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The global social-economic dimension of biological invasions by plankton: Grossly underestimated costs but a rising concern for water quality benefits?

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ABSTRACT

Planktonic invasive species cause adverse effects on aquatic biodiversity and ecosystem services. However, these impacts are often underestimated because of unresolved taxonomic issues and limited biogeographic knowledge. Thus, it is pivotal to start a rigorous quantification of impacts undertaken by planktonic invasive species on global economies. We used the *InvaCost* database, the most up-to-date database of economic cost estimates of biological invasions worldwide, to produce the first critical assessment of the economic dimension of biological invasions caused by planktonic taxa. We found that in period spanning from 1960 to 2021, the cumulative global cost of plankton invasions was US$ 5.8 billion for permanent plankton (holoplankton) of which viruses encompassed nearly 93%. Apart from viruses, we found more costs related to zooplankton (US$ 297 million) than to the other groups summed, including myco- (US$ 73 million), phyto- (43 million), and bacterioplankton (US$ 0.7 million). Strikingly, harmful and potentially toxic cyanobacteria and dinoflagellates are completely absent from the database. Furthermore, the data base showed a decrease in costs over time, which is probably an artifact as a sharp rise of novel planktonic alien species has gained international attention. Also, assessments of the costs of larval meroplanktonic stages of littoral and benthic invasive invertebrates are lacking whereas cumulative global cost of their adults stages is high up to US$ 98 billion billion and increasing. Considering the challenges and perspectives of increasing but unnoticed or neglected impacts by plankton invasions, the assessment of their ecological and economic impacts should be of high priority.

1. Introduction

Invasion scientists, managers, and stakeholders have reported high and rising impacts of invasive species on ecosystems and economies worldwide (Bellard et al., 2016; Diagne et al., 2021a; Cuthbert et al., 2021). In an economically connected world, a more comprehensive assessment of the geographic description and quantification of invasion impacts has been emphasized for the efficient and sustainable management of invasive taxa and invaded habitats (Ricciardi et al., 2020; Haubrock et al., 2022b). The economic burden exhibit more rapid increase in regions historically underappreciated by the invasion science e.g., Africa (Haubrock et al., 2022b) and concerns about protected areas (Rico-Sánchez et al., 2021). Yet, the invasive taxa and the magnitude and distribution of their costs are unevenly reported across types of

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environments and ecosystems with the aquatic invasive species being the most underrepresented when compared to the terrestrial invaders (Cuthbert et al., 2021). Hence, costs of aquatic invasions may be disproportionately low due to a mismatch between high number of non-native species and much lower impact assessments (Crystal-Ornelas and Lockwood, 2020; Cuthbert et al., 2021; 2022).

Aquatic invaders are continuously proliferating as result of the global transport of goods, notable by ballast water (e.g., Casas-Monroy et al., 2015; Bailey et al., 2015; Ricciardi and MacIsaac, 2022), and the electronic commerce (Olden et al., 2021), accelerated over the course of the COVID-19 pandemic (Bhatti et al., 2020). More recently, global attention has also shifted towards climate-driven range extensions and to anthropogenic environmental changes making recipients habitats more susceptible to invasions (Bellard et al., 2016; Seebens et al., 2020; Macêdo et al., 2021, 2022). Likely, the abundant planktonic invaders, including meroplankton, (early planktonic stages of organism with a non-planktonic adult life form), show high propagule pressure colonizing new interconnected aquatic environments (e.g., Czerniawski and Krepski, 2021). Therefore, there has been an appeal to expand our understanding of the impacts of biological invasions at different biological organization levels (Crystal-Ornelas and Lockwood, 2020), and through an interdisciplinary context (Ricciardi et al., 2020, Diagne et al., 2020a, b).

This lack of knowledge is a major concern when it comes to the pelagic habitats, considering planktonic organisms, which themselves have many features that remain primarily overlooked worldwide e.g., abundance, diversity and distribution (Jeppesen et al., 2011; Chust et al., 2017; García-Chicote et al., 2018). Planktonic organisms have a pivotal ecological role in both marine and inland waters where they dictate biogeochemical cycles and mediate energy flow (Kerfoot et al., 1988; Armengol et al., 2019; Naselli-Flores and Padisák, 2022). In addition to the strong and complex trophic links that characterize planktonic relationships: high diversity of taxa, living forms and stages, the interplays between holo- vs meroplankton in the vertical transport of nutrients, novel ecological outcomes can emerge from the examination of non-native planktonic species within native communities and from the context-dependency of their impacts.

To date, invasive plankton impact evaluations are scarce or are biased towards few taxa that caused impacts in developed counties (Dexter and Bollens, 2019) or toward laboratory experiments with limiting extrapolation power (e.g., Oliveira et al., 2019) but see Dexter and Bollens (2020a;2020b). Despite the paucity of evidence, some impacts have been related to plankton invasions: human health through toxin release or parasite hosting (Ito and Olesen, 2017), water quality deterioration from indirect changes in habitat conditions e.g., turbidity (Walsh et al., 2016), massive fish kills through oxygen depletion and histological damage, and bottom-up disruptions of trophic relationships (Amorim and Moura, 2020; Pacheco et al., 2021; González-Madina et al., 2021).

At present, we assume that knowledge gaps on the economic costs of plankton invasions may be a result of the considerable underestimation of their destructive potential, especially if we consider indirect effects and assessment limitations. Using the *InvaCost* database (Diagne et al., 2020b) we address the following questions to understand the current economic dimension of this problem: 1) What are the documented economic costs of invasive planktonic species globally? 2) How do these costs change over time and how are they distributed among main economic activities? 3) What are the costliest invasive species among them all? Also, we discuss the expected gaps of knowledge on meroplanktonic stages, and its implications for costly negative effects in the planktonic habitat and of their adult stages.

2. Materials and Methods

2.1. Data collection

We compared the economic costs of handling invasive holoplanktonic species and organisms with those of meroplanktonic stages using the *InvaCost* database. The *InvaCost* is a comprehensive compilation and description of economic cost estimates of biological invasions worldwide (Diagne et al. 2020a,b). The database was developed following a systematic and standardized methodology to extract information from scientific articles, grey literature, stakeholders, and expert advertisement. All methods and procedures for data search, retention, extraction, validation, collation, and improvements are available in Diagne et al. (2020a,b). We used the most up-to-date version of *InvaCost* (version 4.0, doi: 10.6084/m9.figshare.12668570), which contains 13,123 cost entries referring to a unique cost value (both in local currencies and 2017 US$ rates). There is also a set of specific descriptors of the cost's spatial and temporal information, the taxonomy of the invasive species, the cost typology, the impacted sectors, and the document reporting the cost (Diagne et al. 2020a).

We used a subset of this database focusing on aquatic environments where the costs were estimated and where the invasive species lives, independently of where the cost occurred. We classified holoplanktonic organisms, which fell into the following groups: virioplankton (DNA and RNA viruses with few nanometers in diameter), bacterioplankton (Gram-negative bacteria belonging to Aeromonadaceae family), mycoplankton (fungi-like pathogens, especially oomycetes, with microscopic filamentous dimension), phytoplankton (unicellular algae from families Raphidophyceae, Prymnesiaceae and Cymbellaceae with dimension 10–45 μm), zooplankton (Platyhelminthes 0.5–1.0 mm, Branchiopoda: Cladocera and Anostraca with dimensions 10–15mm, Scyphozoa and Ctenophora with dimension 14–18 cm), and meroplankton (which included animals with early stages in the pelagic zone such as Mollusks, Crustaceans, and some Insects – for a detailed species list see Table S1 and the Glossary for definitions). We extracted all economic costs associated with aquatic organisms filtering the information on the descriptive field "environment". We checked the data subset to remove any missing data on the economic costs. Our final databases had 43 entries of holoplanktonic species (Table S2) and 714 entries of meroplankton (Table S3). Due to the small number of resulting cost information for holoplanktonic species, we also included data classified as having low reliability ($n = 8$; e.g., not fully accessible information) and as potential implementation ($n = 13$; observed or expected through modeling or extrapolations), following Adelino et al. (2021). For meroplanktonic data, we instead retained only the costs classified as "observed" and also those of high reliability (column "method reliability", see Diagne et al. (2020a) for further details). For model analyses, we used the final subset for meroplanktonic organisms (597 entries).

We classified the groups according to the typology of the costs they have promoted, namely: *damage/loss* – for economic losses due to the impact of invaders (e.g., infrastructure alteration, medical care or damage repair); *management* – for economic resources allocated to actions towards avoiding the invasion or dealing with established invaders, (e.g., prevention, control or eradication); *mixed* – when the cost includes both damage and management elements (see also, Vaissière et al., 2022). We also categorized data on which societal or market sectors were impacted by each group, using data from the "impacted sector" descriptive field. *Agriculture* (food and other products produced by human activities through using natural and/plant resources from their ecosystems), *authorities/stakeholders* (governmental services and/or official organizations dedicated to management of biological invasions), *environment* (impacts on natural resources and/or ecosystem services), *fishery* (impacts on fisheries and aquaculture), *health* (cost related to the sanitary demands of people), *public and social welfare* (activities or services related to the human well-being at a broader sense

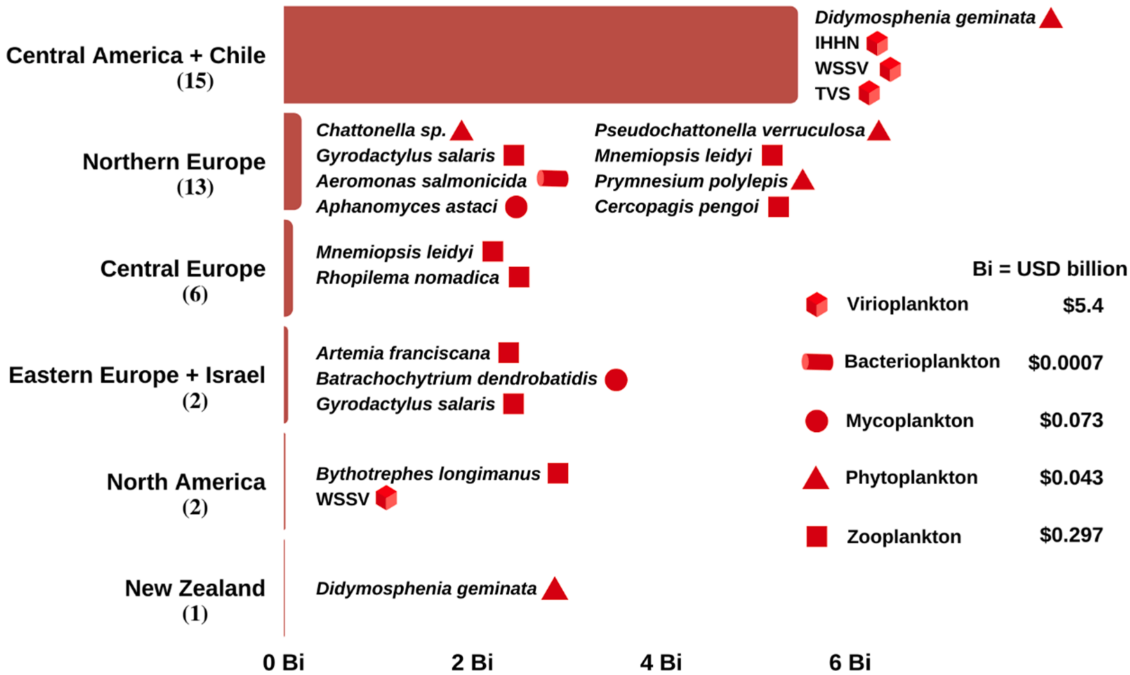

Fig. 1. Global distribution of total economic costs (BI = billion USD) for aquatic invasive holoplanktonic taxa per geographic region. For details of taxa and their individual costs and impacts see Table 2. The number of studies assessing costs is shown in brackets. Costs attributable to more than one country are summed to the corresponding geographic region.

Table 1
Quantitative summary of the cost data and estimates considered in this study for the holoplanktonic (virio-, bacterio-, myco-, phyto-, and zooplankton). Total costs per taxa (between 1960 and 2021) are provided in 2017-equivalent US$ million. A brief description of the effects caused by holoplanktonic invasive species is also provided. Diverse/Unspecified and pooled species were excluded from the individual-specific analysis (see the Material and Methods section for further details).

Holoplankton Family	Group	Taxa	Total cost per taxa (US$)	N (entries)	Impact
Aeromonadaceae	Bacterioplankton	*Aeromonas salmonicida* (Lehmann and Neumann 1896) Griffin et al. 1953	717,924	2	An important pathogen in salmonid aquaculture
Leptolegniaceae	Mycoplankton	*Aphanomyces astaci* Schikora, 1906	73,140,301	2	An emerging filamentous oomycete parasite affecting freshwater crayfish
Artemiidae	Zooplankton	*Artemia franciscana* Kellogg, 1906	3,442	1	Brine shrimp used extensively in aquaculture, the aquarium trade, affecting food webs and primary production in hypersaline ecosystems
Batrachochytriaceae	Mycoplankton	*Batrachochytrium dendrobatidis* Longcore et al. 1999	10,965	4	A zoosporic pathogenic chytrid fungus in amphibians and grows
Cercopagididae	Zooplankton	*Bythotrephes longimanus* Leydig, 1860	6,383,132	1	Spiny predatory waterflea with direct and indirect cascade effects
Cercopagididae	Zooplankton	*Cercopagis pengoi* Ostroumov, 1891	104,101	2	Fishhook waterflea, cited in the WWIS list significant top-down effects on zooplankton
Vacuolariaceae	Phytoplankton	*Chattonella* sp. Biecheler, 1936	2,745,895	1	Marine raphidophytes associated with red tides
Cymbellaceae	Phytoplankton	*Didymosphenia geminata* M. Schmidt, 1899	8,165,085	13	Diatom that produces nuisance growths in stream habitats
Gyrodactylidae	Zooplankton	*Gyrodactylus salaris* Malmberg, 1957	241,328,572	6	Ectoparasite of freshwater fish
Parvoviridae	Virioplankton	IHHN (DNA virus)	1,348,595,783	1	A hematopoietic necrosis virus that affects crustaceans
Bolinopsidae	Zooplankton	*Mnemiopsis leidyi* Agassiz, 1860	49,463,799	2	Ctenophore and major zooplankton predator associated with fishery depletion
Prymnesiaceae	Phytoplankton	*Prymnesium polylepis* Manton and Parke, 1962	27,347,843	1	Potentially toxic marine flagellate algae, found to affect other algae, zooplankton, fish and benthic invertebrates
Florenciellales	Phytoplankton	*Pseudochattonella verruculosa* Hara and Chihara, 1994	5,042,068	1	Phytoflagellate associated with significant impact on the fishing industry
Rhizostomatidae	Zooplankton	*Rhopilema nomadica* Galil, Spannier and Ferguson, 1990	59,110	1	Scyphomedusa with impacts on tourism, human health and fisheries
Dicistroviridae	Virioplankton	TSV (RNA virus)	2,620,354,258	1	A virus disease of penaeid shrimp
Nimaviridae	Virioplankton	WSSV (DNA virus)	1,478,290,764	2	A virus that causes mass mortalities in the aquaculture of shrimps

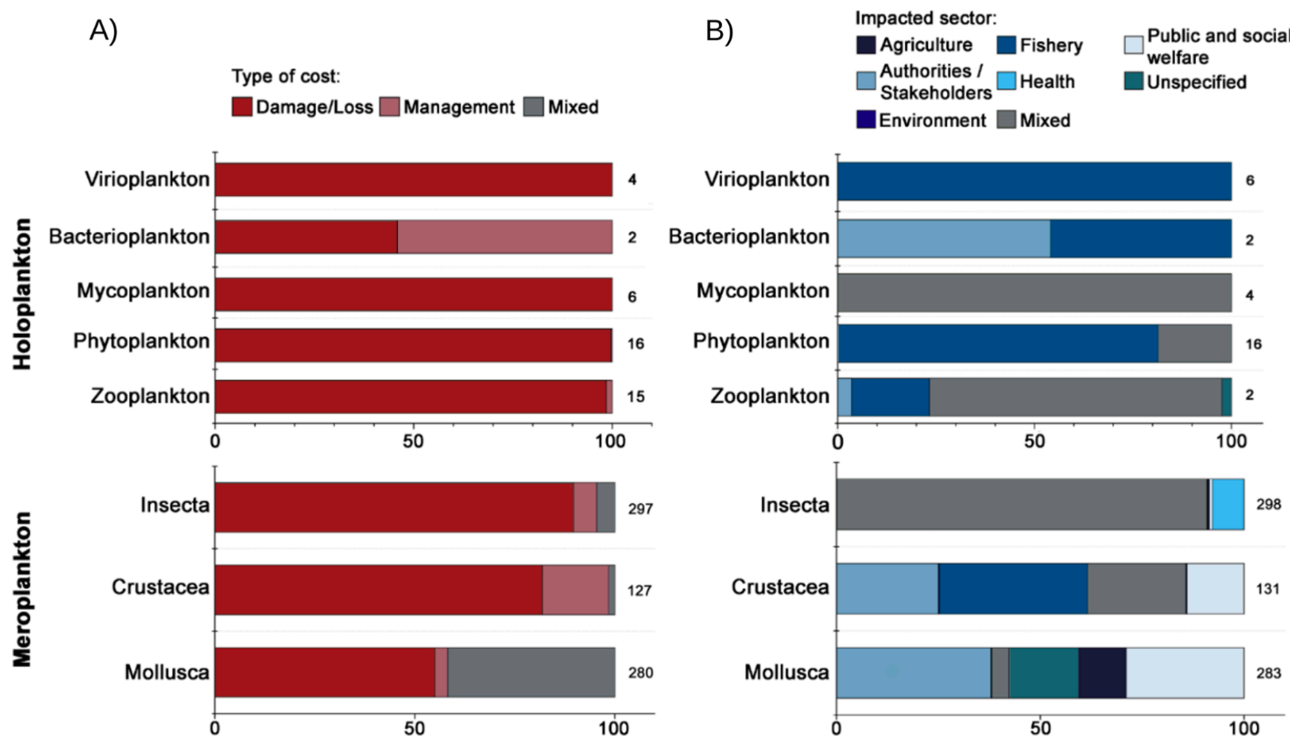

Fig. 2. Distribution of observed costs (using the conservative subset) by A) type of cost and B) impacted sector for each group within holoplankton and adults with meroplanktonic stages (Insecta, Crustacea and Mollusca). The number of entries of each observed cost are given aside the bars. Brief explanation of the cost type and the impacted sectors are provided in the Material and Methods section, but for details and examples mentioned in *Invacost* see Tables 1 and 2 in Diagne et al. (2020a).

such as personal goods or quality of life), and *mixed* (when more than a single sector was involved).

2.2. Data analysis

We performed all analyses in R version 4.1.2 (R Core Team, 2021), using the *InvaCost* R package (Leroy et al., 2020) for analyses and "ggplot2" version 3.3.5 (Wickham, 2011) for data visualization. We first compared the economic costs reported for each group (holo- and meroplankton) using the above classification scheme. Then, we examined annual variations in economic costs. Considering that some of the entries in the database described total costs over multiple years, we used the function "expandYearlyCosts" to determine the annual costs. This function divides the total cost by the number of years and converts it to a cost per year, removing entries with an unspecified period in the database.

We first derived the annual trend of costs caused by planktonic invasive species through the function "summarizeCosts". This function provides a summary of the cumulative costs and the average annual costs of invasive alien species and divides it into regular periods (1970–2020), based on cost estimates as they appeared in the *InvaCost* database. To estimate and predict the trend of the economic costs of invasive planktonic species over time, we fitted models of annual costs using the function "modelCosts" on the $\log_{10}$-transformed cost estimates per year. This function performs different modeling techniques: "ordinary least squares regressions" (linear and quadratic), "robust regressions" (linear and quadratic), "generalized additive models" (GAM), and other analyses not applied to our data—but see Diagne et al. (2020a). We calibrated all models to follow a robust linear regression using cost data as a response variable and time as the predictor. Considering that our subsets for holo- ($n = 43$) and meroplankton ($n = 597$) are too small to make reliable predictions, we used the model approach to detect tendencies for each group. In doing so, we could subsidize our discussion based on the effects of insufficient data on the perceived threat posed by a group of species.

3. Results

The costs of holoplanktonic species were assessed in 17 countries comprising in North America (the United States and Mexico), Central America + Chile, Eastern Europe (Bulgaria, Georgia, Romania, Russia, Turkey, and Ukraine) + Israel, Central Europe (Spain and Scotland), Northern Europe (Denmark, Sweden, Finland, and Norway) and New Zealand. Our sample included three viruses, two fungal-like organisms, one bacterium, four phytoplankton, and six zooplankton taxa (Fig. 1). Geographical and taxonomic disparities associated with costs were perceived, for example, a single species caused damages that cost up to US$ 8 million in New Zealand (one entry), while 8 species in Northern Europe cost altogether US$ 149 million (Fig. 1).

Holoplanktonic taxa listed in the *InvaCost* database were from 13 systematic orders, excluding viruses. Estimated costs and brief descriptive notes of their impacts are also provided in Table 1. All reported costs were from non-urban areas, and only one was from a protected island (Canary Islands) attributable to *Artemia franciscana* Kellogg, 1906 (Anostraca: Crustacea). Altogether holoplanktonic invasive species were responsible for costs around US$ 5.883 billion. The majority of the reported cost estimates was associated with "damage/loss" (US$ 5.877 billion) rather than "management" costs (US$ 0.005 billion) (Fig. 2). This pattern was consistent across groups, except for bacterioplankton, which had slightly larger costs directed to manage invasions and/or to mitigate their impacts (54.1 %). Virioplankton was the costliest (US$ 5.4 billion) group and together with mycoplankton (99.9 %) had the largest share in "damage/loss" costs.

The greatest impact of holoplanktonic invasions was on fishery (US$ 5.5 billion), with virioplankton being responsible for the majority of the costs, followed by phytoplanktonic species (Fig. 2). Many impacts were shared among sectors (US$ 317.9 million), but all of them included fishery. Interventions by the public and private sectors (authorities'/ stakeholders' category) were responsible for 54.1% of the costs related to bacterioplankton. Environmental costs were underrepresented and accounted for less than 1 % as associated with zooplankton.

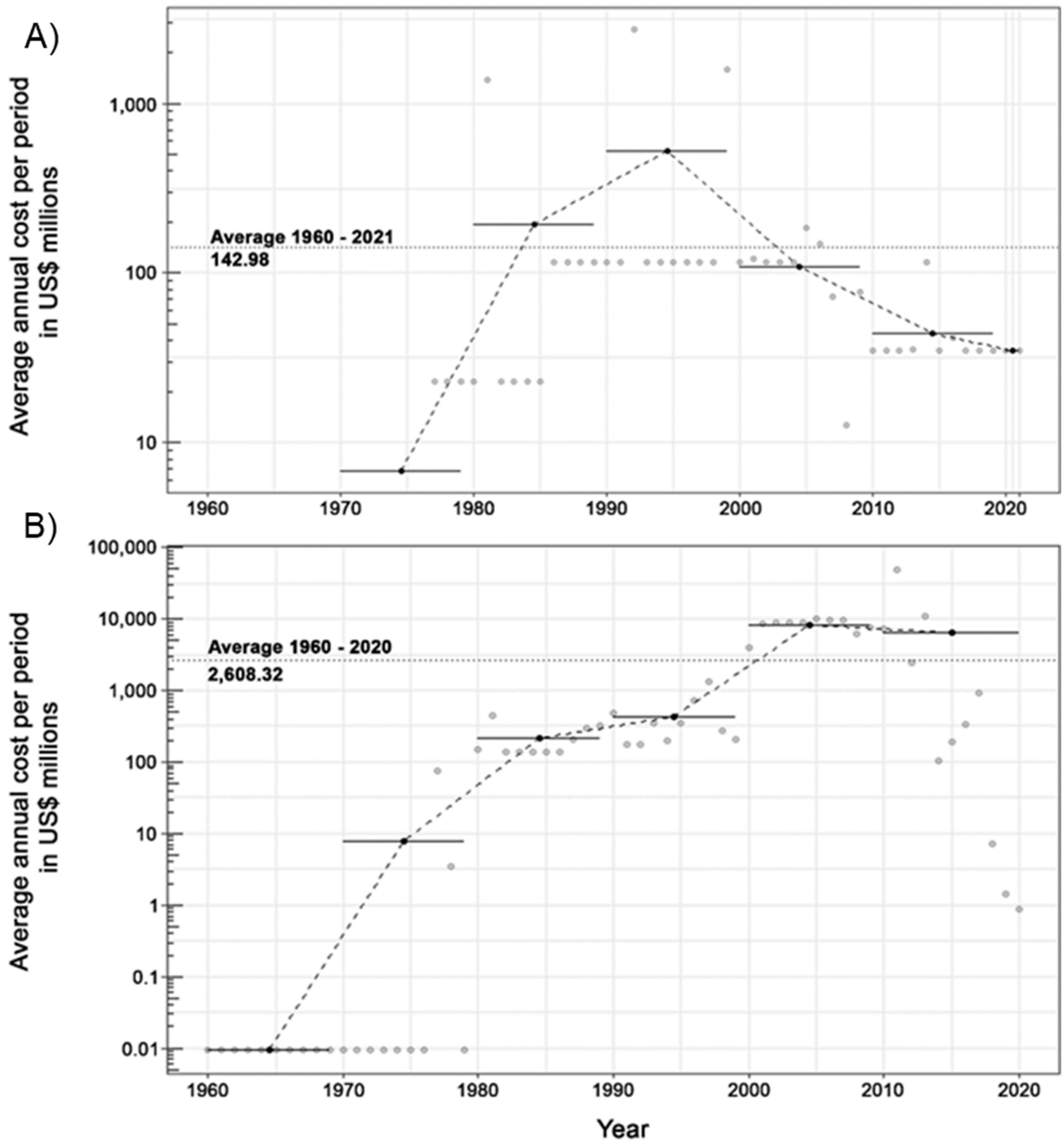

Fig. 3. Temporal trends (1960–2020) of mean annual costs (in year 2017 rate equivalents – US$ millions) of A) holoplankton and B) adults with meroplanktonic stages. We considered the amounts provided for each decade in the conservative subset (excluding “low reliability” and “potential” from the meroplankton database, see the Material and Methods section for further details)

The estimated global cost of Crustaceans (10 taxa), insects (2 taxa), and molluscans (13 taxa), reached US$ 98 billion, mainly attributed to "damage/loss" (US$ 82 billion). However, none of the cost assessments resulted from impacts caused by their early meroplanktonic stages. Most costs associated with Insecta (89.7 %) and Crustacea (81.9 %) were also directed to "damage/loss". In contrast, the costs related to Mollusca were nearly equally attributed to "damage/loss" (55 %) and mixed (41.8 %), with the latter being related to control measures. Mollusks have caused an economic loss of US$ 16.5 billion, mainly spent by authorities and stakeholders (US$ 6.2 billion; 37.9 %) and on public and social welfare (US$ 4.8 billion; 28.9 %). The lowest costs were attributed to crustaceans (US$ 384 million), mostly related to the fishery sector (36.3 %). Health expenditures were exclusively related to the insect group (US$ 6.3 billion) and represented 7.8 % of the total cost caused by this group worldwide (US$ 81 billion).

The costs of biological invasions of holoplanktonic organisms exponentially increased until the ’90s, reaching a peak in 1995 and then steadily decreased towards 2020. During this period, invasions cost on average US$ 142.9 million per year (Figure 3). Costs generated by adult taxa with meroplanktonic stages have, however, exponentially increased, with a mean annual cost of US$ 2 billion. The 2000–2010 decade was the costliest, reaching US$ 8 billion of annual costs, followed by the 2010–2020 year period where nearly US$ 6.5 billion were spent per year to deal solely with adults stages. Although, models indicated a quadratic tendency for holoplankton with a decrease in costs from the 2000s forward (Figure 4A), all modeling techniques confirmed that costs have continuously increased each year since 1970 for adult organisms with meroplanktonic stages (Figure 4B).

4. Discussion

Our global assessment on the economic impacts of plankton

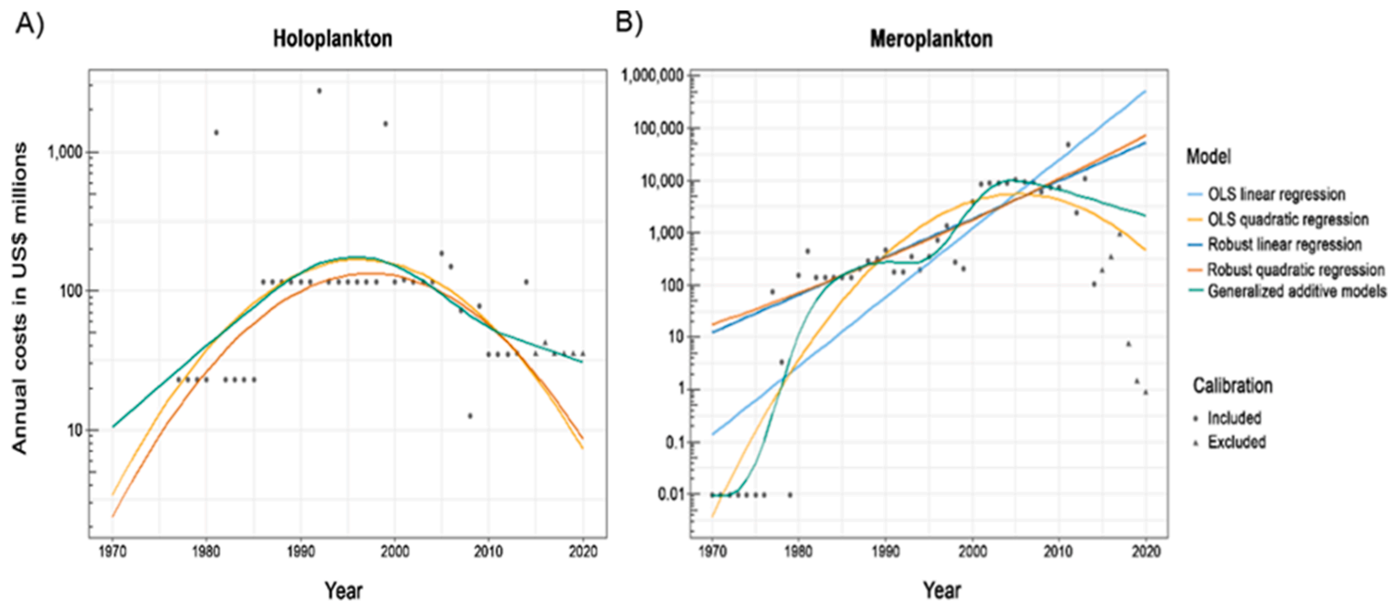

Fig. 4. Temporal trends (1970–2020) of costs (in 2017 equivalent rates –US$ millions) using model predictions for A) holoplankton and B) adults with meroplanktonic stages. We log_{10}-transformed cost estimates, and results were obtained considering models calibrated with at least 75% of cost data completeness from the dataset. OLS: ordinary least-squares.

invasions identified costs of up to US$ 5 billion (holoplankton), between 1960 and 2021. The current economic costs of holoplankton were compiled solely from 16 invasive species, here split within virio- (3 taxa), bacterio- (1), myco- (2 taxa), phyto- (4 taxa), and zooplankton (6 taxa). Reported costs with holoplankton were driven mainly by damage/loss rather than expenses incurred for management. These results are in line with the overall pattern found for the pool of invasive species in *InvaCost* database, indicating insufficient management and the urgent need to increase spending towards more cost-efficient actions, particularly pre-invasion management (Cuthbert et al., 2022). Both fishery and "mixed" sectors were the most compromised economic sectors, respectively caused by microbial pathogens or not clearly distinguished. Overall costs are likely expected to be underreported as the aforementioned taxa can also account for indirect impacts affecting some overlooked economic sectors (e.g., health, environment and public/social welfare).

We illustrated higher costs of invertebrates with meroplanktonic stages (US$ 98 billion; crustaceans, insects, and mollusks). However, costs of their larval stages are absent in *InvaCost* database and studies concerning invasions of meroplanktonic organisms are scarce (Bollens et al., 2002), despite the increasing trend of costs with their adult stages in recent decades. We also advocate that meroplanktonic organisms become a target and priority for invasion early warning (Ernandes-Silva et al., 2016), partly contributing to avoid or minimize the massive negative impact of their adult stages on biodiversity, water quality and economies (mollusks, Haubrock et al., 2022a; insects, Bradshaw et al., 2016; fish, Haubrock et al., 2022b).

4.1. Geographical distribution of costs

We identified an unevenly spatial distribution of costs worldwide with a significant discrepancy between developing and developed countries. Disproportionately more data on invader impacts are available in the "Global North" (Bellard and Jeschke, 2015; Bellard et al. 2016, Dexter and Bollens, 2019). Despite these biased geographical cost estimates, plankton costs represent a higher fraction when compared to the total costs for all groups of aquatic and terrestrial alien species of some regional assessments (e.g., Italy; Haubrock et al., 2021a, México; Rico-Sánchez, et al., 2021, and Singapore; Haubrock et al., 2021b).

Investments in management of invasive species, such as those arising from infectious diseases caused by pathogens (mainly viruses and bacteria) were also geographically skewed towards North America, Europe and Oceania (Haubrock et al., 2022c), although Central America and Chile showed the highest reported costs exclusively handling viruses. In Chile and New Zealand, we found enormous costs associated with a single species of a diatom (*Didymosphenia geminata*) while Northern Europe was the only geographical area that had costs with at least one taxon from each of the holoplanktonic groups. The lack of reported costs for Africa and Asia, as well as the few entries from North America and Oceania, are notable. However, several recent studies have shown raising costs of biological invasions in Australia (Bradshaw et al., 2021), China and India (Liu et al., 2021) or Southern and Eastern Africa (Diagne et al., 2021b). While these increases may be driven by specific taxonomic groups (non-planktonic), Haubrock et al. (2022c) suggest that regions which previously had lower research effort (e.g., Africa) exhibit higher asymptotic increase, comparable to regions historically at the forefront of invasion research (e.g., United States). Costs of planktonic invasive species were also scarce or absent in most South American Country e.g., in Brazil that harbours a significant portion of natural resources with extensive wetlands, groundwater and irrigation systems. Contradictorily, information on the expansion of invasive plankton species in Brazil is rising (Matsumura-Tundisi and Silva, 2002; Anderson et al., 2012; Macêdo et al., 2020; Severiano et al., 2022), but the quantification of their associated impacts were never documented.

4.2. Temporal gaps

While cost estimates of holoplankton have been decreasing over time there is an increasing trend with costs of many other groups included in *Invacost* (Diagne et al., 2020a; Haubrock et al., 2022b). Historically, monetary costs of holoplankton introductions started with Platyhelminthes (*Gyrodactylus salaris*) in 1977, while the most recent register was in 2017 for mycoplankton (*Batrachochytrium dendrobatidis*). There were only two bacterioplankton entries in 2006 and 2009, while phyto- and zooplankton costs were observed mainly in the last two decades. Despite the fact that the harmful effects of algal blooms were recognized as already as the 1970s (Maso and Garces, 2006; Zingone and Enevoldsen, 2000) and some reports of impacts by zooplankton were from

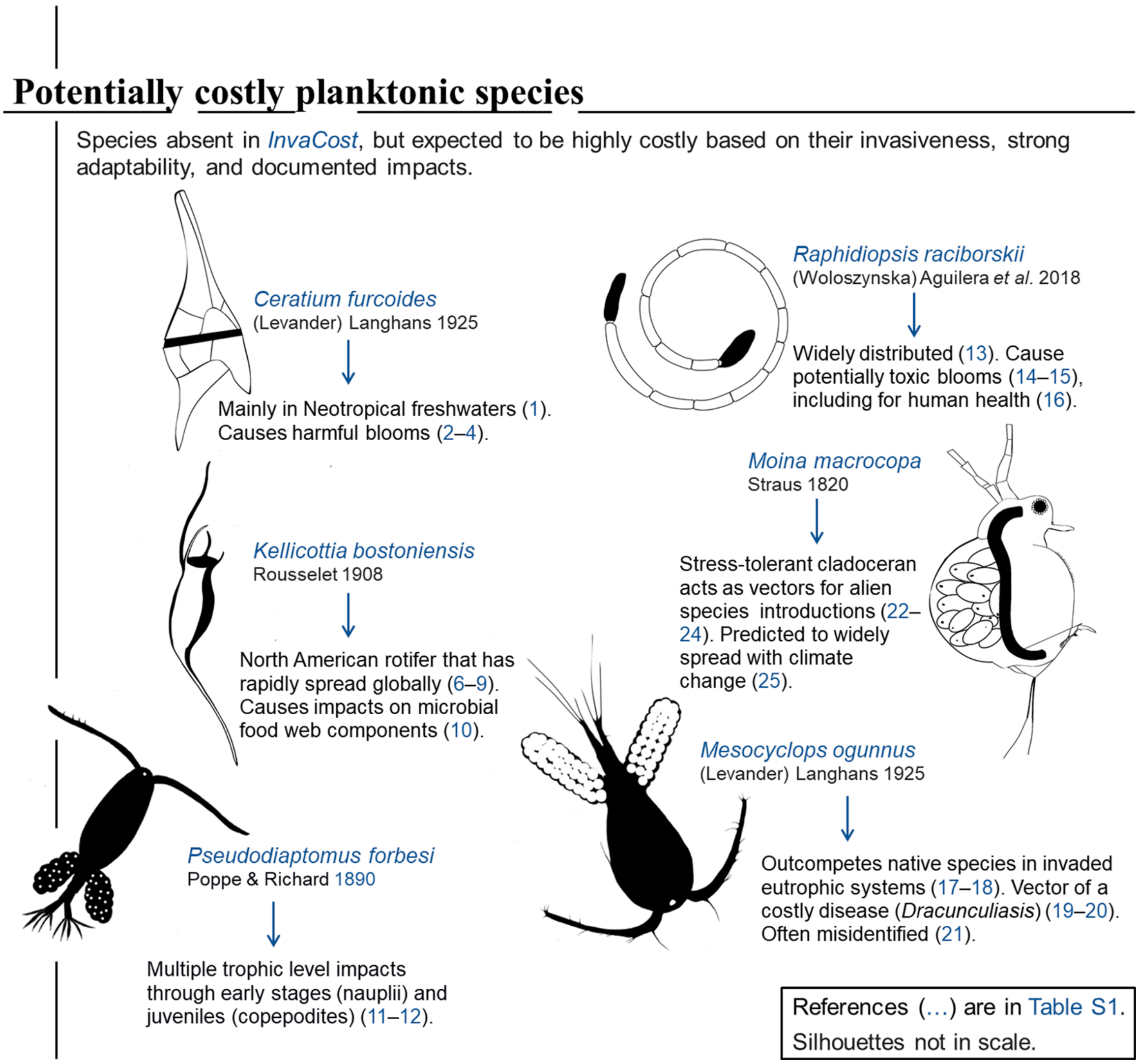

Fig. 5. Potentially costly holoplanktonic invaders not recorded in the *InvaCost* database. We short-listed these species considering their potential to exert dual effects: direct and indirect impacts on biodiversity or human wellbeing (Table S1), which in turn can generate monetary costs to restore vital ecosystem services or public health.

the early 1980s (Moller, 1984; Shiganova et al., 2001), there is a delay in bringing taxa invasion to the attention of the broad scientific community and managers. This may be in part due to misidentifications (e.g., *Mesocyclops ogunnus*, Matsumura-Tundisi and Silva, 2002) or due to delays in labelling as "invasive" species extensively reported in a given area (e.g., the case of *Kellicottia bostoniensis* in Mexico; Nandini et al., 2022).

We assume that the decrease in global economic costs of planktonic species shown in the model estimates to be an artifact because of lack of data and research effort. Also, combining holo- and meroplanktonic invasions than holoplankton alone may show a more realistic trend of costs and potential impacts for the pelagic habitats worldwide. The slightly decrease in costs during 2010-2020 is a lag time in reporting of costs due to the publishing process.

4.3. Taxonomic gaps

There were only 16 species among holoplanktonic invasive causing costs, stressing our plea on the underestimation of their costs worldwide due to a clear taxonomic gap. Dexter and Bollens (2019) in their review on zooplankton invasions pointed out 139 non-native holoplanktonic species and approximately half of the surveyed publications concerned solely four species: *Bythotrephes longimanus* (Leydig, 1860), *Mnemiopsis leidyi, Cercopagis pengoi*, (Ostroumov, 1891), and *Daphnia lumholtzi* (absent in the *Invacost* database). In addition, only 4.3% of the 139 studies informed on their economic impacts. Also, multiple zooplanktonic species have shown much higher non-native distributions than previously reported e.g., *Pseudodiaptomus forbesi, Oithona davisae, Bosmina coregoni, Kellicottia bostoniensis* (Dexter et al., 2020b, Macêdo et al., 2020).

Similarly, phytoplankton was poorly represented in the *InvaCost* database with only four taxa listed (see Table 1). However, the European Alien Species Database (EASIN, 2022) alone lists around 117 phytoplankton taxa as alien in marine and freshwater environments, among them some toxin-producing and bloom-forming algae. These numbers may indicate that less costly species are not less harmful or potentially impactful but probably less studied (e.g., invasive cyanobacteria and microscopic stages of non-planktonic invertebrates). According to Wolf and Klaiber (2017), most of the state and local governments of the United States considered harmful algal blooms to be "somewhat serious" or "very serious" issues. Economic losses related to eutrophication and cyanobacterial blooms have been addressed in several cases (e.g., Dodds et al., 2009; Wolf and Klaiber, 2017; Wurtsbaugh et al., 2019), though in many largely unmeasured or not properly quantified (Carmichael and

Boyer, 2016). However, costs of invasive cyanobacteria are lacking in the *InvaCost* database. The potential negative impacts, and underlying neglected costs, of invasive cyanobacteria might be overwhelming and include changes in the abiotic environment and biogeochemical cycles, shifts in microbial communities, not to mention the effect of single or multiple toxins on biodiversity by acute and sub-lethal effects on consumers and potential competitors (Sukenik et al., 2012; Sukenik et al., 2015). Additionally, the co-occurrence of multiple invasive species (Kokocinski and Soininen, 2019) and harmful impacts in freshwaters of remote oceanic islands (Costa et al., 2021) set the alert for even overwhelming effects of invasive cyanobacteria.

The low observed costs caused by plankton invasions are clearly attributable to taxonomic gaps, but also likely reflects the difficulties in translating their indirect impacts into monetary expenditures, particularly considering the subjective metrics e.g., the aesthetics value of waterbodies (e.g., Jochmsen et al., 1998; Naselli-Flores and Padisák, 2022) or the utilization of inappropriate temporal data (e.g., Arcifa et al., 2020). Water quality is a key ecosystem service commonly affected by nutrient enrichment and pollution, albeit commonly associated with phytoplankton blooms and not to the effect of invasive species (e.g., Amorim and Moura, 2020; González-Madina et al., 2021; Naselli-Flores and Padisák, 2022). Another example is the cascading effect through lakes food web. Through this invasion mechanism the predator *Bythotrephes longimanus* led to losses of US$ 86.5–163 million for restoring water clarity (Walsh et al., 2016). However, the world worst invasive *Cercopagis pengoi,* also a predatory cladoceran responsible for US$ 5 million of economic costs related to impacts on fisheries (Pimentel, 2005), has yet no costs assessments of impacts on environment and ecosystem services. Moreover, many other damaging invasive species are also missing from *INVACOST*: the parasitic copepod *Lernaea cyprinacea*, which infests commercially important fishes, (Soares et al., 2018), *Artemia franciscana*, capable of spreading cysts of protozoan parasites (e.g., *Giardia*) that infect a wide range of vertebrates including humans (Mendez-Hermida et al., 2006). and the dinoflagellate *Ceratium furcoides*, whose frequent blooming negatively affect economically important fish (Pacheco et al., 2021). Therefore, here we suggest some emerging holoplanktonic species of concern for future assessment of costs (Fig. 5). We suggested these species based on their potential to exert dual effects rising economic and public health concerns in a large geographic extension (literature based information, Table S1) e.g., act as disease vectors and lead to environmental problems.

Despite the higher costs of pathogens, free-living life-forms are relevant for our understanding of the trophic relationships in pelagic environments and are most likely to interact with and impact other species e.g., responsible for biomass decline and trophic disruptions (Bowen et al., 2018; Javidpour et al., 2020). Also, early and juvenile stages are more readily dispersed propagules (Flannery et al., 2016; Javidpour et al., 2020), easily transported by several pathways (e.g., as epifauna, within body cavities, via water currents, or ballast water discharges) (Viard et al., 2006). Furthermore, climate change is expected to influence the geographic range, abundance, ontogeny and ultimately the intensity of meroplanktonic invasions by influencing the success of early stages (Walther et al., 2009; Ernandes-Silva et al., 2016; Denley and Metaxas, 2017; Beaury et al., 2020). Lastly, the diversity of taxa and environmental tolerances of the planktonic invaders (e.g., freshwater, hypersaline and marine) can also be taken into consideration to investigate most invasive traits and the invasibility of habitats targeting more efficient monitoring efforts.

5. Conclusions

Our study highlights an uneven distribution of data in reporting costs of holoplanktonic invasions, mainly due to the low number of investigated species (taxonomic gap). While it is difficult to predict and reliably interpret costs of aquatic invaders, a continuous and rising introduction of several groups of planktonic taxa is expected and possibly enhanced by synergistic effects of other environmental human-driven alterations.

As cost types were generally higher for damage/loss than for control or management, we advocate for higher efforts in early detection to avoid or minimize the spread and establishment of invasive populations. For this we can rely on alternative technologies such as molecular tools e.g., environmental DNA and metagenomics. Although not yet sufficiently affordable for most developing countries, this can be primarily helpful in the detection of cryptic species, immature stages of zooplankton and larvae of benthic taxa.

By doing so, we could substantially reduce the costs of plankton invasive species in the future, an issue that reaches beyond a shift in trophic alterations and goes on to affect water quality worldwide.

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.

Data Availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2022.118918.

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