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REVIEW PAPER

Evaluation of the suitability of the parthenogenetic marbled crayfish for aquaculture: potential benefits versus conservation concerns

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Abstract The parthenogenetic marbled crayfish, *Procambarus virginalis*, is currently being discussed as a promising new candidate for aquaculture that could supply people in developing countries with high-quality protein and income. The main advantage of marbled crayfish is parthenogenetic reproduction. Comparison of growth between marbled crayfish and red swamp crayfish, *Procambarus clarkii*, the leading species in crayfish aquaculture revealed inferior body size and considerably slower growth in marbled crayfish. Only a very small proportion of the production would meet the size requirement of the international market and could serve as a cash crop. Aquaculture for local markets in extensive outdoor systems is probably economically feasible in developing countries, but the highly invasive and competitive marbled crayfish could easily escape from such sites, invade natural ecosystems and impair the autochthonous fauna and flora. Culture in closed indoor systems would be a safe alternative but this cost-intensive approach is economically not profitable. Because of small body size and slow growth, conservation concerns, and economic reasons, the marbled crayfish is considered unsuitable for aquaculture. It should not be spread around the globe for aquaculture and sustainable fisheries as was earlier done with the congeneric *Procambarus clarkii*, resulting in devastating ecological effects in numerous countries.

Keywords Marbled crayfish · Aquaculture · Conservation · Growth · *Procambarus clarkii*

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Introduction

The marbled crayfish or Marmorkrebs, *Procambarus virginalis* Lyko, 2017, is the only obligately parthenogenetic freshwater crayfish and decapod crustacean (Scholtz et al., 2003). This unique property appears to make this species particularly suitable for aquaculture. Marbled crayfish was detected in 1995 in the German aquarium trade. It is a triploid descendant of the sexually reproducing slough crayfish, *Procambarus fallax* (Hagen, 1870), that occurs in Florida and southern Georgia (Martin et al., 2010). Marbled crayfish has neither been found in the native range of its parent species nor in historical museum collections giving rise to the hypothesis that it is an evolutionarily young species that even might have originated in captivity (Vogt et al., 2015; Vogt, 2019).

Marbled crayfish is kept by aquarists and research laboratories worldwide. It has frequently been used as a laboratory model for several disciplines including development, neurobiology, toxicology, and epigenetics (reviewed in Vogt 2008, 2018b, 2020a; Faulkes, 2016; Hossain et al., 2018). Marbled crayfish represents a single clone consisting of genetically identical specimens (Martin et al., 2007; Vogt et al., 2008; Gutekunst et al., 2018), and therefore, it is particularly suitable for studying the role of epigenetic mechanisms in shaping of the phenotype and environmental adaptation (Vogt, 2008, 2017, 2018a, 2020b). For these purposes, marbled crayfish colonies are kept safely in closed indoor systems preventing escapes.

Releases have led to the establishment of numerous wild populations in tropical to cold-temperate biomes in Europe (15 countries), Africa (Madagascar) and Asia (Israel and Japan). Detailed information on the invaded sites and the actual status of the populations and respective references are found in Vogt (2020a) and on the Marmorkrebs web page (https://faculty.utrgv.edu/zen.faulkes/marmorkrebs/#Pubs). In Madagascar, marbled crayfish has spread from an initial introduction near the capital Antananarivo in about 2003 (Jones et al., 2009) over more than 100.000 km^2, mostly by human distribution, now inhabiting diverse freshwater ecosystems (Andriantsoa et al., 2019, 2020). Further information on the biology of marbled crayfish and an extensive bibliography are found in Vogt (2018b, 2020a).

In the first scientific paper on marbled crayfish that was published in the journal *Nature* in 2003 we listed the pros and cons of this new crayfish (Scholtz et al., 2003). The pros-list included the possible use of marbled crayfish as a research model and candidate for aquaculture and the cons-list included warnings on the ecological threat that marbled crayfish might exert once released into the wild. At that time, there were only few data available on the biology of marbled crayfish and wild populations were unknown. More recently, the development of a sustainable marbled crayfish aquaculture was propagated by Jurmalietis et al. (2019) and Tönges et al. (2020) aimed at providing people in developing countries with cheap high-quality protein and income. Media even reasoned that marbled crayfish could help to solve the world hunger problem (e.g., https://www.tfhmagazine.com/articles/freshwater/owning-clones). The demand for crayfish products is presently greater than the supply, particularly in China (Wang et al., 2018; https://www.transparencymarketresearch.com/crayfish-market.html), and marbled crayfish aquaculture might help fill this supply gap.

In the following, I will examine the suitability of marbled crayfish for aquaculture considering life history features relevant for aquaculture, possible conflicts with conservation, and economic aspects. In the first section, I give a brief overview on crayfish aquaculture. Thereafter, growth and reproduction are compared between marbled crayfish and red swamp crayfish. *Procambarus clarkii* (Girard, 1852), the most successfully cultured freshwater crayfish. Then the invasiveness and competitiveness of marbled crayfish and its potential effects on invaded ecosystems are examined to identify possible conflicts between aquaculture and conservation. The final sections discuss economic aspects and legal regulations.

Crayfish aquaculture

Freshwater crayfish aquaculture is a rapidly expanding industry with a value of > 10 billion US$ in 2017 (FAO, 2019). Production has tripled since 2008. The following species are cultivated: red swamp crayfish, *Procambarus clarkii*, signal crayfish, *Pacifastacus leniusculus* (Dana, 1852), noble crayfish, *Astacus astacus* (Linnaeus, 1758), narrow-clawed crayfish, *Pontastacus leptodactylus* (Eschscholtz, 1823), yabby, *Cherax destructor* Clark, 1936, red claw, *Cherax quadricarinatus* (von Martens, 1868), and marron, *Cherax tenuimanus* Smith, 1912 (Fig. 1). Red swamp crayfish and signal crayfish are native to North America, the *Astacus* species to Europe and the *Cherax* species to Australia. These species were traditionally fished in their native ranges but were also introduced to other geographical regions for commercial and recreational fishery and aquaculture (Loureiro, 2020).

Although *Procambarus clarkii* is the smallest of the cultured species (Table 1, Fig. 1) it accounts for almost the entire global crayfish production. In 2017, its production was 1.19 mio t (22.7% of crustacean aquaculture production) having a value of 10.0 billion US$ (FAO, 2019). The aquaculture and capture fisheries production of all other crayfish species together was only a few thousand tons. *Procambarus clarkii* is the cheapest freshwater crayfish on the market (~ 5–10 US$ per kg live weight) and the

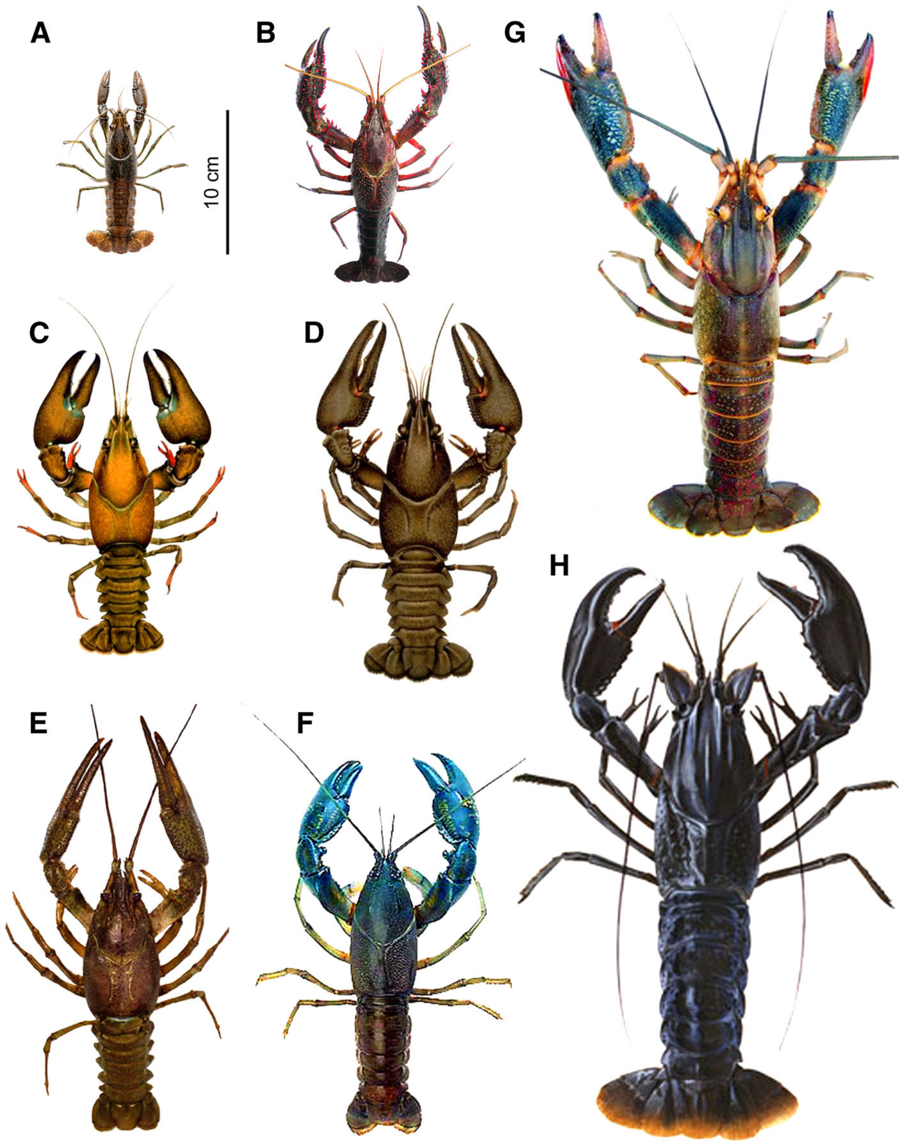

Fig. 1 Comparison of body size and chela size between marbled crayfish and males of cultured crayfish species. **A** Marbled crayfish, *Procambarus virginalis* (from Vogt et al., 2018, modified). **B** Red swamp crayfish, *Procambarus clarkii* (from Koordinationsstelle Flusskrebse Schweiz, 2019, modified). **C** Signal crayfish, *Pacifastacus leniusculus* (from Zimmerman, 2012, modified). **D** Noble crayfish, *Astacus astacus* (from Zimmerman, 2012, modified). **E** Narrow-clawed crayfish, *Pontastacus leptodactylus* (from Huys et al., 2014, modified). **F** Yabby, *Cherax destructor* (from https://insta-stalkerr.com/tag/yabbies-information, modified). **G** Red claw, *Cherax quadricarinatus* (from https://twitter.com/seafooddemand/status/748685733733339136, modified). **H**. Marron, *Cherax tenuimanus* (from WA Department of Fisheries, 2015, modified). **B** and **C** are native to North America, **D** and **E** to Europe and **F–H** to Australia. Scale bar applies to all species

Astacus species and marron are the highest priced species (30–70+ US$ per kg, depending on size).

For economical reasons, all crayfish species are cultured in extensive and, to a lesser extent, semi-intensive outdoor systems (Holdich, 1993). Extensive culture relies on natural food and semi-intensive culture requires supplemental feeding with pellets. Grow-out is generally done in earthen ponds. Rearing of the adults in tanks with recirculating water management is in the experimental stage, for example

Table 1 Comparison of life history features between marbled crayfish and cultured crayfish species. Data from Huner (2002), Lawrence & Jones (2002), Lewis (2002), Skurdal & Taugbøl (2002), WA Department of Fisheries (2015), FAO (2019, 2020a, b) and Gippel (2020)

Species	Total length (cm)	Body weight (g)	Pleopodal egg number	Age at maturity (years)	Longevity (years)	Aquaculture production (t)
Procambarus virginalis	Rarely > 10 Max 12	Mostly < 20 Max 50	50–730	0.4–0.6	2–3 Max 4.5	0
Procambarus clarkii	12 Max 15	30–80 Max 100	100–500 Max 1000	0.3–0.4	2 Max 5	1.19 mio
Pacifastacus leniusculus	F: 12 M: 16	F: 80 M: 200	60–400	1–3 Mostly 2	7–10	< 100
Astacus astacus	F: 15 M: 18	270	80–200	3–5	15–20	< 100
Pontastacus leptodactylus	F: 15 M: 17	200	100–300	3–5	> 10	< 100
Cherax destructor	15	220	30–450 Max 1000	1	3–6	~ 300
Cherax quadricarinatus	25	200–400	300–800	1	5	~ 350
Cherax tenuimanus	30	F: 400 M: 500 Max 2000	200–400 Max 800	2–3	> 10	< 100

F females, *M* males

for *Cherax quadricarinatus* (FAO. 2020b) but appears to be economically not yet profitable. Labour and cost-intensive hatcheries and nurseries are sometimes used for the higher-priced species to reduce mortality and accelerate growth of the early life stages (Parnes & Sagi, 2002; Núñez-Amao et al., 2019).

Comparison of growth and reproduction between marbled crayfish and *Procambarus clarkii*, the leading species in crayfish aquaculture

Since marbled crayfish was not yet reared in aquaculture facilities, I will compare growth of marbled crayfish and *Procambarus clarkii* from comparable natural water bodies and geographical regions. Particular emphasis was given to specimens > 20 g live weight, because this is the minimum target weight required by the international crustacean market (McClain & Romaire, 2004; FAO, 2020a, b; Wang et al., 2018).

Tönges et al. (2020) used specimens from Madagascar and two lakes in southern Germany (mesotrophic gravel pit Reilinger See and recultivated lignite mining site Murner See) to establish a length–weight relationship curve for marbled crayfish. Of the 1537 specimens collected by baited traps, hand nets and scuba diving only 30 specimens (1.95%) were heavier than 20 g and 11 specimens (0.7%) were heavier than 30 g. The heaviest marbled crayfish ever collected or raised had a weight of 49.1 g, and the second and third heaviest marbled crayfish ever recorded had weights of 43 and 39 g (Tönges et al., 2020). In contrast, in a sample from an aquaculture pond in China, more than 50% of the 678 measured *Procambarus clarkii* had weights > 20 g and the heaviest specimen had a weight of 83.4 g (Wang et al., 2011).

Andriantsoa et al. (2019) measured 2458 marbled crayfish collected with traditional fishing tools and hand nets from five distant and ecologically different sites in Madagascar, one pond, one rice field, one lake, and two rivers. None of the analyzed specimens had a weight > 20 g, although subtropical and tropical Madagascar should be an ideal environment for marbled crayfish if one considers that its parent species *Procambarus fallax* is a subtropical species. The same holds for the 552 and 28 specimens sampled by Jones et al. (2009) and Kawai et al. (2009), respectively, in Madagascar. In the highland lake Ranomaimbo (1491 m a.s.l., 28°C at sampling time) all of the 781 measured marbled crayfish were smaller than 12.5 g (Andriantsoa et al., 2019). In contrast, in the highland lake Naivasha in Kenya (1880 m a.s.l., 15.9–20.6°C during sampling period) 72 of 73 captured *Procambarus clarkii* had weights between 20 and 80 g (Oluoch, 1990).

In mesotrophic gravel pit Lake Šoderica, Croatia (south-eastern Europe), which has summer temperatures > 23°C, there were only 5 of 404 trapped marbled crayfish > 20 g and the heaviest specimen had a weight of 23 g (Cvitanić, 2017). In contrast, in comparable mesotrophic Lake Trasimeno, Italy (summer water temperature ~ 26°C), the mean weight of 1168 *Procambarus clarkii* caught by fyke nets was 22.2 g. More than 50% had weights > 20 g and the heaviest specimen weighed 76.7 g (Dörr et al., 2006).

In mesotrophic lake Moosweiher in southern Germany, Central Europe (annual water temperature range 4–26°C), 16 specimens or 3.2% of 496 marbled crayfish caught with baited traps and by hand in different seasons and years had total lengths (tip of rostrum to end of telson) > 93 mm and carapace lengths > 43 mm corresponding to a weight > 20 g (Chucholl & Pfeiffer, 2010; Günter, 2014; Lehninger, 2014; Wolf, 2014; Buri, 2015; Vogt et al., 2018). The biggest specimen had an estimated weight of 31 g (Chucholl & Pfeiffer, 2010). In contrast, about 300 of 313 *Procambarus clarkii* collected with baited traps from mesotrophic gravel pit Riedheimer See in southern Germany (water temperature April–October 11.5–23.9°C) had weights > 20 g and 50 had weights > 50 g (Chucholl, 2011). The largest specimens had carapace lengths of 76.1 mm and 76.0 mm corresponding to total lengths of ~ 16 cm and estimated weights of almost 100 g. These comparisons clearly demonstrate that *Procambarus clarkii* grows on average considerably bigger than marbled crayfish. The other cultured crayfish species obtain much bigger body sizes (Table 1, Fig. 1) and are marketed from 30 g upwards. The market price generally increases with size of specimens.

The growth data also suggest that marbled crayfish grow bigger in higher latitudes than in lower latitudes as was earlier reported for *Procambarus clarkii* (Chucholl, 2011). Bigger body sizes are probably the result of increased longevity in higher latitudes, which was reported for several freshwater and marine decapod species including *Procambarus clarkii* (Chucholl, 2011; Vogt, 2012). Growth over longer life spans apparently over-compensates the lower growth rate in cooler geographical regions.

In the extensive aquaculture ponds of Louisiana, *Procambarus clarkii* grows to marketable sizes > 20 g in less than half a year after hatching (Huner, 2002). McClain & Romaire (2009) raised *Procambarus clarkii* in the laboratory at ~ 28°C, starting with juveniles of 0.013 g and obtained marketable-sized crayfish already after 12 weeks. Specimens raised in rice forage microcosms and fed additionally with formulated pellets (25% crude protein) or rice seeds grew to mean weights of 29.9 g and 23.0 g in 12 weeks, respectively (McClain & Romaire, 2009). In contrast, marbled crayfish raised at 20°C and fed with pellets (47.5% crude protein) plus chironomid larvae had a mean weight of only 2 g after six month (Seitz et al., 2005). A similar weight gain was obtained in my laboratory colony at 20–25°C after six month of feeding with TetraWafer Mix pellets (45.0% crude protein) (Vogt, 2010). Recently, Tönges et al. (2020) made growth experiments with tailored feeds starting with juveniles of a mean weight of 0.11 g (corresponding to an estimated age of ~ 2 months). After 3 months of feeding at 20°C they measured a mean individual weight gain of 1.43 g with a commercial feed and 2.81 g with a feed adjusted to the amino acid composition of marbled crayfish (29% crude protein, methionine supplemented). Although the experimental conditions in the laboratory growth experiments with the two crayfish species were not identical it is quite obvious that marbled crayfish grows much slower than *Procambarus clarkii*. *Cherax destructor* and *Cherax quadricarinatus* obtain maturity and marketable size within a year after hatching but the other species require longer periods of time (Table 1).

In crayfish, males have generally bigger chelipeds and chelae than females, and usually, they grow considerably bigger (Table 1). For example, in *Procambarus clarkii* females have only 50% chela meat when compared to males. Therefore, males are particularly attractive for consumers. However, in the all-female marbled crayfish males are lacking. Marbled crayfish females have only small chelipeds and small and slender chelae (Fig. 1), which is a considerable disadvantage.

Marbled crayfish has a clear advantage over *Procambarus clarkii* and other cultured crayfish species with respect to fertility. Because of parthenogenetic reproduction, all adults are capable of producing offspring. Moreover, marbled crayfish has 40% higher mean numbers of pleopodal eggs than equal-sized *Procambarus clarkii* (Alcorlo et al., 2008; Jones et al., 2009; Hossain et al., 2019a; Jin et al., 2019; Vogt et al., 2019). On the other hand, the maximum egg number ever recorded is higher in *Procambarus clarkii* than marbled crayfish (1017 versus 731) because *Procambarus clarkii* grows bigger and clutch size in crayfish is positively correlated with body size (Oluoch, 1990; Vogt et al., 2019).

Tönges et al. (2020) argued that the monosex population structure of marbled crayfish would allow particularly high stocking densities in aquaculture because of the absence of agonistic interactions between males and females. However, high stocking densities are counterproductive in crustacean aquaculture because they result in increased cannibalism and stunted growth (Barki & Karplus, 2004; McClain & Romaire, 2009). For example, in cultured signal crayfish, *Pacifastacus leniusculus* cannibalism increased with both crayfish size and density even when sexes were separated (Houghton et al., 2017).

Comparison of life history features relevant for aquaculture suggests that marbled crayfish cannot compete with *Procambarus clarkii*, the most successfully cultured freshwater crayfish and the other cultured species in terms of production of marketable-sized crayfish. All marketable marbled crayfish (> 20 g) sampled from ten populations in Madagascar and Germany by baited traps, hand, and scuba diving, which capture the upper proportion of the size-distribution (Jones et al., 2009; Kawai et al., 2009; Chucholl & Pfeiffer, 2010; Günter, 2014; Lehninger, 2014; Wolf, 2014; Buri, 2015; Lyko, 2017; Vogt et al., 2018, 2019; Andriantsoa et al., 2019; Tönges et al., 2020) together had a total weight of less than 2 kg with an estimated total value of only 10–15 US$. Higher fertility in marbled crayfish cannot compensate for the growth disadvantage. The marbled crayfish is simply too small to be grown as a cash crop for the international market. What remains is the production for local markets in developing countries, where much smaller crayfish can be sold. In Madagascar, traded marbled crayfish had a mean fresh weight of only 4.8 g (Andriantsoa et al., 2019).

Conflict of marbled crayfish aquaculture with conservation

Cost-effective production of marbled crayfish for local markets in developing countries is probably possible in extensive outdoor systems depending on natural food (see economics section below) but this type of aquaculture carries the high risk of escapes. Aside of pet shops, aquaculture is the main vector for freshwater crayfish introductions (Chucholl, 2013; Loureiro, 2020).Worldwide, 33 non-indigenous crayfish species (NICS) are known so far, including the aquaculture species *Procambarus clarkii*, *Pacifastacus leniusculus*, *Cherax destructor*, and *Cherax quadricarinatus* (Loureiro, 2020). Crayfish are keystone species in many aquatic water bodies, because they often occur in high densities, feed on detritus, plant material, and animals and are themselves prey for predators (Nisikawa, 2010). Modification of food webs, competition with native species for resources, transmission of diseases, and habitat degradation are the most recurrent threats associated to the establishment of NICS (Kozák et al., 2011; Souty-Grosset et al., 2016; Loureiro, 2020).

The conflict between economic interests and conservation in crayfish aquaculture is best exemplified by *Procambarus clarkii*. This species, which is native to northern Mexico and the southern states of the USA was earlier only fished and cultured in its native distribution range, particularly in Louisiana (McClain & Romaire, 2004). The great success of the traditional Louisiana crawfish capture fishery and aquaculture industry prompted people to introduce this species to other geographical regions for commercial exploitation. Between the 1920s and 1970s it was introduced to other regions of the U.S.A, China, Kenya, and Spain and later to many more countries (Oficialdegui et al., 2019). *Procambarus clarkii* is now one of the most economically valuable cultured freshwater animals. On the other hand, spreading of *Procambarus clarkii* over the world has led to the establishment of wild populations in 34 countries on all habitable continents except Australia (Kawai & Crandall, 2016).

As a result, *Procambarus clarkii* is now the most widespread crayfish on earth and one of the worst invasive species, causing serious negative impacts on native crayfish species and freshwater ecosystems (Loureiro et al., 2015; Souty-Grosset et al., 2016; Oficialdegui et al., 2019). Invasive *Procambarus clarkii* can reduce or replace native crayfish populations by competition for resources and transmission of the crayfish plague, a disease lethal to European astacidean and Southern Hemisphere parastacidean crayfish species (Svoboda et al., 2017). They are potent spreaders of this oomycete disease and have brought a new strain of the disease agent, *Aphanomyces astaci*, from North America to Europe, Asia, and South America (Diéguez-Uribeondo & Söderhäll, 1993; Peiró et al., 2016; Putra et al., 2018; Mojžišová et al., 2020).

Invasive *Procambarus clarkii* can efficiently engineer their new ecosystem. For example, they can increase feeding efficiency on animal prey by reducing submerged macrophytes that serve as shelters, thus increasing their individual growth rate (Nishijima et al., 2017). In streams of the Santa Monica Mountains (California), the invaders disturbed the relationship between the dragonfly nymphs and their mosquito larvae prey (Bucciarelli et al., 2018). The crayfish reduced the dragonfly nymphs, which are more efficient predators of mosquito larvae than crayfish, leading to higher mosquito populations and a loss of ecosystem services related to disease vector control. *Procambarus clarkii* is also an efficient predator of amphibian embryos and larvae and can reduce amphibian populations markedly or completely (Kats & Ferrer, 2003; Cruz et al., 2008). For example, in the Paul do Boquilobo Nature Reserve, central Portugal, 13 species of amphibians were present before the introduction of *Procambarus clarkii*. Eight years later, only six amphibian species were recorded, all in extremely small numbers.

Invasive *Procambarus clarkii* can also cause costly damages to rice fields, irrigation canals, and dams (Souty-Grosset et al., 2016; Oficialdegui et al., 2019). For example, in wet-seeded rice fields in Portugal, it has severely damaged rice production through predation on rice seedlings (Anastacio et al., 2005). In an irrigation canal in Egypt, *Procambarus clarkii* has dug numerous 40–90 cm deep burrows along the shorline of the canal in any time of the year (Abdel-Kader, 2016). Since burrowing animals have been identified as a main cause for levee failures the intensely burrowing *Procambarus clarkii* is considered a severe threat to earthen flood protection dams (Haubrock et al., 2019).

There is no doubt that the congeneric marbled crayfish is a potent invader as well. It has already established many populations in diverse ecosystems and geographical regions, mainly in Europe and Madagascar (reviewed in Vogt, 2020a). Marbled crayfish has a Freshwater Invertebrate Invasiveness Scoring Kit (FI-ISK) score of 22, which was the second highest of the 20 most common crayfish species in the European aquarium trade (Chucholl, 2016). The threshold for being classified as high risk species is a score of $\geq$ 16. The leading species was *Procambarus clarkii* with a FI-ISK score of 39. Because of parthenogenetic reproduction, Jones et al. (2009) called marbled crayfish the "perfect invader" and media called it, more sensational, the mutant monster that overruns the world in a Blitzkrieg (e.g., https://www.dailymercury.com.au/news/cloverfield-crayfish-created-a-new-species-of-self/3328908/).

Marbled crayfish can migrate over land and dig burrows. Specimens were seen escaping from an overpopulated pond in eastern Germany (Wendt, 2011) and crawling on land after cleaning of a canal in the Netherlands (Soes &Koese, 2010). Dead specimens were found in a pedestrian underpass 130 m away from an inhabited large gravel pit in southern Germany well suitable for crayfish (Chucholl et al., 2012). Chucholl and colleagues concluded that migration over land is most likely a dispersal behaviour inherent to marbled crayfish rather than an escape from adverse environmental conditions. Burrowing of marbled crayfish was so far only observed in Madagascar. Jones et al. (2009) found specimens buried deep in the mud of pools with no surface water. However, Frank Lenich has recently detected intense burrowing activity in lake Murner See in Bavaria, Germany (Fig. 2). He found numerous burrows, some as deep as 1 m, and actively burrowing marbled crayfish by scuba diving (Frank Lenich, personal communication).

In contrast to *Procambarus clarkii*, relatively few data are available on the effects of marbled crayfish on invaded ecosystems, but there is increasing information on its high competitiveness. In Madagascar, marbled crayfish is generally considered to "have a negative impact on rice agriculture and fishing" as revealed by a socio-economic survey (Andriantsoa et al., 2020). In Malta, marbled crayfish preyed on

Fig. 2 Marbled crayfish at entrance of burrow in lake Murner See, southern Germany (photo Frank Lenich)

gastropods, tadpoles of frogs, adult fish, and larvae of drone fly (Deidun et al., 2018). In an oligotrophic gravel pit at Leopoldov (south-western Slovakia) marbled crayfish used mostly allochthonous detritus (30%), algae (25%), and autochthonous detritus (21%) as food sources. Zoobenthos and macrophytes contributed 9% and 14% to the diet, respectively (Lipták et al., 2019). Marbled crayfish was also found to be an important food source for fish predators. By combining food-choice laboratory experiments with stable isotope analyses of field samples, Linzmaier et al. (2020) revealed that marbled crayfish occupy a wide range of trophic positions corresponding to a nutritional generalist. In mesotrophic and dimictic lakes they increased grazing pressure on macrophytes and macrophyte-dependent organisms and enhanced decomposition of the allochthonous detritus. Since marbled crayfish can exploit various trophic levels on the one hand and be prey for top level predators on the other hand it has the potential to significantly modify the food webs of invaded ecosystems.

Behavioural laboratory studies revealed that marbled crayfish can well compete with other highly invasive crayfish species such as *Procambarus clarkii*, spiny-cheek crayfish, *Faxonius limosus*, and calico crayfish, *Faxonius immunis* (Jimenez & Faulkes, 2011; Linzmaier et al., 2018; Hossain et al., 2019b, 2020). The co-occurrence of marbled crayfish and *Procambarus clarkii* in Ta' Sarraflu pond, Gozo Island, Malta (Deidun et al., 2018) confirms that marbled crayfish can compete with the red swamp crayfish also in natural environments. In Lake Moosweiher marbled crayfish has established a vivid population since about 2009 despite the presence of the crayfish competitor *Faxonius limosus* that has invaded the lake already before 1990 and effective crayfish predators such as catfish, pike, perch, eel, and great crested grebe (Chucholl & Pfeiffer, 2010; Vogt et al., 2018). *Faxonius limosus* is an invasive species of North American origin that has spread in Central Europe since 130 years. It is now the most common crayfish in this region (Filipová et al., 2011). Marbled crayfish has even established populations in the presence of much bigger crayfish species like the narrow-clawed crayfish, *Pontastacus leptodactylus* on Malta (Deidun et al., 2018) and *Astacoides betsileoensis* and *Astacoides granulimanus* in Madagascar (Andriantsoa et al., 2019).

It is proven that marbled crayfish can also carry and transmit the crayfish plague (Keller et al., 2014), and therefore, it may accelerate spreading of this disease across the globe once introduced for aquaculture. Marbled crayfish can get infected by contact with other plague carrying species of North American origin like *Procambarus clarkii*, *Faxonius limosus* and *Pacifastacus leniusculus*. The Malagasy populations tested so far were free of this oomycete (Jones et al., 2009; Andriantsoa et al., 2019), suggesting that whether an invasive marbled crayfish population carries the pathogen or not depends on the infection status of the founding specimens. The laboratory-raised research colonies tested so far were all free of the disease.

The behavioural and ecological data suggest that marbled crayfish could easily spread from outdoor aquaculture systems into natural water bodies and establish wild populations. In the invaded habitats, it may negatively influence food webs and wildlife biodiversity as observed for *Procambarus clarkii*. To mitigate these problems, Tönges et al. (2020) suggested establishing freshwater ponds for marbled crayfish grow-out in brackish water environments due to the supposedly low salt tolerance of the species. The implementation of this curious idea would, if at all possible, impair the ecologically most valuable mangroves that usually line the brackish water estuaries in subtropical and tropical countries. Moreover, marbled crayfish can not only survive brackish water (0.1–1%

salinity) for many months but even higher salt concentrations, although they do not reproduce under such conditions. Laboratory experiments revealed that 10% of the animals exposed to 0.9% and 1.2% salinity survived the maximally tested exposure time of 155 days and even in 1.8% salinity a specimen survived for 91 days (Veselý et al., 2017). This would give escaped marbled crayfish plenty of time to migrate through the brackish water barriers of such hypothetical aquafarms and search for more suitable habitats in upstream river sections.

Tönges et al. (2020) also proposed the application of an eDNA detection method for marbled crayfish as an additional measure to safeguard aquaculture of marbled crayfish. However, this technique, which can detect very small amounts of environmental DNA released from a crayfish species into the water (Rusch et al., 2020), is only suitable to identify specimens that have already escaped and established populations in the wild but not to prevent escapes. Therefore, the only safe way of culturing marbled crayfish would be rearing of all life stages in closed indoor systems but would this be economically feasible?

Economic considerations

All crayfish species cultured so far are reared in extensive and semi-intensive outdoor systems, even the high-priced ones because closed indoor systems are not profitable. For example, in *Procambarus clarkii* aquaculture in Louisiana, pond size and labour input range from impounded wetlands greater than 120 ha with little management to more intensively managed systems of less than 6 ha. Supplemental feeds are not routinely used (FAO, 2020a). Occasionally, the vulnerable early life stages of higher-priced species are raised in hatcheries and nurseries to reduce mortality (Núñez-Amao et al., 2019) but grow-out is generally done outdoors. Indoor culture of all life stages of crayfish including marbled crayfish is only realized in research institutes that do not have to be profitable.

Collecting marbled crayfish from natural habitats and selling on local markets as done in Madagascar by private people is profitable because there are no production costs. One kg live marbled crayfish is on average sold for ~ 1000 Malagasy Ariary (500–1500 MGA) corresponding to 0.3 US$ (Andriantsoa et al., 2019). This is a bit lower than the price for rice. Since there are no estimates for annual yields per ha and production costs available it is difficult to estimate if the extensive aquaculture of marbled crayfish for local markets, e.g., in monoculture, polyculture with fish, or rotating culture with rice, would be profitable, but I assume that this may be the case.

Indoor culture in closed systems would require buildings, tanks, sophisticated water management, and feeding with artificial feed. It would be much more labour-intensive than extensive outdoor culture. The minimum salary in Madagascar is 333.000 MGA per month (http://www.salaryexplorer.com/salary-survey.php?loc=128&loctype=1), and thus, about 4 t marbled crayfish would be required to earn the annual salary of a single low-wage facility aide.

Another important cost factor is the food. The best food conversion ratio of marbled crayfish that was measured by Tönges et al. (2020) was 1.4. Therefore, one kg food must cost less than ~ 700 MGA to equal the Malagasy market price of 1 kg live marbled crayfish. However, even the cheapest food for cultured fish in Madagascar costs considerably more, e.g., a homemade feed for tilapia consisting of fish meal and local plant material, which had production costs of 1270 MGA/kg (Nguyen, 2015). Chicken feed, which is often used in fish aquaculture, costs ~ 1440 MGA/kg (Nguyen, 2015). These few calculation examples show that intensive culture of marbled crayfish in closed systems would not be profitable in Madagascar, because the feed costs alone would already exceed the sales price.

In summary, in industrialized countries any type of marbled crayfish aquaculture would fail because of high production costs and the lack of demand for such a small crayfish. In developing countries, where small crayfish could be sold, the extensive culture of marbled crayfish relying on natural food may be profitable, but this culture method must be rejected because of the high risk of escapes. The only safe culture possibility, namely closed indoor systems with artificial feeding, is economically not feasible, even not in developing countries with low labour costs.

Legal regulations

There are no specific legal regulations for aquaculture of marbled crayfish yet, but there are regulations in many countries for invasive species including marbled crayfish. In the European Union (27 member states) marbled crayfish is listed among the invasive alien species of EU concern according to EU Regulation No. 1143/2014 (European Parliament and Council of the European Union, 2014; European Commission, 2017). This regulation prohibits keeping and breeding of marbled crayfish within the Union, placing on the market and releasing into the environment. Accordingly, marbled crayfish cannot be cultured and marketed. Keeping for scientific purposes is allowed. In the United States there are regulations for marbled crayfish in at least four states: Idaho, Michigan, Missouri and Tennessee (http://marmorkrebs.blogspot.com/search/label/legislation). For example, in Idaho no person may possess, cultivate, import, ship or transport marbled crayfish without a permit (Idaho Department of Administration, 2010). In Madagascar, the transportation and release of wild marbled crayfish is prohibited (Ministère de l'Agriculture, de l'Elevage et de la Pêche, 2008), but not too many seem to follow this enactment (Andriantsoa et al., 2019).

The problem of exploiting existing marbled crayfish populations

Invasive crayfish populations can be eradicated only in an initial stage and if the invaded water bodies are small (Sandodden, 2019). Rivers and lakes can neither be drained nor poisoned with effective insecticides. Therefore, it was often suggested to exploit the invasive populations to keep them small (discussed in Nuñez et al., 2012). However, experience has shown that this measure is only effective if carried out by licensed fishermen under strict control of the responsible authorities so that no new market can develop. Creating a new market engenders pressure to maintain the invasive species and fosters translocation to previously uninvaded regions, increasing the invader's distribution range (Nuñez et al., 2012; Nunes et al., 2017). This effect is well evidenced by the history of signal crayfish spread in Scandinavia (Bohman et al., 2011). Therefore, the International Association of Astacology (IAA) has recently emphasized in the Gotland Resolution that the control of invasive crayfish species by intensive recreational and commercial fisheries does not represent a feasible method to control the populations (Edsman et al., 2019).

In Madagascar, fishing of the invasive marbled crayfish from natural waters has created a market and fostered its translocation throughout the country to start new populations, which is, to a certain degree, understandable in a poor and highly populated country. This way, the marbled crayfish has spread in only 15 years from a single introduction site over a range of 100.000 km^2 (Jones et al., 2009; Andriantsoa et al., 2019, 2020). This example tells us that once marbled crayfish is introduced in a developing country and used as a food item it will soon be spread by humans across the country.

Conclusions

The present evaluation demonstrates that marbled crayfish is too small a species to compete with the top selling *Procambarus clarkii* as a cash crop on international markets. However, in developing countries it could enrich the food supply on local markets, providing an affordable protein source. Unfortunately, the only economically feasible production system would be extensive outdoor culture in earthen ponds based on natural food but this system does not prevent from escapes. Because of high invasiveness and competitiveness marbled crayfish would surely escape from such ponds, invade natural waters and have detrimental effects on native fauna and flora. Intensive aquaculture of marbled crayfish in closed indoor systems with artificial feeding that would avoid the ecological risks is not profitable, even not in developing countries with low labour costs. Legal regulations on invasive species already prohibit breeding and selling of marbled crayfish in many countries. Due to these reasons, the use of marbled crayfish for aquaculture and its introduction for commercial or subsistence fishery should no longer be propagated.

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