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Identifying economic costs and knowledge gaps of invasive aquatic crustaceans

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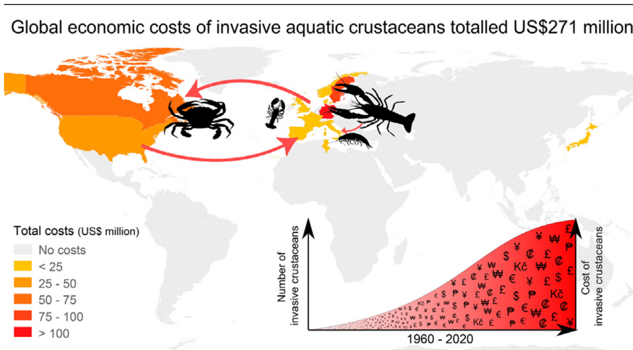
HIGHLIGHTS

- The global economic costs of invasive aquatic crustaceans totalled US$ 271 million.
- Invasive crayfish and crabs had the highest costs, US$ 120.5 and US$ 150.2 million, respectively.
- The signal crayfish was the costliest species (US$ 103.9 million), as seen in Europe.
- Among crabs, the European green crab and the Chinese mitten crab had the highest costs.
- Taxonomic, geographical, and temporal gaps mean that these costs are severely underestimated.

GRAPHICAL ABSTRACT



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ABSTRACT

Despite voluminous literature identifying the impacts of invasive species, summaries of monetary costs for some taxonomic groups remain limited. Invasive alien crustaceans often have profound impacts on recipient ecosystems, but there may be great unknowns related to their economic costs. Using the InvaCost database, we quantify and analyse reported costs associated with invasive crustaceans globally across taxonomic, spatial, and temporal descriptors. Specifically, we quantify the costs of prominent aquatic crustaceans — crayfish, crabs, amphipods, and lobsters. Between 2000 and 2020, crayfish caused US$ 120.5 million in reported costs; the vast majority (99%) being attributed to representatives of Astacidae and Cambaridae. Crayfish-related costs were unevenly distributed across countries, with a strong bias towards European economies (US$ 116.4 million; mainly due to the signal crayfish in Sweden), followed

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by costs reported from North America and Asia. The costs were also largely predicted or extrapolated, and thus not based on empirical observations. Despite these limitations, the costs of invasive crayfish have increased considerably over the past two decades, averaging US$ 5.7 million per year. Invasive crabs have caused costs of US$ 150.2 million since 1960 and the ratios were again uneven (57% in North America and 42% in Europe). Damage-related costs dominated for both crayfish (80%) and crabs (99%), with management costs lacking or even more under-reported. Reported costs for invasive amphipods (US$ 178.8 thousand) and lobsters (US$ 44.6 thousand) were considerably lower, suggesting a lack of effort in reporting costs for these groups or effects that are largely non-monetised. Despite the well-known damage caused by invasive crustaceans, we identify data limitations that prevent a full accounting of the economic costs of these invasive groups, while highlighting the increasing costs at several scales based on the available literature. Further cost reports are needed to better assess the true magnitude of monetary costs caused by invasive aquatic crustaceans.

1. Introduction

Due to their sensitivity to the effects of climate change (Woodward et al., 2010) and a range of other anthropogenic pressures (Darwall et al., 2018; Strayer, 2010), freshwater ecosystems have been characterised as the most threatened in the world (Reid et al., 2019), particularly from biological invasions (Ricciardi and MacIsaac, 2011). Invasive alien species are considered among the most important drivers of biodiversity decline, as well as disruptors of ecosystem functioning and services provisioning (Blackburn et al., 2019; Pyšek et al., 2020), and concerns are increasing as invasion rates continue to rise (Seebens et al., 2017, 2021). Freshwater ecosystems are particularly vulnerable to the introduction of alien species (Frederico et al., 2019), for example, from alien taxa such as bivalves, crustaceans, fishes, and aquatic plants (Ricciardi and MacIsaac, 2011). Despite the recognition of these ongoing losses and risks, the capacity of various countries to effectively combat and prevent biological invasions remains limited. This can be partly attributed to an insufficient understanding of the magnitude of losses and expenditure required to reduce biological invasions and their costs in the future (Early et al., 2016; Faulkner et al., 2020).

In recent years, considerable progress has been made in understanding the ecological impacts of invasive alien species on receiving aquatic ecosystems (e.g. Bradley et al., 2019; Dick et al., 2017; Haubrock et al., 2019a; Jackson, 2015). While frameworks for categorising the socio-economic impacts of invaders have also advanced over time in response to the challenges associated with monetizing economic impacts (Bacher et al., 2018), the scarcity of synthesised costs incurred by invasions weakens the rationale for policy makers to invest scarce resources in prevention, control, and eradication. Pimentel et al. (2000, 2005), followed by Kettunen et al. (2009), summarised the costs of invasive alien species at large spatial scales. Despite the methodological shortcomings of these studies (Charles and Dukes, 2008; Cuthbert et al., 2020a), they have been partly successful in raising awareness of the costs of invasive alien species (Hoffmann and Broadhurst, 2016). Quantifying and communicating these costs provides essential information for policymaking and resource management, as well as for public awareness, and incentives to prevent and manage invasive alien species. Despite recent efforts to analyse invasion costs for specific taxonomic groups (Bradshaw et al., 2016; Haubrock et al., 2021b) across various regions (Crystal-Ornelas et al., 2021; Haubrock et al., 2021c; Liu et al., 2021) or habitat types (Cuthbert et al., 2021b), a detailed collective understanding is still lacking for many taxa, regions, and economic sectors. Filling this knowledge gap is essential to inform policy responses, efficiently allocate resources for management, and avoid future losses, as well as to highlight unevenness in costs reporting at different taxonomic, regional, or sectoral scales.

Invasive crustaceans are important taxa with proven impacts on recipient communities. Among the most notable invasive crustaceans, crayfish are the largest of the freshwater invertebrates and among the longest-lived (Souty-Grosset et al., 2006), with nearly 700 currently known species (Crandall and De Grave, 2017). Due to their substantial individual size, ability to reach high densities, and omnivorous nature, invasive crayfish often play important ecological roles through strong trophic interactions and ecosystem engineering. As a result, they create a severe pressure on many native taxa through predation and competition (Haubrock et al., 2019a; Lipták et al., 2019; Reynolds and Souty-Grosset, 2011; South et al., 2019; Twardochleb et al., 2015; Veselý et al., 2021), impacts on ecosystem services (Lodge et al., 2012) as well as transmission of pathogens and diseases (Longshaw, 2011). Crayfish species native to North America are particularly problematic, as they carry *Aphanomyces astaci* Schikora (Oomycetes), the causative agent of crayfish plague, one of the world's worst panzootics (Martín-Torrijos et al., 2021). Due to its role as an infectious pathogen, this oomycete is listed as one of the 100 worst invasive species by the IUCN (Lowe et al., 2000), mainly due to the high susceptibility and mortality of crayfish species not native to North America. In addition, as a result of the crayfish plague, many populations of native species disappeared, particularly in Europe (Svoboda et al., 2017). Thus, the entire functioning of freshwater ecosystems may be irreversibly altered by the introduction of North American crayfish species (Gherardi, 2007; Lodge et al., 2000).

Similarly, many invasive crabs have also been recognised as a significant threat to the invaded environment and native biota (Howard et al., 2017), with marked adverse ecological and socio-economic effects. Examples include the Chinese mitten crab *Eriocheir sinensis* H. Milne-Edwards, 1853 and the European green crab *Carcinus maenas* (Linnaeus, 1758), both of which are listed in the Global Invasive Species Database and among the 100 worst invasive species in the world (Lowe et al., 2000), implying that they are likely to have high economic effects (Cuthbert et al., 2021a). Other invasive crustaceans, such as amphipods, have also been of great concerns given their ability to spread rapidly via anthropogenic vectors across salinity regimes and displace native communities through competition and predation (Cuthbert et al., 2020b; Dick et al., 2002). A notable example is the ‘killer shrimp’ *Dikerogammarus villosus* (Sowinsky, 1894), which has potential impacts on commercially and biologically important fish species (Taylor and Dunn, 2017), and has often been the focus of management measures to prevent its introduction and spread (Bradbeer et al., 2020).

Despite recent advances in invasion science confirming the ecological impacts of invasive crustacean species, synthesised economic analyses lag behind, and may be partly overshadowed by the benefits provided by the aquaculture and fishing industries. While it is important to consider such benefits in stakeholder decision-making, the direct and indirect costs associated with damages or losses by these taxa remain barely quantified. The lack of data may in turn lead to minimal investment in research and management measures, which are also potentially under-reported. Recent research has identified burgeoning costs of aquatic invasive alien species at the global scale across taxa (Cuthbert et al., 2021a, 2021b), but assessments are needed at finer taxonomic resolutions to better guide management and research in more detail. To address this lack of information, and highlight the uneven reporting and current costs of prominent invasive large-bodied crustaceans (i.e. crayfish, crabs, amphipods, and lobsters), we used the latest version of the InvaCost database (v4.0), which compiles and standardises the reported economic costs of invasive alien species (Diagne et al., 2020). We investigated how reporting of invasive crustacean costs is distributed across space, time, taxonomic groups, cost types, and affected sectors.

2. Material and methods

2.1. Data collection and filtering

To analyse global costs of invasive crustaceans, we used data from the InvaCost database, which primarily presents costs from sources written in English (Diagne et al., 2020), and sources from 16 additional languages (Angulo et al., 2020, 2021). InvaCost captures cost data resulting from both systematic searches of the Web of Science, Google Scholar and Google search engine, and opportunistic contacts with experts and stakeholders. Each recorded cost entry was characterised by various descriptors as described by Diagne et al. (2020) and in the online database repository (https://doi.org/10.6084/m9.figshare.12668570). InvaCost is a dynamic database that allows new cost entries to be corrected and added as they develop or are reported over time. The current version of InvaCost includes 13,123 cost entries (i.e. reported economic costs, or rows of data) of invasive alien species extracted from published peer-reviewed and grey literature (InvaCost version 4.0; as of June 2021). Although there may be costs that we have not captured (e.g., unpublished or outside the search languages), InvaCost is the most up-to-date compilation of invasion costs and therefore the best tool available to draw parallels with the current state-of-the-art in cost reporting and associated knowledge gaps. However, the results may change with future research and as monetary cost data become available for different species, countries, sectors, and other factors.

From the full InvaCost database, we selected a total of 126 cost entries attributed to invasive crustacean species. We identified cost entries attributed to invasive crayfish, based on the “Order” classification by filtering out species belonging to “Decapoda” (n = 117 cost entries) and then those belonging to relevant crayfish families (“Astacidae”, n = 51; “Cambaridae”, n = 64) and diverse/unidentified crayfish (n = 2). No cost entries were found for the families “Parastacidae” or “Cambaroididae”. In addition, we quantified the costs of invasive amphipods (Order: Amphipoda; n = 1), and families belonging to relevant crabs (infra-orders: Brachyura and Anomura; n = 7), and lobsters (Family: Nephropidae; n = 1), based on the costs reported in the InvaCost database. Costs for these groups were extracted using (a) the “Order” column and selecting “Amphipoda”, and (b) the “Family” column and selecting the crab families and the family “Nephropidae”, respectively.

2.2. Temporal cost dynamics, cost descriptors and cost distributions between different crustacean groups

To calculate the total cost of invasions over time, the duration of each reported cost must be taken into account, which was derived from the InvaCost database (columns “Probable starting year adjusted” and “Probable ending year adjusted”; see more details in Leroy et al., 2020). Cost entries in InvaCost were standardised to 2017 equivalent US$ using the World Bank's market exchange rate and accounting for inflation through the Consumer Price Index of the year the cost was estimated in each study. Using duration (in years) and standardised costs in 2017 values (US$), we annualised the data, with each cost entry corresponding to a single year. This step made cost entries of different types and durations comparable. For example, a total cost of US$ 1000 between the years 2000 and 2009 would correspond to US$ 100 per year (see https://doi.org/10.6084/m9.figshare.12668570 for further information). This process allowed us to systematically analyse the total cost throughout the defined period, resulting in 146 expanded cost entries for invasive crayfish, and far fewer for invasive crabs (n = 52), amphipods (n = 6) and lobsters (n = 2). We have provided our final dataset used as a supplement (Supplementary Material 1). Thereafter, we refer only to the expanded cost entries, i.e. those that have been annualised, so that each row of data corresponds to a single year's cost per cost document.

Finally, the available invasion costs were assessed on the basis of the following five descriptors (described in more detail in Diagne et al., 2020; see Supplementary Material 1 and https://doi.org/10.6084/m9.figshare.12668570): (*i*) Method reliability: illustrating the perceived reliability of cost estimates as a function of the type of publication and method of estimation (“High” if costs were described in pre-assessed material, such as peer-reviewed articles and official reports, or in grey material but with documented, repeatable and traceable methods; and “Low” otherwise). We recognise that such a binary classification prevents a full assessment of the relevance of the methodologies employed in each document, but it allowed us to be objective and to obtain a practical number of categories to allow filtering and reliability analysis; (*ii*) Implementation: referring to whether the cost estimate was actually implemented in the invaded habitat (“Observed”) or extrapolated based on cost expectations beyond the invaded habitat and/or predicted over time (“Potential”); (*iii*) Geographic region: describing the geographic origin (i.e. continent) of the cost listed; costs that were not attributable to specific regions were classified under the category “Diverse/Unspecified”; (*iv*) Type of cost merged: grouping costs according to the categories: (a) “Damage”, referring to damages or losses incurred by the invasion (i.e. costs of repairing damage, loss of resources), (b) “Management”, comprising expenses such as surveillance, prevention, control, eradication and (c) “Mixed” costs, including a mixture of categories (a) and (b), which include cases where reported costs were not easily distinguished between damage and management costs; and (*v*) Impacted sector: the activity, societal or market sector that was impacted by the cost (i.e. “Agriculture”, “Authorities-Stakeholders” (governmental departments and/or official organisations such as conservation agencies, forest departments, associations); “Public and social welfare”; “Environment”; “Fishery”). Individual cost entries that were not attributed to a single sector were classified as “Mixed” in the “Impacted sector” column.

In order to assess the available economic costs of invasive crayfish and to describe trends over time, we used the *summarizeCosts* function implemented in the R package “invacost” (Leroy et al., 2020). Using this method, we calculated the absolute and average annual costs observed between the first recorded costs (2000) and last reported costs (2020), considering intervals of 5-years.

Finally, following the analysis of distributions in the reporting of crayfish costs, we similarly quantified the costs of other prominent large-bodied crustacean invaders (crabs, amphipods and lobsters) to better identify inequalities among these taxonomic groups. Specifically, we sought to assess how the total costs of these groups differed by species, geographic regions affected, sectors of the economy and type of cost, with the aim of highlighting knowledge gaps and unevenness in reporting at different scales. All results refer to expanded data (see process details above).

3. Results

3.1. Invasive crayfish costs

3.1.1. Economic costs across taxonomic groups and regions

The reported costs available in the InvaCost database of the 146 freshwater crayfish cost entries amounted to US$ 120.5 million for the period 2000–2020. Most of the cost entries were highly reliable but classified as ‘potential’ (for more details on the ‘Implementation’ descriptor see Section 2.2 and Supplementary Material 2). This total cost was unevenly distributed among crayfish families, with 86.5% inferred from Astacidae (US$ 104.1 million; n = 61 database entries), 12.8% from Cambaridae (US$ 15.4 million; n = 83) and 0.7% (US$ 0.9 million; n = 2) being unspecified.

Costs further differed at the genus-level, with US$ 103.9 million attributed to the genus *Pacifastacus* (specifically the signal crayfish *Pacifastacus leniusculus* (Dana, 1852); n = 59), followed by US$ 11.6 million to the genus *Procambarus* (the red swamp crayfish *P. clarkii* (Girard, 1852); n = 75) and US$ 3.8 million attributed to the genus *Faxonius* (7 entries with reported representative species previously attributed to *Orconectes*, see Crandall and De Grave, 2017: the rusty crayfish *F. rusticus* (Girard, 1852); and the spiny-cheek crayfish *F. limosus* (Rafinesque, 1817)). Diverse or unspecific costs amounted to US$ 1.1 million (n = 5).

All invasive crayfish species with recorded costs in InvaCost were native to North America. The majority of total (‘Observed’ and ‘Potential’) reported costs (US$ 116.4 million; n = 126) were inferred in Europe, where some are widely distributed (Fig. 1), while US$ 3.8 million (n = 2) was related to certain parts of North America (specifically Wisconsin, which is north of the native range of rusty crayfish responsible for these costs) and relatively little in Asia (US$ 309.8 thousand; n = 18) (Fig. 2a). Accordingly, cost information was absent for entire continents, which include South America, Africa, and Oceania (Fig. 2). It is also worth noting that even in regions with relatively high costs (i.e. Europe), many countries invaded by crayfish had no reported costs.

In Europe, the vast majority of total costs from *P. leniusculus* were very unevenly distributed towards Sweden (US$ 86.0 million; n = 2), followed by the United Kingdom (US$ 15.3 million; n = 9), Denmark (US$ 1.8 million; n = 4) and Norway (US$ 145.4 thousand; n = 1). On the contrary, monetary impacts in Italy (US$ 5.6 million; n = 8), Portugal (US$ 4.1 million; n = 2), France (US$ 1.7 million; n = 37) and Spain (US$ 1.6 million; n = 62) were predominantly found from *P. clarkii* (Fig. 2a).

Considering only observed costs, these were again unevenly distributed, with US$ 19.4 million attributed to Europe, US$ 1.9 million to North America, and US$ 309.8 thousand to Asia. Within Europe, 'Observed' costs were incurred most in the United Kingdom (US$ 8.8 million; n = 8), Italy (US$ 5.6 million; n = 8), France (US$ 1.7 million; n = 37), Spain (US$ 1.6 million; n = 62), Portugal (US$ 1.2 million; n = 1), Denmark (US$ 304.5 thousand; n = 2), and Norway (US$ 145.4 thousand; n = 1) (Fig. 2b).

3.1.2. Economic costs among cost types and impacted sectors

With respect to cost types in the available data, 79.9% of total crayfish-related costs were attributed to damages or resource losses, 15.3% allocated to management expenditures on prevention, control or eradication and 4.8% classified as mixed. The majority of costs related to impacted sectors were classified under "Mixed" sectors (US$ 91.6 million; 76.1%; n = 8), followed by impacts to "Authorities-Stakeholders" (US$ 16.9 million; 11.7%; n = 118), impacts to "Fishery" (US$ 8.5 million; 7.1%; n = 16), "Public and social welfare" (US$ 1.5 million; 1.3%; n = 2), and lastly to the categories "Agriculture" (US$ 1.2 million; <1%; n = 1) and "Environment" (US$ 755.8 thousand; <1%; n = 1).

Observed costs differed considerably, with 53.2% of available costs (US $ 11.5 million) being attributed to management expenditure, 19.5% (US$ 4.2 million) to damage-losses, and 27.3% (US$ 5.9 million) classified as mixed costs (Fig. 3a). The majority of observed costs were attributed to

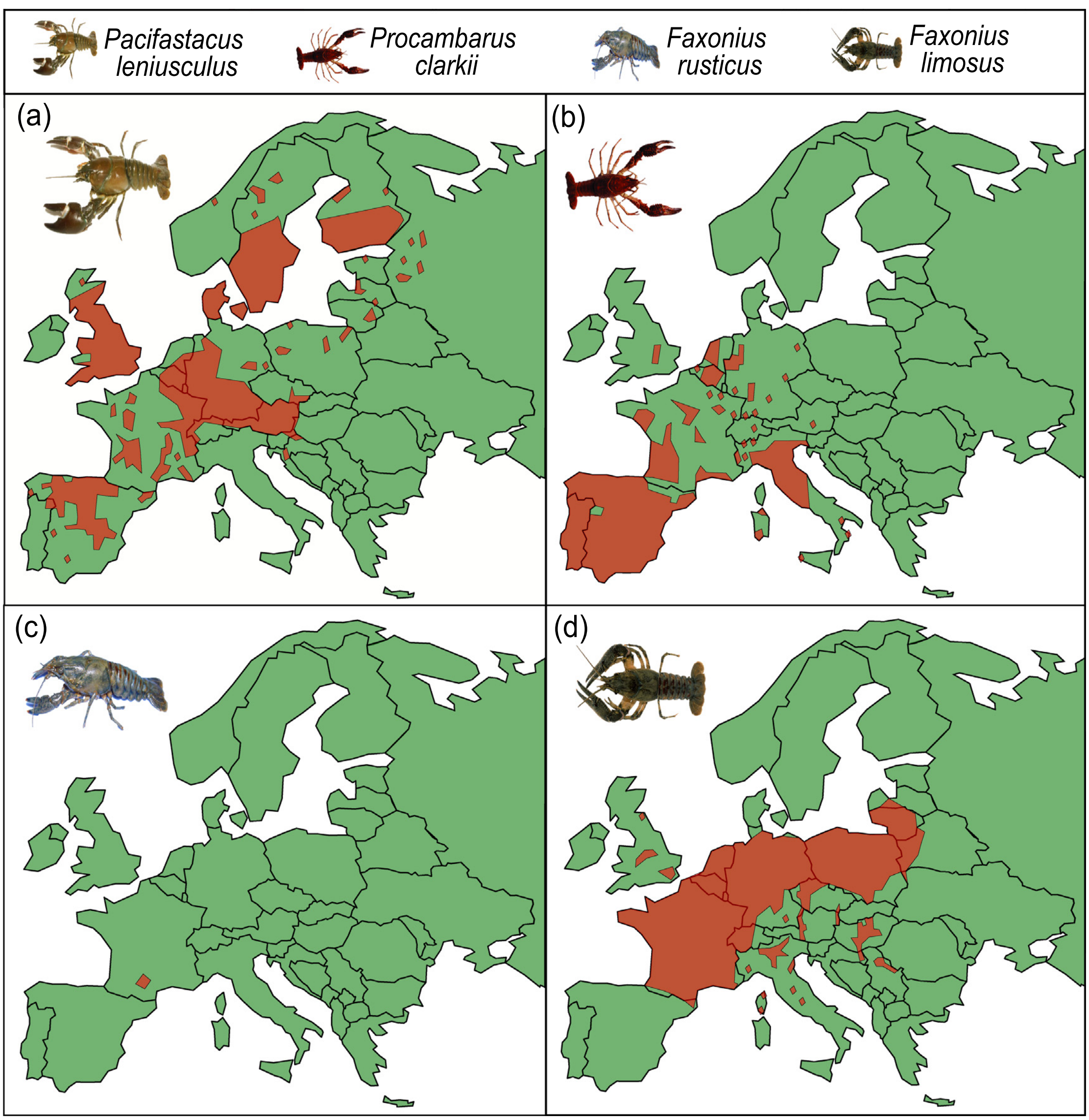

Fig. 1. Indicative distribution (reddish-brown) of *Pacifastacus leniusculus* (a), *Procambarus clarkii* (b), *Faxonius rusticus* (c), and *Faxonius limosus* (d) in Europe (Collas and Andrieu, 2019; Kouba et al., 2014). Note that reported costs of rusty crayfish are exclusively from North America.

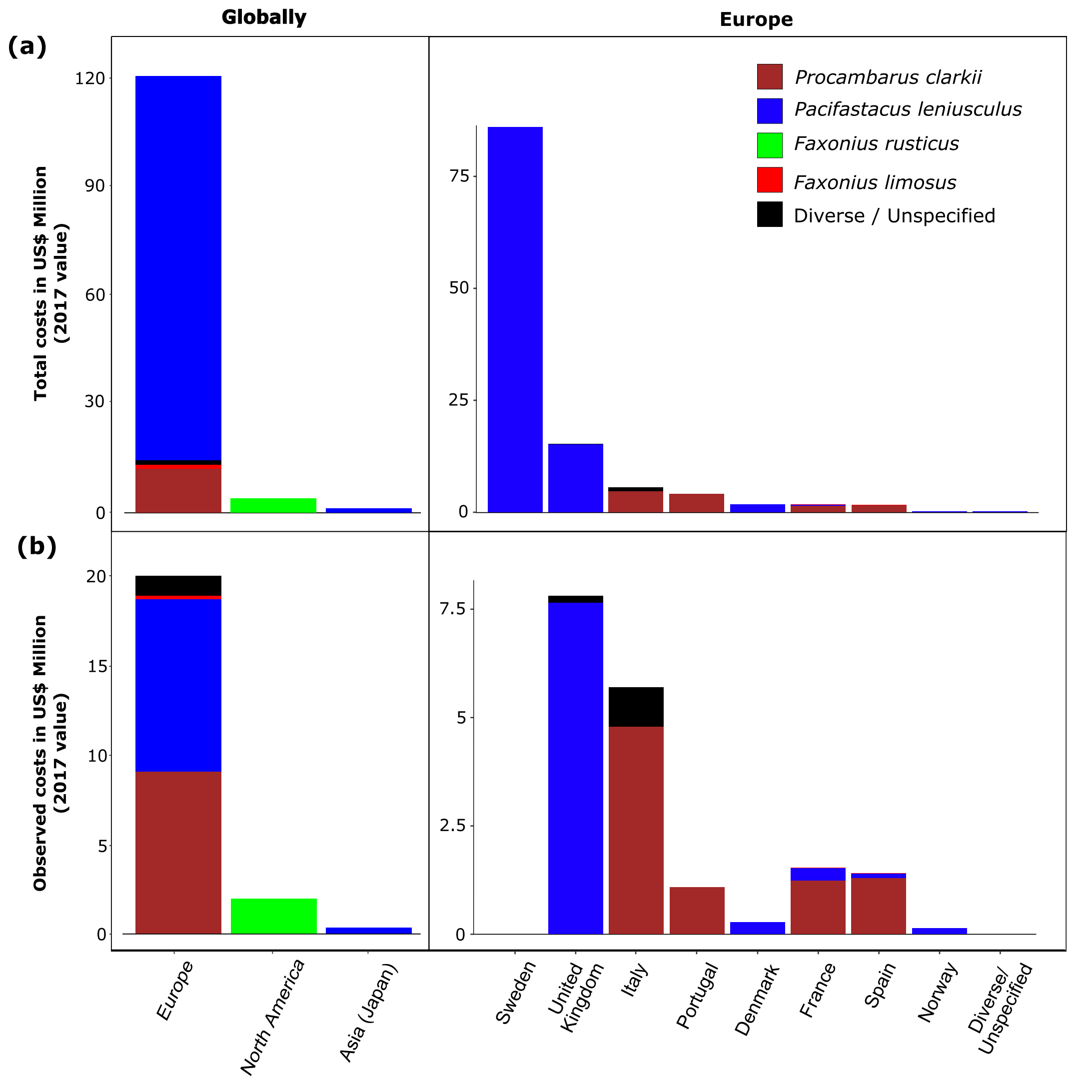

Fig. 2. Distribution of total (a) and observed (b) invasive crayfish costs across continents and European countries.

"Authorities-Stakeholders" (US$ 10.0 million; 46.3%), substantially driven by *P. leniusculus*. This cost was followed by costs to "Fishery" (US$ 6.6 million; 30.6%), inferred only by *F. rusticus* and *P. clarkii*, "Agriculture" (US$ 1.2 million; 5.6%) and lastly "Environment" (US$ 755.8 thousand; 3.5%), both reported only by *P. clarkii*. Costs attributed to "Mixed" sectors totalled US$ 3.0 million (13.9%) (Fig. 3b).

3.1.3. Temporal dynamics of costs

For the available data in InvaCost on invasive crayfish, the recorded total cost of US$ 120.5 million between 2000 and 2020 (Fig. 4) amounted to an average annual cost over the entire period of US$ 5.7 million and US$ 1.0 million when only observed costs were considered. Because the effects of time lags in cost reporting were not incorporated into the analyses, average cost estimates tended to reach a plateau phase or fall in recent years (Fig. 4) — notwithstanding the aforementioned limitations in the available data, which render these costs highly conservative.

3.2. Costs of other prominent invasive crustaceans: crabs, amphipods and lobsters

Since 1960, the reported costs of invasive crabs summed up to US$ 150.2 million, being again unevenly distributed towards a few species: *C. maenas* (US$ 86.4 million; $n = 2$), followed by *E. sinensis* (US$ 62.9 million; $n = 47$), the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (US$ 915.7 thousand; $n = 1$), the blue crab *Callinectes sapidus* Rathbun, 1896 (US$ 20.8 thousand; n = 1), and lastly the flower crab *Portunus pelagicus* (Linnaeus, 1758) (US$ <1 thousand; n = 1). The majority of reported crab invasion costs (57.5%) occurred in North America: US$ 55.1 million (63.8%) in Canada and US$ 31.3 million (36.2%) in USA. The remaining crab invasion costs of US$ 63.8 million (42.5%) were reported in Europe (Germany, Norway, Denmark, and Spain) and Africa (Tunisia; US $ 374.3 thousand; <1%) (see Supplementary Material 3a, b). The few costs reported affected mainly the "Fishery" sector (US$ 55.1 million; 36.7%; n = 1), "Authorities-Stakeholders" (US$ 32.2 million; 21.4%; n = 4), "Environment" (US$ 110.6 thousand; <1%; n = 1), and with 41.8% (US$ 62.8 million; $n = 46$) classified as "Mixed" costs (Fig. 5a). Almost all of the available total costs (99.9%) were attributed to "Damage" costs, with very few attributed to "Management" (Fig. 5a). In the past 60 years, and since the first recorded crab cost in InvaCost, annual costs remained on average at US$ 2.5 million (Supplementary Material 3c). Between 2000 and 2020, crab invasion costs averaged at US$ 3.0 million per year — which is again conservative given a paucity in data for many species and regions.

Overall, only six cost entries were inferred to amphipods, specifically the killer shrimp *D. villosus*, summing to US$ 178.8 thousand. These six costs were classified as "Damage", impacting "Authorities-Stakeholders" solely in Europe (Italy). Lastly, two recorded costs were research-related and inferred to the marine American lobster (*Homarus americanus* H.

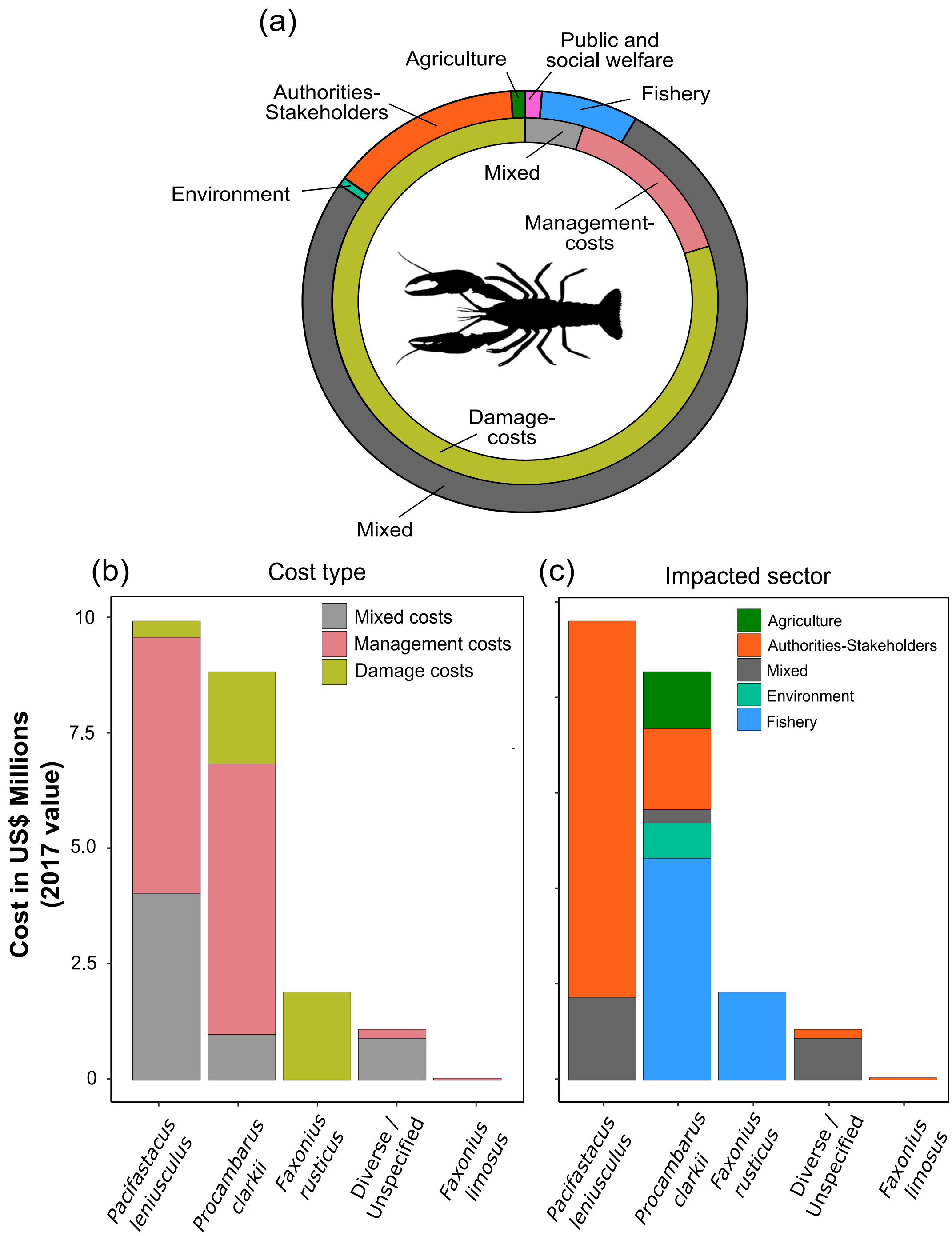

Fig. 3. Share of invasive crayfish total costs (US$ 120.5 million) (a), and their observed cost estimates according to cost type (b) and impacted sector (c).

Milne-Edwards, 1837), summing up to US$ 44.6 thousand and potentially targeting multiple unspecified species. Similar to amphipod costs, those inferred by Nephropidae predominantly impacted Authorities-Stakeholders in Europe (UK) but were attributed to "Management" (Fig. 5b) — specifically relating to research expenditure on unspecified species.

4. Discussion

This study examines the distributions in reported economic costs of major invasive aquatic crustaceans based on data available in the InvaCost database, the most comprehensive compilation of these costs to date. Analysis of several cost descriptors identified key trends and limitations in cost reporting across taxonomic, spatial, and temporal scales, as well as in the types of costs and sectors affected. In the case of crayfish, most of the reported costs were obtained from the peer-reviewed literature and therefore considered "highly reliable". However, most of these were in turn based on predictions or extrapolations from a relatively small number of studies, indicating a lack of empirical studies reporting observed costs. As a result, there was a substantial difference between the realised and predicted/expected costs of invasive crayfish species. While observed costs are important for quantifying actual (and documented) impacts, potential costs were expected to be more important. That is because they are often based on extrapolations from smaller to larger temporal or spatial scales (see Supplementary Material 2). Such efforts may nevertheless have value in informing management by identifying plausible future impacts or over larger areas than observed. We identified uneven cost ratios,

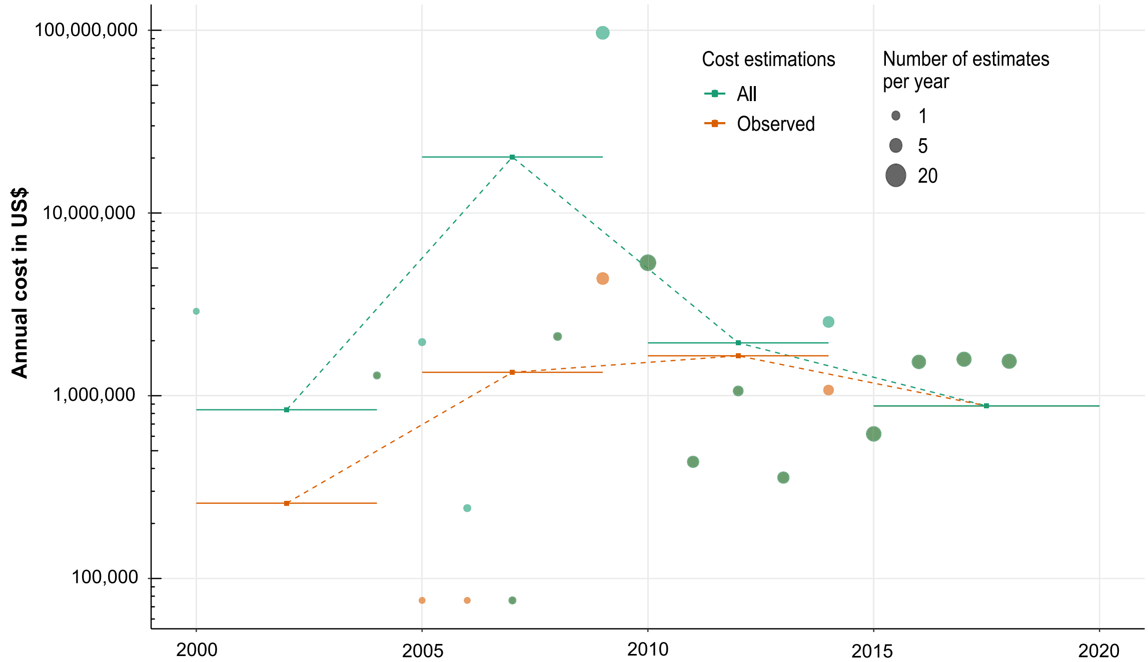

Fig. 4. Temporal development of total (green) and observed (orange) reported annual costs between 2000 and 2020 of invasive crayfish. Points with bars represent decadal means; other points represent annual totals scaled by numbers of estimates. Note that the y-axis is shown on a $\log_{10}$ scale.

particularly towards only four species, *P. leniusculus*, *P. clarkii*, *F. rusticus* and *F. limosus*, while other ecologically and probably economically damaging invasive crayfish were entirely absent from the database. The analysis also compiles the costs of other pertinent large-bodied crustaceans, namely crabs, amphipods and lobsters, with the available data.

4.1. Spatial unevenness

Reported costs for invasive crayfish are mainly incurred in Europe, with relatively few reported costs in North America and Asia (all in Japan). There were no reported costs for other geographic regions, despite the global extent of crayfish invasions (Haubrock et al., 2021b; Lodge et al., 2012; Oficialdegui et al., 2020b; Ribeiro, 2020). The lack of reported costs for Oceania is notable, as the common yabby *Cherax destructor* (Clark, 1936) is known to threaten native fauna in Australia (Coughran and Daly, 2012). Indeed, Australia is the world's second most important crayfish biodiversity hotspot. Equally noteworthy is the lack of reported costs in Africa, as continental and associated island nations are recipients of nine alien crayfish species (Madzivanzira et al., 2020). For example, the 30% loss of gillnet catches attributed to invasive crayfish in Zambia's floodplains results in a shortfall in household catch revenue, which will need to be compensated for by alternative means or increased fishing effort (Madzivanzira et al., 2020, 2021a, in press). A high impact on fisheries recruitment is also likely due to predation by the redclaw crayfish *Cherax quadricarinatus* (von Martens, 1868) on juvenile fishes (Madzivanzira et al., 2021c). However, a recently published study has estimated the cost of crayfish damage to fisheries catches in the invasion hubs of the Zambezi Basin (Madzivanzira et al. in press). Invasive crayfish also cause significant damages to hydraulic and irrigation systems (Haubrock et al., 2019a; Kouba et al., 2016), but information on associated costs is largely lacking (Madzivanzira et al., 2020; Tricarico et al., 2018). This may suggest a lack of management efforts on widely established invasive crayfish species.

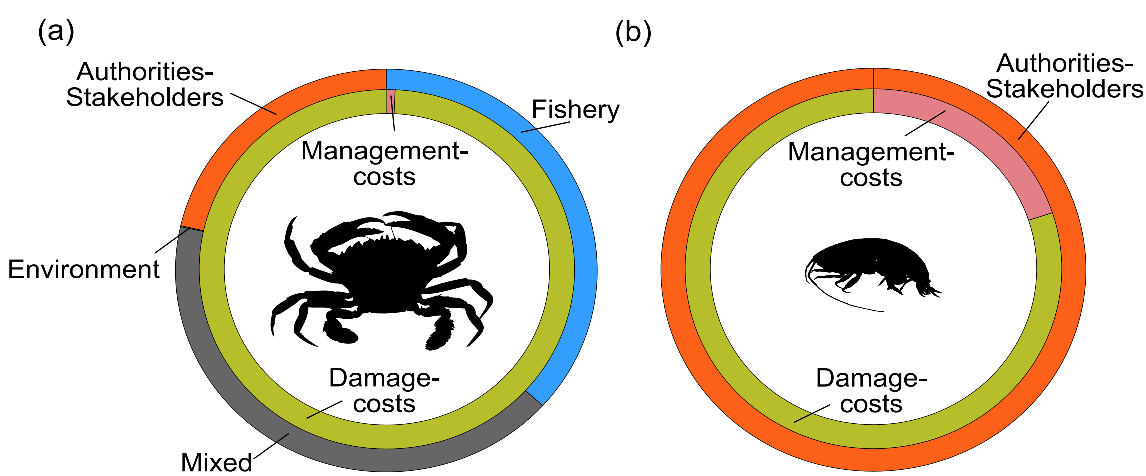

Fig. 5. Share of (a) total crab costs (US$ 150.2 million), and (b) total costs of amphipods (US$ 178.8 thousand) and lobsters (US$ 44.6 thousand) among sectors (outer circle) and cost types (inner circle).

Note, however, that insufficient management could be attributed to the limited capacity to implement large-scale management actions when invasive crayfish populations are so diffuse (see Section 4.5 below). It could also be attributed to a lack of adequate funding for such interventions. Even greater challenges apply to quantifying and assessing the loss of ecosystem services and the many indirect forms of damage (Pejchar and Mooney, 2009; Schröter et al., 2014; Spangenberg and Settele, 2010; Temel et al., 2018).

In Northern European countries, the successful introduction of *P. leniusculus* to replace declining populations of native noble crayfish *Astacus astacus* (Linnaeus, 1758) populations impeded the prioritization of conservation measures for native populations, and eradication efforts for introduced populations (Jussila et al., 2021). While the lack of observed management costs in our database for Sweden is remarkable in this respect, it suggests that the massive potential costs are related to the valuation of declining native crayfish species in culture and traditions (Bohman and Edsman, 2011; Gren et al., 2009). In contrast to northern European countries where potential costs dominate according to our results, southern European countries accumulate the majority of observed costs. One example is the role of *P. clarkii* in Southern Europe, given its impacts on food webs in Mediterranean wetlands (Geiger et al., 2005). This species also has the ability to build large burrows, which have led to the breaking of rice-field dikes and increased flood risk, as well as changes in sediment dynamics. For example, 30% of irrigation canals in Italy have been damaged, resulting in huge costs for management authorities (Haubrock et al., 2019a; Lodge et al., 2012). Dedicated research in recent years has resulted in the inclusion of several crayfish species in the list of invasive alien species of EU concern (European Commission, 2016). As such, Europe incurring the highest costs of crayfish invasion based on our data may reflect the relatively active European astacological community in trying to understand the costs of invasive crayfish species and limit their spread. It may also reflect a proactive stance on behalf of the EU (European Commission, 2014). However, even within Europe, several countries have no costs reported despite being severely affected by crayfish plague and other impacts. Hungary (Mozsár et al., 2021; Weiperth et al., 2020) and Poland (Wiśniewski et al., 2020) can serve as examples.

Costs categorised as damage-losses impacted various sectors such as "Authorities-Stakeholders", "Agriculture", "Fisheries", "Environment" and "Public and social welfare". However, only seven expanded cost entries were reported for crayfish plague, and these were specifically in Norway with only US$ 72.8 thousand listed as potential damage there. The costs associated with the *A. astaci* pathogen causing crayfish plague are highly underestimated, as evidenced by many rapid population extinctions and declines of native crayfish in Europe (Svoboda et al., 2017). However, the pathogen is currently also known from other regions with equally susceptible native crayfish, e.g., South America (Peiró et al., 2016), Indonesia (Putra et al., 2018) and Japan (Martín-Torrijos et al., 2018; Mrugała et al., 2017). The occurrence of chronically infected native crayfish populations remains a relatively rare and poorly understood phenomenon (Mojžišová et al., 2020; Svoboda et al., 2017; Ungureanu et al., 2020). It should be noted that, although largely underestimated, many of the management costs associated with North American crayfish species may have been allocated to crayfish plague mitigation. Therefore, these could increase the costs associated with this infectious disease. In addition, recent research efforts have focused on the role of crabs (Schrimpf et al., 2014; Svoboda et al., 2014b; Tilmans et al., 2014) and shrimps (Mrugała et al., 2019; Putra et al., 2018; Svoboda et al., 2014a) as alternative hosts of this pathogen. However, no mass mortalities have been reported in these groups similar to those observed in non-North American crayfish.

Information on costs of invasive crayfish from South America, Africa, Oceania, and Asia (with the exception of some costs in Japan) was also lacking. Although impacts have probably already occurred and are likely not monetised and/or available, they can increasingly be expected to occur in the near future. This is particularly true given the continued spread of invasive crayfish species and targeted research in these regions (Haubrock et al., 2021b; Horwitz and Knott, 1995; Madzivanzira et al., 2020; Madzivanzira et al., 2021a, 2021b; Nunes et al., 2017; Oficialdegui et al., 2020b). For example, considering the increasing trends in production and wild catches of *P. clarkii* in China in recent years (the world's largest crayfish producing country, exceeding one million tonnes per year recently according to FAO, 2020), it is clear that such production cannot be reached without negative side effects. Indeed, this has become a national food security issue in the country, as larger areas of agricultural land are permanently flooded for crayfish farming, leaving less space for other crops, including rice (Ho, 2020). In addition, these permanently flooded areas and the species' burrowing activity likely contribute to flood dynamics. Similarly, the scarcity of effective biosecurity policies to prevent the entry of non-native crayfish, such as the red swamp crayfish or redclaw crayfish, into South American countries could lead to an underestimation of their current distribution (Ribeiro et al., 2020). Consequently, this could cause an overlooking of the associated environmental and monetary impacts. The lack of reported costs for various regions in the InvaCost database may be due to several reasons, ranging from a shorter introduction history, limited attention to aquatic environments, anecdotal reports, low research effort on this topic and limited available funding, or limited accessibility to relevant cost information. However, this geographical unevenness in reporting is not unique to the costs from invaded aquatic environments or invasive crayfish species (see Cuthbert et al., 2021b; Diagne et al., 2021; Early et al., 2016). Indeed, the paucity of cost data for crayfish and other crustaceans in regions such as Africa, Asia and South America reflects the global distribution of costs. These regions have reported lower costs in general, for example, due to lower research capacity or language barriers (Angulo et al., 2021; South et al., 2020; Cuthbert et al., 2021b; Diagne et al., 2021). Therefore, authorities and research centres should make an effort in these regions to report on the economic impacts of invasive crayfish species.

4.2. Taxonomic unevenness

While the overall costs of invasive crayfish were found to be substantial, we identified an uneven distribution in InvaCost by considering the existing ecological knowledge for high-impact invasive crayfish species. Quantification of the underlying cost covered only a small subset of species from a few regions and was often based on predictions rather than realised costs. For example, *P. leniusculus* accounted for the largest share of the total cost, but its costs were only inferred from northern European countries. In these countries, targeted Action Plans were developed to prevent reduction of native *A. astacus* stocks (Bohman and Edsman, 2011). The second most costly invasive crayfish was *P. clarkii*, reported mainly in southern parts of Europe, where most invaded habitats are located. These increasing costs of *P. clarkii* (US$ 11.6 million) were estimated on the basis of 75 cost entries after expansion over time. The fact that this species is particularly widespread in Europe (Kouba et al., 2014), being already present in more than 40 countries on four continents and with potential for further spread (Oficialdegui et al., 2019; Oficialdegui et al., 2020b), highlights the lack of knowledge on costs at a broader spatiotemporal scale. Other high-profile invasive crayfish that the EU has also listed as significant invaders (European Commission, 2016), but whose invasion costs have not been reported, include the virile crayfish *Faxonius virilis* (Hagen, 1870) and the parthenogenetic marbled crayfish *Procambarus virginalis* Lyko, 2017. The latter has a high potential to spread (Hossain et al., 2018; Kouba et al., 2021) and can be expected to cause considerable damage and costs (Feria and Faulkes, 2011). However, the ecological damage caused by crayfish can often be difficult to quantify in economic terms, given the non-market effects typically associated with ecosystem degradation (but see Hanley and Roberts, 2019). Furthermore, data on the cost of members of the Parastacidae family are lacking, despite their ubiquity in important pathways of introduction such as aquaculture and the pet trade (e.g. *C. destructor* and *C. quadricarinatus*; (Faulkes, 2015; Haubrock et al., 2021b; Madzivanzira et al., 2020).

Given this unevenness among the invasive crayfish species concerned, the costs presented in our study are mainly due to *P. leniusculus*, derived from damage-losses and control actions. Most of these available costs are the result of extrapolations, which may indicate a lack of empirical reporting and monitoring effort, or difficulties in monetizing cost. This asymmetric distribution of costs among taxa is marked, as management efforts do not seem to be devoted to several high-risk species, such as *P. clarkii* (Gherardi et al., 2011; Souty-Grosset et al., 2016) or other emerging invasive species (e.g. *C. quadricarinatus* and *P. virginalis*).

4.3. Temporal unevenness

The complete absence of reported costs before 2000 indicates a significant gap in knowledge about how invasive crayfish have historically impacted human well-being and ecosystems. This is despite the long history of freshwater crayfish introductions worldwide and over 150 years of crayfish plague outbreaks in Europe (Holdich et al., 2009; Kouba et al., 2014). In the case of *P. clarkii*, which is a costly and prominent invader in especially Southern Europe, most studies concerning its impact were not published until the late 1990s, although it was introduced in the 1970s (Oficialdegui et al., 2020b). This delay in bringing crayfish invasions to the attention of the scientific community and managers raises questions about awareness of invasive crayfish, policies, perceptions and the funding available for research before 2000. These factors are further compounded by invasive crayfish being widely considered as an exploitable food source rather than a source of impact. Challenges associated with invasion debt are also important, where the impacts of invasive species can take several decades to become apparent after introduction (Essl et al., 2011). Given current and future global invasion rates (Seebens et al., 2017, 2021), a high likelihood that known costs are largely underestimated and poorly monetised, and trends over the past two decades, we expect future research to shed more light on the true costs of invasive crayfish species.

Data deficiencies across invaded areas may have indirect effects, mainly on the reporting of costs and estimating potential costs over time. For example, the Upper Zambezi catchment has been invaded by *C. quadricarinatus* through multiple introductions since 2001 (Haubrock et al., 2021b; Madzivanzira et al., 2020; Madzivanzira et al., 2021a). There are known impacts of this invasion on fisheries, conferred by scavenging behaviours (Madzivanzira et al., 2020, in press; Weyl et al., 2017) and high consumption effects on juvenile fish affecting recruitment (Madzivanzira et al., 2021c). While the potential ecological impact has been quantified, the economic valuation of these fisheries is often based on inadequate and outdated valuation methods which prevent an economic impact from being estimated from the quantified ecological impacts (Madzivanzira et al., 2021a, 2021c, in press). As a result, assessments are often carried out late if at all, or are sporadic in time depending on the timing of research projects. This conundrum likely applies to other species and countries, such as *P. clarkii* in Kenya (Lowery and Mendes, 1977), *C. quadricarinatus* in Mozambique (Chivambo et al., 2020), and *P. virginalis* in Madagascar (Andriantsoa et al., 2019).

4.4. Costs of other prominent aquatic crustaceans

We identified only five invasive crabs and one invasive amphipod species with reported economic costs, plus only two entries associated with the American lobster. This indicates our data are likely to contain significant knowledge gaps. Invasive crayfish and crabs had costs several times higher than amphipods and lobsters, although the number of reported costs was very unevenly distributed. Indeed, crab costs were of a similar magnitude, yet came from only seven unexpanded cost entries in contrast to the 117 crayfish entries in InvaCost. This unevenness is worth noting firstly because marine commercial fisheries are typically much larger in scale and commercial value than freshwater commercial fisheries, and the same is true for crustaceans (FAO, 2020). Secondly, invasive crab species recorded in InvaCost affect mainly the marine fisheries sector. However, while crayfish are freshwater taxa, marine invasion costs (e.g. for crabs and lobsters) are particularly under-represented in InvaCost (4.0) due to a lack of reporting (Cuthbert et al., 2021b). Invasion costs have not been reported for various notorious and widespread invasive crabs, such as the Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1853) and the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841). These species have significant economic and ecological impacts through predation on shellfish resources, competition, and costs to other commercial fisheries (Boyle et al., 2010; Grosholz et al., 2000; Lohrer, 2001; Zaitsev and Öztürk, 2001). Furthermore, the impacts of invasive crabs in poorly explored aquatic ecosystems, such as Arctic marine waters, remain challenging to quantify due to limited understanding of baseline values (Kaiser and Kourantidou, 2021; Kourantidou et al., 2015). The snow crab *Chionoecetes opilio* (O. Fabricius, 1788) in the Barents Sea is one such prominent example, which continues to expand at the expense of several benthic species (Kaiser et al., 2018). Commercial interest in harvesting this species may also hinder progress towards understanding their invasion costs (Kourantidou and Kaiser, 2019a). The red king crab *P. camtschaticus* is yet another example of high-impact invasion in Arctic waters. Due to its high commercial value, it is mainly managed as a commercial fishery rather than an invasion in the Norwegian part of the Barents Sea, and exclusively as a commercial fishery in the Russian part of the Barents Sea, with damage to ecosystems minimised (Kourantidou and Kaiser, 2019b). As with other species, the current version of the InvaCost (4.0) database does not sufficiently cover the multiple costs associated with bycatches in spatially overlapping fisheries, predation and other deleterious effects on native species (Skonhoft and Kourantidou, 2021). It also does not capture costs spent for baseline research and restoration (Kourantidou and Kaiser, 2021). InvaCost is a living database that continues to be improved as reported costs become available. We hope that these results will encourage more accurate cost reporting in the future (see https://borisleroy.com/invacost/invacost_livingfigure.html).

The reported costs of invasive amphipods have been attributed exclusively to *D. villosus*. This notorious invader from the Ponto-Caspian region has been shown to have marked impacts on a diverse range of prey types, including crayfish eggs/juveniles and fish eggs/larvae, with a greater feeding efficiency than native analogues towards vertebrates and invertebrates (Bollache et al., 2007; Roje et al., 2020; Taylor and Dunn, 2017). Although the economic impacts lack investigation, their ecological impacts may extend to commercial fisheries in inland and coastal waters via predation and parasite transmission. Invasions of *D. villosus* can lead to the extirpation of native freshwater species (Gergs and Rothhaupt, 2015), and once established, populations can dominate native communities in terms of biomass and abundance (Josens et al., 2005; van Riel et al., 2006). Globally, 27 alien gammarid species have been reported. These mainly originate from the Ponto-Caspian region (Cuthbert et al., 2020b), and 96% of the recognised gammarid invaders have no costs reported in InvaCost. This is illustrated by the 'demon shrimp' *D. haemobaphes* (Eichwald, 1841), which has similar ecological effects to *D. villosus* (Constable and Birkby, 2016), but has no costs in InvaCost. Given the range of these species and the impacts they have, these costs remain largely unreported.

4.5. Perception of invasions and implications for management

Despite their importance to socio-economic well-being and their susceptibility to change, aquatic invasions have received less attention overall (Cuthbert et al., 2021b; Lynch et al., 2020; MacIsaac et al., 2011). Often, invaders and their impacts are difficult to monitor, which can lead to delays between reporting of impact and management interventions (Beric and MacIsaac, 2015). As preventive management at an early stage is more effective, management delays can reduce the efficacy of management measures (Coughlan et al., 2020) and potentially increase costs in the long-term (Ahmed et al., 2021). Despite the knowledge gaps presented in our database, large-bodied crustaceans have generally received relatively high public attention, perhaps due to their prominent role in aquatic ecosystems or their popularity as food (Kawai et al., 2015). The introduction of alien crustaceans has led to a considerable turnover of native species compared to alien species (Kouba et al., 2014; Clavero, 2016) but has also led to the loss of cultural heritage and traditions (Edsman, 2004; Kataria, 2007; Swahn, 2004).

Public perceptions are particularly important in the context of management responses (Höbart et al., 2020) and directly affect the way values are formed and thus the reporting of costs of invasions. Like other invasions, aquatic invasions can provide benefits (Christie et al., 2019; King et al., 2006), despite their detrimental properties. Commercial and recreational fisheries for introduced crustaceans also contribute to a greater perceived value of these invasive species (Haubrock et al., 2021b; Kourantidou and Kaiser, 2019a). In low-income areas, they are often valued as a cheap source of protein or can contribute to regional economies (Andriantsoa et al., 2020; Haubrock et al., 2021b). This can lead to limited recognition of costs (especially indirect ones), as well as perhaps limited interest in understanding impacts (Kourantidou and Kaiser, 2019b). The differences in perceptions as well as divergent stakeholder interests in certain species with perceived benefits can trigger conflicts in resource management (Kourantidou and Kaiser, 2019a, 2019b; Oficialdegui et al., 2020a; Zengeya et al., 2017). They can also trigger large changes in socio-ecological systems and economies. In Sweden, for example, the native crayfish *A. astacus* has been largely extirpated by competition with the invasive *P. leniusculus*. Furthermore, associated transmission of the crayfish plague pathogen (Bohman and Edsman, 2011) has caused a considerable monetary impact in Sweden. As a result, the original source of income has been largely replaced by *P. leniusculus* with a lower market price. The Swedish example shows how the almost total loss of a native species and associated environmental and cultural damage, together with the costly control of spread, created additional management costs.

Reporting of management and research costs usually occurs when managers and/or stakeholders have a basic understanding of the invasion and its impact, allowing appropriate management interventions to be implemented (Latombe et al., 2017). These understandings may vary, but ultimately are likely to involve some type of risk assessment (e.g. Bacher et al., 2018; Hawkins et al., 2015), and a classification of invasion status (e.g. Blackburn et al., 2011). Each of these actions contribute to the choice of appropriate management intervention (see Robertson et al., 2020). However, formal risk assessments, specifically for crayfish species, remain limited to date (but see Haubrock et al., 2021b; Roy et al., 2019; Yonvitner et al., 2020). This could be due to a lack of data on crayfish impacts (as in South Africa; Weyl et al., 2020) and/or the intensive nature of compiling contextual impact assessments. Nevertheless, recent horizon scanning exercises have ranked invasive crayfishes, crabs and amphipods among the riskiest species in all habitat types (Lucy et al., 2020; Roy et al., 2019).

It is generally well established in the literature that investment in control and management can reduce losses due to damage (Leung et al., 2002; Ahmed et al., 2021). However, management attempts have largely failed to develop tools which hinder the spread of or successfully eradicate widely established populations of invasive aquatic crustaceans (Gherardi et al., 2011; Haubrock et al., 2018; Stebbing et al., 2014). Indeed, feasible eradications are only possible under a narrow range of specific conditions (relatively small and isolated localities). These include measures such as long-term dewatering or application of non-selective biocides, which can negatively affect the whole aquatic community (Chadwick et al., 2021; Lidova et al., 2019; Manfrin et al., 2019; Peay et al., 2019). Therefore, effective management interventions on large populations of invasive crustaceans are impractical and costly. The development of effective prevention measures for introduction and spread pathways is therefore of paramount importance, as invasive crustaceans can lead to long-term persistence and increasing invasion costs (Krieg and Zenker, 2020).

5. Conclusions

This study highlights the very high economic costs of invasive crayfish and other large-bodied aquatic crustaceans, but also considerable gaps and unevenness in their reporting. The information currently available is generally very fragmented, both spatially and taxonomically. There is an urgent need to better understand the past and current impacts and costs of invasive crustaceans. This will enable national and regional authorities to invest in appropriate policies and measures that can help mitigate these impacts in the future. Given the lack of reported costs in many invaded areas, despite the well-known impacts of some invasive crayfish species, the estimates provided in this study are likely to be very conservative. However, we recognise the presence of challenges in quantifying and monetizing the ecological impacts of these species which likely exacerbate knowledge gaps, and call for more work within environmental and resource economics and interdisciplinary collaborations. These difficulties may arise from non-market valuation methods (e.g. choice experiments, contingent valuation) aimed at eliciting public willingness to pay for improved environmental outcomes from invasion control. Or, from benefit transfer methods which, despite their limitations, may sometimes be considered useful for policy-making. Nevertheless, the available evidence shows that, although represented by a few species, the global economic losses caused by invasive crustaceans are substantial, even in the face of potential data limitations. The costs identified, as well as the sparse data highlighted in this study, call for more effort to understand the impacts of invasive aquatic crustaceans on biodiversity, ecosystem functioning, as well as on social and human well-being.

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CRediT authorship contribution statement

Antonín Kouba: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Francisco J. Oficialdegui:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Ross N. Cuthbert:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Melina Kourantidou:** Conceptualization, Writing – review & editing. **Josie South:** Conceptualization, Writing – review & editing. **Elena Tricarico:** Conceptualization, Writing – review & editing. **Rodolphe E. Gozlan:** Conceptualization, Writing – review & editing. **Franck Courchamp:** Conceptualization, Data curation, Funding acquisition, Writing – review & editing. **Phillip J. Haubrock:** Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Eulogy

This article is dedicated to Professor Olaf L.F. Weyl who passed away suddenly on November 14th 2020. Prof. Olaf Weyl was a hugely influential scientist, mentor and dear friend, who described our African crayfish work as his 'pet project'. His giant presence, in every way, is sorely missed.

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