

Mitigating the role of aquaculture in crustacean invasions

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19 **Importance of aquaculture and its biological invasion risks**

20 Aquaculture plays a critical role in alleviating malnutrition and poverty¹ and stands as the world's fastest growing food sector², especially 21 in developing countries³. Global aquaculture production increased by over 600% from 1990 to 2020⁶, accompanied by a diversification 22 of farmed species, reaching 425 species in 2021⁴. Notably, the number of crustacean species reared commercially has risen from 30 to 23 at least 49 between 2017 and 2020^{5,6}. Many farmed species are non-native in their farmed regions, a trend first observed in 2000 in 24 developing countries such as Cuba, India, Philippines, Chile and Brazil, where 60–95% of all production is non-native species⁷. The 25 growing number of farms and/or farm sizes, along with non-native species farming, increases the risk of intentional or accidental release 26 into the wild³. This is likely to increase propagule pressure⁸ as was seen with the redclaw crayfish (*Cherax quadricarinatus*) which 27 escaped from captivity or abandoned farms and established wild populations in many regions⁹. Farmed species are selected for traits 28 which exacerbate their establishment and spread in the wild¹⁰ such as rapid growth, broad diet and resistance to parasite¹¹.

29 Biological invasions, involving human-related introduction, establishment, expansion and potential impact of species outside of their native ecosystem, pose a significant threat to biodiversity and ecosystem functions12 30 . For example, the red swamp crayfish (*Procambarus* 31 *clarkii*) introduced for aquaculture, is now a global invasive species¹³ which transmits diseases¹⁴ and predates on and competes with 32 native species, thereby altering food webs and habitat structures¹⁵. Notwithstanding biological invasions occasional benefits, they do not 33 outweigh their massive economic impacts¹⁶, estimated to be at least USD 423 billions in damage and management¹², also affecting aquaculture itself17 34 . The signal crayfish (*Pacifastacus leniusculus*) and the European green crab (*Carcinus maenas*), collectively inflict 35 damages totaling US\$271 million¹⁷.

36 We suggest that the rapid development of farms and farmed species is likely to increase the risk of biological invasion¹⁸ unless new 37 biosecurity protocol are developed in parallel¹⁹. While the causal links between aquaculture and biological invasions has been extensively 38 studied for specific countries or species^{20–23}, substantial gaps remain not least in the case of crustaceans, which are significant both as major aquaculture species and as invaders. Therefore, we focus on farmed crustaceans, although our conclusions apply to other taxonomic groups involved in aquaculture. We show why some farmed crustaceans pose an increasing risk of biological invasions and how this risk can be mitigated. Here, we assess commercially farmed crustaceans classifying them by country (native-non-native) and invasive history (lack or presence of invasions historically). Using these classifications, we recommend biosecurity and management strategies while highlighting the gaps in our current understanding.

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- 47 **Distribution of farmed and invasive crustaceans**

 To compile a comprehensive list of farmed crustacean species, we used the most up to date aquaculture dataset of the Food and 49 Agriculture Organization of the United Nations²⁴ (FAO) and supplemented it with our own literature research. For identifying the 50 invasive crustacean species, we cross referenced multiple invasive alien species databases $25-28$ ensuring we removed duplicates and validated scientific names using GBIF. Our final dataset includes 63 crustacean species (Appendix I & II) which have been farmed in 126 different countries globally (Table 1; Appendix III). Here, non-native species are defined as a species outside its natural range in the country where it is farmed. Of these countries, 111 have farmed at least 1 non-native species with 64 farming exclusively non-native species and 15 that farm only native species (Table 1). The whiteleg shrimp (*Penaeus vannamei*) is the most widely farmed species, cultivated across 54 countries. The signal crayfish has only been farmed in non-native countries whereas the giant mud crab (*Scylla serrata*) has been farmed only in native countries (Appendix III). Out of the 63 farmed species, 22 are considered invasive worldwide impacting at least 77 countries (Table 1; Appendix I & IV). Here, we define invasive as actual or probable negative ecological or economic impact documented in at least one population worldwide. The red swamp and the spiny-cheek (*Faxonius limosus*) crayfishes are invasive in over 20 countries (Table 2). There are several pathways by which crustaceans have been shown to spread including ballast water, pet trade and hull fouling (Table 2). However, it is established that aquaculture is a major driver/pathway in invasion crustaceans with at least 19 of the 22 invasive species introduced through aquaculture (Table 2, Appendix V), 14 of those affecting at least 30 62 countries (Table 1; Appendix IV). Causes of their introduction include unintentional escape (e.g. when used as fish food²⁹), intentional 63 release from crustacean aquaculture^{30,31} or transfer through "hitchhiking" on other species as was the case with the Chinese mitten crab 64 (*Eriocheir sinensis*) ^{32–34}. It is important to note that these results are likely underestimated due to the incomplete reporting of both farming and invasions.

Impacts of invasive farmed crustaceans

 These 22 invasive crustaceans farmed in aquaculture originate from diverse regions and environments including marine, brackish, and freshwater (Appendix I). Their introductions into non-native regions have resulted to multiple and severe impacts (Table 2). For instance, the European green crab and Chinese mitten crab outcompete and prey on native species, leading to native population declines; 71 consequently, they are listed among "100 of the worst invasive alien species" ³⁵. Four of these 22 species are also listed on the European list of invasive alien species of concern, the spiny-cheek crayfish, the red swamp crayfish, the signal crayfish, and the Chinese mitten $crab^{36}$.

 The types of impacts and associated mechanisms of these invasive crustaceans are diverse (Table 2). Tiger prawn (*Penaeus monodon*) 75 and red swamp crayfish are vectors of viral diseases such as the white spot syndrome baculovirus³⁷. Crayfish also transmit crayfish 76 plague caused by the oomycete *Aphanomyces astaci*, listed among the 100 worst invasive alien species globally³⁵. Some crustaceans are 77 considered ecosystem engineers^{15,38} that can significantly impact the structure of invaded habitats, thereby affecting other species and altering ecosystem dynamics. The European green crab reduces eelgrass biomass by damaging rhizomes and plant shoots while 79 burrowing for shelter and prey³⁹. Similarly, the red swamp crayfish alters water quality, increasing turbidity and reducing dissolved 80 oxygen levels⁴⁰. These invasive crustaceans can also impact economic activities such as aquaculture, fisheries and agriculture¹⁷. The 81 burrowing behaviour of the common yabby (*Cherax destructor*) can jeopardize dam walls, thus affecting farmers⁴¹. In Lake Naivasha,

 local fishermen estimated that the red swamp crayfish reduced their catch's food provisioning by up to 30% due to crayfish-induced 83 damage to fishing nets⁴². Thus, the risk on human activities results in massive economic consequences since four crabs - *C. sapidus, C. maenas, E. sinensis* and *P. pelagicus* - and three crayfish species – *P. clarkii, P. leniusculus* and *F. limosus* - farmed in aquaculture rank 85 among the costliest invasive crustaceans¹⁷.

A preliminary classification of the risks of invasion of farmed crustacean species

 Despite the acknowledged risks, there is still no global picture of the risk posed by farmed crustacean species in aquaculture. As a first step to address this gap, we propose a simple but widely applicable classification system based on two primary criteria: (1) the species documented global invasion history, and (2) whether the species is farmed outside its native regions. This system creates four possible outcomes, which we used to create a preliminary risk index ranging from limited risk (A) to high (D) (Figure 1). Species farmed in their native range are of low concern if escaped populations establish outside the farm (category A), but of medium concern if they are invasive in other (non-native) range (category B). Conversely, species farmed outside their native range and never reported as invasive (category C) have a high risk of becoming invasive if they escape and establish. The highest concern is for species farmed outside their native range and with a documented invasion history (category D).

 As a preliminary decision and in the absence of more in-depth risk assessments, we suggest applying appropriate management measures 97 of the 63 farmed crustacean species based on their classification. Species with the lowest risk classifications (category $A \& B$), which total 39 species, can continue to be farmed in their native regions, focusing biosecurity efforts on international transport. The seven species farmed in non-native countries (category C), require appropriate biosecurity and monitoring measures to prevent escapes from farms or transports. For the 17 species classified in the highest-risk category (D), farming in non-native regions must be avoided.

 Selecting species for aquaculture that minimise biological invasion risks while boosting economic potential is crucial. Therefore, it is 102 essential to prioritise farming species within their native regions $(A & B)^{10}$, particularly for open pond water farming. However, it is important to note that even native species can have detrimental impacts if released in large quantities (REF Geslin ?). Farming species outside their native region may only be safe if not only species are reared in enclosed structures but also if current and future environmental conditions are unfavourable to their invasiveness. The current and future risks of establishment of non-native species can be predicted with tools such as species distribution models. Thus, conducting local or national spatial prediction analyses before 107 establishing farms may allow the building of non-native farming while lowering the risk that species becomes invasive⁴³. Biosecurity 108 and early response (following regular monitoring) are the most effective ways of managing non-native species^{12,44}. The most basic approaches include: (i) farming sterile or unisex individuals, (ii) isolating farms with closed structures away from natural aquatic habitats, (iii) implementing clean-up protocols and special attire to prevent the spread of eggs and contaminants, (iv) using adequate equipment such as nets to prevent individual escape (e.g., through predation), including equipment maintenance to prevent long-term breakdowns 112 and (v) regularly monitoring surrounding regions^{45,46}. Risks are further reduced through tailored risk assessments^{20,47,48} and updating laws³¹ and regulations at different scales^{20,49,50}. For example, the four species in the European list of invasive alien species³⁶ are forbidden 114 to be farmed⁵¹.

Filling knowledge gaps for safer aquaculture

 We acknowledge that in many cases the long-term negative consequences of biological invasions may be disregarded because of the immediate social and economic benefits of aquaculture or a lack of awareness of the impacts. Our objective here was to highlight these consequences and promote responsible choices in aquaculture, such as selecting native species or implementing specific biosecurity measures, to collectively progress towards sustainable aquaculture with a reduced role in biological invasions. The classification we proposed serves this objective by informing about the risks posed by farmed aquaculture crustacean species. While based on current knowledge, it could be refined as more gaps in our understanding are addressed. Firstly, not all countries farming these crustaceans are 123 currently present in the FAO dataset²⁴. Examples include Venezuela and Brazil which are not present in the FAO despite farming the 124 tiger prawn, also invasive there⁵². The efficient reporting of newly farmed species to the FAO dataset also varies, mostly by country. Secondly, there are species level gaps in the dataset, one example being the brine shrimp (*Artemia franciscana)* which is not included in FAO as of now. Additionally, the FAO often provides information at higher taxonomic levels such as genus or family, thus complicating the identification of all farmed crustaceans, including potentially invasive ones. For instance, the *Metapenaeus* genus may include one of two invasive alien species of this taxonomic group.

 Our study may also underestimate the extent of farms located in non-native regions due to uncertainties in the native regions of some species. This is a problem particularly acute in very large countries (e.g., Australia, Brazil, Russia, USA, China) where farming is reported at the national level, whereas a species is native to specific parts of the country. For example, the smooth marron (*Cherax cainii*) is native to parts of Australia but invasive in others. Further, delays in detecting invasive species in the wild and in quantifying their impact hinder our ability to categorize species as invasive accurately. Finally, information on unregistered or illegal farms is lacking⁹, making it difficult to assign accurate risk categories to some species. Consequently, we cannot rely solely on this dataset to assign a risk category to a given species. Our classification is presented more to illustrate our proposal, enhance understanding of invasion risks related to farmed species crustacean species, assist in prioritizing containment strategies, and inform the selection of future farming locations and species. This approach is also relevant for other farmed aquatic groups like molluscs or fish.

Author's contribution:

 The conception of this study benefited from the collective insights of all authors. EM conducted data collection and crafted the initial draft of the manuscript. BL and FC contributed essential oversight, ensuring a thorough review of the document. All authors engaged in meticulous scrutiny, participating in refining the manuscript through multiple iterations, ultimately leading to unanimous approval for publication.

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- **Appendices:**
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APPENDIX I. Invasive status and native regions of the 63 crustaceans farmed in aquaculture.

333 The majority of native region were found on SeaLifeBase⁸⁶.

 APPENDIX II. Global distribution of the number of farmed crustaceans and invasive crustaceans farmed for aquaculture for the 22 invasive farmed species. The rectangles shown at the centre bottom of this schematic map represent the status of 43 regions (18 islands, 14 countries and 11 overseas territories) that are too small to be depicted. Blue countries are those with no records of farmed crustacean invasion. The large number of countries with purple, red or pink hues are those in which farmed species have become invasive because of aquaculture. Note that a species can be invasive in a country even if it is not farmed within its borders. Consequently, a country may have invasive

- species that exceed those farmed.
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 APPENDIX III. Species farming countries and status (native or non-native) of the 63 crustaceans farmed in aquaculture.

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- **APPENDIX IV.** Invaded countries of the 22 invasive crustaceans farmed in aquaculture.
- Countries where species are farmed and invasive are written in bold.
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- **APPENDIX V.** Classification of the 63 crustacean species farmed in aquaculture.

Figure legends:

- **Figure 1** Species risk classification depending on the farming country (native or non-native) and invasive species status (invasive or
- non-invasive) from lowest (A) to highest risk (D). The numbers in black in each category indicate the number of species involved from the 63 crustaceans currently farmed for aquaculture. The colour gradient indicates the risk index.
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Table legends:

- **Table 1** Overview of farming and invaded countries for the farmed crustacean species. Information related to farming encompasses all
- farmed crustacean species (63 species), while data concerning invasion refers specifically to the 22 invasive farmed crustacean species.
- Among these 22 invasive species, 14 have been documented as invasive in their farming countries.
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- **Table 2** Invasive crustaceans farmed in aquaculture.
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368 **Table 1**

Macrobrachium rosenbergii Cambodia Non-native *Macrobrachium rosenbergii* China Non-native *Macrobrachium rosenbergii* Colombia Non-native *Macrobrachium rosenbergii* Costa Rica Non-native *Macrobrachium rosenbergii* Dominican Republic Non-native *Macrobrachium rosenbergii* Ecuador Non-native *Macrobrachium rosenbergii* El Salvador Non-native *Macrobrachium rosenbergii* Fiji Non-native *Macrobrachium rosenbergii* French Guiana Non-native *Macrobrachium rosenbergii* French Polynesia Non-native *Macrobrachium rosenbergii* Grenada Non-native *Macrobrachium rosenbergii* Guadeloupe Non-native *Macrobrachium rosenbergii* Guam Non-native *Macrobrachium rosenbergii* Guatemala Non-native *Macrobrachium rosenbergii* Guyana Non-native *Macrobrachium rosenbergii* Honduras Non-native *Macrobrachium rosenbergii* India Non-native *Macrobrachium rosenbergii* Indonesia Native *Macrobrachium rosenbergii* Iran Non-native *Macrobrachium rosenbergii* Israel Non-native *Macrobrachium rosenbergii* Jamaica Non-native *Macrobrachium rosenbergii* | Malawi Non-native *Macrobrachium rosenbergii* Malaysia Non-native *Macrobrachium rosenbergii* Martinique Non-native *Macrobrachium rosenbergii* Mauritius Non-native *Macrobrachium rosenbergii* Mexico Non-native *Macrobrachium rosenbergii* Myanmar Non-native *Macrobrachium rosenbergii* New Caledonia Non-native *Macrobrachium rosenbergii* Panama Non-native *Macrobrachium rosenbergii* Paraguay Non-native *Macrobrachium rosenbergii* Peru Non-native *Macrobrachium rosenbergii* Philippines Native *Macrobrachium rosenbergii* Puerto Rico Non-native *Macrobrachium rosenbergii* Réunion Non-native *Macrobrachium rosenbergii* Saint Lucia Non-native *Macrobrachium rosenbergii* Senegal Non-native *Macrobrachium rosenbergii* Singapore Non-native *Macrobrachium rosenbergii* Solomon Islands Non-native

