WITHDRAWN: The Ecological Biases of Zooplankton Invasions: Taxonomic, Geographical And Methodological Perspectives

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The full text of this preprint has been withdrawn by the authors while they make corrections to the work. Therefore, the authors do not wish this work to be cited as a reference. Questions should be directed to the corresponding author.

Abstract

The introduction of non-native species is one of the most important causes of biodiversity loss. Non-native organisms are not recognized by native communities, leading to differential predation rates and differential impacts on a variety of ecological interactions. In this context, the present study was intended to carry out a review of the literature on the impacts of non-native zooplankters on the zooplankton and the dynamics of aquatic ecosystems–literature reviews are a valuable tool that can highlight gaps and find possible biases in our understanding of biological invasions. We carried out a review of the current literature (20 years) looking for any alteration in the natural dynamics of the environment at all ecological levels. A total of 181 studies that addressed some type of non-native zooplankton effect were included in the review. Most studies focused on a just few non-native species and evidenced demographic changes at the population level. A geographic bias in favor of North America was also found. The various gaps in the literature on non-native zooplankton are derived from the same problem, an excessive number of investigations of the same taxa in the same places. Consequently, the recorded impacts are similar since they come from the same groups, and neglect less studied, but not necessarily less impactful, species. A greater focus on studies of lesser-known species could generate more comprehensive knowledge about the effects of non-native zooplankton and contribute to the distribution of conservation efforts beyond the better-known species.

Introduction

Freshwater environments are sources of diverse ecosystem services that contribute to the welfare of human populations but are constantly degraded and in need of new conservation policies (Junk et al. 2014; Maasri et al. 2021). One of the main reasons for the degradation of aquatic systems is the introduction of exotic species, which causes problems in ecosystems around the world, due to the lack of control of these organisms by native species (Darwall et al. 2018).

Several ecosystems from a variety of locations are experiencing problems with large-scale non-native species invasion events (Simberloff and Vitule 2014). Once natural barriers are superseded by anthropic means and biotic and abiotic restrictions are overcome, a species can become invasive, reproducing and generating a population outside its place of origin (Richardson et al. 2000). Through their interactions with native or other invasive species, invaders can cause a variety of changes to the ecosystem, including the decline of native populations and the genetic degradation of local species, as well as economic losses over a period of years (Vitousek et al. 1996; Simberloff and Vitule 2014; Diagne et al. 2021).

Zooplankton species play a key role in the maintenance of natural ecosystems (Lansac-Tôha et al. 2003; Gazulha et al. 2011; Lucena-Moya and Duggan 2011; Rumes et al. 2011). They are primary consumers, using producer communities and other organisms as food (Simões and Sonoda 2009), and thus serve as fundamental components of food webs (Blettler and Bonecker 2007). A common measurable effect of non-native species on natural populations is a change in the spatial distribution of the species within the zooplankton community due, in part, to anti-predatory behavior (Bourdeau et al. 2015). Therefore, knowledge of the impacts caused by invaders on this community would be particularly important.

Literature reviews provide a means to align results and identify problems in important groups, such as zooplankton, in the context of invasions by non-native species. Over the years, many investigations have been carried out with zooplankton as a result of environmental problems related to this group and the increase in the invasion rates of these animals (Dexter and Bollens 2020). Reviews are also able to find evidence of biases in the literature about non-native species (Watkins et al. 2021) and the economic losses associated with them (Diagne et al. 2021). Indeed, research efforts recorded in the literature on non-native species are unbalanced and contain several methodological gaps, and ignore some areas and aspects of biological invasions (Lowry et al. 2013).

Considering the problems generated by non-native zooplankton organisms in natural environments and the possible gaps in the literature about this group, we produced a systematic review of zooplankton associations worldwide in all habitable environments that included effects of the invaders on native communities. We sought to expand on the previous review by Dexter and Bollens (2020) specifying ecological impacts, focusing on studies that used non-native species of zooplankton with some level of impact on the dynamics of the system across ecological levels.

Methods

We conducted a bibliographic review for the years between 2000 and 2020 on non-native zooplankton species and their effects on natural communities. The search for articles was completed in June 2020. Our search focused on the taxonomic groups that make up the range of zooplankton species in continental environments and in the oceans. In order to cover the nomenclature used, we used the following terms: *Zooplankton* AND (*Invasion* OR *invasive* OR *non-native* OR *non-indigenous* OR *introduced* OR *exotic*). The purpose of choosing this combination of words in the search was to cover the largest number of works dealing with zooplankton that also had a relationship with invasive species in their text. The search terms provided results beyond effects and impacts, since we were seeking to obtain the greatest number of studies within the general theme of non-native zooplankton before further refining the results.

The search was carried out in the Web of Science database. After the basic search was completed, the articles were screened for articles that dealt with any level of impact, whether ecosystem, community, population, or individual, caused by components of the zooplankton. The articles were also screened taking into account various aspects such as region, habitat, zones, country, taxonomic group, type of interaction, effects and level of impact, in addition to the basic identification information of each study included in the review.

First, the articles were screened by their titles. At this stage, works far from the topic that, for some reason, were included in the results, or that were related to topic, but did not deal with non-native zooplankton species, were eliminated. Many of these were related to non-native species belonging to other aquatic groups, such as fish. At this point, the remaining works were screened again, this time based on their abstracts. As a result of the second screen a number of articles were selected for full reading. After reading the full text, it was possible to assemble a database for the initial review. In the final phase, the selected articles were screened for some mention of environmental impacts caused by non-native zooplankton species. The results of the final screening were selected for analysis.

The environmental impacts considered were any change in the natural dynamics of ecosystems, at any ecological level, either directly or indirectly (Pyšek et al. 2020). The level at which the impact occurred was considered as recorded in the article, with no extrapolations made beyond what was found by the researchers. Although many studies could carry out inquiries into possible impacts occurring at the time of the research, only those that were actually measured and supported by empirical data were considered. The studies were categorized according to the recorded impacts, showing the ecological level at which, the change occurred and also the effects within that level, adapting the methodology used by Cucherousset and Olden (2011). In this way more than one effect per level could occur and more than one level per ecosystem could be affected. A study, for example, that found changes in behavior, demographic rates and species distribution would have three distinct effects at two ecological levels (individual and population).

Results

The initial search using the keywords resulted in a total of 1,709 articles related to the topic. From these 1,045 were eliminated during the initial screenings of titles and abstracts that eliminated articles outside the scope of the review (mostly based on taxonomic group) and or in a language other than English. More specific screenings were performed on the full text of the remaining articles in order to identify the information needed for the review. This step included 664 articles that addressed non-native zooplanktonic species (Figure 1). These consisted of general works that were subjected to a final screening looking for effects, alterations and ecological impacts of zooplankton species.

Fig.1. Results of searches incorporated in the review. Each step indicates the number of articles and the reason why the articles were withdrawn or included. The inclusion step identifies the levels of impacts recorded (229 levels in 157 studies)

After the final screening, 157 articles were identified as dealing with some type of alteration in the natural environment that could be considered as an impact caused by non-native zooplanktonic species (Figure 1). At first glance, the number of articles with some evidence of impact may seem to be only a small fraction of the total. However, some of these still did not indicate an impact specifically, but recorded in their data effects that could be shown to be caused by non-native species belonging to zooplankton. From the data collected in the articles with impacts, we observed a large number of studies focusing on just a few non-native taxa (Figure 2, A), especially on a single species of the non-native cladoceran *Bythotrephes longimanus* (Leydig, 1860). This can also be seen within taxonomic groups, where the same species has the highest incidence of studies.

Fig.2 Graph of the relationship between species and number of studies. Each point represents a species, studies that included more than one species were counted more than once (n=201). In (B) graph showing the number of articles by taxonomic group

Most of the studies that were within the scope of the review focused on a few species. About 64% of the articles focused their objectives on just five species, out of a total of 60 non-native species recorded in this review. The non-native cladoceran *B. longimanus* was the most frequent taxon in the records (34.85%), followed by the ctenophoran *Mnemiopsis leidyi* (A. Agassiz, 1865) (13.93%), the cladoceran *Cercopagis pengoi* (Ostroumov, 1891) (9.95 %), the ctenophoran *Boroe ovata* (Bruguière, 1789) (5.97%), and the copepod *Pseudodiaptomus forbesi* (Poppe & Richard, 1890) (3.98%), among 201 records (Figure 2, A).

Furthermore, cladocera was the group in which the largest number of studies focused on impact (Figure 2, B). More than twice as many of the articles reviewed dealt with zooplanktonic cladocerans compared to the second most studied group, copepods. Clearly, there is a taxonomic bias in the studies, with a large number of studies involving cladocerans. This is also evident in the large number of studies with impacts on cladocerans. The North American invasive cladoceran *B. longimanus* is the main reason for these results and was addressed in most of the studies in the review.

Regarding global distribution, most studies were carried out in northern hemisphere countries (Figure 3). Large trends were found for studies that recorded impacts, in relation to distribution (region) and focus (species), and these factors are certainly related. According to our review, temperate regions were more extensively studied than tropical regions. A remarkably large number of studies took place in North America and Europe, much larger than in the rest of the world. As was the case for the taxonomic data, a bias is visible in relation to the geographic distribution of studies with non-native zooplankton that cause effects in the environments.

Fig.3 Graph depicting the locations of studies by continent in relation to the number and percentage of the total. The continent where the collection was carried out was considered

We divided the studies into categories based on the level of ecological impact, so that more than one impact could be identified in the same study. In this way, we identified a total of 229 ecological impacts, which led to 236 effects when looked at by level. Changes in vital rates were the most frequent effects for the individual level (n=11). Notably, changes in species demographic rates were much more frequently recorded (n=125), representing 95.42% of population-level effects and 52.97% of the total effects. At the community level, most studies recorded changes in the food webs (n=37), representing half of the effects at this level. At the ecosystem level few impacts were identified, and all were framed as the same effect, abiotic alteration, that is, changes in the physical and chemical environment (n=7).

Fig.4 Chord diagram of impact levels and effects. Within the total number of articles included in this stage of the review (n=157) impacts caused among ecological levels (n=229) by different effects (n=236) were computed. A single study could have more than one level impacted by more than one effect. The levels are: Individual (ID); population (PP); community (CM); and ecosystem (EC). The standardized effects are: vital rates (VR); behavior (BH); morphology (MP); demographic effects (DE); distribution changes (DT); vertical migration (VM); changes in composition, diversity and richness (CDR); food webs changes (FW); species extinction (SE); and biochemical effects (BE)

Discussion

From the results of this review, we can see that the literature is remarkably dominated by a few species, with more than 60% of the studies concentrating on the cladocerans *B. longimanus* (n=62) and *C. pengoi* (n=20), and on the ctenophorans *M. leidyi* (n=28) and *B. ovata* (n=12). This number of target species is small considering the vast taxonomic diversity that certainly causes effects in native environments. There is clearly a taxonomic bias in the literature on non-native zooplanktonic species, as well as for other groups; the literature produced contains several gaps, generated by unequal efforts in specific areas (Lowry et al. 2013). This bias is primarily influenced by the excessive study of the most popular species, or the most “famous” or with positive feeding cycles, simply because they are studied more initially, generating “poster children” species (Watkins et al. 2021). This was already predictable, since these species are related to anthropic environments and are frequently associated with ecological impacts (Dexter and Bollens 2020). The fact that 60 records of non-native species with ecological impacts focused mostly on continental water organisms indicates that taxonomic biases are not exclusive to the oceans and that freshwater environments are underestimated in terms of non-native zooplankton species. This trend is strongly influenced by the incidence of *B. longimanus*, which has been extensively studied and is responsible for a large part of the taxonomic bias.

This does mean that we should ignore the high capacity of the most studied taxa for negative impacts on native environments. Unlike other groups (Lowry et al. 2013) the number of studies of impacts of zooplankton is not frequent, creating an even bigger concern. The predatory and competitive capacity of aquatic invertebrates should not be underestimated, since they are often of more influence in the structuring of native communities than more derived and larger taxa (Bunnell et al. 2011). Since *B. longimanis* was first considered to be an invader in North American environments, several impacts of this species have been recorded, from morphological changes in the formation of the helm of daphnia (Bungartz and Branstrator 2003), to population size restrictions (Dumitru et al. 2001; Barbiero and Rockwell 2008) to changes in species composition (Bunnell et al. 2012).

Even if the information about the potential impact of the species presented in the studies is consistent, the biases are clear and cannot be disregarded; we emphasize that these two facets are linked (Lowry et al. 2013). Records of impacts seen in other reviews are also supported by just a few taxa (see Watkins et al. 2021). The consistency of this pattern makes it safe to say that research efforts are mistakenly and unevenly concentrated, probably because of the high level of impact identified for these species and the consequent advance and intensification of studies involving them (Lowry et al. 2013; Pyšek et al. 2020). As a result, the most incident species in scientific research of ecological impact are increasingly studied, and studies of invasive species end up being biased toward the species with the greatest impact or with impacts that are more conspicuous and easier to recognize. Therefore, the inquiry and extrapolations of these results must be done with care (Guerin et al. 2018) especially when dealing with information that can be used as a basis for the management of natural parks.

We must emphasize the large gap in our knowledge of species in freshwater environments, especially considering that the most studied species invade the North American Great Lakes, which are surrounded by research centers (Bourdeau et al. 2016; de Stasio et al. 2018). The high incidence of studies with the same species from temperate zones raises concerns considering that locations with high diversity are certainly underestimated, these regions receiving little attention and investment, especially in the biodiversity hot spots of tropical zones where financial and conservation efforts should take place (Myers et al. 2000; Jeschke and Heger 2018). Much of this “confusion” within invasion ecology comes from research efforts with theoretical redundancy that could be resolved through the integration of knowledge about invasions (Catford et al. 2009).

The hypothesis that biases are linked to language should be discarded, since only articles in English were used in the review. English, despite being native to the areas with the highest incidence of studies, does not represent an obstacle to the dissemination of the knowledge. On the contrary, it allows science to have a “universal” language. Even so, the standardizations and translations of terms used in research can be confounding factors due to the large number of models and concepts for the ecology of invasions (Blackburn et al. 2014). Certainly, including studies in other languages would have considerably increased the database (Rodríguez-Castañeda 2013). Another point to consider is that basic ecological research, which is often not published in international journals, and includes theses and dissertations, is frequently removed from bibliographic reviews; here it was no different, since most basic research is published in local journals, often in the languages of the region.

Along with these factors, a geographical bias is also clear (Figure 4). The fact is that geographic and taxonomic biases are linked. Although the distributions of the most studied species are not native, they persist and establish themselves in new regions as part of the trophic web (Sinclair et al. 2016), one of their invasive characteristics. Thus, it is evident that studies carried out in these regions will generate more data related to species already well studied (Figure 3). Speaking exclusively of the species with more studies as recorded here, these primarily were found as invaders in countries with larger research centers and resources. The great effort of work carried out in these regions only increases, causing more and more investigations in the same places and with the same species, a factor that also influences gaps in our knowledge in temperate zones (Jeschke and Heger 2018).

The high perception of the impact potential of the most studied species clearly contributes to the biases (Pyšek et al. 2008), an extensive number of studies relating environmental disturbance events caused by the best studied species can be found, certainly related to known events of invasions and environmental impacts, especially in sites sensitive to invasions and widely invaded (Bagheri et al. 2014). this can be seen clearly for the great lakes of North America and the Black Sea (Bilio and Niermann 2004; Yan et al. 2002). Biases are also linked to a cultural issue of research around the world, where the great researchers pass their "legacy" to new researchers who, for the most part, do not stray too far from the research line, and, often, from the species themselves. Furthermore, it is evident and plausible that sites with notable environmental problems end up generating large amounts of work on the same species; this can be observed for the problems with ctenophora in the Black Sea (Gordina et al. 2005). Clearly, worrisome environmental problems should be widely studied, and this does not indicate a lack of useful and important scientific content. However, this factor will inevitably generate more research on the same species and consequently biases in the literature.

Checking the impact potential of the most studied non-native species of zooplankton, examples of notable changes at different ecological levels are easily found, from changes in the behavior of individuals (Bourdeau et al. 2016) to ecosystem functions (Ellis et al. 2011; Brown et al. 2012). However, an ecological impact bias was clearly identified. Quite markedly, the identified effects, for the most part, consisted of changes in demographic rates and within native zooplankton communities. These included reductions in prey number (Foster and Sprules 2010; Rodrigues et al. 2020), reduction in competitor density (Engel and Tollrian 2012), changes in biomass (Rudstam et al. 2015) and even an increase in total abundance of species (Altukhov et al. 2014). Whether it be an increase or a decrease in the natural densities of native populations, these changes cause impacts on the environment, albeit indirectly (Crooks 2002). The lack of diversity in research focuses on impact-causing zooplankton is the main reason for the gap, which raises concerns considering that the effects of non-natives occur in an additive way and more and more impacts and changes can be expected (Braga et al. 2020).

Our results are in agreement with previous reviews on population-level impacts (Crystal-Ornelas and Lockwood 2020). The ecological impact bias is related to two possible points. (i) The impact bias at the population level is linked to the most studied species, since the high incidence of studies on the same invasive populations certainly generates similar effects. Although the environment and native communities influence differences in the intensity of the effects of non-natives (Soares et al. 2018), the biology of the species and its main characteristics of causing accentuated effects of biomass reduction (Bilio and Niermann 2004; Bagheri et al. 2012; Walsh et al. 2018) and the interaction mechanisms of non-native species also influence the results, leaving similar and standardized impacts. (ii) The collection of information on biomass, abundance and density of species is quite frequent and uses simpler methodologies and techniques in comparison to aspects of the individual and ecosystem levels, for example. Thus, a methodological bias exists with respect to research on non-native zooplankton, where numerical data collected from individuals leads to more frequent observations of demographic effects, which could have different results at larger scales of space (Guerin et al. 2018), and time (Sinclair et al. 2016) or with different methodologies. This factor certainly influences the frequency with which studies that show evidence of this type of ecological impact appear in the literature on non-native zooplankton species. In addition, the when differences incumbent on the researchers' own assessments are considered, the uncertainties generated regarding the impact are high, especially when attributed to the severity of the impacts (Clarke et al. 2021).Thus, even though the impacts at the population level are evident, especially in relation to well-studied predatory species (Vehmaa et al. 2018; Hasnain and Arnott 2019; Berges et al. 2020),we must not fail to link these facts with biases, since many of the registered demographic changes are due to the ease of identifying these parameters. We recognize that our impact criteria are not as refined, but we emphasize that we looked for general parameters that could be compared only for the purpose of identifying possible biases.

In short, few species become invasive and even fewer do substantial economic damage, yet, when estimated, the financial losses caused by this minority are quite high (Lovell et al. 2006). It is not surprising that there are gaps in economic data for non-native species, especially given the geographic and taxonomic biases noted (Diagne et al. 2021). Likewise, the biases found here may be influenced by the lack of economic interest in in the majority of the zooplankton. Certainly, the lack of studies does not indicate the lack of economic loss. However, the literature, in general, addresses the best-known species, famous for causing environmental and, potentially, economic damage, again generating taxonomic and geographic biases (Adelino et al. 2021).

Faced with the level of bias, it is not possible to make consistent statements about the species with the greatest impact in records of non-native zooplankton. Other species with fewer records or groups less frequently associated with impacts can cause severe negative effects on natural communities, even if not well studied. Invasive species such as *Hemimysis anomala* have the potential to cause high losses in biodiversity (Penk et al. 2015) despite not having numerical relevance within the present review (n=4); other taxa found in the review may also have their impacts neglected due to biases observed. Obviously, when biases and gaps in the literature concerning impacts are found, less studied groups are underestimated and potential effects may be ignored by inequality in research efforts and considered to be less intense (Lowry et al. 2013). Even though the number of studies on some zooplankton groups is considered sufficient for hypothesis formulations to be extrapolated to other groups (Pyšek et al. 2008). We argue that the discrepancy between the number of studies that address a few taxa for the rest of the world's zooplankton is still very large, and possibly the information limit for the results to be transposed has not yet been reached.

We conclude that all the biases highlighted probably stem from the same problem, excessive research on the same species (poster children) with greater ecological interest. Since the more these species are studied, the greater strength is given to the mechanisms they use, generating more, as recorded here, research, with predation and effective impact level closely related to the most studied species and lead to more effects at the population level, although, as mentioned above, collection methodologies also may be related to the bias toward impacts at the population level. At this point geographic bias is limited to the range of species, such as *B. longimanus* and M. *leidyi*, that are heavily studied, generating results on the disposition of impacts of invasive species across the globe; this extrapolation should be made with caution. There is still much to consider about the effects of non-native zooplankton species and their impacts at different ecological levels, in addition to the ecological consequences of biases found in the literature. Despite the clear implications that invasive species have for native populations, the biases cannot be ignored. These are not unique to non-native zooplankton (Lowry et al. 2013) or inland water communities (Watkins et al. 2021), or of general studies on non-native zooplankton (Dexter and Bollens 2020) and should not be related to invasion ecology, since some of the factors responsible for this result are linked to scientific cultural basis. Greater research efforts are needed in understudied species, as well as better communication between researchers, avoiding uncertainties and replications. The findings of this review can serve as a guide to direct zooplankton researchers where taxonomic, geographic and ecological impact studies are still needed.

Statements & Declarations

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Data availability

All data generated or analysed during this study are included in this published article [and its supplementary information files].

Competing interests

The authors have no relevant financial or non-financial interests to disclose

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection, analysis were performed by Clemerson Richard Pedroso. The first draft of the manuscript was written by Clemerson Richard Pedroso and Jean Ricardo Simões Vitule commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

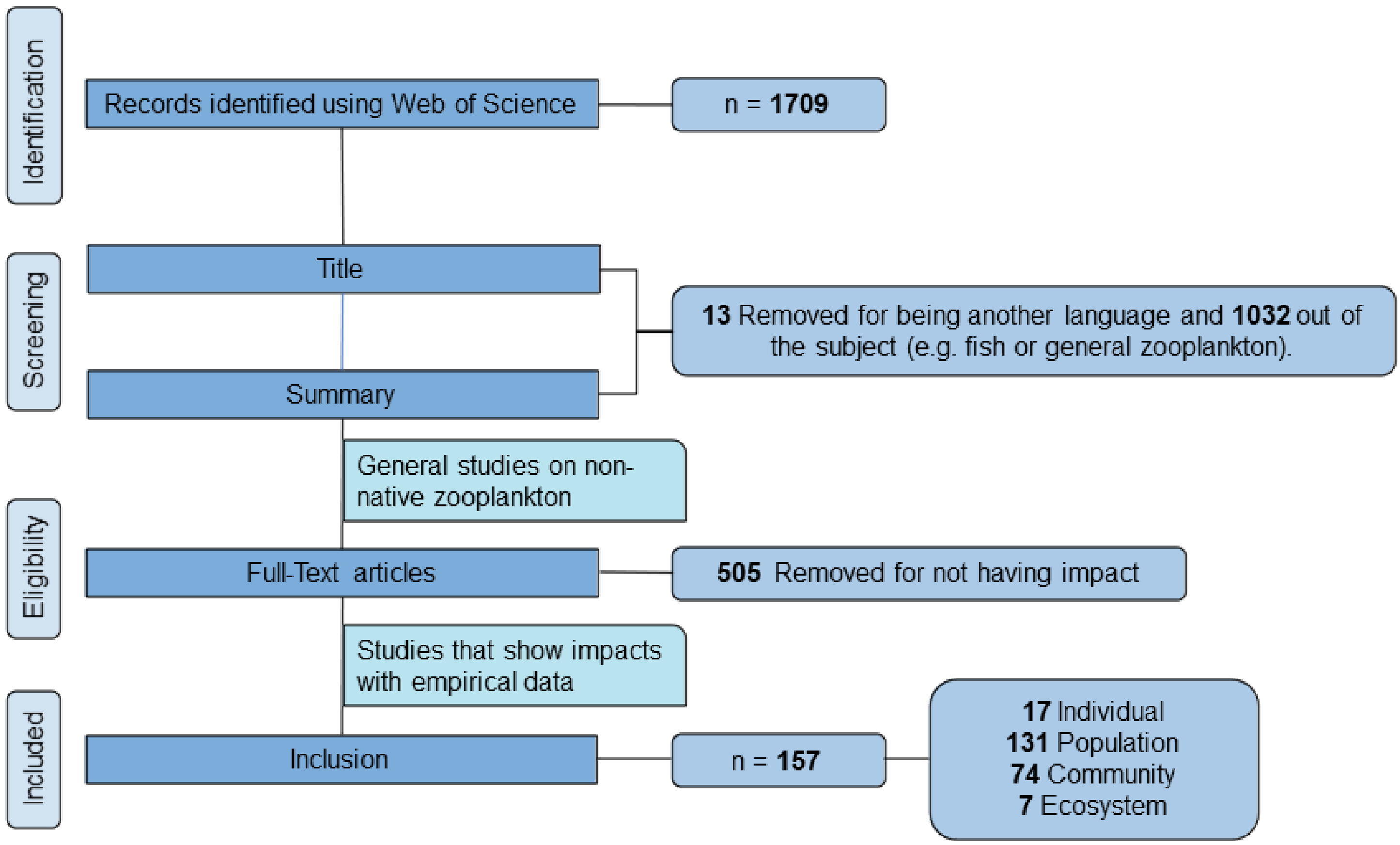

Figure 1

Results of searches incorporated in the review. Each step indicates the number of articles and the reason why the articles were withdrawn or included. The inclusion step identifies the levels of impacts recorded (229 levels in 157 studies)

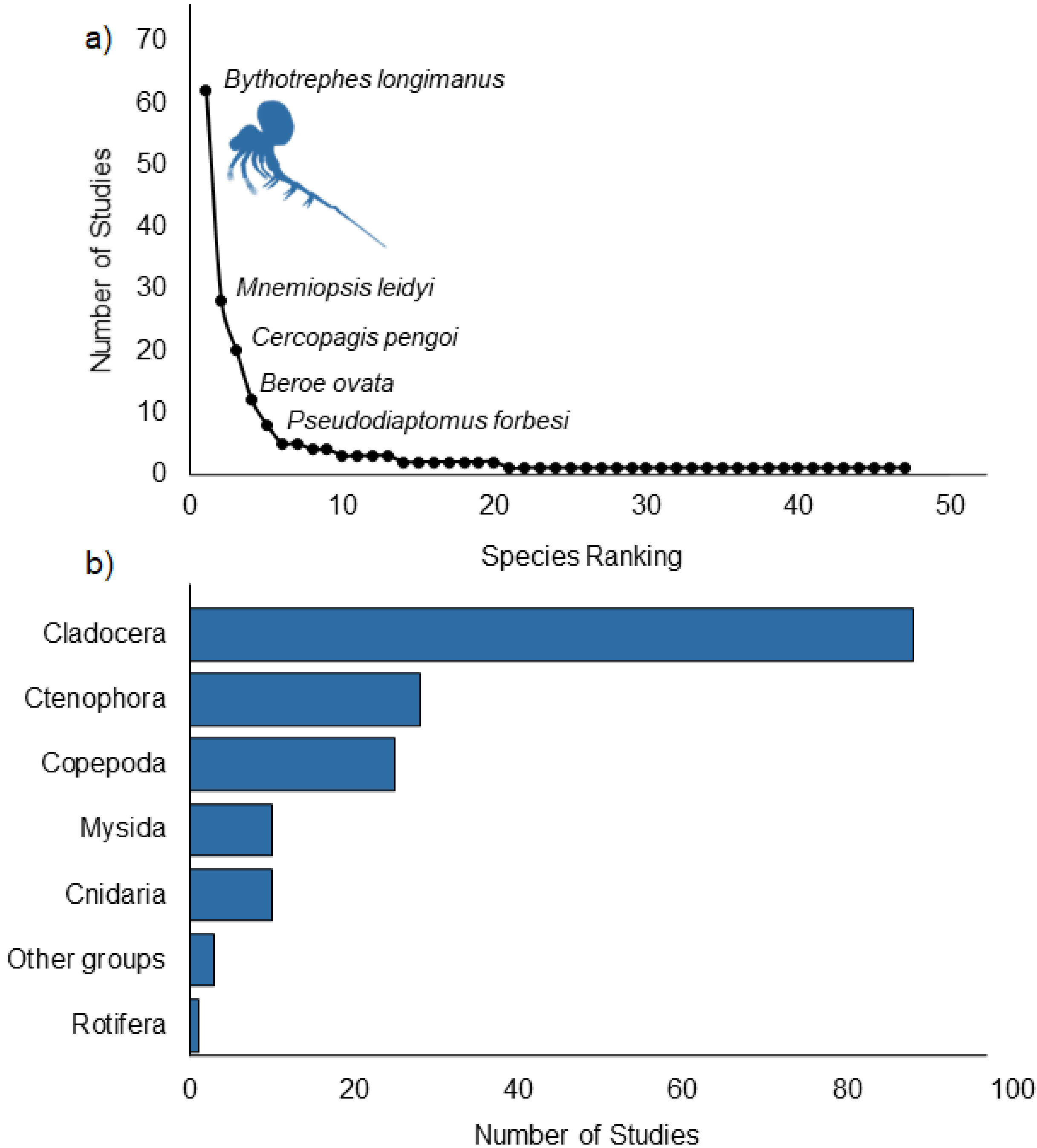

Figure 2

Graph of the relationship between species and number of studies. Each point represents a species, studies that included more than one species were counted more than once (n=201). In (B) graph showing the number of articles by taxonomic group

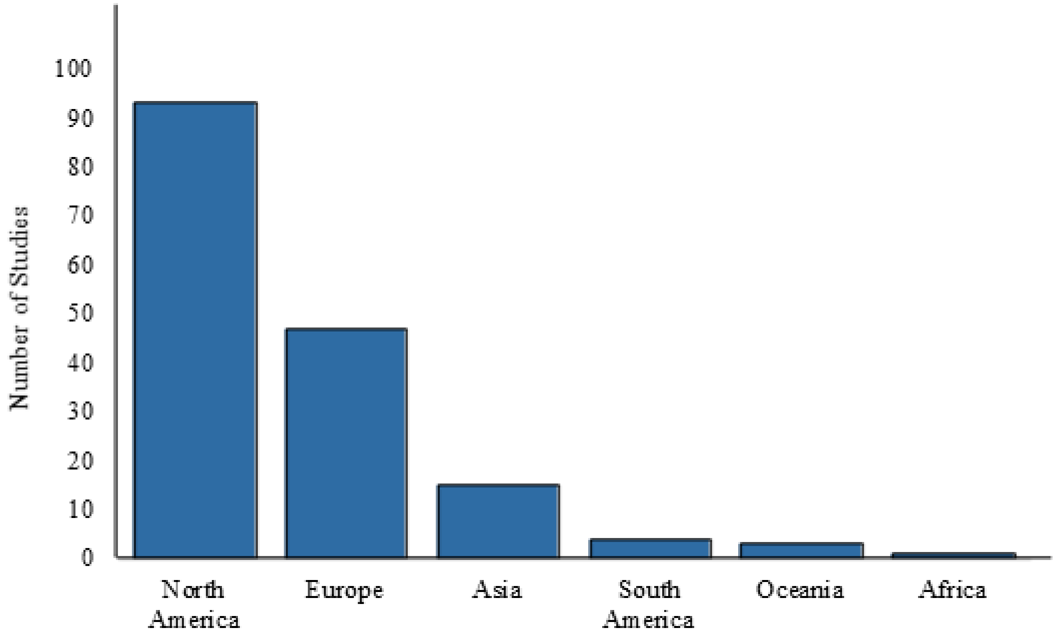

Figure 3

Graph depicting the locations of studies by continent in relation to the number and percentage of the total. The continent where the collection was carried out was considered

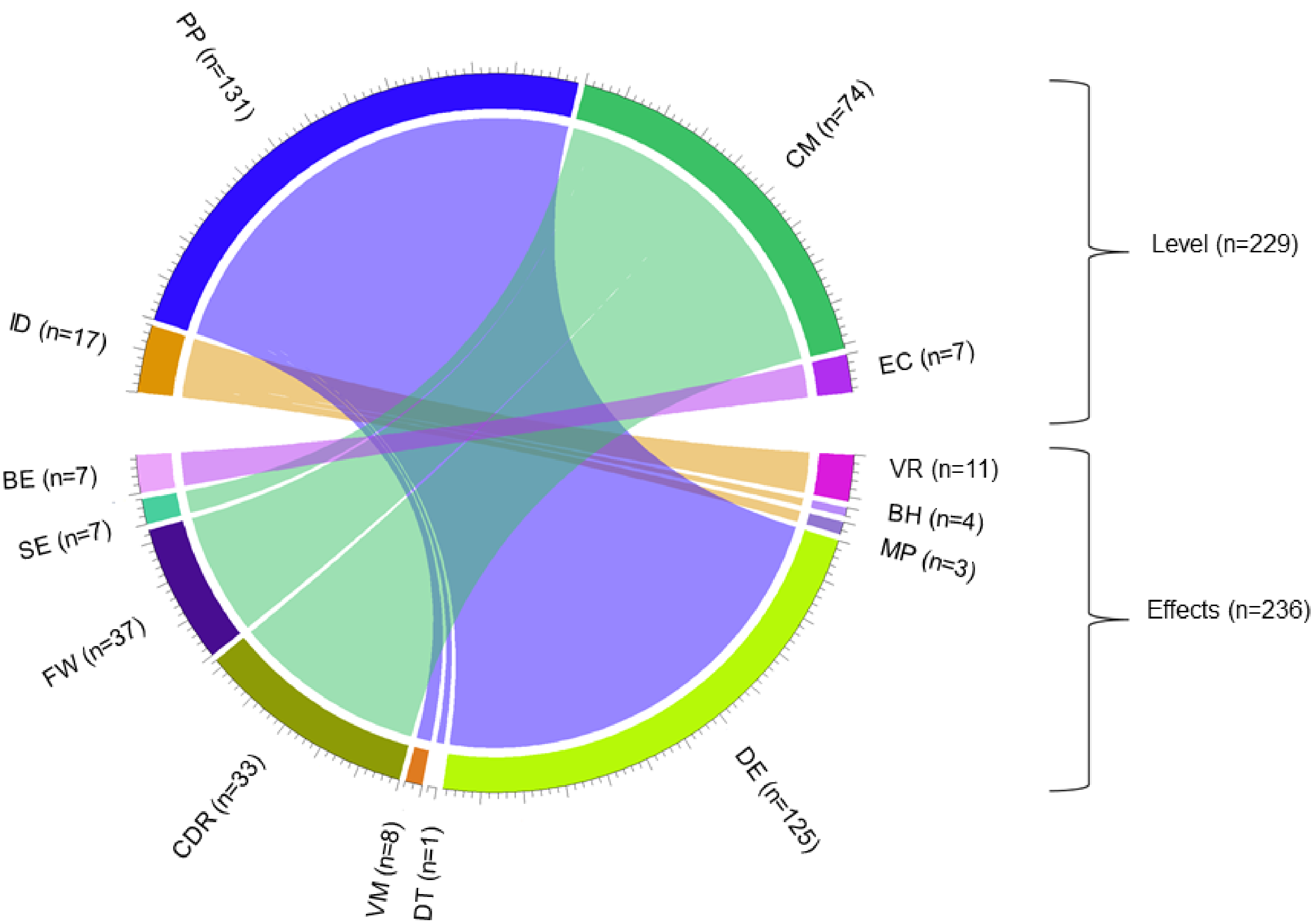

Figure 4

Chord diagram of impact levels and effects. Within the total number of articles included in this stage of the review (n=157) impacts caused among ecological levels (n=229) by different effects (n=236) were computed. A single study could have more than one level impacted by more than one effect. The levels are: Individual (ID); population (PP); community (CM); and ecosystem (EC). The standardized effects are: vital rates (VR); behavior (BH); morphology (MP); demographic effects (DE); distribution changes (DT); vertical migration (VM); changes in composition, diversity and richness (CDR); food webs changes (FW); species extinction (SE); and biochemical effects (BE)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- DatasheetPedrosoandVitule2021.xlsx