010). Marmorkrebs are available through online pet shops and may be readily shipped across borders (Chucholl, 2010; Peay et al., 2010). Additionally, personal contacts between crayfish enthusiasts may lead to cross-border acquisitions (Faulkes, 2010).”

From Lökkös et al. (2016):

“Marbled crayfish attract particular attention because it is the only obligate parthenogenetic decapod known to date (Scholtz et al., 2003) which produces genetically uniform progeny (Martin et al., 2007; Vogt et al., 2008) and is a triploid organism (Martin et al., 2016). Because of this unusual reproduction mode, marbled crayfish is not only an interesting research object for a variety of scientific disciplines but also represents a menace as potential invader since a single individual once released from aquaria into the wild might be able to found a new population (Marten et al., 2004; Faulkes, 2010).”

From Lyko (2017):

“The oldest known record of *P. virginalis* is from a German biologist and hobby aquarist. In a personal conversation with the author (February 2017), he recalled obtaining an uncharacterized batch of "Texas crayfish" from a pet trader specializing in American insects and other invertebrates, at a trade fair in Frankfurt (Germany) in 1995. Animal numbers of this original stock increased rapidly and animals were subsequently distributed to other German aquarists, eventually reaching commercial traders and pet stores. The absence of male animals and the parthenogenetic mode of reproduction were soon recognized among aquarists and subsequently confirmed in the first scientific description of marbled crayfish (Scholtz et al., 2003).”

From Gutekunst et al. (2018):

“These findings are consistent with the model that the marbled crayfish [*P. virginalis*] genome originated from an autopolyploid *P. fallax* gamete and the mating of two distantly related *P. fallax* individuals […], possibly from distant populations and in captivity. Alternative hypotheses involving allopolyploid formation with *P. alleni* appear unlikely due to the lack of hybrid morphological features [Martin et al. 2010a] and the considerable genetic differences.”

# 2 Biology and Ecology

## Taxonomic Hierarchy and Taxonomic Standing

From WORMS (2018):

"Biota > Animalia (Kingdom) > Arthropoda (Phylum) > Crustacea (Subphylum) > Multicrustacea (Superclass) > Malacostraca (Class) > Eumalacostraca (Subclass) > Eucarida (Superorder) > Decapoda (Order) > Pleocyemata (Suborder) > Astacidea (Infraorder) > Astacoidea (Superfamily) > Cambaridae (Family) > *Procambarus* (Genus) > *Procambarus virginalis* (Species)"

"Status accepted"

From Gutekunst et al. (2018):

"The marbled crayfish *Procambarus virginalis* […] is a freshwater crayfish species [Lyko 2017] that holds a unique position among decapod crustaceans due to its parthenogenetic mode of reproduction [Scholtz et al. 2003]. Marbled crayfish are descendants of the sexually reproducing slough crayfish *Procambarus fallax* and reproduce by apomictic parthenogenesis [Martin et al. 2010a; Vogt et al. 2015]."

"These findings are consistent with the model that the marbled crayfish [*P. virginalis*] genome originated from an autopolyploid *P. fallax* gamete and the mating of two distantly related *P. fallax* individuals […], possibly from distant populations and in captivity. Alternative hypotheses involving allopolyploid formation with *P. alleni* appear unlikely due to the lack of hybrid morphological features [Martin et al. 2010a] and the considerable genetic differences."

From Lyko (2017):

"Using morphological characters and molecular markers, Martin et al. identified the sexually reproducing slough crayfish *Procambarus fallax* from Florida as the closest relative of marbled crayfish and suggested the provisional name *Procambarus fallax* forma *virginalis* (Martin et al., 2010). However, the International Code of Zoological Nomenclature (ICZN, 1999) excludes "forma" for names published after 1960 (Article 15.2). Consequently, the provisional name for marbled crayfish was also considered "unavailable" in a recent taxonomic summary of freshwater crayfish (Crandall & De Grave, 2017)."

"Importantly, recent findings have supported the notion that marbled crayfish should be considered as an independent species, for which the scientific name *Procambarus virginalis* was suggested (Vogt et al., 2015)."

## Size, Weight, and Age Range

From CABI (2018):

"The total length can be up to 13 cm, but is more often less than 10 cm."

From Lipták et al. (2016):

"[…] lifespan of 2 to 3 years, […]"

From Vojkovská et al. (2014):

"They live for a maximum of 3 or 4 years (Vogt et al., 2004), […]"

## Environment

From Lökkös et al. (2016):

"For example, marbled crayfish requires for an optimal growth and reproduction water temperatures above 20 °C and breeding completely stops at temperatures below 15 °C (Seitz et al., 2005), but marbled crayfish might be able to withstand low winter temperatures in the European temperate zone (Kaldre et al., 2016, Veselý et al., 2015)."

From Jones et al. (2009):

"We have found *Procambarus* [*virginalis*] in brick pits, drainage ditches, rice fields and fish ponds. The crayfish appear to be quite tolerant to drying; we have found them buried deep in the mud of pools with no surface water remaining and have interviewed vendors who have kept crayfish alive without water for 3 days."

From Veselý et al. (2015):

"Marbled crayfish suffered massive mortality and only a single specimen survived in our [cold water, 2-3°C] experiment. However, due to its parthenogenetic reproduction strategy, theoretically no more than one individual is needed to establish a viable population and potential invasiveness is therefore extremely high [Scholtz et al. 2003; Martin et al. 2007]. The parthenogenetic reproduction strategy combined with fast growth, early maturation, high fecundity, and a capacity for competing with other crayfish species [Seitz et al. 2005; Jimenez and Faulkes 2010] provides this crayfish species an enhanced chance of success. Marbled crayfish are already present and flourish in Germany [Chucholl et al. 2012], Slovakia [Janský and Mutkovič 2010] and likely also in other European states e.g., Italy [Vojkovská et al. 2014] and Croatia [Samardžić et al. 2014] and future spread throughout the Europe is predicted [Chucholl 2014]."

From Bohman et al. (2013):

"Between 15th November and 23rd December 2012, 13 specimens (12 live and one dead) of an unknown alien species of crayfish [determined to be *Procambarus virginalis*], was caught […] and were apparently not affected by the cold water (0–2°C)."

"For example, the Marmorkrebs is known to have survived in water under ice cover during winter (Pfeiffer 2005)."

## Climate/Range

From Lipták et al. (2016):

"Based on our data and on findings from Germany (Chucholl and Pfeiffer, 2010; Chucholl et al., 2012), it is evident that the species survives and successfully reproduces in Central European climatic conditions."

From CABI (2018):

"Recent records from Germany evidence that Marmorkrebs are able to form stable, reproducing populations in temperate zones; […]"

## Distribution Outside the United States

### Native

From Faulkes (2015a):

"There are no known indigenous populations of *P. fallax* f. *virginalis* (Martin *et al.*, 2010a)."

According to Gutekunst et al. (2018), *Procambarus virginalis* arose recently during breeding of *P. fallax* in captivity and therefore there is no native range for *P. virginalis*.

### Introduced

From CABI (2018):

"The first free-living Marmorkrebs was captured from a gravel pit lake near Karlsruhe in southwestern Germany in late 2003 (Marten et al., 2004). In 2005, anecdotal evidence was presented for a population in a sedimentation pond near the city of Braunschweig (Lower Saxony, Germany); however, this has never been verified. Subsequently, single specimens were captured from small brooks near the city of Neu-Ulm (Bavaria) in 2008 (C Chucholl, University of Ulm, Germany, personal communication, 2011) and in Saxony in 2009 (Martin et al., 2010b). The first informal evidence for an established Marmorkrebs population in Germany was published by newspapers in mid-2010 (Privenau, 2010): local media repeatedly reported on Marmorkrebs coming out of an overpopulated small pond in a village near Halle (Saale, Saxony-Anhalt). Shortly after, another research paper evidenced that Marmorkrebs had formed a stable, reproducing population in a small lake near the city of Freiburg (Baden-Württemberg) (Chucholl and Pfeiffer, 2010). The first Marmorkrebs from this population was captured in 2009, but reported observations date back even further. In North-Rhine Westphalia (western Germany), single Marmorkrebs have been found in the Rivers Ruhr and Rhine (LANUV NRW, 2011) and there exist additional records from southwestern and central Germany which are yet unpublished. Chucholl and Pfeiffer (2010) suggested that the published Marmorkrebs records from Germany represent merely the `tip of the iceberg´."

"Free-living Marmorkrebs were also found in the Netherlands (Dordrecht) in 2004 (Soes and van Eekelen, 2006; Souty-Grosset et al., 2006), approximately 30 Marmorkrebs were introduced into a small waterbody in 2003 (Souty-Grosset et al., 2006) and were still present there in 2008 (according to http://www.marmorkrebs.org)."

"In Italy, a single Marmorkrebs was found living in syntopy with a large *Procambarus clarkii* population in 2008 (Nonnis Marzano et al., 2009)."

"Up to date, the Marmorkrebs is most widespread and abundant in Madagascar, where it was probably introduced in 2003 in Ambohimangakely (Jones et al., 2009) and is now present in eight of the country's 22 regions (Heimer, 2010). It is primarily distributed in the central high plains around the capital Antananarivo and is well established in the Ikopa and the Ampasimbe River systems (Jones et al., 2009; Kawai et al., 2009; Heimer, 2010). Large numbers of Marmorkrebs were sold in Moramanga (eastern Madagascar) in 2008 and it might be established in the area by now (Jones et al., 2009)."

"In Japan, one Marmorkrebs was captured from a river in Sapporo City (Hokkaido) in 2006 (Kawai and Takahata, 2010)."

CABI (2018) also lists *Procambarus virginalis* as present in the pet trade in Austria and the UK.

From Gutekunst et al. (2018):

"Finally, our results also demonstrate that the Madagascar population is genetically homogeneous and extremely similar to the oldest known stock of marbled crayfish founded in Germany in 1995. These findings support the notion that the global marbled crayfish population represents a single clone."

"We estimate that between 2007 and 2017, the size of the marbled crayfish distribution area [in Madagascar] increased about 100-fold from $10^3$ $km^2$ to more than $10^5$ $km^2$ […] and that the current population on Madagascar comprises millions of animals."

From Novitsky and Son (2016):

"In the first locality of the localities in Ukraine, – an old flooded quarry in Dnepropetrovsk City […] several alive and dead specimens were sampled in autumn 2015. According to personal communication with local citizens the species appeared in the reservoir in 2014 and was abundant already in the spring of 2015."

"Two female with eggs were caught on 23 October 2015 in water of temperature below $10^oC$. In the second locality – a cascade of ornamental ponds […] in Odessa City three alive individuals were observed in June 2015."

From Chucholl (2013):

"For instance, the Marmorkrebs entered the European pet trade via Germany in the mid-1990s (Scholtz et al. 2002) and were subsequently imported from Germany to other European countries, including the Netherlands, Italy, Great Britain, and Slovakia (Souty-Grosset et al. 2006; Marzano et al. 2009; Peay et al. 2010; Janský and Mutkovič 2010)."

"Marmorkrebs, for which only one established population was known in Central Europe in 2009 (Soes and van Eekelen 2006; Schulz et al. 2009), but at least five established populations were known by mid-2011 (Chucholl and Pfeiffer 2010; Janský and Mutkovič 2010; Wendt 2011; Chucholl unpublished data)."

From Bohman et al. (2013):

"This result suggests that the cambarid crayfishes caught in River Märstaån are doubtless Marmorkrebs and thus, this finding in Sweden is the world's northernmost discovery of Marmorkrebs in natural waters. It is also the first finding in the European "subcontinent" Scandinavia."

"The caught specimens fell into two size classes, with total length of 35 mm (9 individuals) and 80mm (3 individuals) respectively. This may be due to one of two causes: 1) someone emptied an entire aquarium of crayfish into the river (a common phenomenon according to Souty-Grosset et al 2006) or 2) the crayfish had been established for a longer time period and reproduced in the river."

From Lipták et al. (2016):

"Three new established populations of the marbled crayfish have been confirmed in Slovakia."

From Patoka et al. (2016):

"We present here the first records of marbled crayfish from open waters in the Czech Republic from two different, geographically distant sites, in which it seems to have established populations. In an urban pond located in the city of Prague, we could confirm a successful overwintering of the population. In a pond on a post-mining spoil heap close to Bílina, several adult animals were captured, one of which carried eggs in late summer."

From Vojkovská et al. (2014):

"From this point of view, the occurrence and spreading of the invasive crayfish species in the Po River [Italy] watershed is not surprising."

From Pârvulescu et al. (2017):

"Forty-two adult individuals were found for the first time in Romania in the semi-natural ponds in Băile Felix, near Oradea. Nine ovigerous females were captured as evidence that the population is breeding in the wild."

## Means of Introduction Outside the United States

From CABI (2018):

"In Europe, Marmorkrebs have become popular as food source for ornamental turtles in recent years (C Chucholl, University of Ulm, Germany, personal communication, 2011). Since ornamental turtles may be kept in open ponds, this use of Marmorkrebs may facilitate accidental introductions."

From Chucholl et al. (2012):

"In at least three instances, Marmorkrebs were observed to migrate over land […] 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."

From Novitsky and Son (2016):

"The most probable pathway of invasion to these localities is the trade of aquarium pets. Marbled cryfish [sic] is popular in large pet markets of Odessa and Dnepropetrovsk and in online trade, where they are cheaper than other exotic cambarid species. The parthenogenetic breeding mode, unique for decapod crustaceans and rapid growth (Martin et al. 2010a) make it [sic] population difficult to control even in aquaria. This may lead to market saturation, which promotes illegal releases of commercially unprofitable and unwanted juveniles to urban waters."

From Callaway (2018):

"Julia Jones, a conservation scientist at Bangor University, UK, led the team that first surveyed [Jones et al. 2009] the spread of marbled crayfish in Madagascar after their discovery in 2007. She says that the species' spread is due largely to their popularity as a food source. In 2009, she met a man on a bus carrying a plastic bag full of them that he planned to dump into his rice fields in the hope of creating a sustainable stock, she says."

From Lökkös et al. (2016):

"As described above, Lake Hévíz [Hungary] and its outlets is a preferred site for illegal introductions by aquarium hobbyists and thus, it is very likely that marbled crayfish get into the wild in the same way."

From Jones et al. (2009):

"We believe *Procambarus* were first introduced to Madagascar in 2003 in Ambohimangakely. The reason for the introduction remains mysterious but there may be a link with a road building project carried out by foreign contractors in 2003/2004."

## Short Description

A detailed diagnosis can be found in Lyko (2017).

From Lyko (2017):

"Color notes. The marmorated coloration of the carapace, which prompted the informal names "marbled crayfish" or "Marmorkrebs", is particularly prominent in aquarium stocks. It is often less pronounced in wild animals, which usually present in dark shades of brown or green with spotted patterns on the lateral cephalothorax and pleon […]."

"Marbled crayfish are morphologically similar to *P. fallax* and to *P. alleni* (Kawai et al., 2009; Martin et al., 2010). A discrimination according to the taxonomically highly relevant first pleopods of breeding (Form1) males (Hobbs, 1972, 1989) is not possible as there are no male marbled crayfish (Scholtz et al., 2003). However, marbled crayfish/*P. fallax* females can be discriminated from *P. alleni* by the annulus ventralis (Kawai et al., 2009; Martin et al., 2010). This important morphological character of cambarid females (Hobbs, 1972, 1989) is bell-shaped with an S-shaped sinus in marbled crayfish and *P. fallax*, but differently shaped in *P. alleni* […]. The specific morphology of the annulus ventralis is highly conserved among marbled crayfish from various sources (Kawai et al., 2009; Martin et al., 2010; Vogt et al., 2015; Vojkovska et al., 2014). Specific morphological characters that discriminate marbled crayfish from *P. fallax* are not known, which is likely related to the very recent speciation of marbled crayfish 20-30 years ago (Vogt et al., 2015)."

## Biology

From CABI (2018):

"**Genetics**
The Marmorkrebs propagates apomictically and produces genetically uniform clones (Martin et al., 2007). Developmental variation, however, leads to numerous phenotypes, even when reared under identical conditions (Vogt et al., 2008)."

"**Reproductive Biology**
The Marmorkrebs is unique in the manner that it is the only known decapod crustacean that reproduces by apomictic parthenogenesis: there exist only females which lay unfertilized eggs that develop into genetically uniform offspring (Scholtz et al., 2003; Martin et al., 2007; Vogt et al., 2008). No males have been found in laboratory or introduced, wild populations (Seitz et al., 2005; Jones et al., 2009)."

"The available data suggest that the Marmorkrebs is a fast growing species, which exhibits r-selected life history traits like early maturation, an extended breeding period and high fecundity. Parthenogenesis permits a high reproductive potential and since the females do not need to mate in order to reproduce, one single specimen is sufficient to create a new population."

"Reproduction and growth of the Marmorkrebs have been studied in the laboratory by Seitz et al. (2005). They found that growth rate was largely temperature dependant [sic] and highest at 30°C, while highest survival occurred at 20°C. Marmorkrebs exposed to low water temperatures (8-10°C) mostly survived and some individuals moulted at 10°C."

"Females reared at a temperature of 20-25°C started reproduction at an age of 141-255 days (carapace length = 14-22 mm). Fecundity ranged between 45 and 416 pleopodal eggs and increased with the size of the mother. Brooding took between 22 and 42 days and interclutch periods varied between 50 and 85 days."

"The fecundity of free-living Marmorkrebs in Madagascar was slightly higher and ranged between approximately 50 and 525 pleopodal eggs (Jones et al., 2009). Three ovigerous Marmorkrebs captured in southwestern Germany carried seven, 160 and 724 pleopodal eggs (Chucholl and Pfeiffer, 2010)."

"Only limited information is available on the timing of reproduction in free-living Marmorkrebs populations: In Madagascar, ovigerous females have been observed in March, June, July-September and December (Jones et al., 2009). In southwestern Germany, ovigerous females were found from early June to mid-October, at water temperatures between 26 and 15°C (Chucholl and Pfeiffer, 2010; M Pfeiffer and C Chucholl, University of Ulm, Germany, personal communication, 2011). Seitz et al. (2005) reported that Marmorkrebs in the laboratory ceased to reproduce at temperatures of 15°C or below."

"**Nutrition**
Like most crayfish species, the Marmorkrebs is most likely a polytrophic omnivore. It probably feeds on detritus, algae, plants and invertebrates and may also impact on higher trophic levels (e.g. fish). Vegetable substances dominated the stomach content of ten free-living Marmorkrebs sampled in Madagascar (Kawai et al., 2009)."

"Introduced Marmorkrebs have been found in both lentic and lotic freshwater habitats (e.g. Marten et al., 2004; Martin et al., 2010b). 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). Established populations in Germany are known from lentic habitats only (Chucholl and Pfeiffer, 2010; Privenau, 2010)."

From Gutekunst et al. (2018):

"Our results unambiguously demonstrate the clonality of the marbled crayfish genome, consistent with the proposed mode of reproduction by apomictic parthenogenesis [Vogt et al. 2004; Martin et al. 2007]."

From Lyko (2017):

"Reproductive incompatibility. The marbled crayfish genome is triploid, which represents a major cytogenetic roadblock for meiotic chromosome segregation (Martin et al., 2016; Vogt et al., 2015). As such, most triploid organisms are apomictic parthenogens (Saura et al., 1993) and thus reproductively isolated from sympatric sexually reproducing relatives. In crossbreeding experiments, marbled crayfish females and *P. fallax* males showed typical courtship behavior and mating (Vogt et al., 2015). However, offspring of marbled crayfish females that had been mated with *P. fallax* males were exclusively female and exclusively showed the microsatellite markers of the marbled crayfish mother […]. These findings are in agreement with the notion that the *P. fallax* male did not contribute to the genome of the offspring and that the progeny is the product of apomictic parthenogenesis in the marbled crayfish mother. Taken together, the data suggest that marbled crayfish are reproductively isolated from *P. fallax* (Vogt et al., 2015)."

"Their morphological similarities notwithstanding, life history traits have been found to be markedly different between marbled crayfish and *P. fallax* […]. Specifically, mean carapace length and clutch size were found to be significantly higher in adult marbled crayfish than in *P. fallax* (Vogt et al., 2015). These findings suggest important phenotypic differences between marbled crayfish and *P. fallax* that are independent of the taxonomically relevant morphological characters."

From Lipták et al. (2016):

"It is estimated that under the laboratory conditions, the marbled crayfish can complete up to seven reproduction cycles during its lifespan of 2 to 3 years, and the generation time is about 6-7 months (Vogt, 2010). The amount of juveniles increases with each cycle in relation to size increase of the maternal individuals (Vogt, 2011), and may reach very high values for large females. Under laboratory conditions, Vogt (2011) reported the maximum number of 427 juveniles in one clutch. Some field-collected individuals were nevertheless even more fecund: one female from Madagascar studied by Jones et al. (2009) carried approximately 530 eggs […], and Chucholl and Pfeiffer [2010] reported as many as 724 eggs in a single marbled crayfish clutch from a German population. Thus, 455 juveniles carried by one marbled crayfish from the Koplotovce site do not seem to be exceptional, even under Central European conditions, and this number confirms a substantial reproduction potential of this invasive species."

## Human Uses

From CABI (2018):

"**Economic Value**
The Marmorkrebs is a popular pet species in Europe and North America (Chucholl, 2010; Faulkes, 2010). In Germany, Marmorkrebs are sold at approximately 5 € per specimen (C Chucholl, University of Ulm, Germany, personal communication, 2011)."

"In Madagascar, Marmorkrebs are sold in markets for human consumption (Jones et al., 2009, Kawai et al., 2009; Heimer, 2010). However, Heimer (2010) and Jones et al. (2009) concurrently indicate that Marmorkrebs are of low economic value."

"**Social Benefit**
The Marmorkrebs was suggested as laboratory model organism for development, epigenetics and toxicology. Its high number of genetically identical offspring and its undemanding nature are, among other peculiarities, ideal prerequisites for this role (Vogt, 2008; 2010). Recent publications document its increasing use as model organism (e.g. Jirikowski et al., 2010; Rubach et al., 2011)."

From Chucholl and Wendler (2017):

"Red swamp crayfish (*P. clarkii*), Marmorkrebs (*P. fallax* f. *virginalis*), signal crayfish (*P. leniusculus*), and spiny-cheek crayfish (*O. limosus*) are included on the list of IAS of Union concern (European Commission 2016). Species on this 'black list' can be subjected to trade regulations, as well as a ban on import and keeping."

From Chucholl (2013):

"[…] Marmorkrebs are still widespread and readily available through wholesalers, the retail trade, and online marketplaces (Lukhaup and Pekny 2009)."

## Diseases

**Crayfish plague (infection with *Aphanomyces astaci*) is an OIE-reportable disease.**

From Mrugała et al. (2015):

"Viability of *A*[*phanomyces*] *astaci* was confirmed by its isolation to axenic cultures from three host taxa, including the parthenogenetic invader Marmorkrebs (*Procambarus fallax* f. *virginalis*)."

From CABI (2018):

"Rickettsiosis and coccidiosis have both been found in Marmorkrebs and *Psorospermium* sp. is known to infect *P. fallax* in its indigenous range (Souty-Grosset et al., 2006)."

## Threat to Humans

No information on threats to humans from *Procambarus virginalis* was found.

# 3 Impacts of Introductions

The following details ***potential***, ***anecdotal***, or ***highly generalized*** information on impacts of introduction from *Procambarus virginalis*. Scientifically defensible documentation of actual impacts was not found.

From CABI (2018):

"Anecdotal observations from Madagascar suggest a significant impact on fish populations. Local fishermen reported that Marmorkrebs have destroyed fishing in their area (Jones et al., 2009; Heimer, 2010). Inland fisheries in Madagascar rely mostly on introduced fish (e.g. small carp and tilapia) and are an important source of protein and income (Jones et al., 2009; Heimer, 2010). Although the Marmorkrebs may represent a substitute for fish, preliminary data of Jones et al. (2009) suggest that it is of lower economic value and in less demand."

“There is also substantial concern that the invasion of Marmorkrebs will negatively impact rice culture in Madagascar (Jones et al., 2009; Kawai et al., 2009; Heimer, 2010). Introduced, non-indigenous crayfish are mostly considered a pest in rice paddies worldwide, because they damage young rice plants as well as irrigation systems and dams (e.g. Anastacio et al., 1995; Souty-Grosset et al., 2006). Preliminary stomach content data stress the ability of Marmorkrebs to feed on plant matter (Kawai et al., 2009) and Heimer (2010) indicated that Marmorkrebs may indeed damage young rice plants. Given the strong dependence of Madagascar’s economy on rice culture, a reduction in rice productivity would involve serious economic damage (Jones et al., 2009).”

“**Impact on Habitats**
Marmorkrebs act probably as polytrophic omnivores and were found at very high densities in Madagascar (Jones et al., 2009). Given that, they might have a profound impact on ecosystem functioning and integrity, although specific information is currently lacking.”

“Marmorkrebs pose a threat to indigenous crayfish species in Madagascar and Europe, due to competition for food and space and crayfish plague transmission (Jones et al., 2009; Kawai et al., 2009; Chucholl and Pfeiffer, 2010).

“Jimenez and Faulkes (2011) studied direct aggressive interactions between Marmorkrebs and *Procambarus clarkii* and concluded that Marmorkrebs have the potential to compete with other crayfish species. Furthermore, Marmorkrebs differ ecologically from indigenous crayfish in Europe and Madagascar in having a fast growth rate, a very high fecundity and an extended breeding period (Seitz et al., 2005; Jones et al., 2009; Chucholl and Pfeiffer, 2010). These life history traits might give an additional competitive advantage to Marmorkrebs.”

“The risk of devastating consequences for indigenous crayfish would dramatically increase if Marmorkrebs are infected with crayfish plague: Any contact of Marmorkrebs to susceptible crayfish (i.e. all crayfish native to Europe, Madagascar, Asia, Australia, and South America) would almost certainly result in mass mortalities among the susceptible species (Souty-Grosset et al., 2006; Jones et al., 2009).”

From Jones et al. (2009):

“We lack direct information on the effects of *Procambarus* invasion but anecdotal observations of the effect of *Procambarus* on fish populations (so far only in areas where only introduced fish are present) suggest that they may have a significant impact. […] We have spoken to many fishermen who say that *Procambarus* has destroyed fishing in their local area. Inland fisheries, mostly based on introduced species, are very important to the economy of many parts of Madagascar and provide an important protein source. Although *Procambarus* may to some extent act as a substitute for fish, our preliminary work suggests they are of lower value and in less demand than fish.”

From Lökkös et al. (2016):

“Apart from the fact that introduced alien species are generally unwelcome as adulterating elements in national parks that were founded to conserve regional ecosystems of great significance, marbled crayfish could also have an immediate negative impact on the sensible natural balance of this unique marshland biotope. Since freshwater crayfish have not occurred in the area for more than a half century (Puky et al., 2005), a sudden abundant appearance of such a keystone taxon might dramatically change the diversity and structure of the food web of the area. For example, crayfish can be effective grazers on the water vegetation (e.g. Carpenter and Lodge, 1986; Feminella and Resh, 1989; Nyström, 1999; van der Wal et al., 2013) and thus, a high marbled crayfish density could lead to a significant decline of submerged macrophytes and therefore to an increasing of the nutrient load. This, in turn, would reverse the above-described positive effect of the ecological restoration of Kis-Balaton, which has made the wetland to a retention basin of nutrients from River Zala, leading to the current good water quality of the adjoining Lake Balaton. Also, direct negative effects of crayfish by predation on the macrozoobenthos fauna and amphibians are well documented (Nyström et al., 2001; Moorhouse et al., 2014), whereas their influence on fishes is rather indirect by reduction of macrophytes which serve the vertebrates as breeding sites and shelter. On the other hand, crayfishes are an important transformer of energy to higher trophic level which can also result in a positive effect on predatory fishes. […] The biggest impact through introduced crayfish, however, is on the autochthonous crayfish fauna, as shown in Europe, where ICS have been replaced by North American species in large parts of the continent. At first sight, this effect does not seem to be of great importance in the area affected by marbled crayfish since autochthonous crayfish species have become extinct in Lake Balaton and the lower stretch of its inflowing River Zala in the 1960s due to crayfish plague and the introduction of the European eel *Anguilla anguilla* Linnaeus 1758 (Padisák, 1999; Puky et al., 2005). However, future projects for the reintroduction of ICS such as started in the Balaton Uplands National Park at the early 1990s (Puky et al., 2005) could fail in areas already settled with marbled crayfish because of its capability to transmit the crayfish plague (Keller et al., 2014) what would lead to the immediately death of the just resettled native crayfishes.”

From Veselý et al. (2015):

“Although not as well studied, other alien crayfish species , [sic] e.g., the marbled crayfish *Procambarus fallax* f. *virginalis*, yabby *Cherax destructor* and the redclaw *Cherax quadricarinatus* etc. are considered to cause detrimental impacts once established in the natural environment [Dukes and Mooney 1999].”

From Soes and Koese (2010):

“The Marbled crayfish possibly has a similar ecology as the other *Procambarus* species in the Netherlands. Evidence for this is based on the fact that the species has shown to have a relatively large portion of plant organic material in the gut in the wild in Madagascar (Kawai et al. 2009). Additionally, the species has been found amongst red swamp crayfish in the wild. The Dutch climate might be relatively disadvantageous for the Marbled crayfish compared to the other

*Procambarus* specimens. However, the fact that only a single individual can be the source of an entire population (see below) still posesses [sic] a large threat."

From Faulkes et al. (2012):

"Marmorkrebs live in rice paddies in Madagascar and consume rice."

"Marmorkrebs have damaged rice paddies in Madagascar […]"

# 4 Global Distribution

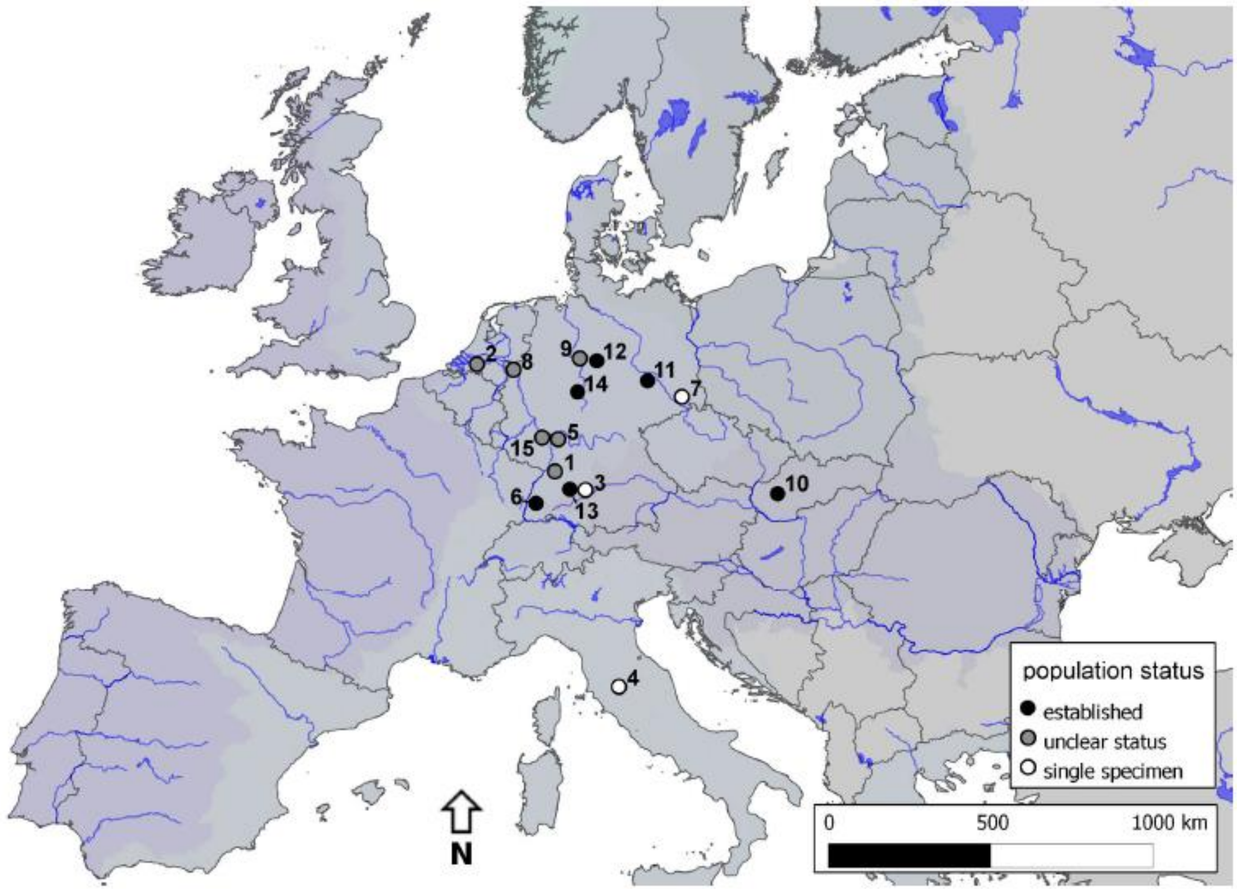


**Figure 1.** Known distribution of *Procambarus virginalis* in Europe as of 2012. Map from Chucholl et al. (2012).

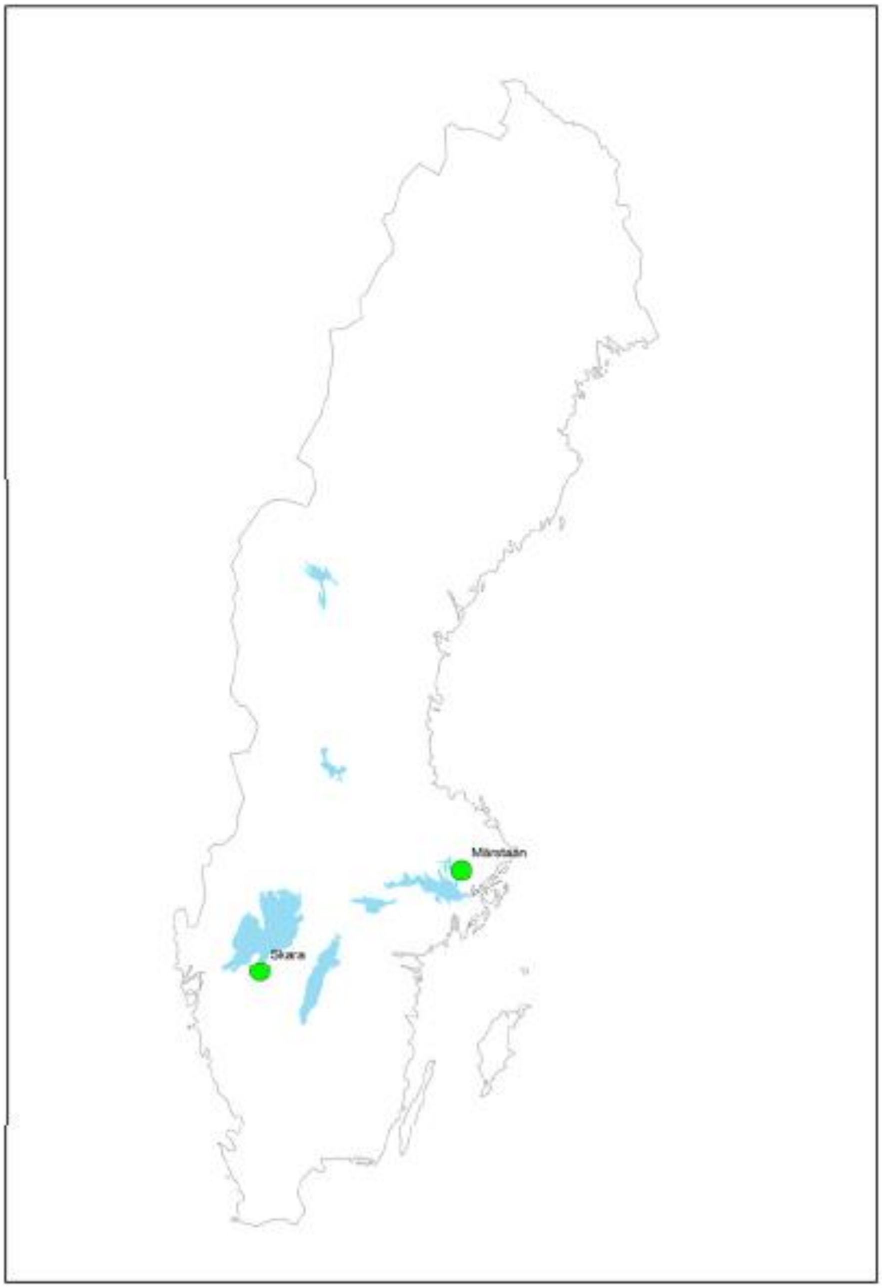


**Figure 2.** Locations of confirmed (green dot on right) and potential (green dot on left) populations of *Procambarus virginalis* in Sweden as of 2012. Map from Bohman et al. (2013).

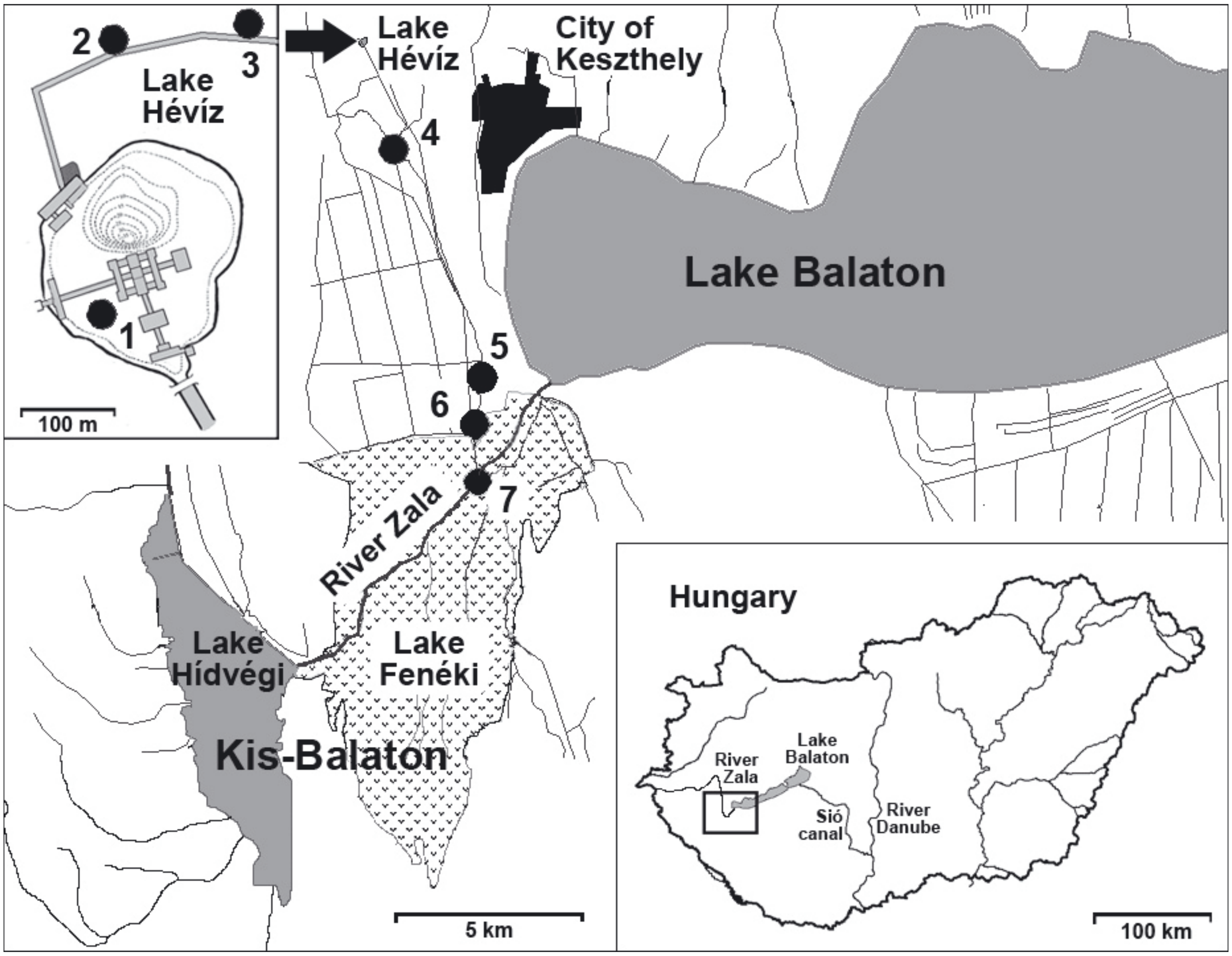


**Figure 3.** Known distribution of *Procambarus virginalis* in Hungary as of 2014. Map from Lökkös et al. (2016).

**Figure 4.** Location of the first known established population of *Procambarus virginalis* in Romania, detected in 2017. Map adapted from Pârvulescu et al. (2017).

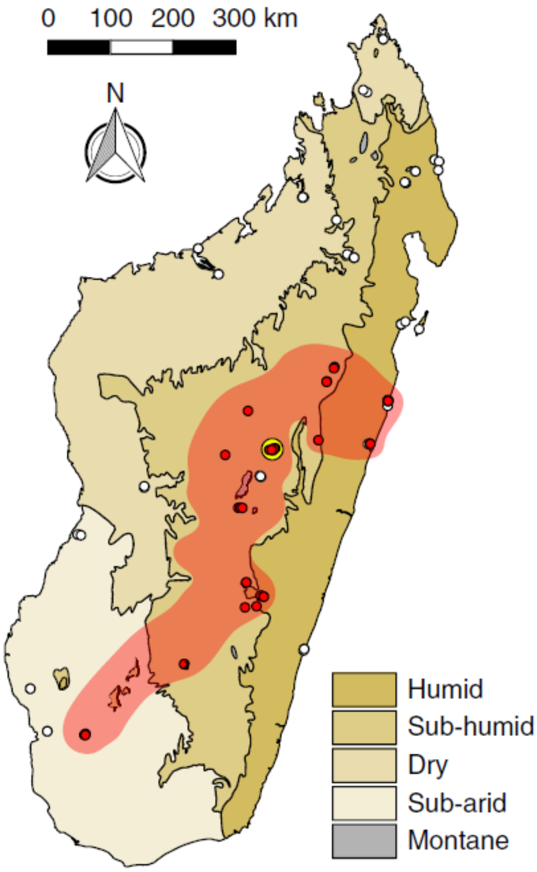


**Figure 5.** Known distribution of *Procambarus virginalis* in Madagascar as of March 2017. Red dots indicate *P. virginalis* presence; white dots indicate survey locations where *P. virginalis* was not detected. Map adapted from Gutekunst et al. (2018).

# 5 Distribution Within the United States

No records of wild populations of *Procambarus virginalis* in the United States were found.

# 6 Climate Matching

## Summary of Climate Matching Analysis

The climate match (Sanders et al. 2014; 16 climate variables; Euclidean Distance) for *Procambarus virginalis* is moderate to high in portions of the Great Lakes region, and moderate in the central U.S., Northeast, and Mid-Atlantic regions. Low climate match is seen along the Pacific coast and in the southern Appalachians. The Climate 6 score (Sanders et al. 2014; 16 climate variables; Euclidean distance) for the contiguous U.S. was 0.164, high. The following states had individually high climate scores: Arizona, Arkansas, Colorado, Delaware, Illinois, Indiana, Iowa, Maryland, Michigan, Missouri, Montana, New Jersey, New Mexico, New York, Ohio, Pennsylvania, Utah, Vermont, Virginia, West Virginia, and Wisconsin.

Crayfishes have been observed to establish populations in climates different from that found within their native range (M. Hoff, U.S. Fish and Wildlife Service, personal communication).

The climate match shown here may be an underestimate of climate suitability for the establishment of *P. virginalis* because of the close relationship with *P. fallax* of Georgia and Florida.

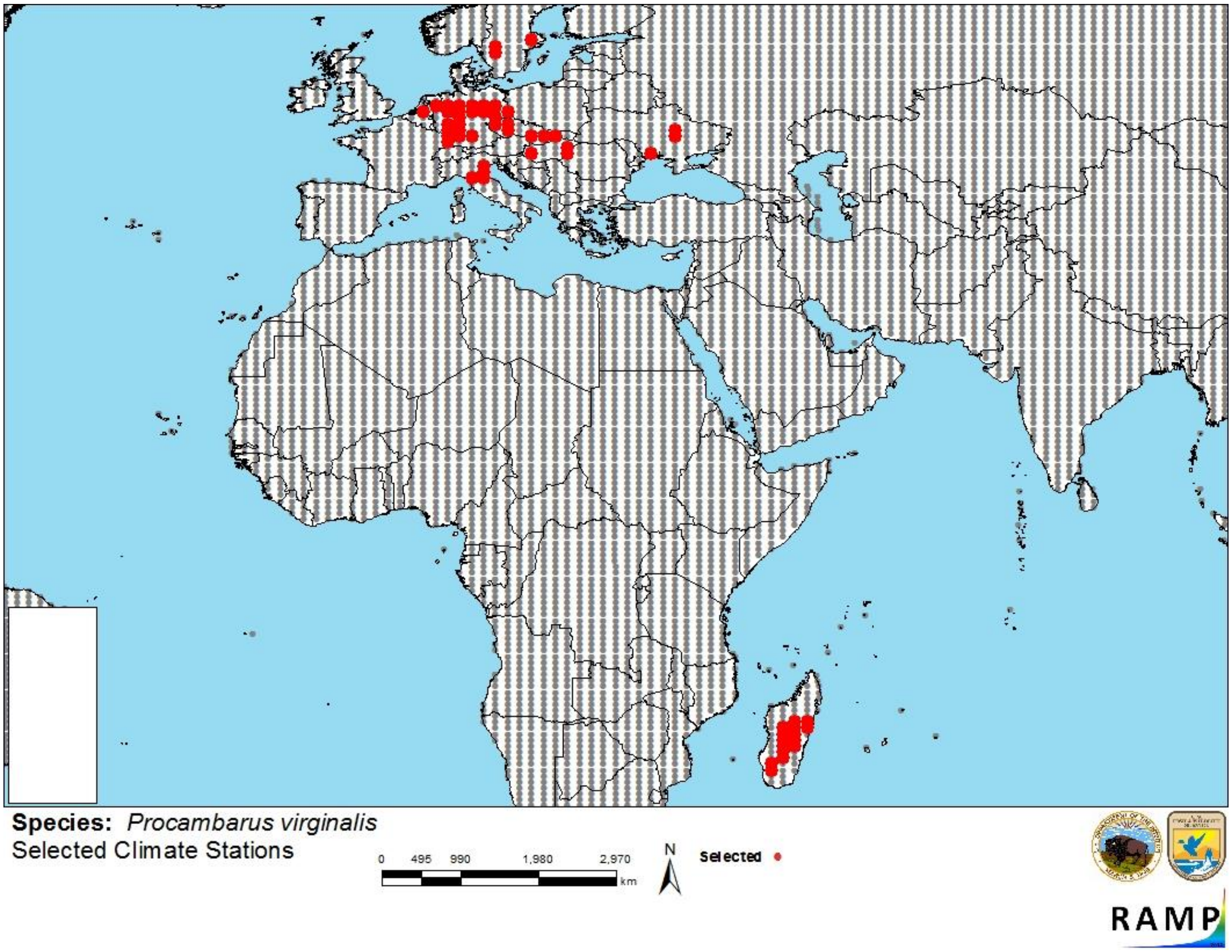


**Figure 6.** RAMP (Sanders et al. 2014) source map showing weather stations selected as source locations (red) and non-source locations (gray) for *Procambarus virginalis* climate matching. Source locations from Chucholl et al. (2012), Bohman et al. (2013), Vojkovská et al. (2014), Lipták et al. (2016), Lökkös et al. (2016), Novitsky and Son (2016), Patoka et al. (2016), Pârvulescu et al. (2017), and Gutekunst et al. (2018). These source locations include only the known introduced range of the species; there is no native range.

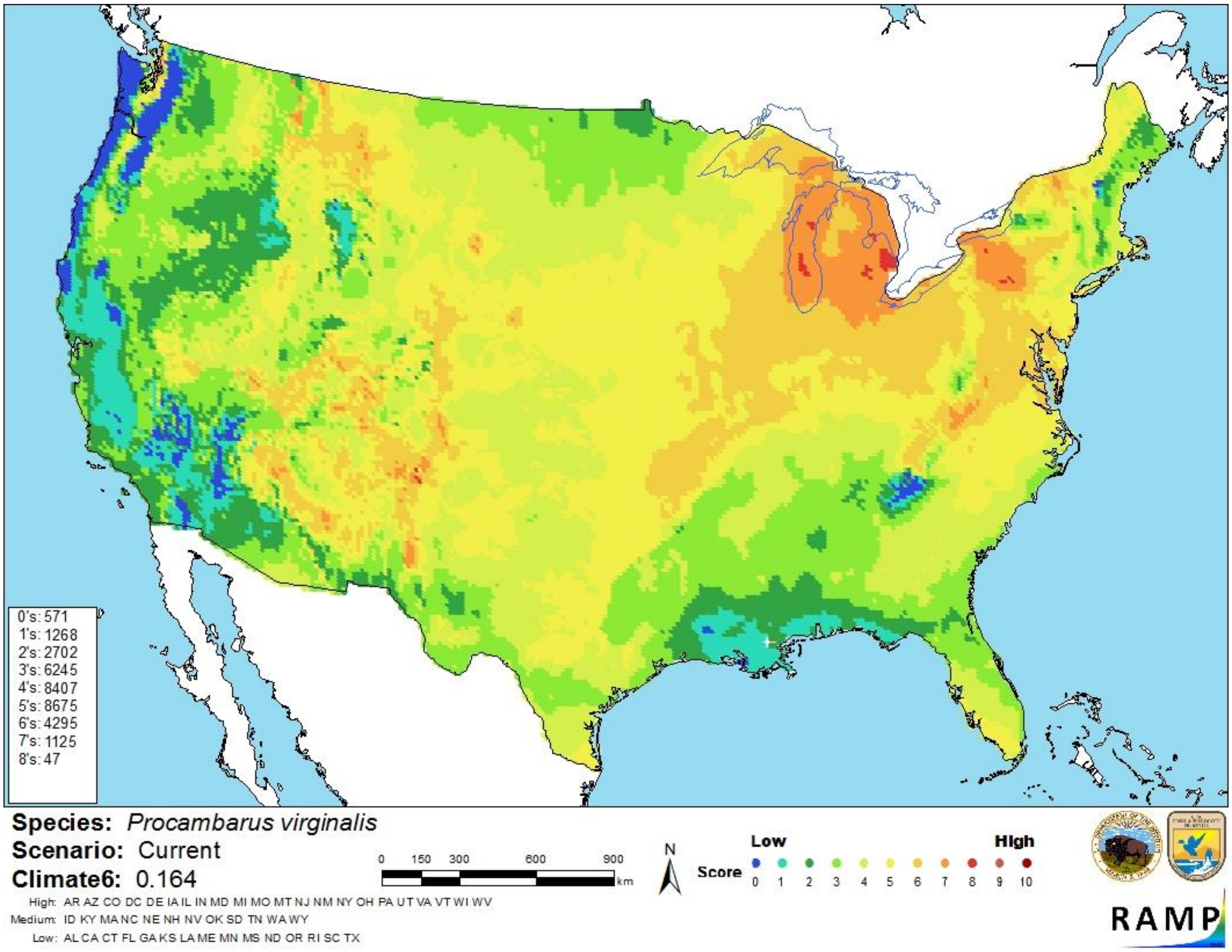


**Figure 7.** Map of RAMP (Sanders et al. 2014) climate matches for *Procambarus virginalis* in the contiguous United States based on source locations reported by Chucholl et al. (2012), Bohman et al. (2013), Vojkovská et al. (2014), Lipták et al. (2016), Lökkös et al. (2016), Novitsky and Son (2016), Patoka et al. (2016), Pârvulescu et al. (2017), and Gutekunst et al. (2018). 0= Lowest match, 10=Highest match. Climate match scores are tabulated on the left.

The “High”, “Medium”, and “Low” climate match categories are based on the following table:

| Climate 6: Proportion of (Sum of Climate Scores 6-10) / (Sum of total Climate Scores) | Climate Match Category |
|---|---|
| 0.000≤X≤0.005 | Low |
| 0.005<X<0.103 | Medium |
| ≥0.103 | High |

# 7 Certainty of Assessment

The certainty of assessment for *Procambarus virginalis* is medium. The biology of *P. virginalis* has been studied extensively in captivity. Recently, uncertainty regarding taxonomy and origin of the species has been resolved. However, information on its ecology and impacts on native ecosystems is not well understood. Further direct study of its impacts is necessary.

# 8 Risk Assessment

## Summary of Risk to the Contiguous United States

The history of invasiveness for *Procambarus virginalis* is not documented. *P virginalis* is a parthenogenetic lineage of *Procambarus fallax* that was created during captive breeding. *P. virginalis* has become established in Madagascar and Europe, primarily due to the release of aquarium pets and due to its value as a food source in Madagascar. There is much concern over the high reproductive capacity of the species, the potential for established populations to originate from introductions of a single individual, and the close relationship of the species to *P. clarkii*, for which negative impacts of invasion are well-documented. However, negative ecological impacts of *P. virginalis* have yet to be scientifically documented. Anecdotal evidence suggests impacts to native crayfish and fish populations, as well as to rice culture. High densities of *P. virginalis*, achievable through its parthenogenetic form of reproduction, could have important effects on ecosystem processes. The species is a carrier of crayfish plague, and so poses a risk to native crayfish on all continents except North America. Climate match of this species to the contiguous U.S. is high. The certainty of assessment is medium. Overall risk posed by this species is uncertain.

## Assessment Elements

- **History of Invasiveness (Sec. 3): None Documented**
- **Climate Match (Sec. 6): High**
- **Certainty of Assessment (Sec. 7): Medium**
- **Remarks/Important additional information:** Reproduces by parthenogenesis. Due to this reproduction method, new populations can become established after the release of a single individual.
- **Overall Risk Assessment Category: Uncertain**

# 9 References

**Note: The following references were accessed for this ERSS. References cited within quoted text but not accessed are included below in Section 10.**


Bohman, P., L. Edsman, P. Martin, and G. Scholtz. 2013. The first Marmorkrebs (Decapoda: Astacida: Cambaridae) in Scandinavia. BioInvasions Records 2(3):227–232.

CABI. 2018. *Procambarus fallax* f. *virginalis* (Marmorkrebs) [original text by C. Chucholl]. Invasive Species Compendium. CAB International, Wallingford, UK. Available: https://www.cabi.org/isc/datasheet/110477. (February 2018).

Callaway, E. 2018. Super-invasive crayfish revealed to be a genetic hybrid. Nature 554:157–158.

Chucholl, C. 2013. Invaders for sale: trade and determinants of introduction of ornamental freshwater crayfish. Biological Invasions 15:125–141.

Chucholl, C., K. Morawetz, and H. Groβ. 2012. The clones are coming – strong increase in Marmorkrebs [*Procambarus fallax* (Hagen, 1870) f. *virginalis*] records from Europe. Aquatic Invasions 7(4):511–519.

Chucholl, C., and F. Wendler. 2017. Positive selection of beautiful invaders: long-term persistence and bio-invasion risk of freshwater crayfish in the pet trade. Biological Invasions 19:197–208.

Faulkes, Z. 2015a. The global trade in crayfish as pets. Crustacean Reasearch 44:75–92.

Faulkes, Z. 2015b. Marmorkrebs (*Procambarus fallax* f. *virginalis*) are the most popular crayfish in the North American pet trade. Knowledge and Management of Aquatic Ecosystems 416:20.

Faulkes, Z., T. Feria, and J. Muñoz. 2012. Do Marmorkrebs, *Procambarus fallax* f. *virginalis*, threaten freshwater Japanese ecosystems? Aquatic Biosystems 8:13.

Gutekunst, J., R. Andriantsoa, C. Falckenhayn, K. Hanna, W. Sten, J. Rasamy, and F. Lyko. 2018. Clonal genome evolution and rapid invasive spread of the marbled crayfish. Nature Ecology and Evolution doi:10.1038/s41559-018-0467-9.

Jones, J. P. G., J. R. Rasamy, A. Harvey, A. Toon, B. Oidtmann, M. H. Randrianarison, N. Raminosoa, and O. R. Ravoahangimalala. 2009. The perfect invader: a parthenogenic crayfish poses a new threat to Madagascar's freshwater biodiversity. Biological Invasions 11(6):1475–1482.

Lipták, B., A. Mrugała, L. Pekárik, A. Mutkovič, D. Gruľa, A. Petrusek, and A. Kouba. 2016. Expansion of the marbled crayfish in Slovakia: beginning of an invasion in the Danube catchment? Journal of Limnology 75(2):305–312.

Lökkös, A., T. Müller, K. Kovács, L. Várkonyi, A. Specziár, and P. Martin. 2016. The alien, parthenogenetic marbled crayfish (Decapoda: Cambaridae) is entering Kis-Balaton (Hungary), one of Europe’s most important wetland biotopes. Knowledge and Management of Aquatic Ecosystems 417:16.

Lyko, F. 2017. The marbled crayfish (Decapoda: Cambaridae) represents an independent new species. Zootaxa 4363(4):544–552.

Mrugała, A., E. Kozubíková-Balcarová, C. Chucholl, S. Cabanillas Resino, S. Viljamaa-Dirks, J. Vukić, and A. Petrusek. 2015. Trade of ornamental crayfish in Europe as a possible introduction pathway for important crustacean diseases: crayfish plague and white spot syndrome. Biological Invasions 17(5):1313–1326.

Novitsky, R. A., and M. O. Son. 2016. The first records of Marmorkrebs [*Procambarus fallax* (Hagen, 1870) f. *virginalis*] (Crustacea, Decapoda, Cambaridae) in Ukraine. Ecologica Montenegrina 5:44–46.

Pârvulescu, L., A. Togor, S.-F. Lele, S. Scheu, D. Şinca, and J. Panteleit. 2017. First established population of marbled crayfish *Procambarus fallax* (Hagen, 1870) f. *virginalis* (Decapoda, Cambaridae) in Romania. BioInvasions Records 6(4):357–362.

Patoka, J., M. Buřič, V. Kolář, M. Bláha, M. Petrtýl, P. Franta, R. Tropek, L. Kalous, A. Petrusek, and A. Kouba. 2016. Predictions of marbled crayfish establishment in conurbations fulfilled: evidences from the Czech Republic. Biologia 71(12):1380–1385.

Sanders, S., C. Castiglione, and M. Hoff. 2014. Risk Assessment Mapping Program: RAMP. U.S. Fish and Wildlife Service.

Soes, D. M., and B. Koese. 2010. Invasive crayfish in the Netherlands: a preliminary risk analysis. Bureau Waardenburg, interm report EIS2010-01, Culemborg, Netherlands.

Veselý, L., M. Buřič, and A. Kouba. 2015. Hardy exotics species in temperate zone: can "warm water" crayfish invaders establish regardless of low temperatures? Scientific Reports 5:16340.

Vojkovská, R., I. Horká, E. Tricarico, and Z. Ďuriš. 2014. New record of the parthenogenetic marbled crayfish *Procambarus fallax* f. *virginalis* from Italy. Crustaceana 87(11–12):1386–1392.

WORMS. 2018. *Procambarus virginalis*. *In* World Register of Marine Species. Available: http://www.marinespecies.org/aphia.php?p=taxdetails&id=1049466. (February 2018).

# 10 References Quoted But Not Accessed

**Note: The following references are cited within quoted text within this ERSS, but were not accessed for its preparation. They are included here to provide the reader with more information.**

Anastacio, P. M., S. N. Nielsen, J. C. Marques, and S. E. Jorgensen. 1995. Integrated production of crayfish and rice-a management model. Ecological Engineering 4:199–210.

Carpenter S. R., and D. M. Lodge. 1986. Effects of submersed macrophytes on ecosystem processes. Aquatic Botany 26:341–370.

Chucholl, C. 2010. Invaders for sale: does the ornamental freshwater crayfish trade constitute an actual and overlooked risk? Page 108 *in* C. Souty-Grosset, F. Grandjean, and C. Mirebeau, editors. Abstracts of the European crayfish, food, flagship & ecosystem services conference, Poitiers, France. Imprimerie Copy-Media, France.

Chucholl, C. 2014. Predicting the risk of introduction and establishment of an exotic aquarium animal in Europe: insights from one decade of Marmorkrebs (Crustacea, Astacida, Cambaridae) releases. Management of Biological Invasions 5:309–318.

Chucholl, C., and M. Pfeiffer. 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(4):405–412.

Crandall, K. A., and S. De Grave. 2017. An updated classification of the freshwater crayfishes (Decapoda: Astacidea) of the world, with a complete species list. Journal of Crustacean Biology 37(5):1–39.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14:135–139.

European Commission. 2016. Commission implementing regulation (EU) 2016/1141 of 13 July 2016 adopting a list of invasive alien species of union concern pursuant to regulation (EU) No 1143/2014 of the European parliament and of the council. Off J EU 59:4–8

Faulkes, Z. 2010. The spread of the parthenogenetic marbled crayfish, Marmorkrebs (*Procambarus* sp.), in the North American pet trade. Aquatic Invasions 5(4):447–450.

Faulkes Z. 2013. How much is that crayfish in the window? Online monitoring of Marmorkrebs, *Procambarus fallax* f. *virginalis* (Hagen, 1870) in the North American pet trade. Freshwater Crayfish 19:39–44.

Feminella, J. W., and V. H. Resh. 1989. Submersed macrophytes and grazing crayfish: an experimental study of herbivory in a California freshwater marsh. Holarctic Ecology 12:1–8.

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

Hobbs, H. H. J. 1972. Crayfishes (Astacidae) of North and Middle America. Biota of Freshwater Ecosystems. Identification Manual 9. Environmental Protection Agency, Washington, DC.

Hobbs, H. H. J. 1989. An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae, and Parastacidae). Smithsonian Contributions to Zoology 480:1–236.

ICZN. 1999. International Code of Zoological Nomenclature, 4th edition. The International Trust for Zoological Nomenclature, London.

Janský, V., and A. Mutkovič. 2010. Rak *Procambarus* sp. (Crustacea: Decapoda: Cambaridae)–Prvŷ Nález na Slovensku. Acta Rerum Naturalium Musei Nationalis Slovaci 56:64–67.

Jimenez, S., and Z. Faulkes. 2010. Establishment and care of a colony of parthenogenetic marbled crayfish, Marmorkrebs. Invertebrate Rearing 1:10–18.

Jimenez, S. A., and Z. Faulkes. 2011. Can the parthenogenetic marbled crayfish Marmorkrebs compete with other crayfish species in fights? Journal of Ethology 29(1):115–120.

Jirikowski, G., S. Kreissl, S. Richter, and C. Wolff. 2010. Muscle development in the marbled crayfish-insights from an emerging model organism (Crustacea, Malacostraca, Decapoda). Development Genes and Evolution 220(3-4):89–105.

Kaldre, K., A. Mězenin, T. Paaver, and T. Kawai. 2016. A preliminary study on the tolerance of marble crayfish *Procambarus fallax* f. *virginalis* to low temperature in nordic climate. *In* T. Kawai, Z. Faukles, and G. Scholtz, editors. Freshwater crayfish: a global overview. CRC Press, Boca Raton, Florida.

Kawai, T., and M. Takahata. 2010. Biology of crayfish. Hokkaido University Press, Sapporo, Japan.

Kawai, T., G. Scholtz, S. Morioka, F. Ramanamandimby, C. Lukhaup, and Y. Hanamura. 2009. Parthenogenetic alien crayfish (Decapoda: cambaridae) spreading in Madagascar. Journal of Crustacean Biology 29(4):562–567.

Keller, N. S., M. Pfeiffer, I. Roessink, R. Schulz, and A. Schrimpf. 2014. First evidence of crayfish plague agent in populations of the marbled crayfish (*Procambarus fallax* forma *virginalis*). Knowledge and Management of aquatic ecosystems 414:15.

LANUV NRW. 2011. Marmorkrebs (*Procambarus* spec.). Available: http://neobiota.naturschutzinformationen-nrw.de/nav3/ArtInfo.aspx?ART=Tiere&ID=bd1e22a8-46ab-4a55-ab68-69c7d834386b.

Lukhaup, C., and R. Pekny. 2009. Flusskrebse in der Aquaristik. Pages 129–132 *in* L. Füreder, editor. Flusskrebse: Biologie, Ökologie, Gefährdung. Veröffentlichungen des Naturmuseums Südtirol, volume 6. Folio Verlag, Bozen, Italy.

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

Martin, P., N. Dorn, T. Kawai, C. van der Heiden, and G. Scholtz. 2010a. The enigmatic Marmorkrebs (marbled crayfish) is the parthenogenetic form of *Procambarus fallax* (Hagen, 1870). Contributions to Zoology 79(3):107–118.

Martin, P., S. Hong, G. Füllner, and G. Scholtz. 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(4):397–403.

Martin, P., K. Kohlmann, and G. Scholtz. 2007. The parthenogenetic Marmorkrebs (marbled crayfish) produces genetically uniform offspring. Naturwissenschaften 94(10):843–846.

Martin, P., S. Thonagel, and G. Scholtz. 2016. The parthenogenetic Marmorkrebs (Malacostraca: Decapoda: Cambaridae) is a triploid organism. Journal of zoological systematics and evolutionary research Zeitschrift für zoologische Systematik und Evolutionsforschung 54(1):13–21.

Marzano, F. N., M. Scalici, S. Chiesa, F. Gherardi, A. Piccinini, and G. Gibertini. 2009. The first record of the marbled crayfish adds further threats to fresh waters in Italy. Aquatic Invasions 4.

Moorhouse, T. P., A. E. Poole, L. C. Evans, D. C. Bradley, and D. W. Macdonald. 2014. Intensive removal of signal crayfish (*Pacifastacus leniusculus*) from rivers increases numbers and taxon richness of macroinvertebrate species. Ecology and Evolution 4:494–504.

Nonnis Marzano, F. N., M. Scalici, S. Chiesa, F. Gherardi, A. Piccinini, and G. Gibertini. 2009. The first record of the marbled crayfish adds further threats to fresh waters in Italy. Aquatic Invasions 4(2):401–404.

Nyström, P. 1999. Ecological impact of introduced and native crayfish on freshwater communities: European perspectives. *In* F. Gherardi, and D. M. Holdich, editors. Crayfish in Europe as alien species. How to make the best of a bad situation? A. A. Balkema, Rotterdam, Netherlands.

Nyström, P., O. Svensson, B. Lardner, C. Brönmark, and W. Granéli. 2001. The influence of multiple introduced predators on a littoral pond community. Ecology 82:1023–1039.

Padisák J. 1999. A Balaton természettörténete. História 21:50–53.

Peay, S., D. M. Holdich, and J. Brickland. 2010. Risk assessments of non-indigenous crayfish in Great Britain. Freshwater Crayfish 17:109–122.

Pfeiffer, M. 2005. Marmorkrebse überleben im Eis. Fischer & Teichwirt 2005(6):204.

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

Puky, M., J. D. Reynolds, and P. Schád. 2005. Native and alien Decapoda in Hungary: distribution, status, conservation importance. Bull. Fr. Pêche Piscic. 376–377, 553–568.

Rubach, M., S. Crum, and P. van den Brink. 2011. Variability in the dynamics of mortality and immobility responses of freshwater arthropods exposed to chlorpyrifos. Archives of Environmental Contamination and Toxicology 60(4):708–721.

Samardžić, M., A. Lucić, I. Maguire, and S. Hudina. 2014. The first record of the marbled crayfish (*Procambarus fallax* (Hagen, 1870) f. *virginalis*) in Croatia. Crayfish News 36:4.

Saura, A., J. Lokki, and E. Suomalainen. 1993. Origin of polyploidy in parthenogenetic weevils. Journal of Theoretical Biology 163(4):449–456.

Scholtz, G., A. Bradand, L. Tolley, A. Reimann, B. Mittmann, C. Lukhaup, F. Steuerwald, and G. Vogt. 2002. Parthenogenesis in an outsider crayfish. Nature 421:806

Scholtz, G., A. Braband, L. Tolley, A. Reimann, B. Mittmann, C. Lukhaup, F. Steuerwald, and G. Vogt. 2003. Parthenogenesis in an outsider crayfish. Nature 421:806.

Schulz, H., H. Groß, C. Dümpelmann, and R. Schulz. 2009. Flusskrebse Deutschlands. Pages 71–81 *in* L. Füreder, editor. Flusskrebse: Biologie, Ökologie, Gefährdung. Veröffentlichungen des Naturmuseums Südtirol, volume 6. Folio-Verlag, Bozen, Italy.

Seitz, R., K. Vilpoux, U. Hopp, S. Harzsch, and G. Maier. 2005. Ontogeny of the Marmorkrebs (marbled crayfish): a parthenogenetic crayfish with unknown origin and phylogenetic position. Journal of Experimental Zoology A 303(5):393–405.

Soes, M., and R. van Eekelen. 2006. Rivierkreeften, een oprukkend probleem? De Levende Natuur 107(2):56–59.

Souty-Grosset, C., D. M. Holdich, P. Y. Noel, J. D. Reynolds, and P. Haffner. 2006. Atlas of crayfish in Europe. Muséum National d´Histoire Naturelle, Paris.

van der Wal, J. E. M., M. Dorenbosch, A. K. Immers, C. Vidal Forteza, J. J. M. Geurts, E. T. H. M. Peeters, B. Koese, and E. S. Bakker. 2013. Invasive crayfish threaten the development of submerged macrophytes in lake restoration. PLoS One 8:e78579.

Vogt, G. 2008. Investigation of hatching and early post-embryonic life of freshwater crayfish by in vitro culture, behavioral analysis, and light and electron microscopy. Journal of Morphology 269(7):790–811.

Vogt, G. 2010. Suitability of the clonal marbled crayfish for biogerontological research: a review and perspective, with remarks on some further crustaceans. Biogerontology 11(6):643–669.

Vogt, G. 2011. Marmorkrebs: natural crayfish clone as emerging model for various biological disciplines. Journal of Biosciences 36:377–382.

Vogt, G., C. Falckenhayn, A. Schrimpf, K. Schmid, K. Hanna, J. Panteleit, M. Helm, R. Schulz, and F. Lyko. 2015. The marbled crayfish as a paradigm for saltational speciation by autopolyploidy and parthenogenesis in animals. Biology Open 4:1583–1594.

Vogt, G., M. Huber, M. Thiemann, B. Gvan den, O. J. Schmitz, and C. D. Schubart. 2008. Production of different phenotypes from the same genotype in the same environment by developmental variation. Journal of Experimental Biology 211(4):510–523.

Vogt, G., L. Tolley, and G. Scholtz. 2004. Life stages and reproductive components of the Marmorkrebs (marbled crayfish), the first parthenogenetic decapod crustacean. Journal of Morphology 261:286–311.

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