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Biological invasions via ballast water: evaluating the distribution and gaps in research effort by geography, taxonomic group, and habitat type

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While crucial for maneuverability and safety of commercial ships, ballast water (BW) has long served as a major vector for the distribution of non-native species in coastal ecosystems. Species transfers via shipping can alter community composition, ecosystem function, economies, and human health. In recent decades, a significant body of research has focused on BW, including many *in-situ* studies, but this is unevenly distributed across global regions. Here, we conducted a literature review to evaluate the distribution of published BW studies across geographic regions, taxonomic groups, and habitats, highlighting some current knowledge gaps. Of 2,088 publications on BW in our review, 270 (13%) reported on *in-situ* sampling from ballast tanks across 194 unique geographic locations. For both number of publications and sampling effort, approximately 85% were from the northern hemisphere. Considering planktonic organisms sampled in BW, only 12% of publications were from the southern hemisphere, and no study reported analyses of benthic communities in ballast tanks outside of North America and Europe. While we recognize that our review does not capture all existing data, such as technical reports and regional journals, it provides a relative measure of research effort to date, highlighting the disparity among regions in taxonomic and habitat analyses of ballast communities. In particular, the low frequency of *in-situ* measures for many regions (especially the southern hemisphere) limits current understanding of BW species transfers, including changes over time in response to evolving management and policy across the globe.

KEYWORDS

ballast water, biological invasion, non-indigenous species, sampling, shipping

1 Introduction

Over 80% of international trade involves shipborne transportation, which is expected to increase by 240–1,209% by 2050, with a commercial fleet of 105,493 vessels moving goods through an extensive network of ports (Miller et al., 2011; Sardain et al., 2019; UNCTAD, 2023). Shipping is obviously critical for international trade (Hoffmann and Kumar, 2013), being the cheapest method of transporting goods around the world (Khalikov et al., 2020). In addition to transporting goods, ships also comprise many sub-vectors, such as hull, propeller, rudder and ballast tanks, which act as habitats or niches that allow for marine and freshwater organisms to be transported to new locations (Hewitt et al., 2009). Most of these unintentional species transfers take place through ballast tanks or biofouling (Sardain et al., 2019), and ballast water (BW) and hull fouling alone are considered responsible for 60–90% of marine bioinvasions (Hewitt et al., 2009; Ruiz et al., 2015; Bailey et al., 2020).

When pumping BW on board, ships entrain free-living organisms in ballast tanks as adults, larvae, cysts, and eggs. Organisms associated with port sediments can also be re-suspended and taken on board as well (Gollasch et al., 2019; Sardain et al., 2019).

Non-native species can cause changes at different levels of biological organization, from genetic structure to the alteration of communities (Lehtiniemi et al., 2015). The impacts are interdisciplinary, from ecological to economic, including biodiversity loss, habitat changes, species distributions, biotic interactions such as predation, parasitism, competition, shifts in community structure, modification of productivity and nutrient cycling, alteration of food chain resources, and introduction of pathogens (Cabral et al., 2019; Kholdebarin et al., 2020). Overall, it has been estimated that around 5% of the world's annual economy is lost due to the negative impact of invasive species transported to new ecosystems via anthropogenic activities, by disrupting fisheries, fouling ships' hulls (e.g., increasing drag and fuel consumption), and clogging intake pipes for water supplies, which are critical for industry, agriculture, and public use (Erol et al., 2020; Tamburri et al., 2020; Davidson et al., 2021). Some species can even directly impact human health by spreading disease (Ruiz et al., 1997; Pimentel et al., 2001).

BW was suggested as a potential vector for species transfers and invasions over 100 years ago; however, it was only in 1973 that the presence of live zooplankton in a vessel's ballast tank was documented after a transoceanic voyage (Ostenfeld, 1908; Peperzak and Gollasch, 2018).

At an international scale, the International Maritime Organization (IMO), the United Nations body that administers the international regulatory regime for shipping, adopted in 2004 the International Convention on the Control and Management of Ships' Ballast Water and Sediments, the most comprehensive international agreement on BW management to date (Gollasch and David, 2017). It is the latest global effort to deal with the discharge of organisms in BW aimed at limiting the potential for invasions of non-native species in BW and its associated sediment discharge (Sardain et al., 2019). The two management standards

recognized by the IMO Convention are to be implemented sequentially, representing a stepwise reduction in organism transfers in ships' BW (Minton et al., 2005; National Research Council, 2011). These include:

- Regulation D-1, which requires vessels to exchange their BW pumped in coastal areas for BW taken in the open ocean, whenever possible, 200 nautical miles away from the nearest land and 200 meters in depth; this aims to reduce concentrations of coastal organisms, which could invade coastal ports and habitats.
- Regulation D-2, which sets limits for viable density of organisms that can be discharged in BW systems to coastal waters for particular types and sizes of organisms, using water treatment to achieve this standard, which is lower than concentrations achieved by BW exchange (IMO, 2004).

The aim of this paper is to evaluate the extent of knowledge about various dimensions of the BW biota, with a particular focus on *in-situ* measures from ballast tanks, including both planktonic and benthic communities. More specifically, we seek to examine the distribution of published research on BW biota across global regions, taxonomic groups, and habitats (i.e., planktonic versus benthic communities of ballast tanks). Using a literature analysis, we explore the relative distribution of *in-situ* analyses across these three axes. While the review is not intended to be exhaustive, it provides insight into the spatial and taxonomic distribution of the existing knowledge base and gaps, which are relevant to evaluating the extent of species transfers and ongoing changes due to management and policy in various global regions.

2 Methods

Using the Thomson Reuters Web of Science TM, we conducted a search for all publications including the topic search term “ballast water”. The search was conducted on September 7, 2022, for all years available in the Web of Science Core Collection (1900–2022). Not all publications are indexed in the Web of Science, but this is a publisher-neutral repository that is home to more than 170 million records covering over 34,600 journals. Our intention was to capture and portray the general landscape of publications and readily available knowledge on BW, recognizing that technical reports and some publications may not be included.

Overall, our initial search resulted in 2,088 publications. We further refined this count by reading publication titles, abstracts, or full text to assess whether BW was the focus of the research or not. We defined a BW study as any original research whose focus was BW, which includes analyses through sampling, modeling, experiments, or simulated BW conditions. Publications not related to species transfers or invasions through BW (e.g. naval architectural, draft calculations) were removed, along with those studies that only referenced BW within their text, including those restricted to conceptual frameworks and discussions.

Following this first data filter, a total of 810 publications were considered for future analysis. In each of these publications, we extracted information on whether there was *in situ* sampling or if it was not (e.g. experimental/modeling studies) and, if applicable, what the target taxonomic group(s) of organisms analyzed from BW or sediment samples collected on ships were.

Target groups were classified according to the following categories: (a) microorganisms (i.e. bacteria and viruses), (b) non-autotrophic protists, (c) phytoplankton, (d) zooplankton, and (e) benthic. We included (f) a 'broad' classification that covered all cases where the main focus of the publication was not one single group, but a broad range of groups was analyzed and discussed (e.g., through metabarcoding studies or when no specific group was declared as the focus of the study). The (g) N.A. category was created to account for non-biological targets (i.e. sediment elemental analysis, heavy metals, fluoride and chloride levels, as well as optical signatures).

A second filter was applied only on those studies that actually analyzed samples of BW or sediment. The following information was extracted: (1) which habitat was sampled inside ballast tanks: BW, sediment or both; (2) number of samples/ships analyzed and, (3) sampling location, when available, since the country in which the samples were taken did not always match the country of the author's affiliation. In some cases, it was not specified in the study exact areas where the samples were taken, and other times it was detailed in the Supplementary Material for example. Samples taken in-transit (e.g., during a multi-day voyage from one country to another) were considered for analysis only when we could identify in which country they were collected, since we wanted to evaluate the countries/regions where BW/sediments were most studied *in situ* — as the number of sampling events below.

To estimate where the samples were collected, approximate coordinates were obtained using Google Maps (google.ca/maps/) based on the sampling locations provided in publications; in some cases, samples were used from previous studies, so the sampling sites were obtained from the cited publication. It's worth mentioning that these publications were still taken into account since they worked with real ballast samples under a different approach. Where specific sampling locations could not be identified, either because no information was provided in the publication, if it was an on-route study, or the site could not be confidently located based on the descriptors provided (e.g. samples from ships in European ports), sites were not included in any visualizations of geographic distribution or included in the sampling effort estimations.

For the calculations, we considered each paper as a sampling event, and a paper may have one or more distinct geographic locations or sites where ships were sampled. The number of ships sampled was not included in many papers. Thus, we evaluated the total number of unique papers (events) and the total number of unique locations sampled per paper, as well as the number of papers with samples at each specific location. We also evaluated the cumulative number of locations sampled across papers as an additional measure of sampling effort. For example, one paper may have sampled ships at 5 distinct locations for BW, another may have sampled ships at 3 locations for BW, yielding a total

sampling effort of 8; this was intended to provide some measure of effort, but did not account for the actual number of ships sampled or samples/ship (which were only available for a subset of papers).

Frequency distribution curves were calculated based on the actual number of BW/sediment samples collected per location, as available and reported in the publications.

3 Results

3.1 Overview, sample sites and media collected

From 1932 to September 2022, the Web of Science recorded 2,088 publications on BW, with over half originating from the United States, China, and Canada (Figure 1). However, only 38.8% of these studies specifically focused on BW, and 12.9% (270 studies) included actual samples from inside BW tanks, covering at least 194 sampling locations. Overall, 85.5% of these studies (231) analyzed BW samples across 186 sites, while only 23.7% (64 studies) focused on sediment, covering 62 sites (Table 1). Additionally, 9.3% of all publications (n = 25) analyzed both BW and sediment. On average, the number of BW samples reported per publication was higher than that for sediment samples, with averages of 64.7 and 53.1, respectively (Figure 2).

Overall, 22% of these 270 studies collected samples in-transit or did not specify in which region samples were collected. When considering the other 210 publications, 5.4% of the sampling events could not be assigned to a specific country and, for 13.3% of sampling effort, we note that the specific locations were not available or evident (Supplementary Material). North America had more sampling events than other global regions (Table 1), accounting for 53.5% of the total, and greater sampling effort, with 60.8%, across 93 locations (47.9%). Asia accounted for 25.4% of sampling events, with a high representation of studies conducted in China, which made up 32.8% of the sampling events in this area. Europe contributed 10.1% of sampling events.

The southern hemisphere accounted for only 14% of all sampling events. Regions like New Zealand, South America, and

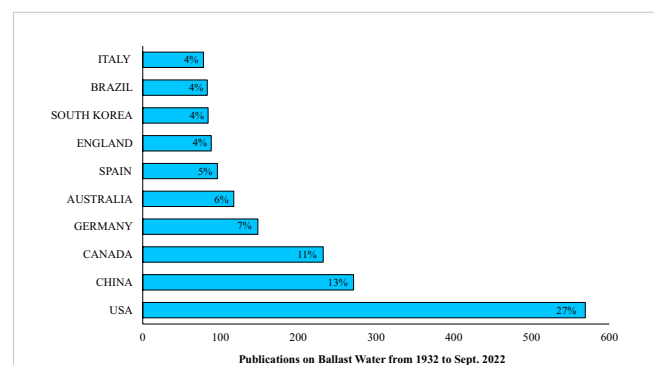


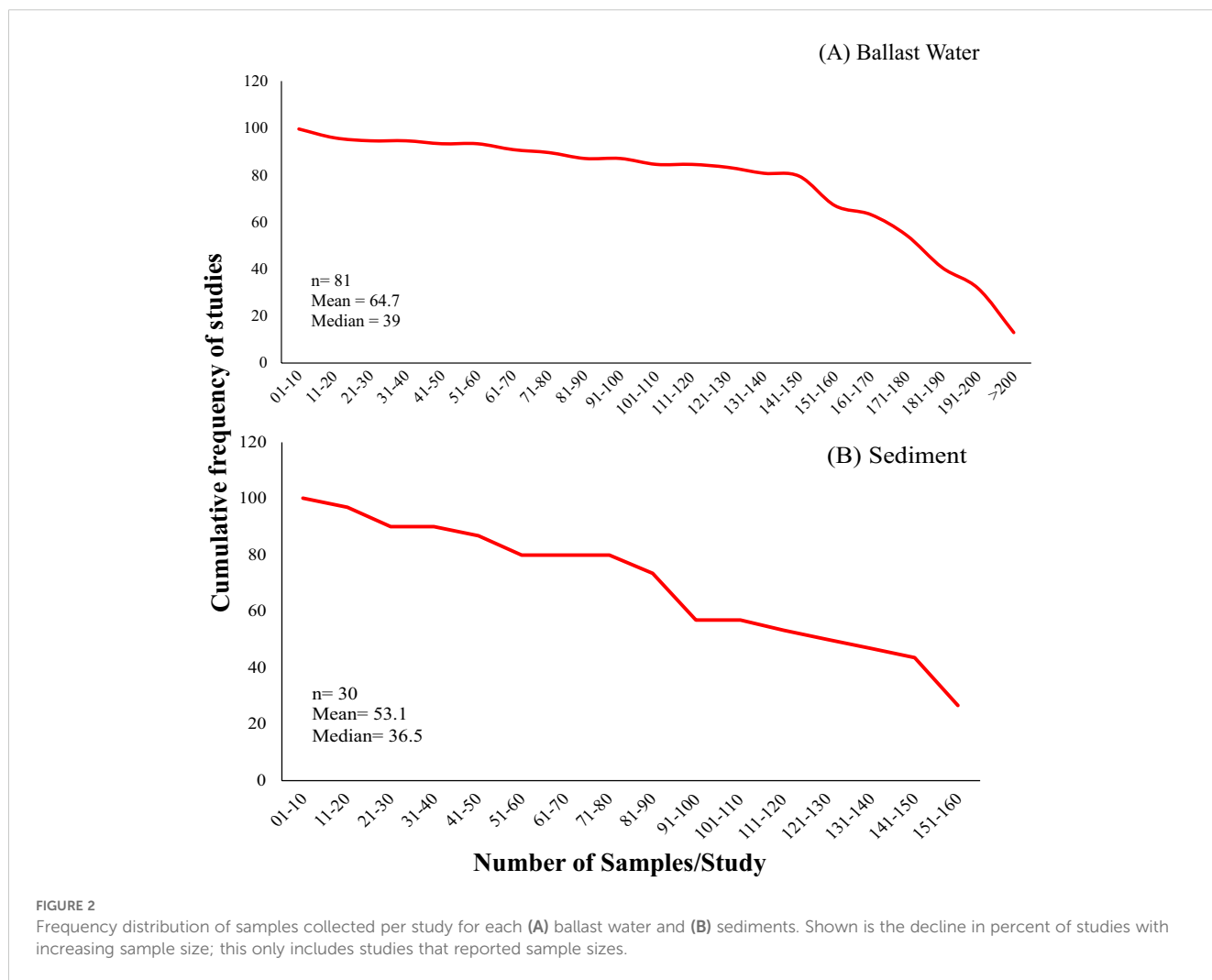
FIGURE 1

Ten countries with the highest number of publications on ballast water according to the Web of Science from 1932 to 2022. In blue is the total number of publications on ballast water with the respective percentage highlighted in black.

TABLE 1 Distribution of sampling events and effort across geographic regions, hemispheres, and global scales — for ballast water, sediment and total (ballast water + sediment; n=270).

	Region							Hemisphere		Total
	North America	Asia	Europe	Australia	Africa	South America	New Zealand	North	South	
1. Sampling Events										
Total	53.5%	25.4%	10.1%	5.3%	4.0%	1.3%	0.4%	86.0%	14.0%	
Ballast Water	51.3%	27.5%	9.8%	4.7%	4.7%	1.5%	0.5%	85.0%	15.0%	85.5%
Sediment	56.4%	20.0%	10.9%	12.7%	–	–	–	87.3%	12.7%	23.7%
2. Sampling Effort										
Total	60.8%	13.9%	5.6%	10.4%	3.7%	4.9%	0.7%	82.8%	17.2%	
Ballast Water	56.2%	16.5%	6.0%	9.3%	4.8%	6.3%	0.9%	82.0%	18.0%	77.3%
Sediment	58.2%	8.5%	2.8%	30.5%	–	–	–	69.5%	30.5%	32.7%
3. Unique Locations	47.9%	12.9%	10.3%	11.3%	5.2%	10.8%	1.6%	75.3%	24.7%	

For the sampling effort, publications where specific sampling location was not provided are not included.



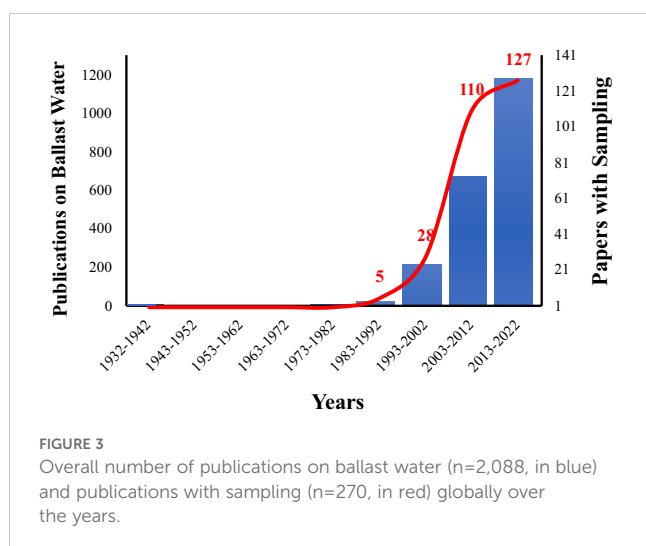
Africa had relatively few sampling events, with 0.4%, 1.3%, and 4% of the studies respectively, and also exhibited lower sampling efforts at 0.7%, 4.9%, and 3.7% respectively. For instance, South America had 21 sites sampled, each with only one sampling event, representing 1.3% of the total (Table 1). Moreover, no sampling events were reported for sediment sample analyses in these three regions.

3.2 Temporal and geographical patterns

Approximately 56% of all 2,088 publications on BW detected in our literature search were published in the last decade (2013-2022), totaling 1,179 studies. However, only 127 of these studies included sampling, averaging fewer than 13 publications per year that analyzed BW/sediment samples across 27 countries in the last 10 years; notably, the United States, Canada, and China contributed to 56.7% of these publications.

BW studies have been consistently published at an increasing rate since the late 1980s (Figure 3), with a notable increase in 2017 following new BW management specifications, resulting in 739 studies from 2017 to 2022. Additionally, there has been a rising trend since 2003 in studies that report BW/sediment sampling, with the last decade seeing the highest number of these studies, accounting for 47% of all BW/sediment sample analyses.

Most of the sampling effort to study BW was concentrated in North America (Table 1), not only due to the higher number of sampling locations and events but also because of sampling frequency (Figure 4). This aligns with our initial finding that the United States leads in overall BW publications (n=570; Figure 1). Overall, the United States had the highest number of sampling events (30.7%), with 59 unique locations across 72 publications, and BW sampling conducted at all these locations. Canada followed with 21.9% of the sampling events across 33 locations and 50 publications. However, the sampling effort was higher in Canada (35%) compared to the United States (25.5%), as the same locations in Canada were sampled multiple times (Figure 4).



Although Australia ranks fifth in the total number of BW publications (n=117; Figure 1), it is the third most sampled region in terms of identified sites and sampling frequency, with 22 sites across 12 publications. Notably, during the first half of the review period (1988-2007), Australia was highly represented in sampling sediment from ballast tanks, conducting sediment analysis in 21 out of the 22 locations, making it also the country with the second highest sediment sampling effort (sediment sampling effort: Canada=42.5%, Australia= 30.5%, US=15.6%) (Table 1; Figure 4B).

China had only eight identified sampling sites. However, due to frequent sampling at these locations across different publications and the collection of both BW and sediment samples, it ranks as the fourth best-sampled country (Figure 4), despite being home to the busiest ports in the world.

Germany ranks fourth in the number of BW-related studies published (n=148; Figure 1). However, many of these publications analyzed samples not necessarily collected in Germany; often, the samples were from in-transit samplings, or the publications focused on experiments, regulatory data evaluation, or recommendations. Despite this, the number of sampling sites and events in this region has helped to highlight Europe as a significant area for BW studies (Table 1).

Other countries, such as Brazil, had only two publications analyzing BW samples and none analyzing sediments, despite having a total of 83 publications on the topic (Figure 1), which primarily consisted of reviews and discussions.

3.3 Target groups

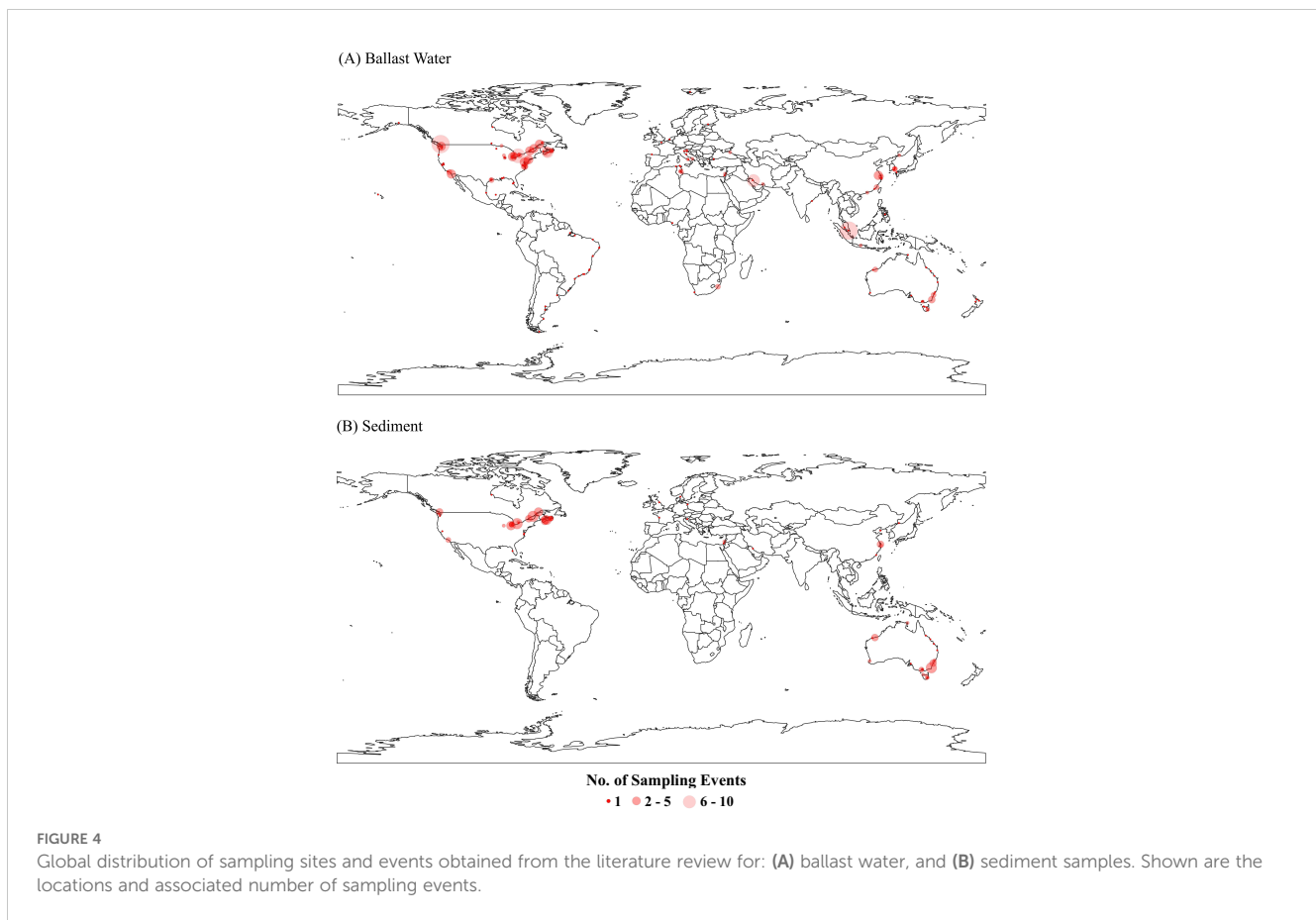
The same publication can focus on more than one group, and the majority of the total sampling events and the highest sampling effort were in North America (55.5% and 63%, respectively) (Table 2).

Across all regions, most studies focused on phytoplankton (29%), followed by microorganisms (25.7%) and zooplankton (24.6%) (Figure 5; Table 2). However, the sampling effort for phytoplankton was up to two times greater than for the other groups (41.7%, Table 2).

Phytoplankton was exclusively examined in 57 studies (21.1%). Microorganisms, including viruses and primarily bacteria, were exclusively analyzed in 58 publications (21.5%). Non-autotrophic protists were studied in 12 publications (4.4%), with only 5 exclusively focusing on this group (1.8%). Zooplankton was the sole focus of 48 studies (17.8%). Benthic specimens were included in 12 publications (4.4%), with 5 exclusively focusing on this group (1.8%).

Regarding publications that looked through whole samples without focusing on specific groups (Figure 5F), 46.7% had samples collected in North America (Table 2): 33.3% of these studies in the US, followed by Canada with 13.3%. Studies not focused on the biological content of BW/sediment (Figure 5G) were more frequent in Asia (40.9%; with Iran representing 66.7% of the studies in this region), followed by North America (36.4%), with Canada representing 62.5% of these publications in North America.

Overall, the trend throughout this study was consistent, with North America having the highest number of sampling events for 5



out of the 7 categories analyzed. The number of sampling events for microorganisms was very similar in both North America and Asia though (41.4% and 42.8%, respectively). However, Asia had the highest number of ballast analyses that did not focus on biological content (40.9%; Table 2).

4 Discussion

BW is considered a major vector for species introduction for several key reasons, including the extent, frequency, and magnitude of biotic transfers across the globe. Ships move goods and hitchhiking species across an extensive, world-wide network that connects >300 major ports and countless regional subnetworks (Miller et al., 2011; UNCTAD, 2017; Sardain et al., 2019). A global commercial fleet of > 100,000 commercial vessels of 100 gross tons and above (UNCTAD, 2023) is in nearly constant motion, carrying billions of tonnes of BW annually (David et al., 2015, 2016) and providing frequent species transfers and invasion opportunities in space and time. Moreover, a single ship can carry >100,000 metric tons of BW (Smithsonian Environmental Research Center and United States Coast Guard, 2024), transferring literally millions to billions of organisms - in the absence of BW management - in a single discharge event (National Research Council, 2011; Carney et al., 2017; Darling and Frederick, 2018; Desai et al., 2018; Lohan et al., 2020).

While the role of BW in invasion dynamics is recognized broadly, and has been a focus of increasing research and policies since the 1980s, there are still major gaps in knowledge about biotic transfers, especially for particular geographic regions, taxonomic groups, and habitat types. Of the 2,088 studies evaluated in our review, 270 publications (12.9%) involved *in situ* analysis of actual BW/sediment samples. When we partitioned this by geography, it is evident that the global south has very limited representation. Furthermore, although we did not evaluate distribution of studies by latitude, it is also evident that the data is primarily from temperate versus tropical latitudes (Figure 4).

The geographic variation in *in situ* publications and sampling effort is even more apparent and amplified when focused on particular taxonomic groups. For several geographic regions we detected no *in situ* data among the publications evaluated in our literature review.

Regarding the habitats analyzed, while many benthic organisms can be displaced from shallow areas or be captured as larvae during ballast operation (Gollasch et al., 2019; Sardain et al., 2019), the distribution of this work also shows a strong disparity among global regions, with no studies focused on *in situ* sampling of benthic communities in ballast tanks for the entire southern hemisphere, and only 23.7% of the studies analyzed sediment from ballast tanks. Yet, sediment transported by merchant ships can harbor a diverse assemblage of organisms as adults, larvae, cysts, and eggs (Gollasch, 2002; Gollasch et al., 2019). Therefore, it represents a unique

TABLE 2 Distribution of sampling events and effort by region and groups studied.

	Region							Hemisphere		Total
	North America	Asia	Europe	Australia	Africa	South America	New Zealand	North	South	
1. Sampling Events										
Plankton										
A. Microorganisms	41.4%	42.8%	8.6%	–	4.3%	2.9%	–	80.0%	20.0%	25.7%
B. Non-Autotrophic Protists	70.0%	20.0%	10.0%	–	–	–	–	100.0%	–	3.7%
C. Phytoplankton	53.2%	16.5%	13.9%	10.1%	6.3%	–	–	88.6%	11.4%	29.0%
D. Zooplankton	74.6%	7.5%	10.4%	4.5%	3.0%	–	–	95.5%	4.5%	24.6%
E. Broad	46.7%	13.3%	26.7%	6.7%	–	6.7%	–	80.0%	20.0%	5.5%
Benthic	88.9%	–	11.1%	–	–	–	–	100.0%	–	3.3%
N.A.	36.4%	40.9%	9.1%	4.5%	4.5%	–	4.5%	90.9%	9.1%	8.1%
Total	55.5%	22.4%	11.8%	4.8%	4.1%	1.1%	0.4%	88.6%	11.4%	
2. Sampling Effort										
Plankton										
A. Microorganisms	43.3%	28.9%	8.2%	–	3.1%	16.5%	–	81.4%	18.6%	19.2%
B. Non-Autotrophic Protists	73.3%	20.0%	6.7%	–	–	–	–	100.0%	–	3.0%
C. Phytoplankton	62.1%	7.1%	6.6%	18.5%	5.7%	–	–	81.0%	19.0%	41.7%
D. Zooplankton	84.2%	2.5%	7.5%	0.8%	5.0%	–	–	99.2%	0.8%	23.7%
E. Broad	42.9%	9.5%	4.8%	19.0%	–	23.8%	–	57.1%	42.9%	4.1%
Benthic	95.5%	–	4.5%	–	–	–	–	100.0%	–	4.3%
N.A.	20.0%	45.0%	10.0%	5.0%	5.0%	–	15.0%	70.0%	30.0%	4.0%
Total	63.0%	11.9%	7.1%	8.9%	4.4%	4.1%	0.6%	85.4%	14.6%	

For the sampling effort, publications where specific sampling location was not provided are not included.

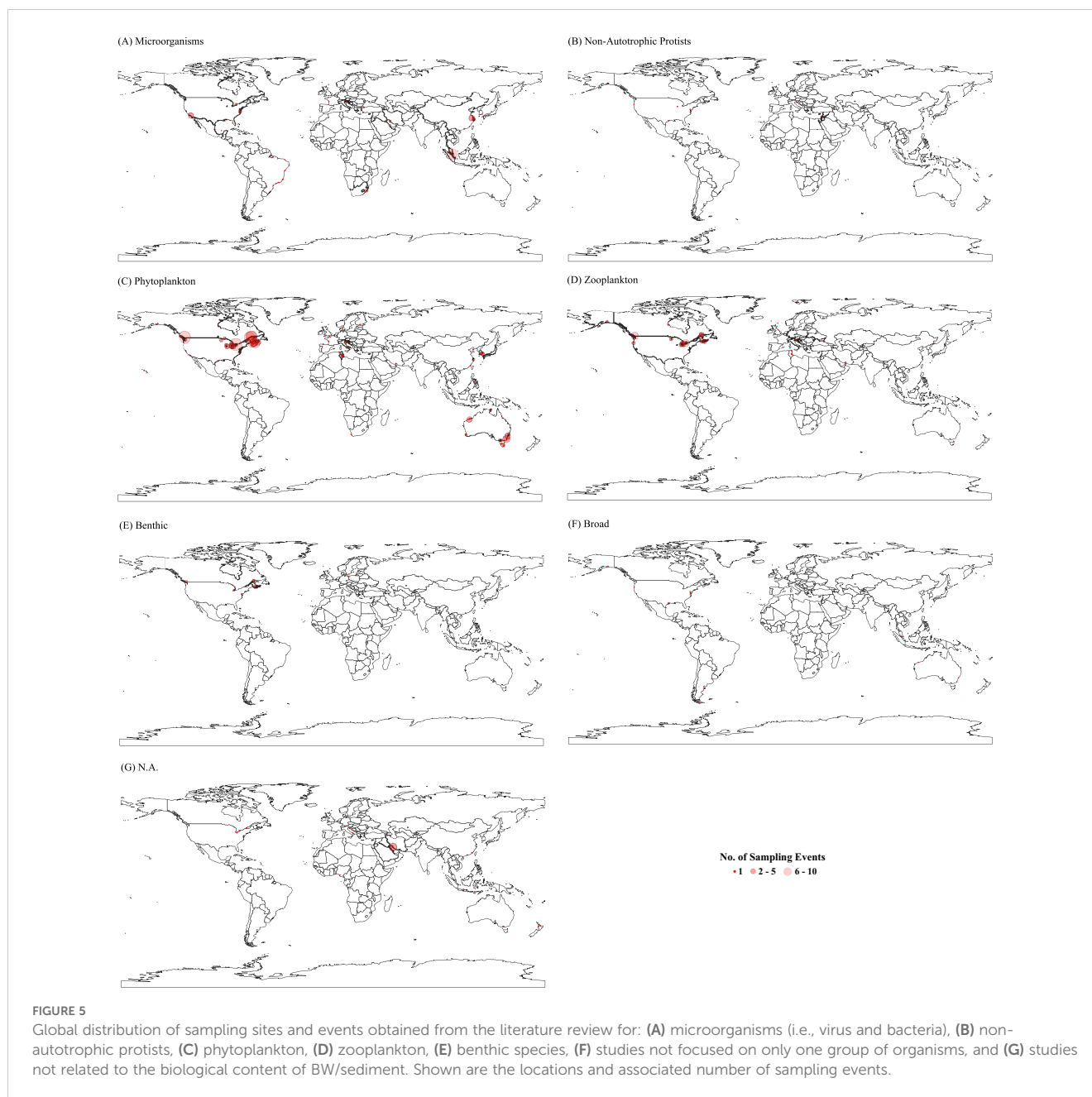
habitat, with different abiotic conditions, including infaunal and soft-sediment biota that may differ from those in BW samples (Gollasch et al., 2015). This habitat is also especially worthy of attention from a management perspective: no matter what type of treatment the BW receives, if the sediment is not properly managed, the organisms in it can contaminate the water again, as many of them can develop resistant stages and survive in tanks for long periods (Branstrator et al., 2015).

It is well known that many aquatic species have a planktonic or waterborne dispersal phase in their life cycles, which allows them to be entrained and transferred in BW (Lehtiniemi et al., 2015; Gollasch et al., 2020). Moreover, many of the known invasions are benthic species. As an example, from all non-native marine species recorded for Brazilian waters, about 77% are benthic species (Teixeira and Creed, 2020). Most marine species spend part of their life cycle within the water column, and meroplanktonic species can be transported by a greater potential number of mechanisms associated with shipping, whether related to the larval phase in BW or as adult/juvenile settled in ballast sediments or encrusted as fouling (Lopes, 2004; Lehtiniemi et al., 2015).

The limited information across geographic, taxonomic, and habitat axes for *in situ* analyses of ballast tank biota has several

significant implications. First, this likely results in gross underestimates of biodiversity associated with ships' BW (and associated sediments). Earlier work by Darling et al. (2020) demonstrated extensive sampling is needed in single ports to estimate diversity in arriving BW, and our study indicates that many regions, especially the southern hemisphere and tropics, remain largely unstudied. Importantly, we expect biodiversity transferred in ships' BW to differ in both space and time, and many regions have limited (or no) analyses available to date. Second, these knowledge gaps also represent obvious biases in the distribution of samples among regions and lead to important questions about whether these regions are representative more generally. For example, do BW analyses from the northern temperate latitudes provide sufficient insight and proxies for the southern hemisphere or tropical latitudes?. Currently, there is insufficient data or comparison across these spatial scales to answer this question.

While the phenomenon of species transport by ships' BW is clearly general to all global regions, the differences in community composition, abundance, and characteristics among regions are largely unexplored by direct *in situ* measures. Although frequently used to estimate risk of invasion by shipping, the



number of ship arrivals and ballast volume discharged are not highly informative in this regard, due to the wide variability in the density and diversity of organisms recorded from BW samples, and if used alone can yield erroneous conclusion (Minton et al., 2005; National Research Council, 2011; Bailey et al., 2011; DiBacco et al., 2012; Ruiz et al., 2013; Bailey, 2015). Ships with the greatest quantity of BW on board and most water discharged do not necessarily represent the highest propagule pressure (Verling et al., 2005; DiBacco et al., 2012). Importantly, the species composition, characteristics, densities, and viability of organisms in BW vary with source regions, transit routes, time (e.g., season and year), and BW management type (Cariton and Geller, 1993; Verling et al., 2005; Kaluza et al., 2010; Keller et al., 2011). The potential for regional differences in organism delivery becomes

especially important in implementing treatment technologies to reduce concentrations of organisms transferred in ships' BW.

BW treatment technologies being used now to meet discharge standards, such as chlorination, ultraviolet radiation, and ozonation (often in combination with filtration), are sensitive to differences in temperature and multiple water quality parameters (Bradie et al., 2023; Gollasch et al., 2024), which vary among global regions. Thus, measures of performance or compliance in one global region may not adequately predict or serve as a proxy for different regions, due to both differences in BW/sediment biota and water conditions among regions. Although these BW treatment systems are subject to type approval or initial evaluation of performance under standard conditions (Marine Environmental Protection Committee, 2001), the conditions for type approval represent a very limited range of

real-world conditions found across ports of the world. Thus, it remains critical to address current gaps in *in-situ* analyses going forward, to adequately evaluate the performance of BW management to reduce organism delivery and meet existing discharge standards. Systematic *in situ* measures across regions remain an important goal that can provide essential information, regarding the risk of invasion and advance understanding of invasion science (Darling and Frederick, 2018; Holbech and Pedersen, 2018), especially under rapidly evolving management and policy.

Author contributions

FC-A: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. GR: Investigation, Resources, Supervision, Writing – review & editing. FB: Project administration, Resources, Supervision, Visualization, Writing – review & editing.

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Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2025.1389559/full#supplementary-material>

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