Check for updates

Received: 16 September 2020 | Revised: 13 February 2021 | Accepted: 8 March 2021

DOI: 10.1111/conl.12802

Conservation Letters
A journal of the Society for Conservation Biology
Open Access
WILEY

REVIEW

Research biases create overrepresented "poster children" of marine invasion ecology

Hannah V. Watkins | **Helen F. Yan** | **Jillian C. Dunic** | **Isabelle M. Côté**

Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, Canada

Correspondence
Isabelle M. Côté, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.
Email: imcote@sfu.ca

Authors Hannah V. Watkins and Helen F. Yan contributed equally to this work.

Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: Discovery Grants Program

Abstract

Nonnative marine species are increasingly recognized as a threat to the world's oceans, yet are poorly understood relative to their terrestrial and freshwater counterparts. Here, we conducted a systematic review of 2,203 research articles on nonnative marine animals to determine whether the current literature reflects the known diversity of marine invaders, how much we know about these species, and how frequently their impacts are measured. We found that only 39% of nonnative animals listed in the World Register of Introduced Marine Species appeared in the peer-reviewed English literature. Of those, fewer than half were the subject of more than one study. There is currently little focus on the consequences of marine introductions: only 9.9% of studies quantified the impact of nonnative species. Finally, our knowledge of nonnative marine species is heavily limited by strong taxonomic biases consistent across all phyla, resulting in one or two disproportionately well-studied representatives for each phylum, which we refer to as the "poster children" of invasion. These gaps in the literature make it difficult to effectively triage the most detrimental invasive species for management and illustrate the challenges in achieving the global biodiversity goals of preventing and managing the introduction and establishment of invasive species.

KEYWORDS
biological invasions, biotic introductions, introduced marine animals, invasion ecology, systematic review, taxonomic bias

1 | INTRODUCTION

Marine species have been transported and introduced to areas beyond their native ranges in virtually all parts of the coastal ocean (Molnar et al., 2008; Rilov & Crooks, 2009). Many translocated species appear to have no impact on native communities and ecosystems (e.g., Anton et al., 2019). Some are truly benign, while for others, an apparent lack of effect is due to a lack of power at detecting these effects (Davidson & Hewitt, 2014) or delayed manifestation of impacts due to lag times in the invasion process (Crooks, 2005; Iacarella et al., 2015). However, some translocated species become readily invasive; they increase in abundance, competing effectively for resources with native species or preying on them (Blackburn et al., 2019; Molnar et al., 2008; Pyšek et al., 2020; Vitousek et al., 1996; Wallentinus & Nyberg, 2007). In some cases, these species can ultimately trigger declines in native populations, resulting in losses in ecosystem services (Blackburn et al., 2019). Nevertheless, potential benefits of some invasive species have been highlighted: they can be ecosystem engineers, increasing habitat or prey availability for native species, or replace ecological functions that would otherwise be lost following the decline or disappearance of native species (Davis et al., 2011; Katsanevakis et al., 2014; Schlaepfer et al., 2011).

Whether measurable impact should be at the core of any definition of invasiveness is an academic question that has important implications for marine conservation. Blackburn et al. (2014), for example, proposed a general framework for the prioritization of invasive species for management that relied heavily on demonstrated negative impacts. However, Ojaveer et al. (2015) argued that such a framework might underestimate the risk of nonnative marine species because the impacts of marine invaders take a long time to manifest and might be subtle in comparison to the effects of invasive species on land. Indeed, the effects of nonnative marine species are generally not well known and are taxonomically biased (Crystal-Ornelas & Lockwood, 2020; Florencio et al., 2019; Katsanevakis et al., 2014; Lowry et al., 2013; Ruiz et al., 1999; Vilà et al., 2010). For example, recent global meta-analyses of invasive marine species impacts tend to be dominated by studies of primary producers (e.g., 60% of studies in Guy-Haim et al., 2018; 41% of species in Anton et al., 2019), even though plants and algae only account for 25% of all introduced species recorded in the World Register of Introduced Marine Species (WRiMS; Ahyong et al., 2020). Perhaps for this reason, concerns have been raised about the inclusion of only one nonnative marine species (i.e., *Plotosus lineatus*) on the list of invasive alien species of concern to the European Union (Tsiamis et al., 2020), despite the well-known high risk of marine introductions into the Mediterranean Sea (Galil, 2008; Zenetos et al., 2017). Furthermore, even for the better studied primary producers, the impacts of only 10% of known nonnative seaweeds have been studied (Davidson et al., 2015; Schaffelke & Hewitt, 2007; Williams & Smith, 2007), a proportion that might apply to marine invaders in general (Anton et al., 2019). In fact, even the most basic ecological knowledge about nonnative marine species, which could hint at their invasiveness and potential impact, seems to be lacking (Braga et al., 2018; Lowry et al., 2013). A case in point is the lack of any information about reproductive behavior or ontogenetic habitat shifts by Indo-Pacific lionfish (*Pterois* sp.) in the western Atlantic, which is arguably one of the best documented recent marine invasions (Côté & Smith, 2018).

Here, we conducted a systematic review of the published English-language literature to survey what is currently known about nonnative marine animals. More specifically, we asked whether the relatively poor understanding of invasive algae is mirrored in major groups of nonnative marine animals. Using the eight most speciose marine animal phyla in WRiMS (Ahyong et al., 2020), as well as the intensively studied phylum Ctenophora, we examined the topics and locations of studies of nonnative marine animals to assess their relevance to our understanding of ecological impact. Finally, we also documented variation in study intensity across species to determine if there are marked taxonomic biases in what scientists choose to study.

2 | METHODS

2.1 | Literature search and selection criteria

Using the ISI Web of Science database, we conducted a comprehensive systematic literature review focusing on nine major phyla of marine macro-animals: Porifera, Ctenophora, Cnidaria, Bryozoa, Annelida, Mollusca, Arthropoda, Echinodermata, and Chordata (separated into Tunicata and fishes). The terminology used to describe nonnative species is inconsistent and highly varied among invasion biologists; some classify all nonnative species as "invasive," others delineate "introduced" and "invasive" based on spread or impact, and some even classify certain native species as invasive (Lockwood et al., 2013). We therefore chose to use broad search terms to capture as much of the relevant literature possible (i.e., invasive, introduced, nonnative, nonindigenous, alien, exotic). In this review, we specifically use "nonnative" to refer to any species found outside of its native geographical range as a consequence of human activity (whether direct or indirect) and "invasive" to refer to any of these species that have been shown to have significant and detrimental impacts in these nonnative habitats. We searched each taxon separately with taxon-specific search terms for "all years" ending June 2018 (see online supplement for full search strings). To ensure that using a single database was adequate, we conducted the same search for one phylum, Cnidaria, using the Aquatic Sciences and Fisheries Abstracts database. This search yielded only seven additional studies that met our inclusion criteria, or just 5% of the number obtained with Web of Science.

We first refined and excluded all obviously irrelevant articles, such as medical articles, using Web of Science Categories. We then rejected articles on the basis of the title, or the abstract when the title was insufficiently informative. Articles were rejected if they were (1) not about one of the target taxonomic groups, (2) not about a marine species (including articles on euryhaline species in freshwater), or (3) not about a nonnative species. We only accepted articles

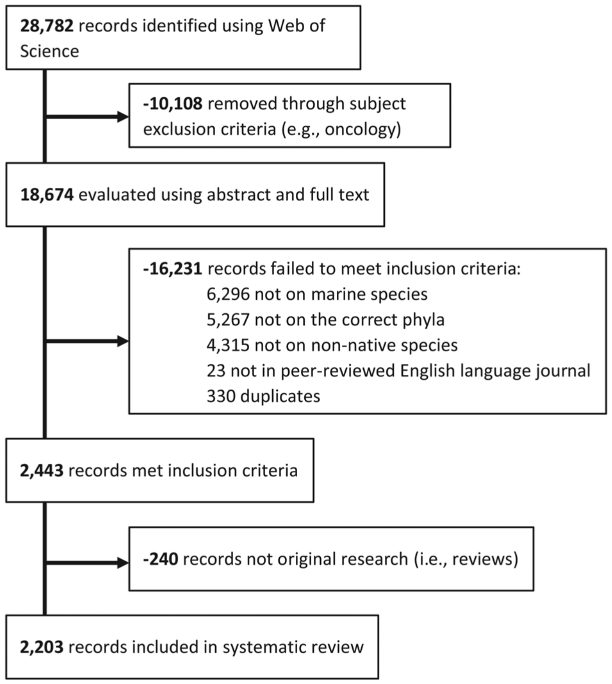

FIGURE 1 Flow chart showing the steps taken in evaluating studies for inclusion in this systematic review

when the nonnative species was studied or collected from its invaded region. Whether or not climate-driven range-shifting species should be classified as introduced or invasive is a contentious debate in invasion biology (Urban, 2020; Wallingford et al., 2020); to limit reviewer subjectivity and to include studies in which the source of introduction was unclear, we accepted all studies in which the authors described the focal species as being out of its native range. If the nonnative species was introduced for aquaculture, we only accepted articles when the species had escaped from aquaculture facilities and was studied in the wild. We noted the reason for rejection for each article (Figure 1).

2.2 | Accepted articles and impact

For all accepted articles, we recorded the topic and location of study, the nonnative species and habitat types examined, and whether the article assessed impact. We categorized articles into eight main topics: (1) taxon (the taxonomic description of a new species), (2) descriptive (descriptions of life-history traits or body morphology), (3) distribution (record in a new location, overall richness, range extensions, or confirmation of presence), (4) toxin (toxin content or uptake by invader), (5) genetics (population genetics, genome studies, identification of cryptic species, phylogeography), (6) timing (estimates of time since invasion), (7) management and methods (mitigation of impacts, methods of control or removal, or descriptive methods for detecting the invader), and (8) ecology. We further categorized ecological studies into eight subtopics (see online supplement for details). For each study, we recorded the marine province(s) in which the study took place (sensu Spalding et al., 2007) and the latitude and longitude of the study site. If there were multiple sites within a province, we selected coordinates at approximately the center of the study area. If multiple provinces were studied, we recorded one set of coordinates in each province. Finally, we recorded the habitat type(s) examined in each study, following the International Union for Conservation of Nature (IUCN) Habitats Classification Scheme (IUCN, 2020; see online supplement for full breakdown of habitat and subhabitat types).

Impact is often poorly and inconsistently defined across the biotic invasion literature (Jeschke et al., 2014). In the most basic sense of the word, all nonnative species necessarily have an impact just by being present in a new location (Ricciardi et al., 2013). More commonly though, in the context of invasions, the definition generally comprises three key, interacting factors: range, abundance, and per capita effects of the invader (Parker et al., 1999). To broadly capture all studies within our search that may be used for decision-making processes, we accepted all studies that included effects, even when estimates of range or abundance were missing. We therefore adapted the definition from Ruiz et al. (1999), and considered impacts as quantifiable changes in native populations, communities, ecological processes, or habitats. Under this definition, for instance, a trophic study analyzing the gut contents of a nonnative predator would not be considered an impact study, while a trophic study measuring changes in native prey density in the presence of the nonnative predator would. These are much broader inclusion criteria than those used in recent meta-analyses (Anton et al., 2019; Guy-Haim et al., 2018), which require specific parameters (e.g., means, sample sizes, variance) to compare effects across studies. However, since invasive species management relies on all available evidence of impact, including less rigorous studies, we believe that our more general definition is better suited to our analysis. For articles measuring impact, we also noted the study method (i.e., observational study, field experiment, or mesocosm or lab experiment).

2.3 | Global list of marine invasive animals

To determine the proportion of known nonnative marine species that have been studied, we compared our list of species derived from the literature survey with that of

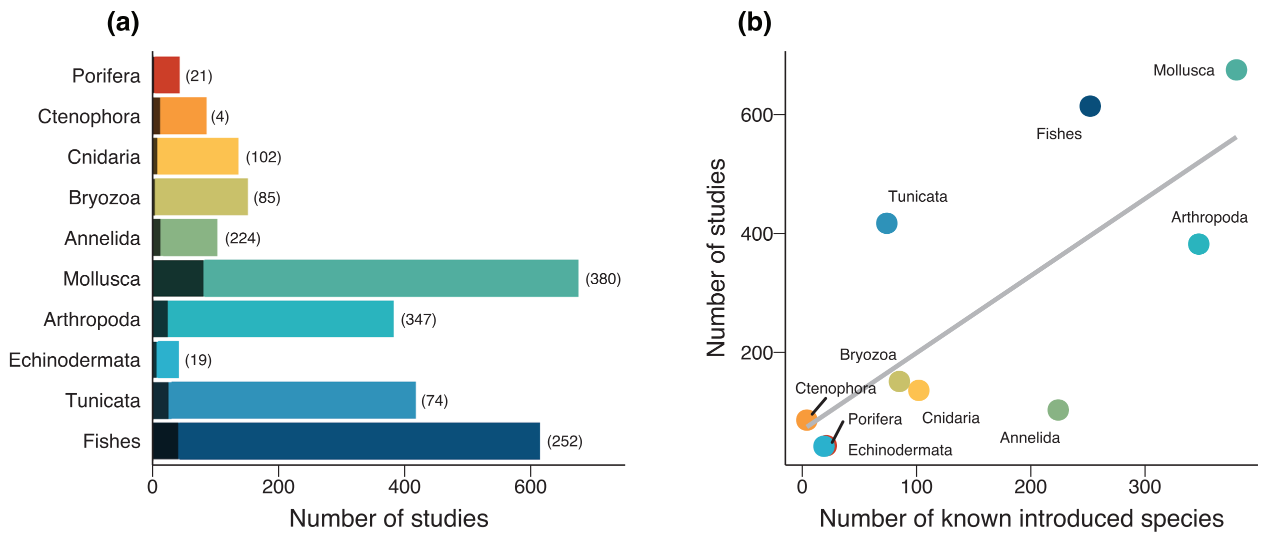

FIGURE 2 **(a)** Number of studies of nonnative marine animal species in each phylum found in this review, with the number of studies measuring impact of the introduced species shaded in black. The number of known introduced species from the World Register of Introduced Marine Species (WRiMS; Ahyong et al., 2020) in each phylum is given in parentheses. The phylum Chordata has been divided into fishes and Tunicata. Studies including more than one species within a phylum are only counted once per phylum. **(b)** Number of studies on each phylum found in this review in relation to the number of introduced species reported in WRiMS. The regression line is shown. Phyla above the line have been studied disproportionately more than expected from the phylum-specific number of species reported in WRiMS

a global database of introduced marine organisms. We obtained the total number of nonnative species from each phylum and the introduced geographical distributions of each species from the World Register of Introduced Marine Species (WRiMS; Ahyong et al., 2020). This database records the marine species from the World Register of Marine Species (WoRMS; WoRMS Editorial Board, 2020) that have been introduced by human activities to novel geographic areas outside their respective native ranges. The WRiMS list includes both accepted species names and synonyms, so we removed taxonomic duplicates to avoid overestimating the number of known introduced species. We then cross-referenced our own list of species with the appropriate accepted synonyms on WoRMS to make the lists directly comparable. Finally, we assigned the appropriate marine province code(s) (sensu Spalding et al., 2007) to each species' recorded distribution to examine any geographic biases in the dataset and their similarity to those in the published literature. Using the number of known introduced species in each province as a proxy for the expected research effort for that location, we determined areas of disproportionately high or low research effort by calculating the ratio between the number of studies found in this review and the number of species in each province as recorded in WRiMS.

Because WRiMS excludes species that colonized new locations naturally (i.e., range extensions), even if in response to human-induced climate change, we compared our species list both (1) without removing any species and (2) removing studies that focused solely on distribution as a main topic, which includes range expansions due to climate change. We chose to compare our results with the species list from WRiMS because it combines many global and regional databases of invasive species (e.g., ISSG Archives, Global Invasive Species Database, and the European Alien Species Information Network) with peer-reviewed articles (e.g., Molnar et al., 2008) to create a comprehensive, taxonomically corrected list of marine introduced species. We calculated all summary statistics and created all figures in R v.3.6.2 (R Core Team, 2019) using the ggplot2 (Wickham, 2016), ggrepel (Slowikowski, 2019), patchwork (Pedersen, 2019), fishualize (Schiettekatte et al., 2020), and PNWColors (Lawlor, 2020) packages.

3 | RESULTS

Our initial searches yielded 18,674 articles, with the highest number of articles for Chordata ($n = 11{,}815$), followed by Mollusca ($n = 2{,}860$), Arthropoda ($n = 2{,}116$), Echinodermata ($n = 509$), Porifera ($n = 313$), Annelida ($n = 301$), Bryozoa ($n = 296$), Cnidaria ($n = 293$), and Ctenophora ($n = 171$). We ultimately accepted 2,443 studies, which were unevenly distributed across all taxa. Chordates (fishes and tunicates combined) accounted for the largest proportion of studies (38%), while echinoderms accounted for less than 2% (Figure 2a). Fishes, tunicates and molluscs have been studied disproportionately more often than expected given their phylum-specific number of species reported in the global database of marine intro-

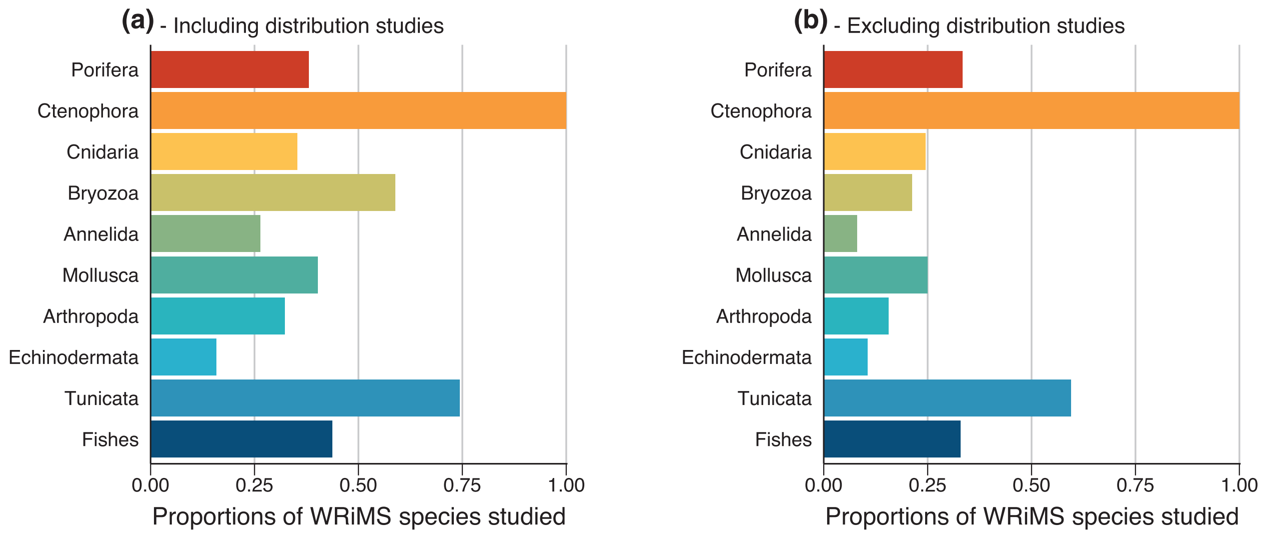

FIGURE 3 Proportions of species listed in the World Register of Introduced Marine Species (WRiMS) that were the subject of at least one study found in this literature review, (**a**) including and (**b**) excluding studies that exclusively looked at distribution

duced species (WRiMS), whereas the converse holds in particular for annelids and arthropods (Figure 2b). In total, there were 240 reviews, which we removed from further analyses as they did not present novel information pertaining to nonnative species.

3.1 | Proportions of known nonnative taxa studied

Few nonnative marine species have been studied in the peer-reviewed literature compared to the list of introduced species from WRiMS. Fishes and Mollusca were the groups with the most species studied ($n = 254$ species and $n = 203$, respectively), followed by Arthropoda ($n = 197$), Tunicata ($n = 88$), Bryozoa ($n = 77$), Annelida ($n = 68$), Cnidaria ($n = 56$), Porifera ($n = 17$), Echinodermata ($n = 6$), and Ctenophora ($n = 4$; Table S1). All Ctenophora species listed in WRiMS have been the subject of at least one study (Figure 3). For other taxa, the proportion of WRiMS-listed species that have been studied ranged from 74.3% for tunicates to 15.8% for echinoderms (Figure 3). Many nonnative species that have been studied were not in WRiMS. Fishes and Arthropoda had the largest number of species that were not listed ($n = 142$ and $n = 89$, respectively), followed by Mollusca ($n = 53$), Tunicata ($n = 36$), Bryozoa ($n = 30$), Cnidaria ($n = 22$), Annelida ($n = 16$), Porifera ($n = 9$), Echinodermata ($n = 3$), and Ctenophora ($n = 0$; Figure S1). The numbers of "missing" species are lower, particularly for fishes ($n = 74$) and Arthropoda ($n = 20$), when studies of distribution—which include records of climate-related range expansions not in WRiMS—are omitted (Figure S1).

3.2 | Biases in study topics

Across the eight topics used to categorize articles, nearly three-quarters of all articles focused on either ecology (41.0%) or distribution (35.4%). The remaining studies were divided into genetics (10.9%), descriptive (5.1%), management and methods (4.1%), taxon (1.4%), toxin (1.1%), and timing (1.1%; Figure S2). Within ecological studies, each of which may contain more than a single subtopic ($n = 1{,}054$ studies with a combined $n = 1{,}209$ subtopics), more than half were about habitat (26.2%) or trophic interactions (24.7%; Figure S3). More than half of all studies, each of which could contain more than a single habitat type ($n = 2{,}203$ studies with $n = 2{,}585$ recorded habitat types), were conducted in neritic habitats (52.3%), while artificial substrates (18.8%) and intertidal habitats (17.1%) were studied less frequently (Figures 4 and S4). Coastal/supratidal habitats only accounted for 4.1% of studies, while 7.6% of studies did not specify habitat type.

Relatively few studies assessed ecological impact (i.e., 217 out of 2,203 studies, or 9.9%). The largest proportions of studies assessing ecological impact were for echinoderms (18.4%), ctenophores (16.4%), molluscs (12.9%), and annelids (12.9%; Figure 2a). In contrast, fewer than one in every 10 studies of all other taxa documented impact; the extreme was bryozoans, which only had four out of 151 studies measuring impact (2.6%; Figure 2a). Overall, only 5.4% of the introduced species on the WRiMS database have been the subject of any studies measuring impact. Most studies (55%) assessing ecological impact were done observationally as correlational relationships in the field. The remaining studies used field experiments (30.0%) or

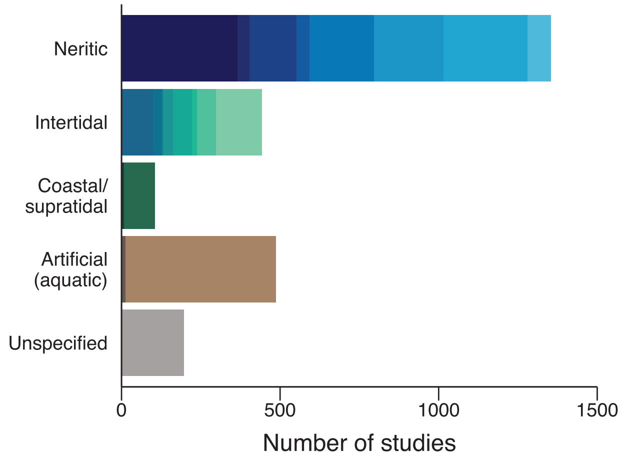

FIGURE 4 Habitat types examined in studies of nonnative marine animals, following the IUCN Habitats Classification Scheme, Version 3.1 (IUCN, 2020). Studies covering more than one habitat type are counted once for each habitat type ($n = 2,203$ studies and $n = 2,585$ cases). The variable shading within bars corresponds to subhabitat types (see online supplement for subhabitat type list)

ex situ experiments in laboratories or mesocosms (15.0%, Figure S5).

3.3 | Geographic biases

We found strong geographic biases in the locations of nonnative marine animals recorded in WRiMS (Figures 5a and S6), with substantially higher numbers recorded in Europe and North America than anywhere else in the world. We observed a similar trend in the distribution of study sites found in this review, with most European and North American regions the sites of hundreds of studies, while many other marine provinces were unstudied (Figure 5b). Despite these broad trends, there were interesting discrepancies between these two data sets. For instance, while South America and Australia host similar numbers of introduced species according to WRiMS, most South American provinces were studied more frequently than expected while most Australian provinces were studied less frequently (Figure 5c).

3.4 | Taxonomic biases

We also found strong taxonomic biases in the species studied, with 55.2% of species appearing in a single study, and only 7.7% of species appearing in 10 or more studies (Figure 6). In each of four phyla, one species was studied more than twice as often as the next most-studied species and emerged as a clear "poster child" (i.e., a disproportionately well-studied representative) of invasion for that phylum (Figure 7a). These phyla include Ctenophora, which was dominated by studies of *Mnemiopsis leidyi* (with 69 studies, accounting for 93.2% of all studies and 100% of all impact studies done on the phylum), Echinodermata (*Asterias amurensis*, 16 studies, 48.5%, 71.4%), Porifera (*Paraleucilla magna*, 16 studies, 43.2%, 0%), and fishes (*Pterois volitans/miles*, 177 studies, 37.4%, 58.5%; Figure 7a). In other phyla, research effort was more even and multiple species were studied at least half as often as the most-studied species (Figure 7b). The most extensively studied species in these taxa include the bryozoan *Watersipora subtorquata* (36 studies, 26.7%, 25.0%), the tunicate *Botrylloides violaceus* (70 studies, 20.3%, 26.9%), the cnidarian *Tubastraea coccinea* (16 studies, 15.8%, 37.5%), the annelid *Ficopomatus enigmaticus* (11 studies, 13.6%, 30.8%), the arthropod *Carcinus maenas* (38 studies, 11.4%, 24.0%), and the mollusc *Magallana gigas* (67 studies, 11.1%, 20.1%; Figure 5b).

4 | DISCUSSION

Nonnative marine species are consistently understudied relative to their freshwater and terrestrial counterparts (e.g., marine species account for only 21.7% of the studies reviewed in Crystal-Ornelas & Lockwood, 2020). Here, we found that within the limited body of research on nonnative marine animals, there are clear biases toward research on specific phyla, topics, habitats, locations, and species. Chordates (fishes and tunicates) and molluscs are studied disproportionately frequently, but fewer than one-quarter of known introduced marine species have been studied in most taxonomic groups. Only 9.9% of all studies assessed the impact of introduced animals, and less than 6% of known introduced marine animals have been the subject of any studies measuring impact. Research bias is particularly evident at the species level. More than half of studied species appear in a single study, while only 7.7% appear in 10 or more studies. Indeed, a fair amount of work has been conducted on the detrimental effects of a few nonnative marine animals—often just one species per phylum—while very little is known about the rest. The extent to which these representatives of marine invasions reflect the threats posed by less well-studied species is a concern both for the development of invasion ecology theory and for management and conservation.

There is a mismatch between the peer-reviewed literature and what is arguably the most comprehensive database of introduced marine species. Overall, we found studies for only 38.9% of species listed in WRiMS, while our review uncovered many papers on nonnative species that were not listed in this database. As both WRiMS and our own review show a strong geographic bias in

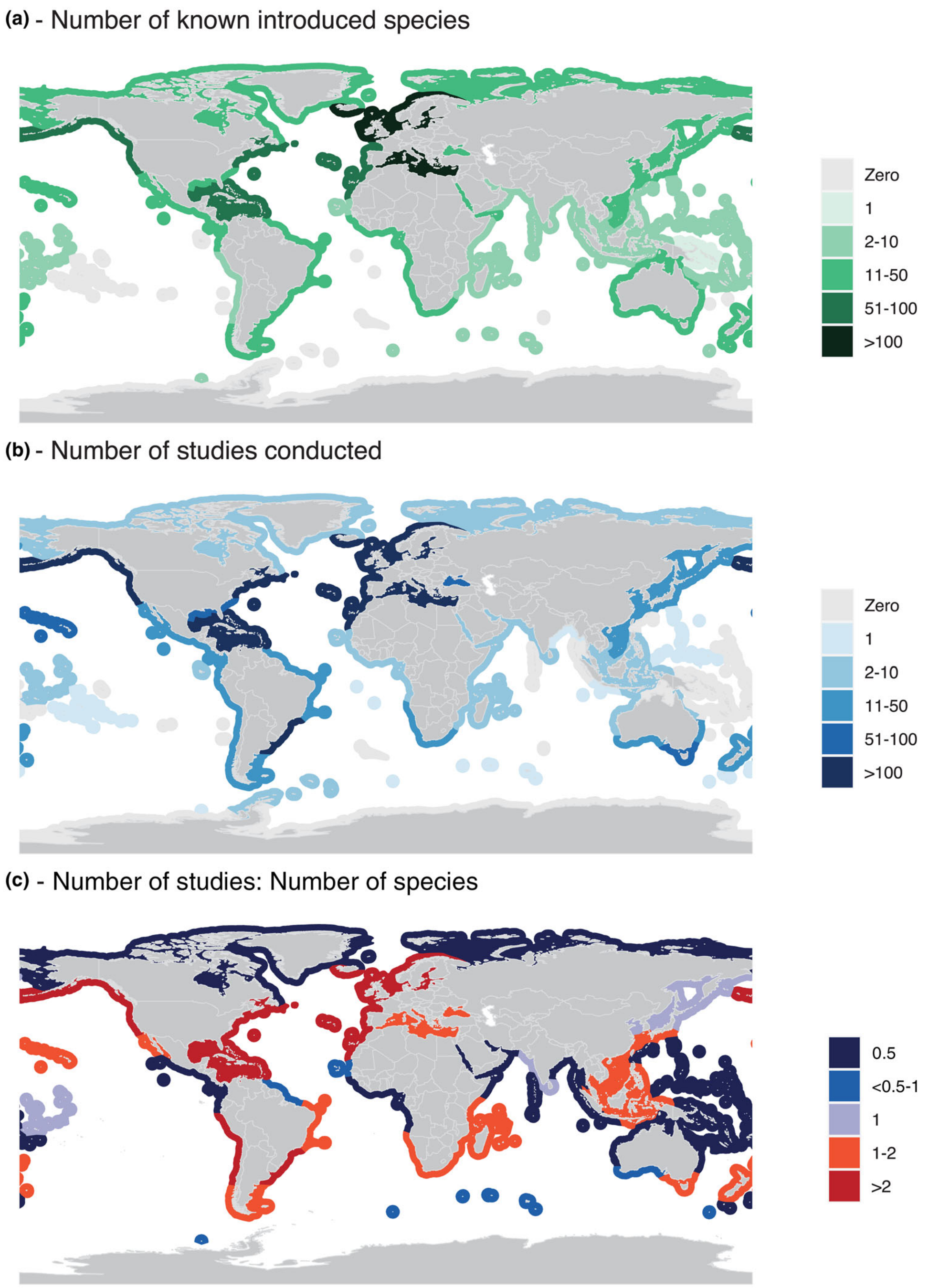

FIGURE 5 Distribution of nonnative marine animals across marine provinces (sensu Spalding et al., 2007) in terms of (**a**) number of known introduced species in the World Register of Introduced Marine Species (WRiMS; Ahyong et al., 2020), (**b**) number of studies included in this review, and (**c**) the ratio of the number of studies to the number of species. A high ratio (red shades) indicates that a province has received more research attention than expected given its number of known introduced species, while a low ratio (blue shades) indicates the opposite

studies on nonnative marine animals toward English-speaking regions (Figure 5), our decision to restrict our search to the English-language literature seems unlikely to explain this disconnect. Rather, these mismatches are more likely due in part to the lack of standardization in the language used to classify nonnative species (Blackburn et al., 2011; Lockwood et al., 2013). These problems manifested in two ways. First, inconsistencies in terminology made it difficult to develop search strings that adequately captured all published studies. It is possible that our search terms did not capture studies that did not clearly specify that a species was nonnative, which may have contributed in part to the low proportions of introduced species listed in WRiMS that were the subject of at

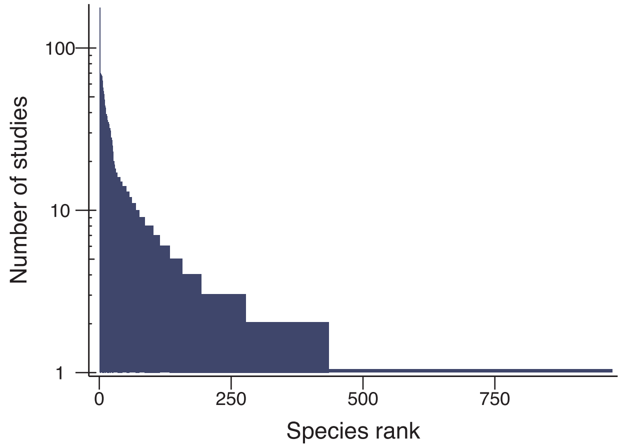

FIGURE 6 Frequency distribution of number of studies of all nonnative marine animal species included in this review. Each bar represents one species ($n = 972$) and the height of each bar represents the number of unique studies on each species. Studies including more than one species are counted once for each species ($n = 2,203$ studies and $n = 3,870$ cases). Note the *y*-axis is on a $\log_{10}$ scale

least one study (Figure 3). However, given that our initial searches yielded more than 18,000 studies, this issue is unlikely to explain the major discrepancies between our results and WRiMS. Second, WRiMS draws data from many other databases, each with their own distinct categorization of "invasive" or "introduced." For instance, the Global Invasive Species Database (GISD)—one of the databases contributing to WRiMS—considers some native species as invasive. It includes, for example, the crown-of-thorns seastar, *Acanthaster planci*, which has eruptive population dynamics and causes deleterious impacts on corals (e.g., Baird et al., 2013; Leray et al., 2012), but which has not been introduced beyond its native range. Such inconsistencies might also explain only a small fraction of the mismatch. Rather, it seems more likely that many of the species present in WRiMS, but never formally studied, have only been recorded on unpublished surveys and in the grey literature. Simply put, it seems as though scientists are unable to keep up with the ever-growing number of new species introductions (Seebens et al., 2017).

Our results also highlight the paucity of empirical evidence of impacts of nonnative marine species. Consistent with the literature on nonnative algae (Davidson et al., 2015; Schaffelke & Hewitt, 2007; Williams & Smith, 2007), the impacts of only a small proportion of known nonnative marine animals have been examined. Even with our relatively broad inclusion criteria for impact papers, which cast a wide net over studies that would be excluded from more restrictive quantitative reviews, only 9.9% of the studies (i.e., 217 out of 2,203 unique studies), covering 5.4% of known introduced animals listed in WRiMS (i.e., 81 out of 1,508 known species), quantified any measure of ecological impact. This major gap in research may explain the reliance of marine managers and policy makers on anecdotal evidence of invasive species impacts (Davidson et al., 2015; Katsanevakis et al., 2014; Parker et al., 1999), which can have major ecological and economic implications (e.g., Hager & McCoy, 1998). Furthermore, only 4.8% of the studies (i.e., 106 out of 2,203) assessed the effectiveness of any type of management strategy.

Taxonomic biases are prevalent across much of the invasion literature (e.g., Davidson et al., 2015; Florencio et al., 2019; Pyšek et al., 2008), though much this work has focused on interphyla or interguild differences. However, the most striking biases we observed were at the species level in the marine animals studied here. For instance, *Mnemiopsis leidyi* alone accounts for 93.2% of all studies and 100% of impact studies on nonnative ctenophores. Even among the more speciose nonnative fishes, the Indo-Pacific lionfish, *Pterois volitans/miles*, accounts for more than one-third of all studies and nearly two-thirds of all impact studies. Though the "poster children" of marine invasions have been studied exhaustively and have reached levels of scientific scrutiny and public awareness comparable to the most well-studied terrestrial invaders, most documented marine invaders are poorly represented, or outright missing, from the literature. The clear imbalance in research effort shown in Figure 6 mirrors the results from a recent review on terrestrial and aquatic invaders (Crystal-Ornelas & Lockwood, 2020), though the disparities between the most and least-studied species are far more extreme in marine animals than in other groups. For instance, of the species listed in WRiMS that were studied, more than half were only found in a single study.

Taxonomic bias in nonnative species research is thought to be driven by the perceived large impact of these over-represented species (Pyšek et al., 2008), in which case a disproportionate investment in research may be warranted to aid in management and minimize the negative effects of the worst offenders (Blackburn et al., 2014). However, this reasoning is circular: the few species for which impacts are already known will continue to be targeted for future research, further entrenching the divide between the current "poster children" of invasion and understudied nonnative species (Guerin et al., 2018). If the current literature reflected a greater diversity of nonnative species, then perhaps uneven allocation of research efforts could be justified. Additionally, given our narrow understanding of nonnative marine species, it is unclear whether the well-studied representatives of invasion really do have larger impacts than less-studied nonnative species. For instance, a recent meta-analysis of nonnative marine species found little to no ecological effect of the most well-studied marine

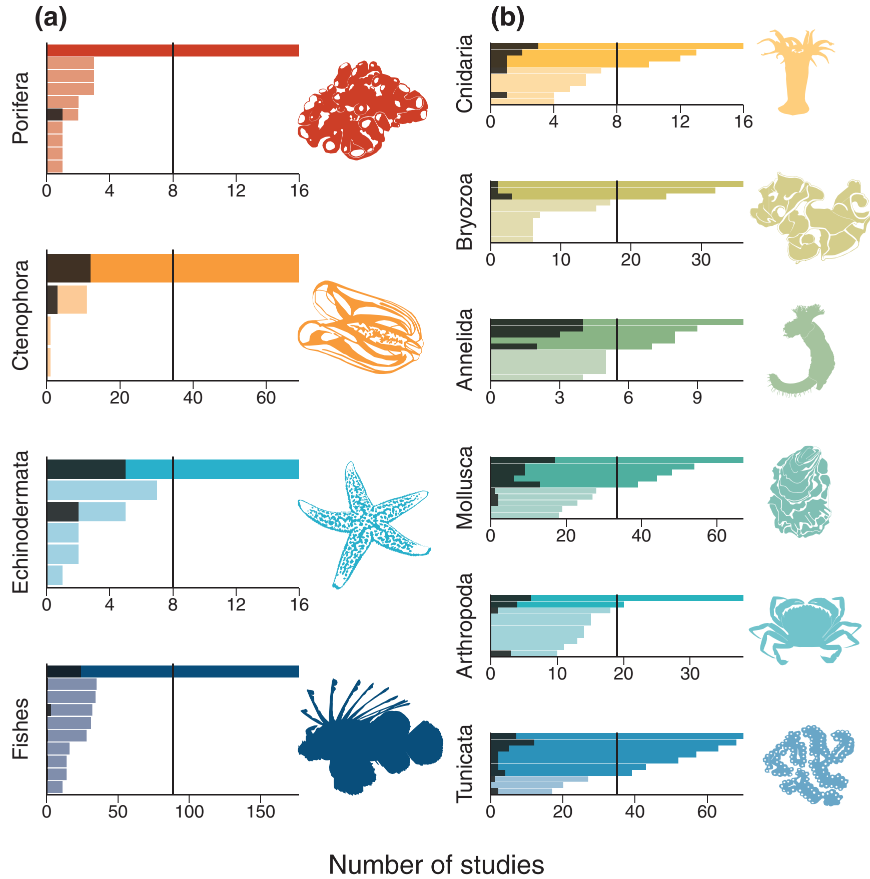

FIGURE 7 Frequency distributions of number of studies of nonnative marine animals in each phylum. Each plot shows the top 10 most-studied species in each phylum. The number of studies measuring the impact of the nonnative species are shaded in black. For phyla with fewer than 10 species studied, all species are shown. The vertical lines represent half of the number of studies on the most-studied species in each phylum. Note that the *x*-axis range is different for each phylum. **(a)** Phyla with "poster children" of invasion, that is, when the second most-studied species has been the subject of less than half as many studies as the most-studied species in the same phylum. "Poster children" are (from top to bottom): *Paraleucilla magna* (Porifera), *Mnemiopsis leidyi* (Ctenophora), *Asterias amurensis* (Echinodermata), and *Pterois volitans/miles* (Fishes). **(b)** Phyla in which several species have been studied more than half as often as the most-studied species. From top to bottom, the most-studied species are: *Tubastraea coccinea* (Cnidaria), *Watersipora subtorquata* (Bryozoa), *Ficopomatus enigmaticus* (Annelida), *Magallana gigas* (Mollusca), *Carcinus maenas* (Arthropoda), and *Botrylloides violaceus* (Tunicata). See Table **S1** for the full list of species

invaders (Anton et al., 2019), which would suggest a discrepancy between perceived and actual effects (but see Thomsen, 2020 regarding the issues with data aggregation in this meta-analysis).

Many attempts have been made to synthesize the invasion literature and develop robust, unified hypotheses and management frameworks (Blackburn et al., 2011; Catford et al., 2009), but there are risks in basing so much of our understanding on a few model organisms. Despite the fact that several hypotheses in invasion ecology have been developed and tested on only a few taxa (e.g., terrestrial plants), Pyšek et al. (2008) suggested that most groups have been studied extensively enough to derive general hypotheses that can be confidently applied across taxa. Akin to the species–area relationship, in which increasing the area of a habitat beyond a certain point results in few additional species, Pyšek et al. (2008) proposed the existence of a "species–information" relationship: once a threshold number of case studies has been reached, there is little need to study more species to improve generalizations. Based on the extreme intraphyla biases toward only a few highly studied species uncovered in this review, we suggest that the proposed information threshold may not have yet been reached for marine animals, putting into question any broad generalizations about marine invaders. Moreover, the inclusion of many studies of a few invaders with large impacts may bias the results of reviews toward overall negative impacts of nonnative species (Florencio et al., 2019), despite little to no empirical evidence of impact for most nonnative species. An exaggerated perception of effects can, in turn, misguide prioritization effort and management action (Guerin et al., 2018).

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) specifically highlighted these issues of threat prioritization and resource allocation as key focal points in their development of an assessment of invasive alien species (IPBES, 2018). With neither evidence of impact nor clear strategies for management prevalent in the literature, it will be a challenge to effectively address these concerns. Currently, marine managers must make a key decision in allocating limited resources to combatting the negative impacts of nonnative animals: they can either (1) assume that well-studied invaders are representative of all nonnative species, thus spreading resources thinly and inefficiently across many species; or (2) assume that only these "poster children" are cause for concern, leading to more targeted management efforts but leaving marine ecosystems vulnerable to the potential impacts of other species. A concerted effort from the scientific community to address this information deficit, by diverting focus from the "poster children" toward understudied nonnative species, would greatly aid managers in balancing this trade-off. A study on a poorly understood nonnative species could have greater value in helping managers to effectively triage species for management than a similar study on a species whose detrimental impacts are already known.

As the world becomes increasingly interconnected, there is a growing global concern over the early detection and mitigation of nonnative marine species. In 2010, countries signatory to the Convention on Biological Diversity of the United Nations addressed the issue of filling the knowledge gap on invasive species and highlighted the urgency for greater understanding of their impacts. Aichi Biodiversity Target 9 specifically aimed to identify invasive alien species, prioritize species for management, and effectively control or eradicate these priority species by 2020 (UNEP/CBD/COP/DEC/X/2, 2010). For marine animals, it is clear that we are far from reaching that goal; our results highlight striking gaps in even our basic understanding of the ecology of the majority of marine invaders. Only through diversifying research to a wider array of nonnative marine species can we begin to build a stronger foundation upon which this growing threat can be confidently addressed.

ACKNOWLEDGMENTS

We thank Catherine Reynolds for assistance with data cleaning. We also thank Dr. Jane Catford and two anonymous reviewers for feedback that greatly improved the manuscript. This work was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to I.M.C.

AUTHORS' CONTRIBUTIONS

IMC conceived the study. HVW and HFY conducted the literature search. HVW and JCD created summary statistics. HVW and HFY created the figures. HVW, HFY, and IMC drafted the manuscript and all authors provided feedback and approved the final version.

ETHICS STATEMENT

Ethics approval was not required for this study and no ethical restrictions apply because the data were obtained from public databases.

DATA ACCESSIBILITY STATEMENT

Data and code related to this review are available at https://github.com/hannahvwatkins/open-access-data-and-code/tree/main/poster-children-marine-invasions.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ORCID

Hannah V. Watkins https://orcid.org/0000-0002-6134-1939
Helen F. Yan https://orcid.org/0000-0002-9428-9882
Jillian C. Dunic https://orcid.org/0000-0002-0729-3083
Isabelle M. Côté https://orcid.org/0000-0001-5368-4061

REFERENCES

Ahyong, S., Costello, M. J., Galil, B. S., Gollasch, S., Hutchings, P., Katsanevakis, S., … Zhan, A. (2020). World Register of Introduced Marine Species (WRiMS). https://doi.org/10.14284/347 Retrieved from http://www.marinespecies.org/introducedon2020-07-01.

Anton, A., Geraldi, N. R., Lovelock, C. E., Apostolaki, E. T., Bennett, S., Cebrian, J., Krause-Jensen, D., Marbà, N., Martinetto, P., Pandolfi, J. M., Santana-Garcon, J., & Duarte, C. M. (2019). Global ecological impacts of marine exotic species. *Nature Ecology and Evolution*, *3*(5), 787–800. https://doi.org/10.1038/s41559-019-0851-0

Baird, A. H., Pratchett, M. S., Hoey, A. S., Herdiana, Y., Campbell, S. J. (2013). *Acanthaster planci* is a major cause of coral mortality in Indonesia. *Coral Reefs*, *32*(3), 803–812. https://doi.org/10.1007/s00338-013-1025-1

Blackburn, T. M., Bellard, C., & Ricciardi, A. (2019). Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment*, *17*(4), 203–207. https://doi.org/10.1002/fee.2020

Blackburn, T. M., Essl, F., Evans, T., Hulme, P. E., Jeschke, J. M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Wilson, J. R. U., Winter, M.… Bacher, S. (2014). A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biology*, *12*(5), e1001850. https://doi.org/10.1371/journal.pbio.1001850

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R P., Jarošík, V., Wilson, J.R.U., Richardson, D.M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, *26*(7), 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Braga, R. R., Gómez-Aparicio, L., Heger, T., Vitule, J. R. S., & Jeschke, J. M. (2018). Structuring evidence for invasional meltdown: Broad support but with biases and gaps. *Biological Invasions*, *20*(4), 923–936. https://doi.org/10.1007/s10530-017-1582-2

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*(1), 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Côté, I. M., & Smith, N. S. (2018). The lionfish *Pterois* sp. invasion: Has the worst-case scenario come to pass? *Journal of Fish Biology*, *92*, 660–689. https://doi.org/10.1111/jfb.13544

Crooks, J. A. (2005). Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Écoscience*, *12*(3), 316–329. https://doi.org/10.2980/i1195-6860-12-3-316.1

Crystal-Ornelas, R., & Lockwood, J. L. (2020). The "known unknowns" of invasive species impact measurement. *Biological Invasions*, *22*(4), 1513–1525. https://doi.org/10.1007/s10530-020-02200-0

Davidson, A. D., & Hewitt, C. L. (2014). How often are invasion-induced ecological impacts missed? *Biological Invasions*, *16*(5), 1165–1173. https://doi.org/10.1007/s10530-013-0570-4

Davidson, A. D., Campbell, M. L., Hewitt, C. L., & Schaffelke, B. (2015). Assessing the impacts of nonindigenous marine macroalgae: An update of current knowledge. *Botanica Marina*, *58*(2), 55–79. https://doi.org/10.1515/bot-2014-0079

Davis, M. A., Chew, M. K., Hobbs, R. J., Lugo, A. E., Ewel, J. J., Vermeij, G. J., Brown, J. H., Rosenzweig, M. L., Gardener, M. R., Carroll, S. P., Thompson, K., Pickett, S. T. A., Stromberg, J. C., Tredici, P. D., Suding, K. N., Ehrenfeld, J. G., Philip Grime, J., Mascaro, J., & Briggs, J. C. (2011). Don't judge species on their origins. *Nature*, *474*, 153–154. https://doi.org/10.1038/474153a

Florencio, M., Lobo, J. M., Bini, L. M. (2019). Biases in global effects of exotic species on local invertebrates: A systematic review. *Biological Invasions*, *21*(10), 3043–3061. https://doi.org/10.1007/s10530-019-02062-1

Galil, B. S. (2008). Alien species in the Mediterranean Sea—Which, when, where, why? *Hydrobiologia*, *606*(1), 105–116. https://doi.org/10.1007/s10750-008-9342-z

Guerin, G. R., Martín-Forés, I., Sparrow, B., & Lowe, A. J. (2018). The biodiversity impacts of non-native species should not be extrapolated from biased single-species studies. *Biodiversity and Conservation*, *27*(3), 785–790. https://doi.org/10.1007/s10531-017-1439-0

Guy-Haim, T., Lyons, D. A., Kotta, J., Ojaveer, H., Queirós, A. M., Chatzinikolaou, E., Arvanitidis, C., Como, S., Magni, P., Blight, A. J., Orav-Kotta, H., Somerfield, P. J., Crowe, T. P., & Rilov, G. (2018). Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: A global review and meta-analysis. *Global Change Biology*, *24*(3), 906–924. https://doi.org/10.1111/gcb.14007

Hager, H. A., Mccoy, K. D. (1998). The implications of accepting untested hypotheses: A review of the effects of purple loosestrife (*Lythrum salicaria*) in North America. *Biodiversity and Conservation*, *7*(8), 1069–1079. https://doi.org/10.1023/A:1008861115557

Iacarella, J. C., Mankiewicz, P. S., & Ricciardi, A. (2015). Negative competitive effects of invasive plants change with time since invasion. *Ecosphere*, *6*(7), 1–14. https://doi.org/10.1890/ES15-00147.1

IPBES. (2018). Information on scoping for a thematic assessment of invasive alien species and their control (deliverable 3 (b) (ii)). In *Plenary of the intergovernmental science-policy platform on biodiversity and ecosystem services*. Retrieved from: https://ipbes.net/sites/default/files/ipbes-6-inf-10_en.pdf

IUCN. (2020). *Habitats classification scheme (Version 3.1)*. Retrieved from https://www.iucnredlist.org/resources/habitat-classification-scheme

Jeschke, J. M., Bacher, S., Blackburn, T. M., Dick, J. T. A., Essl, F., Evans, T., Gaertner, M., Hulme, P. E., Kühn, I., Mrugała, A., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Winter, M., & Kumschick, S. (2014). Defining the impact of non-native species. *Conservation Biology*, *28*(5), 1188–1194. https://doi.org/10.1111/cobi.12299

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M. E., Oztürk, B., Grabowski, M., Golani, D., Cardoso, A. C. (2014). Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. *Aquatic Invasions*, *9*(4), 391–423. https://doi.org/10.3391/ai.2014.9.4.01

Lawlor, J. (2020). *PNWColors: Color palettes inspired by nature in the US Pacific Northwest*. . *R package version 0.1.0*. Retrieved from https://cran.r-project.org/package=PNWColors

Leray, M., Béraud, M., Anker, A., Chancerelle, Y., & Mills, S. C. (2012). *Acanthaster planci* outbreak: Decline in coral health, coral size structure modification and consequences for obligate decapod assemblages. *Plos One*, *7*(4), 1–10. https://doi.org/10.1371/journal.pone.0035456

Lockwood, J. L., Hoopes, M. F., & Marchetti, M. P. (2013). *Invasion ecology* (2nd ed.). Oxford: Wiley-Blackwell ISBN: 978-1-444-33364-0

Lowry, E., Rollinson, E. J., Laybourn, A. J., Scott, T. E., Aiello-Lammens, M. E., Gray, S. M., Mickley, J., & Gurevitch, J. (2013). Biological invasions: A field synopsis, systematic review, and database of the literature. *Ecology and Evolution*, *3*(1), 182–196. https://doi.org/10.1002/ece3.431

Molnar, J. L., Gamboa, R. L., Revenga, C., Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, *6*(9), 485–492. https://doi.org/10.1890/070064

Ojaveer, H., Galil, B. S., Campbell, M. L., Carlton, J. T., Canning-Clode, J., Cook, E. J., Davidson, A. D., Hewitt, C. L., Jelmert, A., Marchini, A., Mckenzie, C. H., Minchin, D., Occhipinti-Ambrogi, A., Olenin, S., & Ruiz, G. (2015). Classification of non-indigenous species based on their impacts: Considerations for application in marine management. *PLoS Biology*, *13*(4), e1002130. https://doi.org/10.1371/journal.pbio.1002130

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., Williamson, M. H., Von Holle, B., Moyle, P. B., Byers, J. E., Goldwasser, L. (1999). Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, *1*(1), 3–19. https://doi.org/10.1023/A:1010034312781

Pedersen, T. L. (2019). *patchwork: The composer of plots*. . *R package version 1.0.0*. Retrieved from https://cran.r-project.org/package=patchwork

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H.…Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, *95*, 1511–1534. https://doi.org/10.1111/brv.12627

Pyšek, P., Richardson, D. M., Pergl, J., Jarošík, V., Sixtová, Z., Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, *23*(5), 237–244. https://doi.org/10.1016/j.tree.2008.02.002

R Core Team, (2019). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, *83*(3), 263–282. https://doi.org/10.1890/13-0183.1

Rilov, G., & Crooks, J. A. (2009).Eds. *Biological invasions in marine ecosystems: Ecological, management and geographic perspectives*. Berlin: Springer. ISBN: 978–973-540-79236-9

Ruiz, G. M., Fofonoff, P., Hines, A. H., & Grosholz, E. D. (1999). Non-indigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. *Limnology and Oceanography*, *44*(3 II), 950–972. https://doi.org/10.4319/lo.1999.44.3_part_2.0950

Schaffelke, B., & Hewitt, C. L. (2007). Impacts of introduced seaweeds. *Botanica Marina*, *50*, 397–417. https://doi.org/10.1515/BOT.2007.044

Schiettekatte, N. M. D., Brandl, S. J., & Casey, J. M. (2020). *fishualize: Color palettes based on fish species. . R package version 0.2.0*. Retrieved from https://cran.r-project.org/package=fishualize

Schlaepfer, M. A., Sax, D. F., & Olden, J. D. (2011). The potential conservation value of non-native species. *Conservation Biology*, *25*(3), 428–437. https://doi.org/10.1111/j.1523-1739.2010.01646.x

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H.,… Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 1–9. https://doi.org/10.1038/ncomms14435

Slowikowski, K. (2019). *ggrepel: Automatically position non-overlapping text labels with "ggplot2." R package version 0.8.1*. Retrieved from https://cran.r-project.org/package=ggrepel

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, Al, Lourie, S. A., Martin, K. D., Mcmanus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience*, *57*(7), 573–583. https://doi.org/10.1641/B570707

Thomsen, M.S. (2020). Indiscriminate data aggregation in ecological meta-analysis underestimates impacts of invasive species. *Nature Ecology and Evolution*, *4*(3), 312–314. https://doi.org/10.1038/s41559-020-1117-6

Tsiamis, K., Azzurro, E., Bariche, M., Çinar, M. E., Crocetta, F., De Clerck, O., Galil, B., Gómez, F., Hoffman, R., Jensen, K. R., Kamburska, L., Langeneck, J., Langer, M. R., Levitt-Barmats, Ya', Lezzi, M., Marchini, A., Occhipinti-Ambrogi, A., Ojaveer, H., Piraino, S.,… Cardoso, A. C. (2020). Prioritizing marine invasive alien species in the European Union through horizon scanning. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *30*(4), 794–845. https://doi.org/10.1002/aqc.3267

UNEP/CBD/COP/DEC/X/2. (2010). *The strategic plan for biodiversity (2011-2020) and the Aichi biodiversity targets*. Retrieved from https://www.cbd.int/doc/decisions/cop-10/cop-10-dec-02-en.pdf

Urban, M. C. (2020). Climate-tracking species are not invasive. *Nature Climate Change*, *2020*, 1–3. https://doi.org/10.1038/s41558-020-0770-8

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., & Hulme, P. E. (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, *8*(3), 135–144. https://doi.org/10.1890/080083

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., & Westbrooks, R. (1996). Biological invasions as global environmental change. *American Scientist*, *84*(5), 468–478.

Wallentinus, I., & Nyberg, C. D. (2007). Introduced marine organisms as habitat modifiers. *Marine Pollution Bulletin*, *55*(7–9), 323–332. https://doi.org/10.1016/j.marpolbul.2006.11.010

Wallingford, P. D., Morelli, T. L., Allen, J. M., Beaury, E. M., Blumenthal, D. M., Bradley, B. A., Dukes, J. S., Early, R., Fusco, E. J., Goldberg, D. E., Ibáñez, I., Laginhas, B. B., Vilà, M., & Sorte, C. J. B. (2020). Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. *Nature Climate Change*, *10*(5), 398–405. https://doi.org/10.1038/s41558-020-0768-2

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Retrieved from https://ggplot2.tidyverse.org

Williams, S. L., & Smith, J. E. (2007). A global review of the distribution, taxonomy, and impacts of introduced seaweeds. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 327–359. https://doi.org/10.1146/annurev.ecolsys.38.091206.095543

WoRMS Editorial Board. (2020). World Register of Marine Species. http://www.marinespecies.orgon2020-07-01.

Zenetos, A., Çinar, M. E., Crocetta, F., Golani, D., Rosso, A., Servello, G., Shenkar, N., Turon, X., & Verlaque, M. (2017). Uncertainties and validation of alien species catalogues: The Mediterranean as an example. *Estuarine, Coastal and Shelf Science*, *191*, 171–187. https://doi.org/10.1016/j.ecss.2017.03.031

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Watkins HV, Yan HF, Dunic JC, Côté IM. Research biases create overrepresented "poster children" of marine invasion ecology. *Conservation Letters*. 2021;*14*:e12802. https://doi.org/10.1111/conl.12802