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ORIGINAL PAPER

The assessment of marine bioinvasion diversity and history

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Abstract A significant challenge in comparing and contrasting regional reviews of non-native marine species diversity is that evaluation methods vary widely, resulting in highly inconsistent taxonomic, habitat and historical coverage even in ostensibly well-studied regions. It is thus difficult to interpret whether strikingly different numbers of non-native species in different regions reflect differential invasion patterns or different assessment criteria and capabilities. We provide a comprehensive guide to the methods and techniques to assess the diversity and timing history of non-native and cryptogenic marine species. We emphasize the need to broaden taxonomic and habitat breadth when documenting invasions, to use a broader and deeper search term menu (including using older terms), to thoroughly access global systematic and invasion literature for local, regional records, and to delve deeper into invasion timing to avoid the use of dates-of-publication to assess invasion tempo and rates. Fundamental in all invasions work is the reassessment of the status of ostensibly native species which in fact may have been introduced decades or centuries earlier. We expand to 14 categories the criteria for the recognition of non-native species. Without thorough and vetted modern and historical assessments of the scale of invasions across temperate, subtropical, and tropical marine ecosystems, our ability to look deep into marine community ecology, evolution, and biogeography is strikingly compromised, as is our ability to frame robust invasion policy and management plans.

Keywords Exotic · Alien · Non-indigenous · Non-native · Cryptogenic · Inventory · Introduced · Vector · Estuarine · Maritime · Range expansions

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Introduction

Many regional reviews and assessments have appeared around the world in recent decades seeking to document the diversity of non-native marine species. A significant challenge in comparing and contrasting these studies—with a goal, for example, of identifying global bioinvasion patterns—is that the methods employed to evaluate non-native (and at times cryptogenic) species diversity vary widely, resulting in inconsistent coverage of taxonomic diversity, habitats and historical depth, even in ostensibly well-studied regions. It may thus be difficult to interpret whether strikingly different numbers of non-native marine species in different areas of the world, or within the same taxonomic groups across regions, reflect (1) differential invasion patterns or (2) different assessment criteria and capabilities.

Spatial invasion patterns of interest may center on invasion susceptibility and resistance, including whether temperate marine regions are more invaded compared to tropical regions (Hutchings et al. 2002; Freestone et al. 2013; Giachetti et al. 2020) or to high-latitude regions (de Rivera et al. 2011), whether at the same latitudes there are asymmetric invasion patterns across oceans (Torchin et al. 2021), whether invasions differ between regions influenced by maritime versus continental climates (Ruiz et al. 2000, 2015), or whether some habitats are more susceptible to invasions than others (Wasson et al. 2005; Ruiz et al. 2011, 2015). Similarly, temporal patterns of invasions may be of interest, to assess invasion rates or the effectiveness of management strategies (Byers et al. 2015; Seebens et al. 2017; Bailey et al. 2020). However, the accuracy of species' first collection or detection dates provided in such assessments is often highly variable as well, varying from coarse- to fine-grained, creating potential challenges for resolving clear patterns and making global comparisons.

Differences in the breadth, depth, and accuracy of the assessment of invasion diversity may result from a number of different factors and approaches. A number of authors have discussed the potential limitations, challenges, and errors inherent in assembling inventories of non-native species (Wasson et al. 2000; Ruiz et al. 2000; McGeoch et al. 2012; Rocha et al. 2013; Ojaveer et al. 2014a, b; Marchini et al. 2015; Marchini and Cardeccia 2017; Katsanevakis and Moustakas 2018; Albano et al. 2021). Many studies do not (1) acknowledge the diversity of understudied taxonomic groups (such as protists, flatworms, nemerteans, nematodes, sponges, hydroids, polychaetes, bryozoans, and many others) which may have not been assessed thoroughly (if at all) for the presence of non-native species. Many studies also do not (2) appear to capture the full extent of the regional historical biodiversity literature, resulting in overlooking a potentially large number of earlier records if not earlier invasions. Further, independent of historical work, by not considering the potential (3) phyletic (even if well studied) and (4) habitat breadth that might include or support non-native species, many invasions documented in more modern literature in a region may also be simply overlooked. Critically, most studies do not appear to (5) employ the reassessment techniques available to expose the diversity of non-native species that may have long been incorrectly regarded as native.

Thus, simply reviewing and summarizing databases and selected literature on previously reported invasions for a given region in order to produce a working list of non-native species may result in overlooking a substantial fraction of the non-native biota. Concomitantly, accepting at face value species reported without sufficient justification as being non-native may be problematic. More challenging may be a widespread but rarely stated assumption that online databases that provide lists of non-native species are both comprehensive and have been expertly vetted. Finally, the advent of molecular techniques as a tool by which to assess invasion diversity, in the absence of expert morphological taxonomic confirmation of the results obtained from sequencing, may lead to significantly inaccurate reports of non-native species, as discussed below.

By employing an extensive suite of research techniques that we detail here, work in the Hawaiian Islands resolved the previous recognized number of marine bioinvasions from 90 to 333 (Carlton and Eldredge 2009, 2015), in the Galápagos Islands from 5 to 53 (Carlton et al. 2019) and in Argentina/Uruguay from 29 to 129 (Schwindt et al. 2020). Nevertheless, and despite the significant expansion in recognition of the actual scale of non-native species present in these locations, these assessments remain incomplete relative to historical and cryptic invasions. The biogeographic status of many of these newly-recognized non-native species was often not discussed in the pertinent regional literature, because they were long assumed, in the absence of systematic investigation, to be native species.

Our objective is to present a comprehensive guide to the methods and techniques that we have developed and applied over the past 50 years to assess the diversity of non-native and cryptogenic marine species and to either resolve or estimate the timing of first detection of such species. Many of these approaches are also applicable to investigations in freshwater and terrestrial systems. We discuss the following topics, summarized in Fig. 1, that permit a deeper unveiling of the often remarkable, but hidden, diversity of non-native species and their potential detection dates.

Preamble I: Definitions and Terminological Considerations
Preamble II: The *Sine Qua Non* of a Robust and Reliable Taxonomic Foundation

Establishing Assessment Breadth

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- IB. *Habitat Diversity*

Searching for Invasions

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- IVA. *Colonization Substrates (Passive Sampling)*
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- IVC. *Extended Site Surveys*
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Filtering the Record

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- VA. *Species to be excluded from calculations of regional marine invasion diversity*
- VB. *Review of criteria for recognition of non-native species*
- VC. *Retention in invasion assessments of species not recently reported*
- VD. *Type localities are not default native regions*

Establishing Invasion Timing

VI. **Methods for Establishing the Timing of Invasion Records, and the Importance of Not Using Publication Dates**

- VIA. *Methods for Determining Earlier Dates of Collection or Detection*

Not treated in depth in the present essay are methods by which to determine (1) the known or probable geographic origin of a recognized invasion—that is, the presumptive native (indigenous or endemic) region, and (2) the known or probable vectors involved in transporting a species of concern to a new location.

Preamble I: definitions and terminological considerations

Community species diversity generally changes in three ways. Species populations increase and decrease, new species arrive, and species disappear. Our consideration here focuses on species arrivals—the additions—to communities over space and time. A core question in community ecology and evolution is how the addition of novel species may alter community structure and function, in terms of the abundance and distribution of resident species, predator–prey and parasite-host dynamics, competitive networks, and energy flow, among other phenomena.

Additions to marine communities may occur in two ways: species may be transported by, for example, ocean currents or birds, or be transported by human activity. In ecological and evolutionary literature, both are considered ***biological invasions.*** For example, Braun (1921), Lindroth (1957), and Simberloff (1976) described the natural processes of historical plant movements, the arrival in Iceland of certain beetle and moth species, and the experimental colonization of mangrove islands, respectively, as invasions. Chapter 2

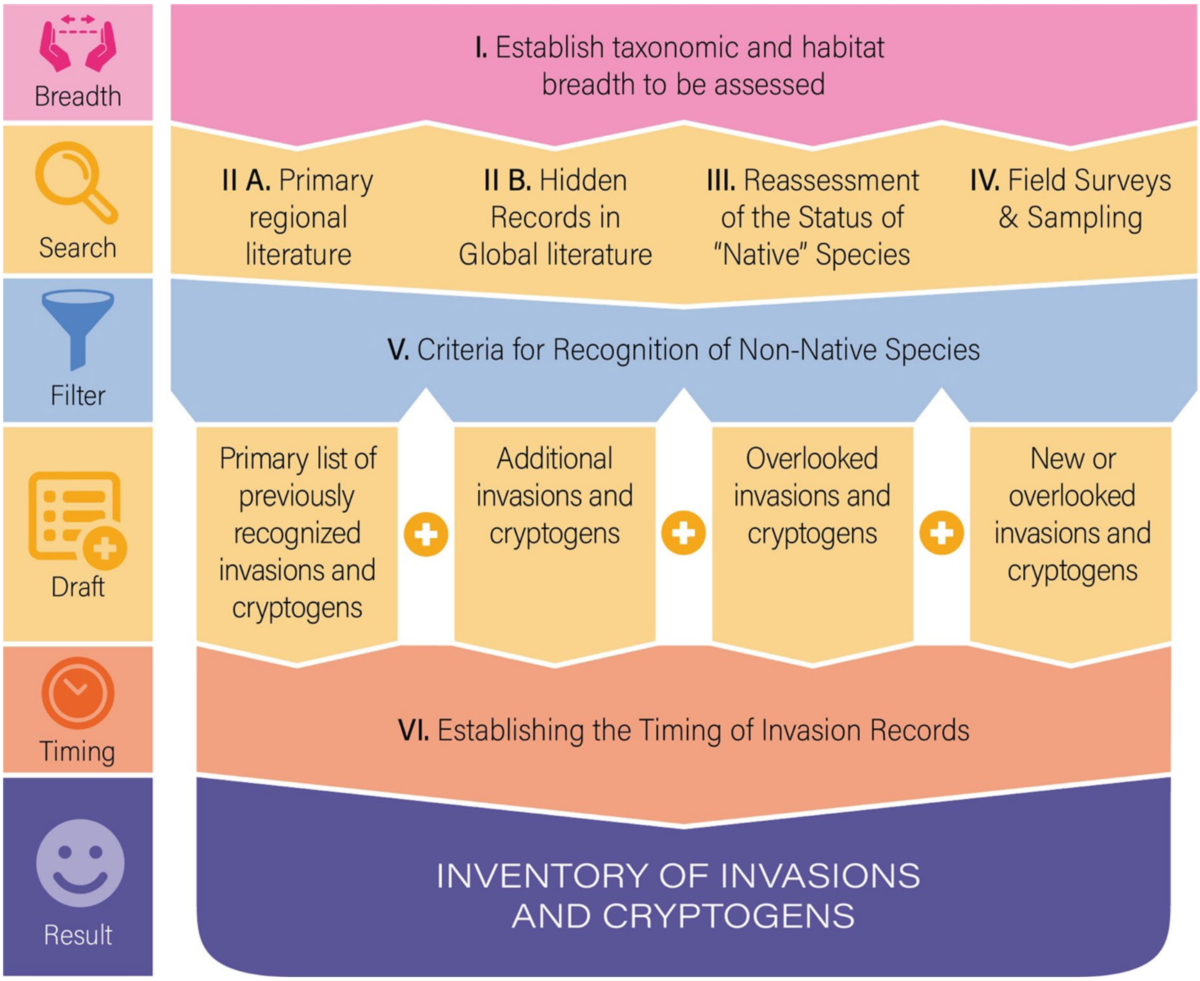

Fig. 1 Schematic workflow by which to assess the diversity and history of marine bioinvasions and cryptogens. The first step is to consider candidate species across the fullest possible taxonomic and habitat *breadth* to *search* for species from four different literature and field sources. The second step is to *filter* the resulting species inventory with the criteria for recognition of non-native species, which will produce the first *draft* of an invasions and cryptogen assessment. The third step is to perform a deeper exploration of invasion *timing*, resulting in a vetted inventory of the diversity, history, and timing of bioinvasions and cryptogens for the region under consideration

of Charles Elton's 1957 "*The Ecology of Invasions by Animals and Plants*" is devoted to examples of natural species range expansions (Elton 1957). MacArthur and Wilson (1967) described the "fundamental process" of biogeography as "dispersal, invasions, competition, adaptation, and extinction." Carlton (1987) noted that "Biological invasions in marine communities occur through two processes, range expansions and introductions." Williamson (1996) wrote that "Biological invasion happens when an organism, any sort of organism, arrives somewhere beyond its previous range," and, "Invasions have been an important component of the evolutionary process throughout geological history." Vermeij (1996) emphasized that, "By invasion I mean the geographical expansion of a species into an area not previously occupied by that species. Invasions may occur as the result of climatic and tectonic changes as well as through introduction by humans."

Historic and geological movements of species have also long been described as invasion, invading, and invader phenomenon (Linderg 1991; Vermeij 1991). The Great American Biotic Interchange (GABI)—the late Cenozoic range expansion of diverse species between North America and South America following the creation of the Isthmus of Panama—has been framed for decades as a textbook model of biological invasions (di Castri 1989; Leite et al. 2014). Knapp et al. (2021) delve into paleogenetic tools relative to "ancient biological invasions."

However, commencing in the early 2000s, the concept of "invasion" became restricted, relative to "alien flora," to "where the distribution and abundance of plants changes as a result of human activity" (Pyšek et al. 2004). In essence, the definition of biological invasions changed to a focus on the vector. This redefinition gained subscription in the years to follow (for example, Wilson et al. 2016; Blackburn et al. 2020; Robinson et al. 2020; Hulme 2021; Convention on Biological Diversity (https://www.cbd.int/invasive/WhatareIAS.shtml, accessed August 2023)).

Anchored by fundamental interests in community dynamics, and the ecological, evolutionary, economic, and other consequences of species additions, we continue here the long-standing definition that biological invasions include both human-mediated introductions and range expansions.

Biological invasions, or in shortened form, ***bioinvasions***, thus refer to the process of species arriving by any vector and establishing reproducing populations in a geographic region where they did not exist in historical time. Bioinvasions may also be defined as those species found outside of their native range, usually thus having transgressed one or more physical or climatic barriers to dispersal. However, for a great many marine species it may be challenging if not impossible to unequivocally assess accurately the true boundaries of their native, natural ranges. Anthropogenic movement of many marine species began centuries if not millennia prior to the onset of biological studies (Carlton 1999b; Ojaveer et al. 2018) and thus the assumed native range of a potentially large number of species is in reality not known. Through archeological, historical, genetic or other evidence it may be possible to delineate prehistoric ranges before human-mediated transport commenced, but in the absence of such data, the purportedly extraordinarily broad latitudinal and longitudinal (especially "pantropical") ranges of many marine species should not be assumed to be natural (Carlton 1987; Darling and Carlton 2018).

For historical biogeographers, paleoecologists (Webb; 2006; Bacon et al. 2015) and ecologists (Mooney and Drake 1986), a fundamental interest in bioinvasions is how a community may respond to the arrival of novel species, in terms of, for example, potential changes in resident species' abundance, diversity, distribution and interactions. For the public and government, including environmental managers, interest may further focus on how invasions do or will impact the quality of ecosystem services, the viability of rare and endangered native species, cultural values, the economy, and public health, as well as how to institute potential pre-invasion or post-invasion management strategies (Ruiz and Carlton 2003; Veitch et al. 2011; Wan et al. 2017; Giakoumi et al. 2019; Zengeya and Wilson 2020; Simberloff 2021).

We note that *invasion* (defined above), *invasive* (a non-native species that "spreads" or has some measure of "impact") and *invasiveness* ("The features of an alien organism, such as their life history, traits and modes of reproduction that define their capacity to invade, i.e., to overcome various barriers to invasion" (Richardson et al. 2011)) are three distinct concepts and are not synonyms.

Introduced species (synonyms and related terms are treated below in Section "IIA. Regional invasion and taxonomic literature, and the need for search term diversity") are those which have been transported by human activities into a region where they were previously absent and which have become established as evidenced by the presence of self-sustaining reproducing populations. Introductions have occurred for many reasons over millennia and result in a vast array of impacts ranging, along imperceptible gradations, from difficult to detect (in the absence of experimental or pre-invasion quantitative evidence) to significant changes in the recipient community. We note that the lack of reports of impact is not equivalent to the lack of impacts. Introductions are facilitated by a long list of anthropogenic vectors (Ruiz and Carlton 2003; Williams et al. 2013; Grosholz et al. 2015; Fowler et al. 2016; Ojaveer et al. 2018), including, now, rafting marine debris (Carlton et al. 2017; Rech et al. 2018a, b; Haram et al. 2021).

While we suggest no fixed before-after dates by which to recognize a species as transported by human activity, we note the following examples that would all be considered introduced species from both an ecological and evolutionary point of view: the introduction of dingoes into Australia by humans more than 3500 years ago (Fillios and Tacon 2016; Cairns 2021), the plants and animals introduced to Britain by Romans (AD 43–AD 410; Webb 1985; Witcher

2013) as well as the introduction by Polynesians (commencing circa AD 1000–1100; Athens et al. 2014) of plants and animals to the Hawaiian Islands. Webb (1985) succinctly captured this concept: "The frequent practice of treating long-established aliens as equivalent to natives gives rise to confusion in discussions of phytogeography or quaternary history: the former may be hard to distinguish from natives, but they are aliens none the less." Crees and Turvey (2015) provide examples of even older introductions.

In concert with this, we do not find compelling ecological or evolutionary support for distinguishing, as archaeophytes and neophytes, human-mediated introductions that occurred in Europe before and after, respectively, Columbus' first voyage in 1492 (Richardson et al. 2000; Essl et al. 2018), long after transatlantic anthropogenic introductions had commenced (Dugmore et al. 2005; Essink and Oost 2019). We note that certain regional cultural, social, economic, political, or legal—but not scientific—perspectives may regard some earlier introductions as "native".

Native (indigenous, endemic, autochthonous) species are those that have been historically present in a region, as determined by paleontological, archeological, biogeographic, molecular, and other evidence (see Crees and Turvey 2015) for a nuanced and extended discussion).

Cryptogenic species are taxa of a known identity (to varying taxonomic levels, as discussed below) whose evolutionary and biogeographic origins are poorly described or not yet known, and thus cannot yet be resolved as either non-native or native (Carlton 1996). As noted by Carlton (2009), cryptogenic species are not (1) non-native species of uncertain geographic origin, (2) cryptic invaders, or (3) introductions whose mechanism of transport is uncertain. We underscore the latter: Evans et al. (2020) inaccurately extended the definition of cryptogenic to "include species for which uncertainty exists as to whether their introduction was human-mediated or not," and thus calculated the number of "true newcomer" fish in the Mediterranean that were "cryptogenic." The term "polyvectic" (below) correctly covers this concept. Cryptogenic species are also not (4) non-native species represented by both native and introduced genes (Yund et al. 2015), (5) species whose introduction occurred long ago and were not witnessed (Zenetos et al. 2005), nor (6) species whose type locality (the location where a species was originally described) is outside of the region under study. Critically, assigning a species cryptogenic status should (7) not mean that they should be evaluated as if they were not-native (Blackburn et al. 2014) or imply that "it is guilty of being introduced until it is proven otherwise" (Campbell et al. 2018). By definition, a cryptogenic species is one that has not yet been determined to be non-native or native.

It is important to emphasize that in some cases species may be considered, based upon biogeographic or other evidence, as non-native or cryptogenic even if only resolved to family or genus level. That is, taxa that cannot be resolved to species level do not automatically default to an unassigned status. Biogeographers regularly recognize taxa, unresolved to lower taxonomic levels, as members of clearly allochthonous clades that are demonstrably not, or unlikely to be, native to a given continent or ocean (Carlton and Eldredge 2009). Cryptogenic (and introduced) species may also include undescribed taxa, as discussed below (Sections "III. Reassessment of the status of "native" species" and "VD. Type localities are not default native regions").

Unassigned taxa are insufficiently resolved taxonomically to be assigned a status of non-native, cryptogenic, or native. These taxa are also referred to as *unresolved, undetermined, indeterminate, uncategorized, unidentified* (sensu Carlton 2009) or *data deficient* (sensu Essl et al. 2018).

Range expansions typically refer (in a marine context) to the movement of species along shore, shelf, or island corridors, as well as to poleward movements in the open ocean, into regions where they were previously absent. Rare possible non-corridor exceptions exist, such as the ostensibly natural transoceanic dispersal of the cattle egret (*Bubulcus ibis*) from Africa to South America (Cele and Downs 2020). Range expansions include both the movements of recent introduced species whose post-introduction ranges expand to their natural physiological limits, and native species or older introduced species that are responding to environmental changes (such as habitat alterations or climate shifts). The phrase *range extension* is used in the literature, often without distinction, for two distinct phenomena: (1) range expansions as defined here, and (2) the discovery that a species' presumed native range is more extensive than previously known. Such discoveries may be due to increased sampling effort, to the development of new sampling techniques, or to exploration of new areas (Lonhart 2009), rather than the establishment of new populations.

Once a species has arrived and established, further range expansions may be facilitated by both natural vectors (such as currents, winds, and birds) and by anthropogenic vectors (Richardson et al. 2011, the latter thus constituting introductions as well as range expansions.). Thus, after a species is introduced to a region, both (for example) coastal currents and ships (or other human vectors) may move it to a new region within a biogeographic province or between adjacent provinces.

Similarly, many native species responding to climate change and expanding poleward may potentially do so *both* by currents and by human vectors that are transporting them to regions which were historically not amenable to colonization. Indeed, such species may have been transported for centuries to higher latitudes, only now to find warmer temperatures now suitable for reproduction. Rather than assuming that species moving poleward are doing so naturally, the relative roles of natural dispersal versus anthropogenic transport must be determined and documented if possible. If evidence suggests that both natural and human-mediated vectors may be in play relative to the movement of a species, these would be considered ***polyvectic*** species (Carlton and Ruiz 2005, who note that “polyvectism is a significant management challenge”). We emphasize that if it is not known if a range-expanding species has been moved by, for example, ocean currents or vessel hull fouling, the assignable vector is not “unknown”: possible vectors are often in fact well known, but which vector(s) is or are responsible for a given introduction event may not be resolved (Carlton and Ruiz 2005). The term *unknown vector* (***cryptovectic***) is reserved for those very rare instances where no known dispersal mechanism explains the arrival of a new colonist (Carlton and Ruiz 2005). In the absence of data, however, the default is not natural dispersal.

Regardless, a vast number of species have been, are, and will be expanding their ranges poleward in both hemispheres as a result of warming waters due to human-induced climate change. These species are thus not in the category of fundamentally “natural” expansions uninfluenced by human actions, even if transported by ocean currents or birds. While some species may be *dispersing* naturally, those responding to anthropogenic habitat and climate change are not *expanding* naturally. Species responding to climate change and moving poleward, whether by natural or anthropogenic means, are not native in the regions which they have newly colonized and where they were historically absent.

The fact that range expansions of species may not be accommodated in legal, policy, or other definitions of introduced (alien, non-native) species in regional or international protocols does not mean they should be disregarded. To omit range expansions in treatments of regional invasions discounts their potentially significant impacts (see, for example, Ling et al. 2009; Strain and Johnson 2009, 2013; Henry and Sorte 2021). Our concerns relative to potential economic, societal, or ecological repercussions relative to the arrival and establishment of historically absent species remain fundamentally the same, whether a species is from overseas, or moving naturally poleward from lower latitudes, or is a human-transported native species from an adjacent region. The fact that species invading from adjacent provinces may (but not necessarily) have deeper ecological and evolutionary relationships with resident species in the invaded region (Sorte et al. 2010) *versus* with species from distant provinces, while of no small interest, does not remove the former from the category of biological invasions.

Preamble II: the *sine qua non* of a robust and reliable taxonomic foundation

Nearly all of the analytical methods that we describe below operate at the mercy of taxonomy—that is, the presumption of a robust and reliable taxonomic foundation, whether analyzing phyletic or habitat diversity of invasions, re-assessing a species’ biogeographic history, or in biological survey data. A working assumption is typically that the identifications of species being considered and lists of species being analyzing have been expertly vetted to the extent that our current understanding permits (acknowledging that molecular genetics and finer-grained morphological work may reveal that many taxa now under the umbrella of one scientific name are in fact species complexes; Darling and Carlton 2018). Thus, establishing at the outset the quality of both past and present taxonomic work, relative specifically to identifications of non-native species, is extremely critical. This said, given that the ability of non-specialists to assess taxonomic quality assurance and quality control may be limited (or non-existent), a path of least resistance is to simply take on faith the reported species names. The fundamental assumption of presumptive taxonomic expertise may be reflected in part by the fact that some genetic databases (discussed below) do not require reporting the name of the person who identified the species in question.

The detailed means by which ecologists, geneticists, biogeographers, modelers, and others could judge the taxonomic quality of a body of work is beyond the scope of the present work. However, we note several basic steps that can be taken. In the process of attempting to determine the identity and number of non-native species in a given area, regional and local species lists (see Section "II. Searching for invasions: literature surveys") based on biodiversity or ecological surveys may be useful. Researchers should seek evidence that taxonomic experts were involved in such lists and surveys, either in the authorship or acknowledgments. If none of the authors are specialists in any of the taxonomic groups considered, and if the methods refer solely to the use of local keys or guides, if voucher specimens have not been archived in a recognized depository, and if no experts are acknowledged for the taxa considered, then acceptance of the identifications of the species, and certainly key species of interest, must proceed carefully (Bortolus 2012a, b). Researchers should pay special attention to reports of species otherwise previously known only from another ocean or another hemisphere and newly reported by non-specialists for the first time. Such reports would require verification by taxonomic experts through direct examination of specimens. Indeed, for key species of interest, re-examination and verification by experts may be of value. We discuss "verification" of species identifications by genetic analyses below.

Matches with DNA (nucleic acid)-Based Species Databases may not yield the correct identification

The availability of public databases with molecular sequences of "identified" species has often proven to be of exceptional value in potentially yielding the scientific names, based on genetic data, of unidentified specimens, especially if morphological taxonomists are not available, if the material in hand alludes morphological identification, if species complexes are involved, or in eDNA metabarcoding of whole community samples or species-specific qPCR assays (Section "IVD. eDNA metabarcoding surveys and qPCR assays"). Newly generated molecular sequences (from whatever sources) are compared with online sequences deposited by others to produce a purported identification. Non-specialists may thus assume that a 99–100% (or sometimes lower) "match" produces a "correct" identification of the material in hand, resulting in common statements in the literature such as "identification was confirmed by molecular analysis." This said, it is critical to remember that all first-time species entries in genetic databases are based on morphological identifications, identifications which may or may not have been made by expert taxonomists.

The reliability of GenBank, as an example, as a tool for verifying species identifications has generated a number of discussions (see Leray et al. 2019, 2020; Locatelli et al. 2020; Dupérré 2020; Ricciardi et al. 2021; Hayes 2021; Sigwart et al. 2021). To add sequences to GenBank does not require sequence providers to document the name of the person who identified the species, a photograph of specimens, or the institutional deposition of specimens, nor details about the collection site (GenBank Submissions Handbook https://www.ncbi.nlm.nih.gov, accessed August 2023). The iBOL alliance however requires saving the specimen from which a DNA sample was taken, a photo, and the name and contact of the person who identified the specimen. However, most sequences are uploaded to GenBank; critical baseline taxonomic and curatorial information may or may not be in a supporting publication. At least in the marine systematics community it is widely discussed, often privately, that many species in genetic databases are either known or probable misidentifications. Better of course is published evidence in the peer-reviewed literature that mistakes have been made, although only those who deposited the original sequences can then correct the identification. Fehlauer-Ale et al. (2015) stipulated the GenBank numbers for three species of marine bryozoans that were incorrectly identified in that database, and provided the correct identifications. As of August 2023, none of these identifications had been changed in GenBank. Sigwart et al. (2021) noted that more than 6%, or 62 of 942 sequences deposited in GenBank for species of the oyster genus *Magallana* "represent identification errors," while Fort et al. (2021) found that up to one-third of all deposited sequences in GenBank of foliose species of the green alga *Ulva* were misidentified. Gauff et al. (2023) note that for species in the bryozoan genus *Watersipora,* there are "pervasive erroneous identifications in GenBank, which in turn perpetuate further errors in recent studies."

The extent to which the use of GenBank can influence identifications is reflected in an increasing number of papers that report improbable or impossible records of species, based solely on "confirmation" to matched sequences. Thus, molecular genetic "identification" alone, absent expert morphological confirmation, of remarkably disjunct species occurrences, may result in the mis-identification and thus mis-reporting of species. As an example, the Asian barnacle *Megabalanus rosa* was reported, based on a molecular match in GenBank, as established in the rocky intertidal of southern California, but in fact was the native California barnacle *Megabalanus californicus* (Hagerty et al. 2018, and Corrigendum; Hagerty et al. 2019). Ardura et al. (2021) have listed many cold-water species as invasions from French Polynesia, based solely on genetically-based identifications, which we comment on further below.

We are aware of the challenges of verifying genetic matches with expert identifications based on morphology. The dearth—or complete unavailability—of taxonomists for many marine taxa in many regions is well-known. For those taxonomists who are available, the queue to obtain an expert opinion may be very long. In many areas of the world there are no scholarly taxonomic guides to the marine fauna or flora in general, nor to many specific taxonomic groups. However, none of these situations mean that genetic-only identifications should automatically be considered valid, especially when they produce eyebrow-raising names of species previously known only from another ocean or another continent, or with serious climatic mis-matches, unaccompanied by a museum-deposited specimens or even a photograph. Erroneous identifications may have further consequences relative to the understanding of ecological interactions as well as in management decisions (Bortolus 2008).

With these preambles considered, we outline here suggested "best practices" approaches that would permit more thorough and accurate assessments of bioinvasion diversity.

I. Establishing target taxonomic and habitat breadth to be assessed

IA. Phyletic diversity

An attempt should be made to capture the broadest possible range of marine and maritime taxa in reviews of bioinvasion diversity. We review below the historical and taxonomic impediments that may make it challenging to do so. Examples of inventories that have attempted to include a broad range of taxa include Carlton and Eldredge (2009, 2015, Hawaiian Islands), Carlton et al. (2019, Galápagos Islands), Schwindt et al. (2020, Argentina and Uruguay), Mead et al. (2011a, b, South Africa), Katsanevakis et al. (2020, Mediterranean Sea), Galil (2009, Mediterranean Sea), and Minchin et al. (2013, British Isles).

Examples of the range of taxa that could be captured in invasion inventories are shown in Table 1. Documented marine invasions include viruses, bacteria, fungi, a wide range of additional microorganisms (including foraminiferans, ciliates, dinoflagellates), algae, seagrasses and salt marsh halophytes, many invertebrate phyla, and fish, birds, and mammals (we discuss below the inclusion of introduced mammals in marine invasion inventories). Invasion inventories omit many of these groups, not necessarily because of the lack of reports of such invasions (which we discuss below), but because the authors may not have investigated whether invasions were in fact already reported in many taxa, and, as we further discuss below, because authors may lack taxonomic resources and expertise.

The desire to assess invasions across a wide range of marine taxa also quickly encounters long-term and long-discussed critical challenges in the adequate censusing of many groups of marine organisms, challenges which are often linked to the "taxonomic impediment" (Carlton and Fowler 2018; Dupérré 2020; Ricciardi et al. 2021). Carlton and Fowler (2018) listed examples of 29 phyla and classes of marine invertebrates and fish that are currently subject to global and coastal transportation by a wide range of anthropogenic vectors. Of these, they noted that a review of the past 20 years of surveys suggest that 27 of these 29 groups appear to be "globally under-reported as invasions." These under-represented groups, all marked by a serious and growing lack of taxonomic expertise world-wide, range from sponges and hydroids to flatworms, nemerteans and polychaetes, as well as to many groups of small crustaceans and bryozoans.

Thus, the breadth and depth of capturing invasion diversity varies strikingly by location, and in many cases will mirror local interest and available taxonomic expertise. Non-native marine copepods and mysids have been well explored in San Francisco Bay, California (Orsi and Walter 1991; Orsi and Ohtsuka 1999; Slaughter et al. 2016) and in the American Pacific Northwest (Cordell et al. 2007a, b, 2008) but in many regions of the world no introduced copepods or mysids are reported at all, reflecting the lack of investigation, rather than a lack of invasions.

Similarly, despite the fact that a reasonable assumption would be that many species of diatoms and dinoflagellates (among many other microbial groups) have been transported and successfully introduced by ballast water for more than 150 years, their recognition as non-native species in marine coastal systems around the world is highly variable and often absent. Wyatt and Carlton (2002) remarked that "most modern phytoplankton invasions have simply been overlooked," detailing evidence for this suggestion. Long-standing complexities of diatom and dinoflagellate taxonomy, the lack of historical data bases, the existence of dinoflagellate resting cysts that may remain undetected for long periods of time, and the boom-and-bust cycles of many phytoplankton species, among other challenges, have all served to obfuscate the detection and verification of phytoplankton invasions. Perhaps no better example is found in San Francisco Bay, California, USA, which hosts nearly 300 non-native species of algae, invertebrates, and fish (Carlton 2009). The Bay also supports 500 distinct phytoplankton taxa, with 396 identified to species level—none of which are recognized as non-native species by phytoplankton researchers, although many of the same species bear cosmopolitan names, have been found in ballast water, and are not known from ocean currents (Carlton 2009). We further note below (Section "VB. Review of criteria for recognition of non-native species") the "smalls" rule of invasion biology—the inverse correlation of body size with the ability to be recognized as non-native (Carlton 2009). Nevertheless, we encourage researchers to consider the potential for, at least, cryptogenic phytoplankton taxa in the communities in which they work.

The way forward: how to embrace phyletic diversity of invasions

To more fully clarify or investigate the phyletic diversity of invasions under consideration, researchers should,

- *Taxonomic Lacunae* Explicitly discuss the taxonomic groups that are missing from the regional treatment, in order to weigh the potential scale of invasion underestimation. Thus, if a regional marine invasion inventory considers no polychaetes or amphipods, these lacunae should be clearly flagged as a lack of knowledge of the biogeographic history of taxa in the study area (if such is the case), rather than the implication that such taxa have been investigated and no non-native species are present.
- *Earlier Non-Invasion Literature* Search regional taxonomic and natural history literature which did not appear in searches using invasion terms, particularly searches that use more "modern" words (such as invasion, invasive, or non-indigenous) for non-native species. Earlier literature may refer to non-native species as "introduced," or simply suggest that a species was historically transported by ships to the present location.
- *Tap Specialist Knowledge* Consult with both local and global taxonomic specialists to determine if they are aware either of literature that does or may contain records or suggestions of non-native species in the region in question, or of species that they themselves consider certain or likely non-native candidates, regardless of whether the biogeographic status of such species in a given region has been previously published.
- *Mining Non-Regional Literature* Search in global taxonomic, and particularly monographic, literature. As we review below (Section "II. Searching for invasions: literature surveys"), non-native species present in a given region may be reported as such in non-regional literature.

IB. Habitat diversity

Few invasion inventories explore the full range of potential habitat diversity occupied by marine and estuarine non-native and cryptogenic species (Table 2).

Non-native species have invaded virtually every marine habitat (Table 2), including the deep sea (Carlton 2002, 2003), in many habitats prominently so. We consider 22 habitats which support non-native species, grouped under Water Column, Intertidal (including Dunes and Supralittoral), Sublittoral, and Deep Sea.

Water Column, Marine and Estuarine

Coastal (neritic) waters
Oceanic neuston-pleuston (neopelagic)

Dunes, Supralittoral, and Intertidal, Marine and Estuarine

Maritime sand dunes
Supralittoral (strand zone)
Maritime wharves
Rocky intertidal (exposed coast)
Rocky intertidal (protected coasts and estuaries)
Other hard-bottom intertidal (e.g. oyster reefs, serpulid tubeworm reefs)
Soft-bottom intertidal (e.g. mudflats, sandflats, clay-peat banks, sandy beaches, mixed sediments),
Sandy beaches and surf zones (exposed coast)
Salt marshes
Rocky salt marshes
Mangroves
Coral reefs (intertidal)

Subtidal (Sublittoral)

Fouling (intertidal and subtidal)
Wood-boring (largely in harbors and ports)
Hard-bottom subtidal to shelf (including rocky, to 200 m)
Soft-bottom subtidal to shelf (mixed sediments, to 200 m)
Seagrasses
Kelp beds
Coral reefs (subtidal)

Deep Sea

Deep Sea mixed bottoms (> 200 m)

Only 3 of these 22 habitats involve human-created environments (acknowledging that all of the other habitats have sustained human modification)—maritime wharf communities, intertidal and subtidal fouling communities, and wood-boring communities, largely in harbors and ports. Bays and estuaries are typically highly invaded (Table 2), and include water column, natural hard-bottom and soft-bottom intertidal and subtidal substrates, mangroves, intertidal and subtidal fouling and wood-boring communities and seagrass (including eelgrass) communities. As many of these are studied as distinct habitats within bays and estuaries, and given that there has been a concentration of work on artificial substrates, some of these habitats may remain largely unexplored for invasions (or, if invasions are reported in such environments, as we note below, may be overlooked in invasion reviews).

Importantly, non-native species found in three of the above habitats—maritime (ocean) sand dunes, supralittoral zones, and salt marshes—may often be either overlooked or intentionally omitted in assessments of marine invasion diversity. We argue for their inclusion in assessments of marine bioinvasion diversity based upon ecological and evolutionary physiological grounds, given that species in these habitats typically require an ocean—that is, a saline—environment in order to reproduce, feed, grow and survive. For example, the European beachgrass (marram grass) *Ammophila arenaria* is a member of the non-native maritime beach dune community on the Pacific coast of North America and the North American cordgrass *Spartina alterniflora* is a prominent non-native species in salt marshes in countries around the world. Both plants require a salt-based environment to exist. Salt marshes are inundated by tidal ocean waters daily, and non-native species occurring in this habitat thus qualify as members of the marine bioinvasion community, rather than terrestrial ecosystems.

Similarly, often under-reported globally are invasions in the marine supralittoral zone, also known as the strand-line, wrack-line, drift-line, and maritime community. Terrestrial entomologists and botanists recognized as early as the 1700s that rock, shingle, sand, and shore debris ballast transported in ocean-going ships had begun the movement of coastal insects and plants around the world (Lindroth 1957; Mack 2003). Despite Roux's early (1828) mention of the probable transport of a non-native shore isopod

(*Ligia exotica*) in a ship's hold (Carlton 2011), recognition lagged behind in marine literature that a great many other littoral invertebrates were also likely dispersed for centuries in "solid" ballast. Examples of the latter include talitrid amphipods ("beach-hoppers," "marsh-hoppers" and "sand-hoppers"), halophilic oniscoid isopods, insects, and gastropods. Importantly, even well-recognized non-native maritime plants and insects are often omitted in treatments of marine bioinvasions—and may also be omitted in treatments of terrestrial invasions! Supralittoral animal and plant species are included in bioinvasion reviews for South Africa (Mead et al. 2011a, b), Argentina (Schwindt et al. 2020), the Galápagos Islands (Carlton et al. 2019), and the Hawaiian Islands (Carlton and Eldredge 2009) (Table 3), but are generally absent in marine invasion reviews.

We further argue that certain non-native species of birds and mammals, albeit not requiring the ocean for reproduction or survival, should be critically considered for inclusion in coastal invasion inventories based upon their ecological roles in marine communities. The roles of non-native birds and mammals as consumers and predators in marine environments may often be overlooked by marine invasion researchers. In fact, non-native terrestrial mammals (Carlton and Hodder 2003) and non-native birds (below) utilize and may impact coastal marine and estuarine communities. The marine invasion inventories for Chesapeake Bay (Ruiz et al. 1999) include introduced terrestrial mammals utilizing salt marshes. In contrast, the same introduced mammals invasions are omitted from the treatment of introduced aquatic and marine species in the Great Lakes and the North and Baltic Seas (De Lafontaine and Costan 2002; Reise et al. 1999; Gollasch et al. 2009). The non-native duck *Anas platyrhynchos* is included in the inventory of marine bionvasions of the Hawaiian Islands (Carlton and Eldredge 2015) because these birds feed in brackish water habitats on Oahu. Similarly, the Eurasian mute swan *Cygnus olor* is included among marine bioinvasions of New England (Williams 2007) and British Columbia (Levings et al. 2002), where it is a common consumer in coastal waters. We regard these and other species as members of marine intertidal communities, and include them in lists of marine bioinvasions, as discussed earlier.

However, resident non-native species that neither rely on a marine environment for reproduction, nor regularly act as competitors or predators in marine communities, should, in general, not be treated as members of marine or brackish ecological communities. A great many species of terrestrial plants, for example, live in a broadly-defined "sea spray" or "salt spray" zone (but not the wave splash zone), and many of these same plants are found well inland in cities, gardens, roadsides, grasslands, and farms, far from the ocean. Anton et al. (2019) included well-known terrestrial plant invaders, such as Australian pine (*Casuarina equisetifolia*), velvet grass (*Holcus lanatus*), bitou bush (*Chrysanthemoides monilifera*) and turf grass (buffalo grass, St. Augustine grass) (*Stenotaphrum secundatum*), the latter a common lawn grass, in their review of the "global ecological impacts of marine exotic species," because these plants appeared in studies that included "environments getting sea spray," and in searches with the word "coastal." While we do not doubt the abundance and potential ecological engineering roles of these and many other terrestrial species that tolerate but do not require a saline habitat, marine bioinvasion ecology would be fundamentally redefined by extending an umbrella over these species.

A broad suite of open ocean habitats have sustained invasions, include near-shore planktonic ecosystems (by diatoms and dinoflagellates, jellyfish, and fish), soft-bottom subtidal communities, kelp beds, open coast sandy beaches, coral reefs and deep sea. For the latter, Voight et al. (2012) have offered a sobering example of how scientific equipment used to study deep-sea hydrothermal vents has the ability to transport species between vent systems. Likewise there have been newly-detected invasions of the high seas by coastal species colonizing plastic marine debris (e.g., Haram et al. 2021). In particular, exposed rocky intertidal shores support (and in some areas have long supported) highly abundant invaders in regions as widespread as Europe, the Western North Atlantic, Argentina, Chile, and the Hawaiian Islands (Table 2). In contrast is an older view, as expressed by Zevina and Kuznetsova (1965), that "an open coast is not suited to the introduction of new organisms. Only closed inlets and bays, from which the larvae will not be carried into the open sea, and in which they will be able to set in close proximity to each other, are suitable."

Certain habitats that appear to support few invasions may have simply not benefitted from focused study on their invasion history, a hypothesis that, as far as we can determine, has not been tested. The absence of reports of large number of invasions from any given habitat (such as open coast sandy beaches or deeper ocean waters) should not be interpreted as a general dearth of invasions (see Preisler et al. 2009; Bumbeer and Rocha 2016), even if some habitats are less invaded than others. As we comment earlier in this essay, phytoplankton invasions may be extensively underreported globally.

Perhaps again because of the general focus on invasions in port and harbor habitats, there appear to be few global reviews of the presence and impact of non-native species in most of the habitats and communities shown in Table 2. The exceptions include Williams' (2007) review of invasions in seagrass ecosystems, a brief review of selected zooplankton invasions (Bollens et al. 2002), a brief review of animal invasions in salt marshes (Byers 2009), and a review of certain invasions in mudflats (Ruesink 2018).

The way forward: how to embrace habitat diversity of invasions

To more fully clarify or investigate the habitat diversity of invasions, researchers should,

- *Habitat Lacunae* Explicitly identify those habitats that are missing from the regional treatment, in order to weigh the potential scale of invasion underestimation. Thus, if a regional marine invasion inventory fails to consider supralittoral, salt marsh, or mud-sand habitats, these omissions should be clearly flagged as being uninvestigated, rather than the implication that such habitats have been investigated and no non-native species were found to be present.
- *Habitat-Specific Literature* Search specific regional habitat literature—such as the literature on salt marshes or soft-sediment infauna—if these habitats do not surface using (in parallel to the above phyletic considerations) search terms for non-native species.
- *Tap Specialist Knowledge* Consult with both local and global habitat specialists to determine if they are aware of either literature that does or may contain records or suggestions of non-native species in the region in question, or of species that they themselves consider certain or likely non-native candidates, regardless of whether the biogeographic status of such species in a given habitat has been previously published.

II. Searching for invasions: literature surveys

It is critical to recognize at the outset of reviewing regional invasion literature that many researchers, including systematists, biogeographers, and ecologists, still do not recognize the trichotomy of native, non-native, and cryptogenic species, despite the introduction of the cryptogenic concept more than 25 years ago (Carlton 1996). Thus, a researcher is often faced with lists of "native" or "non-native" species, a result of the general long-term default in biogeography and ecology to categorize species as native even if the evolutionary and distributional history of a given species is not known (Carlton 2009). We address this situation in Section "III. Reassessment of the status of "native" species". Linked to this is that the nineteenth century concept of natural "cosmopolitanism" of shallow-water coastal species remains alive and well in the hearts of many scientists working with many small-bodied and poorly known taxa (Darling and Carlton 2018; this, too, remains one of the greater challenges in resolving invasion diversity. We address both of these topics in further detail below as well (Section "III. Reassessment of the status of "native" species").

Here we present the multiple ways in which literature, often from many different sources, can be critically evaluated.

IIA. Regional invasion and taxonomic literature, and the need for search term diversity

Taxa reported in regional (in-country) invasion literature and databases typically yield the first working lists of non-native and cryptogenic species. If the desire is to publish an authoritative, scholarly review of regional marine invasions, all records derived from both regional and global databases should be verified by examination of primary original sources. While this can be both time-consuming and challenging (if not annoying), doing so will avoid errors passed down from one secondary source to another.

A standard approach is to use web-based search systems, such as Web of Science, SciELO, BIOSIS

Citation Index, CABI, Scopus, and ASFA. We note however, that users should be aware that these databases do not cover all languages, and thus sites such as Google Scholar may be important to find more regional non-English literature. Researchers may often unnecessarily restrict their use of search terms and search combinations. We emphasize that it is important to use a broad range of search terms, given that standardized terminology in invasion science is far from stabilized (Occhipinti-Ambrogi and Galil 2004; Falk-Petersen et al. 2006; Richardson et al. 2011). We further emphasize that ceasing one's search, after using multiple search terms and standard databases, may result in overlooking many invasions, as we detail in the sections below.

If the resources to do so are available, the following terms (not a selection of them) should be used in searches, in pertinent combinations, in order to reveal previously reported invasions in a given region. Naturally, these words should be translated into appropriate languages and any additional common regional terms should also be included.

Invasion terms adventitious, adventive, alien, allochthonous, biopollution, climate migrant, colonist, colonization, colonizing, cosmopolitan, cryptogenic, exotic, extralimital, foreign, hitchhiker, immigrant, imported, introduced, introduction, invaded, invader, invasive, migrant, naturalization, naturalized, neobiota, neocosmopolitan, neophyte, neozoa(n), non-indigenous, nonindigenous, non-native, nonnative, pseudoindigenous, stowaway, tramp, transfer, translocated, transplant, transported, waif, weed, xenodiversity

Biogeography terms cosmopolitan, cryptogenic, expand, expansion, extension, "first discovery", "first record", new, "new record", northward, novel, poleward, range expansion, range extension, southward, spread, spreading

Vector terms aquaculture, aquarium industry, ballast, biofouling, biological supply, canals, fisheries, Fouling, habitat restoration, mariculture, marine debris, marine litter, oil and gas drilling platforms, rafting, seafood, ship, vessel

Habitat terms aufwuchs, biofouling, brackish, coastal, estuarine, estuary, fouling, marine, maritime, ocean, sea; see also Table 2

IIB. Global taxonomic and invasion literature with "hidden" invasion records

McGeoch et al. (2012) noted that the significance of incomplete information searches in alien species listing is "assumed to be small where significant effort is invested in thorough searches," which presumes that the searcher knows how and where to search. In contrast, non-native species may be reported in global taxonomic and invasion literature, unbeknownst to regional researchers who may not be aware that the species in question even exists in their country. For example, Herbert (2012) noted that the European salt marsh snail *Myosotella myosotis* was a non-native species in South Africa, but that "this information, published in a taxonomic revision of western Atlantic Ellobiidae … escaped the attention of the South African marine science community"—although the record was published in 1996 and this snail had been present there since the 1880s. *Myosotella myosotis* is a global invader that was inadvertently re-named as a new species many times after its introductions around the world (Martins 1996; Carlton 2009). It has similarly been overlooked as an invasion in Peru, where it has been present since the 1830s, and in Bermuda (Martins 1996).

We provide additional examples of such hidden records in Table 4, in three categories:

(1) Taxonomic literature with hidden invasion records in which the authors indicated that the species in question is introduced elsewhere, but these records largely appear to have gone unnoticed in the regions indicated,
(2) Invasion literature with hidden invasion records for other countries or regions,
(3) Taxonomic literature with invasion records not identified as such in the cited references (but are so suggested in Table 4, as examples)

The way forward: how to address hidden invasion records

To investigate potentially "hidden" records of invasions, researchers should,

- *Search Other Regional Invasion Literature* Using the local region or country name, search invasion inventories in other regions for species that have been flagged as non-native in parts of their known range.

- *Search Regional or Global Systematics Literature* Using the local region or country name, search papers and monographs that review the taxonomy and distribution of selected marine taxa on an ocean-wide basis if not global basis, for species that have been flagged as non-native in parts of their known range. The depths to which such records may exist but can be overlooked are frustrating: for regions that we know well, such as Argentina and the Hawaiian Islands, we have no doubt that buried in the other invasion literature or taxonomic literature are records of non-native species that we have not yet discovered.
- *Tap Specialist Knowledge* As suggested above, relative to embracing taxonomic and habitat diversity, consult with experts in specific taxonomic groups that often encompass large numbers of non-native taxa. Examples include corophiid and caprellid gammarid amphipods, sphaeromatid isopods, balanoid barnacles, campanulariid hydroids, diadumenid anthozoans, spionid and serpulid polychaetes, bugulid bryozoans, and ascidians.

III. Reassessment of the status of “native” species

Many hundreds, and perhaps thousands, of species of marine protists, invertebrates, fish, algae, and maritime and marsh higher plants were transported around the world long before scientific investigations commenced (Carlton 1987, 2003, 2009; Ojaveer et al. 2018). Thus, in any given coastal marine community there may be scores or hundreds of species whose biogeographic status as native has never been questioned, a situation underlain by the “shifting baseline” assumption that species first recorded at a location, especially in the 1700s, 1800s or early 1900s, were native (Carlton 2009; Ojaveer et al. 2018). Heavily layered upon this assumption was the common (and in a surprising number of cases still enduring) usage of the same scientific name for species occurring in far-reaching locations around the world, leading to a persistent view that literally thousands of coastal species of marine animals and plants were (or are) “naturally cosmopolitan” (Darling and Carlton 2018). Carlton (2009) has reviewed in detail the consequences of these assumptions and views relative to the multi-century obfuscation of the scale of invasions. In reviewing an earlier suggestion that “nearly 1000 coastal species” may have been overlooked as invasions (Carlton 2003), Carlton (2009) suggested that, “in retrospect, the number 1000 now seems too low.”

While global invasions commenced prior to the 1500s, a great many invasion inventories report the oldest known invasions as beginning only in the mid-1800s, with rare earlier records. Despite this temporal disconnect of several centuries between the apparent onset of invasions and their first detection, there has been an overall reluctance, as noted above, in most invasion inventories to re-assess the biogeographic status of ostensibly “native” species (Table 3). As examples, of 22 study regions in four oceans (North and South Atlantic and North and South Pacific) representing 11 continental margins or island systems, only 8 studies re-assessed selected “native” species and re-assigned some of these to a non-native status (9 did the same for cryptogenic species) (Table 3). We know of no studies (including our own) that attempt a “deep dive”—a daunting task—into even a significant number of candidate taxa deserving biogeographic re-assessment relative to how many may represent earlier invasions. For the 8 study areas noted here that have benefitted from some re-examination of the native biota, re-assessment is typically limited to relatively few taxa or taxonomic groups, leaving the bulk of the “native” biota unquestioned. In turn, identification of cryptogenic species, foraged from “native” lists, are, without exception, only *examples* of cryptogens, with most of the marine biota similarly remaining biogeographically unexcavated.

Beyond the shifting baseline, several additional reasons may account for this reluctance to re-consider species’ indigenous (or even endemic) status:

(1) A general hesitancy to challenge “conventional wisdom,” as held by senior in-country zoologists or botanists, including reluctance to question the biogeographic status of “iconic” native species (see for example Bortolus et al. 2015 relative to the history of the understanding of the biogeography of the marsh grass *Spartina alterniflora* in South America).

(2) An assumption that re-constructing the origin and dispersal history of a species that may have been subject to centuries of human-mediated dispersal may be nearly impossible (a resistant belief now potentially set aside, in part, by the advent of molecular genetics that could tease apart a species' history over time and space, such as the work resolving the origin of the widespread supralittoral isopod *Ligia exotica* as being in East and Southeast Asia Hurtado et al. 2018), and work resolving the octocoral *Carijoa riisei*, formerly thought to be native to the Caribbean (from where it was first described in 1860), as native to the Indo-West Pacific (Concepcion et al. 2010)).

(3) The assumption that a species' type locality (which may be in the study area in question) is the native region (see Section "VD. Type localities are not default native regions", below).

and,

(4) What may simply appear to be the daunting knowledge required of the obscure and complex systematic and biogeographic literature of a taxon, often under older species names and in multiple languages, accompanied by a similar complex and unsynthesized literature on historical anthropogenic vectors applicable to the potential historic movement of any one species.

Yet, abundant evidence suggests that a great many non-native species may be hidden under an indigenous-endemic umbrella. As Carlton (2009) outlined, many non-native species are *pseudoindigenous*, having been, (a) mistakenly re-described as new in the introduced region (i.e., already described in their native regions), (b) first described as new (with the presumption they were native) where they were actually introduced, and then later discovered in their native regions, and (c) described as new after being introduced (as determined post-description by other researchers, by the application of criteria discussed below), but nevertheless remain unknown elsewhere.

Pseudoendemic is an unrelated term, having been introduced independently multiple times, including meaning a population largely dependent on constant immigration (Redfield and Beale 1940), a species found only in one sampled location (although known to occur in other locations), as opposed to the number of species common to two or more sampled locations (Balinsky 1967), endemic species whose range has been inadequately or unevenly sampled (Daniels et al. 1995), species "already known from other countries or not being genuinely distinct species" (Fraser-Jenkins 2008), and species "now confined to one or a few islands, but that had much larger ranges (prior to) human contact" (Steadman 2006), among other meanings.

Relative to the three pseudoindigenous categories noted above, Carlton (2009) provided 94 examples of species in category (a); in many cases, species were redescribed as new in different regions (up to 11 times for one species), for a total of 159 cases of mistaken re-description amongst these 90-some species alone. Carlton (2009) also provided examples of 21 species in pseudoindigenous category (b), and 7 species in category (c), the latter, as defined above, thus being *sui generis* designations as introductions by later work. Soledade et al. (2013) have described cases in category (a) as a "precautionary tale when describing species in a world of invaders."

Descriptions of non-native species as new species in the above categories were not recognized by authors as introduced at the time of description (Carlton 2009), a situation that continues to the present day (Soledale et al. 2013; Aguilar et al. 2022). However in a small number of cases, authors recognized that a species, albeit apparently undescribed, was not likely native (Carlton 2009, Table 2.4): as examples of species recognized at the time of their description (or mistaken redescription) as non-native, Carlton (2009) offered examples of 7 species in category (a), 5 species in category (b) and 7 species in category (c). Recognition of marine species as undescribed but introduced dates back to at least the 1870s. Cooper (1872), in describing the brackish-water snail *Alexia setifer* as a new species from San Francisco Bay (now known as *Myosotella myosotis*, the same species long-overlooked in South Africa as discussed above) noted that the Bay had been searched for mollusks "for more than twenty years," and concluded that it might not be native, speculating that it may have been brought from China on ship hulls, or "as ova in damp nets or otherwise." Authors recognizing non-native species at the time of their description have used trivial names such as *aliena, alienense, enigmatica,* and *exotica* (Carlton 2009) *nomadica* (Galil et al. 1990), *invadens* (Reise et al. 2011), *perambulata* (Louis and Menon 2009), and *ingressus* (Engin et al. 2018), among others.

An important derivative from these examples is that a number of demonstrably non-native species remain known only from where they have been introduced (Carlton 2009 Tables 2.3 and 2.4-C). Of course, some of these species may yet be found to be described elsewhere, with earlier descriptions (and thus names) not yet being matched to the satellite populations of these species. However, in many if not most cases, it appears likely that the biota in the native or presumptive native regions of these taxa (as judged by criterion 6 in Section "V. Criteria for recognition of non-native species") is simply not sufficiently known, and that these species have come to light only by being introduced to regions under greater investigation, or by the vagaries of fortuitous encounters (such as the discovery of a new species of bryozoan, *Bugula tsunamiensis*, known only (at this time) from rafting debris in the North Pacific, but for reasons detailed in McCuller et al. (2018) appears to find its origin in Honshu, Japan). The scale of pseudoindigenous diversity is unknown, but as a phenomenon it further contributes to the strong likelihood that the number of "endemic" or "indigenous" species miscategorized as such is under-estimated—and thus that the number of introductions in any one region is likely higher than estimated.

In contrast to the earlier lack of recognition of new species as potential candidates for having been introduced, an increasing number of undescribed or potentially undescribed marine invertebrate species from well-studied shallow-water areas are now recognized as being non-native at the time of discovery and description, a sign of greater awakening of an understanding of the scale of invasions. We provide examples of these in Section "VD. Type localities are not default native regions", below.

In addition, non-native species have been initially misidentified as already-described native species, with well-known cases including mistaking the Japanese seastar *Asterias amurensis* for a native seastar in Tasmania (Buttermore et al. 1994), the Western Atlantic comb jelly *Mnemiopsis leidyi* for a native ctenophore in The Netherlands (Faasse and Bayha 2006), and the Mediterranean mussel *Mytilus galloprovincialis*, mis-identified as the native mussel *Mytilus edulis* (now *Mytilus trossulus*) for many decades in southern California (Geller 1999). It is unlikely that all such cases have been recognized.

In sum, while the most common approach in creating invasion inventories is to rely on species already reported as non-native, as discussed above, in reality the historical biogeographic status of many species in a given region may not have been properly assessed, if assessed at all. Jaric et al. (2019) have categorized the underestimation of non-native species diversity as "crypticity in biological invasions," encompassing the multiple challenges of undescribed species, taxonomically difficult species complexes, pseudoindigenous species, cryptogenic species, and undetected species.

IIIA. Targeting candidate "native" species for re-evaluation of biogeographic status

Of hundreds or thousands of species in a regional biota, which taxa or taxonomic groups potentially representing overlooked invasions would bear investigation? Put another way, in which taxa should considerable time and effort be invested to tease out those species which may have been introduced long before formal scientific work began?

While we have argued (above, and Table 2) that non-native species are found in a broad range of marine habitats, the following specific groups and habitats bear early consideration. We recognize that our considerations here overlap with our admonitions to more fully explore both phyletic and habitat diversity of non-native species:

1. "Native" species that occur largely or primarily in habitats known to support well-recognized non-native species. Such species fall under one of the criteria for recognizing non-native species (Section "V. Criteria for recognition of non-native species"), that is, close association with known invaders. Thus—again noting our emphasis of the wide habitat diversity of invasions—low-hanging fruit includes re-consideration of species in local biofouling communities that have not been previously considered as possible non-native taxa.
2. Habitats and thus taxonomic groups not previously considered in a given region as supporting possible or probable invasions, such as *supralittoral maritime amphipods* and *isopods* (often omitted in considerations of marine bioinvasions) and *teredinid shipworms* and *limnoriid isopods*.
3. Taxonomic groups such as campanulariid hydroids and shipworms that have been his-

torically dismissed as "naturally cosmopolitan" because of unfounded assumptions of "natural rafting" (see Carlton 1999a; Carlton and Eldredge 2009).

(4) Symbionts, commensals, and parasites of recognized invaders. These may include host invader taxa supporting (a) species-specific symbiotic and commensal ciliates, (b) folliculinid ciliates found with limnoriid isopods ("gribbles") and other hosts, (c) commensal isopods such as *Iais* spp. found with their sphaeromatid isopod hosts, or (d) host-specific marine fungi associated with non-native maritime plants, such as mangroves.

Species that thus come under consideration as potential invaders are then analyzed through the lenses of the criteria outlined in Section "V. Criteria for recognition of non-native species".

IV. Field surveys and sampling

If no field surveys for non-native species have been conducted for more than 5 years, efforts should be made to deploy standard assessment methods (below) to determine if any new invasions have occurred. This requires access to taxonomic expertise across as many phyla as possible, which may be challenging within country. Despite the abundance and diversity of, for example, sponges, flatworms, hydroids, polychaetes, bryozoans, ascidians and other taxa in marine communities, there may be no in-country experts to identify specimens, or, as discussed earlier, available experts may not have the time to examine material. In this case, effort should be made to contact taxonomic experts in other countries who may be available.

Whether in-country or not, taxonomists are invited to be co-authors of papers resulting from the survey work (that is, rather than being simply acknowledged). Unfortunately, funds are rarely available to engage professional for-hire taxonomists or taxonomic consulting companies, and we acknowledge that those involved in those trades are rarely inclined to exchange their services for the honor of co-authoring papers. Regardless, we have commented earlier that in the absence of the availability of morphological taxonomists, genetic analyses must not be substituted *in toto* to generate identifications.

We outline here some standard survey methods, which may variously be quantitative, qualitative, or a mixture of the two. Applying more than one method will increase the detection of non-native and cryptogenic species (Schwindt et al. 2014). Campbell et al. (2007) provide an overview of selected methods.

We note the rapidly expanding and highly beneficial role of the public ("citizen scientists"), social network sites such as iNaturalist (https://www.inaturalist.org/), and the increasing availability of reporting applications in documenting the occurrence of novel invasions, the spread of older invasions, and invasion diversity in general (Pearson et al. 2019; Martínez-Laiz et al. 2020; Hermoso et al. 2021; Kaminas et al. 2022; Howard et al. 2022).

IVA. Colonization substrates (passive sampling)

Standardized plates (panels), made of a wide variety of materials, are deployed to capture the recruitment of both sessile and mobile species in different sites, in different locations within sites, different habitats and depths, and over varying lengths of time (Bumbeer and Rocha 2012; Schwindt et al. 2014; Maraffini et al. 2017; Ramalhosa et al. 2021; Loureiro et al. 2021; Leclerc et al. 2021; Chebaane et al. 2022). Substrate deployments have a rich history (Jarvis 1853; Parker 1924; Visscher 1928; Coe and Allen 1937; Miyazaki 1938; Edmondson and Ingram 1939; McDougall 1943; Edmondson 1944; Millard 1952), with these earlier studies often providing an important baseline for fouling community diversity. Holmes and Callaway (2020) experimented with a "mixed material survey" (MMS) (substrates of different materials deployed simultaneously) to assess non-native species colonization; the MMS attracted a greater proportion of non-native species compared to the deployment of standard acrylic settlement plates. Plates may be deployed in different configurations, including vertically- and horizontally-oriented panels, the latter leading to algae and/or sediment accumulation on upper surfaces but providing shading for negatively phototactic species on lower surfaces. Some deployments employ both methods (Collin et al. 2015), given that larval settlement may be influenced by (among many phenomena) physical factors such as light, gravity, and water flow. Plates may also be caged to exclude predators accompanied by uncaged (open) treatments (Freestone et al. 2013; Oricchio et al. 2016; Giachetti et al. 2020), noting that unattended biofouling on cages can alter the treatment, and that predators may recruit into (and be trapped in) cages. Once retrieved, plates may be sampled at various intensities (all taxa or selected taxa, and for morphological and/or genetic analyses). Expert taxonomists may be involved at the time of plate retrieval (for live analysis) or later.

IVB. Rapid assessment survey (RAS)

An RAS consists of typically assembling a team of taxonomic experts and support personnel to sample a series of sites and habitats along a length of coastline over a defined period of time (Pederson et al. 2021). In a marina-based RAS, for example, about 15 small boat harbors may be sampled along a distance of 400 km over a period of 7 days by a team of 15 to 20 personnel. As with all survey methods, RASs have limitations, including restricted temporal and spatial coverage, that may result in underestimating the number of non-native species present (Rohde et al. 2017). RASs have been conducted since the 1990s in a number of countries, including, for example, the following sites, with the referenced works providing extensive details of sampling and analytical methods: the United States Pacific coast (Cohen et al. 2005, and earlier surveys reviewed therein), the U.S. New England coast (Mathieson et al. 2008; Pederson et al. 2021, as well as earlier surveys reviewed therein)), England (Arenas et al. 2006), Scotland (Ashton et al. 2006; Nall et al. 2015; Collin et al. 2015), Ireland (Minchin 2007, based on a one-person survey extending over 18 months), Brazil (Marques et al. 2013) and Korea (Park et al. 2017). The first RAS known to us was conducted in June 1970 in San Francisco Bay (California) by James T. Carlton and the late Neil A. Powell.

This method is similar to bioblitzes, which are also intensive time and space limited surveys, but differ in assembling teams of observers, collectors and taxonomists at one site, who may then fan out across a relatively small region and bring specimens back to a central processing area (Ashton et al. 2020).

We note that taxon-specific (target taxa) surveys can also be conducted (Minchin 2012; Minchin et al. 2016). These conceivably could further focus on detecting species in the wild that have been documented to date only on arriving or regional vessels (for example, Meloni et al. 2020) or known to be released into local waters, such as the same species repeatedly released in a port or bay (Carlton and Geller 1993). "Watch lists" for potential invaders are common throughout much of the world, but often highlight species not actually known to be arriving on specific vectors into a given region. Concentrating on species known to have arrived (and potentially (via vessel biofouling) or likely (via ballast water) released), or known to be present on in-country vessels may be lower-hanging fruit.

IVC. Extended site surveys

Extended surveys may be conducted over time involving multiple sites (and potentially multiple habitats), either within a region (Rohde et al. 2017), or throughout country (Campbell et al. 2007). The resulting greater sampling and necessarily increased taxonomic effort would typically require greater funding resources. Examples include marine bioinvasion surveys conducted around the Australian continent (Campbell et al. 2007, with multiple sampling strategies), along the coast of Patagonia, Argentina (Schwindt et al. 2014), and around the United States (Bastida-Zavala et al. 2017, employing fouling plate deployments).

IVD. eDNA metabarcoding surveys and qPCR assays

Increasingly advanced molecular genetic techniques are permitting the early detection, and monitoring the spread of, non-native species using water, sediment and marine debris samples (Zaiko et al. 2015; Borrell et al. 2017; Holman et al. 2019; Pearman et al. 2020; Suarez-Menendez et al. 2020; Ibabe et al. 2019, 2021). eDNA or qPCR sampling may also permit species-specific detection and monitoring (for example Jerde et al. 2011; Willis et al. 2011; Gargan et al. 2022). Agersnap et al. (2022) and Miya et al. (2022) have presented models for combining citizen science or community-based collection of water samples with eDNA or qPCR monitoring. As discussed above, limitations center on correct species identifications, even with 99–100% sequence matches, given that identifications mounted on genetic bank websites may not be correct or that the nearest matches may still not represent the species sequenced. As noted above, Ardura et al. (2021) reported apparently in error a large number of North Atlantic Ocean cold-water species in tropical Pacific Islands based only on genetically-based identifications. Other limitations include only partial sampling of non-native species present using metabarcoding (Couton et al. 2022), a limitation of course with all sampling methods. Metabarcoding surveys do not completely replace visual surveys nor collections of actual specimens that would permit morphological confirmation of identifications made through DNA assays.

IVE. Invited experts: focus on specific taxonomic groups

It may prove fruitful to invite expert taxonomists to a country or a region to work on a specific taxonomic group to determine regional richness, with a focus on assessing or resolving the presence of non-native species. Rationales for funding such work include resolving the scale of native vs. non-native diversity in severely under-reported groups (Carlton and Fowler 2018), establishing a biodiversity baseline by which to detect future invasions in understudied regions (for example, the Arctic and Antarctic), as well as, critically, determining which species, if any, that have been the subject of key ecological research (such as studies on ecological engineers) may in fact not be native, despite presumptions to that effect.

V. Filtering the Records: Criteria for recognition of non-native species

The majority of non-native species yielded by standard literature searches (IIA) do not, in general, require re-assessment as to their invasion status, having been (presumably) vetted repeatedly. Exceptions are those species which are listed as introductions but fail to meet minimum criteria of residency in marine waters, are not established in the wild, and other eliminating considerations, as outlined below (Section "VA. Species to be excluded from calculations of regional marine invasion diversity"). For the re-evaluation of species thought to be native but which may be introduced, robust distinguishing criteria are required, which we review below (Section "VB. Review of criteria for recognition of non-native species"). These same criteria may be applied to newly described species whose native status is uncertain but which may fall within the realm of new species that have been recognized as non-native at the time of their description (Section "VD. Type localities are not default native regions").

VA. Species to be excluded from calculations of regional marine invasion diversity

The following categories of species should not be included in the calculations of the total number of non-native marine species in a given region. In particular, we strongly discourage (as noted below) listing species held only in mariculture (aquaculture) facilities as being resident non-natives, no more than species found solely in zoos or botanical gardens should be included. In summary, the categories discussed below are,

- Species indicated as non-native without supporting evidence
- Native species mistaken as introductions
- Species intercepted on incoming vectors, found only in aquaculture, mariculture or aquarium facilities, or demonstrably not established in the wild
- Species not found alive
- Temporary range expansions
- Failed invasions

Species indicated as non-native without supporting evidence

Not all species categorized as non-native (or cryptogenic) in the literature should be accepted at face value. Without supporting evidence, such taxa should be excluded from non-native diversity calculations pending evaluation. For example, Moro et al. (2003) assigned hundreds of species of marine plants and animals in the Canary Islands to the following categories, but none of these assignments are accompanied by supporting literature reference or other data: *Nativo Seguro, Nativo Probable, Nativo Posible, Introducido Seguro No Invasor, Introducido Seguro Invasor, Introducido Probable* (the "probable" and "possible" assignments would be considered cryptogenic in invasion literature). Similarly, Subba Rao (2005) reported more than 200 species as introduced post-1960 to Indian Seas, the majority without specific evidence as to their non-native status. While such lists are of potential value to highlight possible non-native species, the history and status of each species would require investigation.

Native species mistaken as introductions

As Carlton (2009, Sect. 2.5, "The Overestimation of Invader Diversity") noted, mis-categorizing native species as introduced is relatively rare, in part because, as discussed earlier (Section "II. Searching for invasions: literature surveys") a default in biogeography is to consider a species native. Application of the criteria detailed here (Section "V. Criteria for recognition of non-native species") may highlight such cases, but the scale of misconstruing natives as introductions is unknown.

Examples include three species previously treated as non-native in the Hawaiian literature re-assigned to native status (Carlton and Eldredge 2009): the marine snails *Bulla vernicosa* (a sporadically-blooming native species first thought to be a World War II-era introduction from Guam) and *Vitularia miliaris* (also thought to be a WWII-era introduction, but in fact a previously overlooked native species long resident in the Islands and in the Hawaiian fossil record), and the mantis shrimp *Gonodactylellus hendersoni* (now *G. demanii*) a relatively small and easily overlooked species. The copepod *Centropages maigo*, initially thought to be a ballast-water introduction in Japan, is more likely native (Ohtsuka et al. 2007).

Yund et al. (2015) resolved that the ascidian *Botryllus schlosseri*, previously often considered as introduced in the Northwest Atlantic, appears to be primarily composed of native populations. Villalobos-Guerrero and Carrera-Parra (2015) demonstrated that what was thought to be the introduced North Atlantic polychaete *Alitta succinea* in the Eastern Tropical Pacific is a regional endemic species. The bryozoan *Membranipora rustica* (Florence et al. 2007), a native species in South Africa, was formerly thought to be the non-native North Atlantic species *Membranipora membranacea,* Carlton (2009) further reviewed the curious case of the misinterpretation of the history of the native xanthid crab *Pilumnoides rubus* in South Africa.

In the above cases, a combination of biology, ecology, natural history, biogeography, genetics or higher resolution taxonomy served to resolve these cases, all at the heart of the criteria laid out in Section "VB. Review of criteria for recognition of non-native species".

Species intercepted on incoming vectors, found only in aquaculture, mariculture or aquarium facilities, or demonstrably not established in the wild

A large number of regional records of non-native species may be in hand that are not, or are not likely, based upon established wild populations. These include, (i) species arriving on, in, or with vectors, even if released into the environment (Marchini et al. 2015), although, as noted above, such species provide fodder for taxa-specific searches; (ii) species released into the environment with no evidence of establishment; (iii) species held solely in captivity; and (iv) species raised in mariculture operations but showing no evidence of wild, established reproducing populations (for example, Sherwood and Carlile 2012, relative to a red alga in Hawaii), even if occasional volunteers are found outside of aquaculture sites. Examples of the latter are the common occurrences of non-cultured non-native oysters attached to natural substates within a several kilometer halo of oyster farming operations in regions around the world.

Species not found alive

These include dead specimens that may have arrived with vectors, such as species that may have fallen off ships, or arrived with marine debris. These are of interest and should be recorded, but not listed as non-native species (Marchini et al. 2015). For example, the marsh snail *Myosotella myosotis* was incorrectly reported as non-native in Uruguay, but these records were based only on empty shells (Orensanz et al. 2002), and only years later it was found alive (Schwindt et al. 2020).

Temporary range expansions

Ephemeral expansions of species beyond their normal documented ranges and that do not result in permanently established reproducing populations should be excluded. Such expansions may be related to aperiodic phenomena such as Pacific Decadal Oscillations (PDOs), El Niño–Southern Oscillations (ENSOs) and other marine heat waves, and La Niña events (Victor et al. 2001; Montagne and Cadien 2001; Lluch-Belda et al. 2005; Lonhart 2009; Goddard et al. 2018; Sanford et al. 2019; Lonhart et al. 2019), or to cyclonic weather systems, such as hurricanes.

Failed invasions

Non-native species that failed to become established (for many reasons; see Simberloff and Gibbons 2004; Miller et al. 2007; Miller and Ruiz 2009; Zenni and Nuñez 2013; Bosso et al. 2022) should not be included in invasion diversity calculations. *Failed invasions* are defined as non-native species populations (F1 generation or more) either known to have (1) been reproducing, or (2) transiently settled in the wild from spawning adults on an arriving vector, but in either case are then documented by survey work to no longer be present. Examples of (1) include the establishment of a European sea anemone (*Sagartia* sp.) in Massachusetts from 2000 to 2010 (Wells and Harris 2014) and the presence of the Atlantic quahog (clam) *Mercenaria mercenaria* in a Southern California lagoon from the 1960s to the 1980s (Burnaford et al. 2011). Examples of (2) include the transient settlement of the mussel *Mytilus galloprovincialis* in Pearl Harbor, Hawaii, spawned from adult mussels arriving on a vessel from the State of Washington (Apte et al. 2000; Carlton and Eldredge 2009), and the transient settlement of the southern serpulid worm *Hydroides elegans* in Eel Pond, in Woods Hole, Massachusetts (Bastida-Zavala et al. 2017), spawned from adult populations arriving on a visiting vessel.

It is difficult to interpret many occasional discoveries, often bundled under a "failed invasion" category, including whether these may have represented transient reproducing populations, were collected off a visiting vessel (without mention of such), or represented recruits spawned from the biofouling on an arriving vessel. While these occurrences may be of interest in terms of prospective invasions, such records do not constitute new records for, nor additions to, the local biota, nor should they be treated as additions to the list of marine bioinvasions. Examples include the discovery of a single specimen of the Australasian barnacle *Austrominius modestus* on an experimental panel in Cape Town in 1949 (Sandison 1950, published in *Nature* in more halcyon days), admitted to the list of South African invasions in Robinson et al. (2020) and the Western Pacific ascidian *Styela plicata*, long admitted to the lists of Uruguayan biota, although based on a sole 1880s record (Traustedt 1883; Scarabino et al. 2018).

Failed invasions do not include the discovery of single or a few adult individuals of a species that likely are the result of direct release, whether accidental (such as the one-off occurrences of green crabs *Carcinus maenas* around the world, particularly in the 1800s Carlton and Cohen 2003) or intentional (such as the discovery of the Atlantic blue crabs *Callinectes sapidus* in Hawaii, Carlton and Eldredge 2009), in the absence of evidence of successful reproduction. Nevertheless, scattered one-time records of *Carcinus* around the world, including in tropical waters where they cannot live, were long included in inventories of where the green crab had invaded.

VB. Review of criteria for recognition of non-native species

Criteria for the often difficult task of distinguishing native from non-native species have been proposed and discussed by Lindroth (1957), Carlton (1979), Webb (1985), Chapman and Carlton (1994), Essl et al. (2018), Campbell et al. (2018) and others. Quell et al. (2021) have proposed a series of biological traits which may characterize some non-native marine invertebrates, but such traits do not function as criteria to distinguish native from non-native species. In Table 5 we define 14 criteria, provide caveats and critiques for each, and identify examples of non-native species fitting each criterion.

In outline these criteria are,

1. Prior absence in region of concern/interest: Absence from the historical, archeological, or recent fossil record
2. Global Biogeography: Globally disjunct distributions
3. Global Biogeography and Temporal History
4. Regional Biogeography: Highly restricted distribution
5. Regional Biogeography: History of geographic expansion
6. Allochthonous (exotic) evolutionary origin
7. Limited Natural dispersal potential for transoceanic and interoceanic colonization
8. Anthropogenic Dispersal Potential
9. Invasion Founder Effect: Reduced genetic variation

(10) Invasion Founder Effect: Reduced morphological or physiological variation
(11) Invasion Founder Effect: Reduced variation in reproductive strategies
(12) Ecology: Predatory, symbiotic, commensal, or parasitic association with non-native species
(13) Ecology: Prevalence or restriction to disturbed, anthropogenic habitats (including artificial substrates) often with concentrations of non-native species
(14) Ecology: Rapid increase in population size

The application of these criteria is highly dependent on the taxon and location in question, the history and depth of regional biodiversity investigation, and the quality and quantity of biological, genetic, physiological, and ecological data available. Thus which, and how many, criteria are applied and applicable will vary considerably. As an example, if the well-known Asian crab *Hemigrapsus sanguineus*, a recognized invader of the North Atlantic Ocean, should be introduced and become established in Argentina, if correctly identified, then criterion (1) would be sufficient to recognize it as non-native to South America.

Robust evidence of prior absence, in particular, is one of the strongest criteria for recognizing a non-native species, especially for large, conspicuous species unlikely to have been overlooked for decades or centuries in well-studied areas. The Indo-Pacific octocoral *Carijoa riisei*'s appearance in the 1960s in the Hawaiian Islands is a classic example of a prominent, easily recognized species not detected in the Archipelago since scientific collections began in the 1800s. Although species can be missed in ecological and biodiversity surveys, no evidence suggests that *C. riisei* would fall into such a "missed" category. First thought to be found in Hawaii in 1972, it was later determined to have been photographed in Hawaii in 1966, leading Concepcion et al. (2010) to conclude that this 6-year gap "demonstrates that lack of precedence is a weak foundation for classifying" non-native species. Lack of precedence, in fact, remains one of the strongest foundations; it is not uncommon to discover that species were found by members of the public years before occurring in scientific samples (Carlton 2008). There is, further, thus no evidence that *C. riisei* is cryptogenic in the Hawaiian Islands, as suggested by Salimi et al. (2021).

An instructive lesson in the synergism between the ability to establish prior absence in a region, and enduring assumptions about the probability of natural colonization (dispersal) of species from a source area, is the history of the introduction of two marine species from the South American mainland to the Galápagos Islands (Carlton et al. 2019). A baseline barnacle survey was conducted in the Islands in 1964, and baseline crab surveys in the 1930s. In 1966 a large barnacle from the South American mainland, *Megabalanus coccopoma*, was discovered in fouling communities in the Galápagos, introduced by vessel traffic (Carlton et al. 2019). The edible mangrove crab *Cardisoma crassum*, common in Ecuador, was found in the wild on Santa Cruz Island in 1993, with local knowledge establishing that it was intentionally introduced that year (Carlton et al. 2019). Both species remain established today in the Islands. A critical lesson here is that had the barnacle been first found in the Galápagos in 1964 or earlier, or had the crab been introduced (without anyone knowing) intentionally half-a-century earlier, Galápagos biogeographers would assume that both species had naturally dispersed from the mainland. Other than these 2 species all remaining marine species that are found both on the mainland and in the Islands are considered natural colonists in the Galápagos (Carlton et al. 2019).

As Carlton et al. (2019) concluded, anthropogenic movements of marine species from South America to the Galápagos may be underestimated, as it would appear highly unlikely that the only two marine species to be transported accidentally or intentionally from the mainland to the Archipelago happen to be species that arrived since the 1950s. In fact, the distance between South America and the Galápagos, although less than 1000 km, may exceed the dispersal capabilities of many species, although such dispersal is consistently invoked.

Other species (Table 5) are recognized as probable introductions based solely on criterion (12). For some species, the application of various criteria may change over time and result in finer-scale resolution. For example, as noted earlier, Roux (1828) invoked prior absence (our criterion 1) to recognize that the littoral isopod *Ligia exotica* was not native to the Mediterranean, but it was work 90 years later (Hidalgo et al. 2018) that resolved its origin as the Indo-Pacific through criterion (9).

For a great many species, data for criteria 5, 9, 10, 11, and 14 may simply not be available without extensive historical study or laboratory and field research. For many soft-bodied species with no preservable hard parts, application of the archeological or recent fossil record is inapplicable. For very small, including microbial, inconspicuous and historically undersampled (or never sampled) species, criterion (1) may especially not be applicable, although the inability to establish prior absence has led in some circumstances to the application of the "smalls rule"—an assumption that small species, in general, are naturally very widely distributed (see Carlton 2009).

The above aside, whenever possible, as many applicable criteria should be mustered to bolster the case that a given species is or may be non-native; conversely, not all criteria must be met to do so (Bortolus et al. 2015; Miranda et al. 2018). For many species, the data may at this time be insufficient to resolve a species status; such species are thus cryptogenic.

VC. Retention in invasion assessments of species not recently reported

How long to continue to retain species not recently re-reported on inventories of non-native species is an unresolved question in invasion science. Ruiz et al. (2000) noted that the "population status was considered unknown for introductions with no records within the past 20–30 years." Robinson et al. (2016) set aside records for South Africa for species not recorded "in the past 25 years." For larger, well-known macroscopic species—for example, large gastropods and bivalves, or large crabs—no records for several decades may indeed suggest that the species is no longer present. Intensive expert searching in the same habitat in the same sites for species not reported for decades, regardless of species size, would also suggest that the species be removed from the register of currently recognized established invasions.

While the above scenarios provide *evidence of absence,* a fixed time period for confirming the population status for a great many cryptic, small, and especially taxonomically challenging species may inadvertently imply that there is a probability that the species is no longer present, when in fact there may have been no attempts to confirm such—nor, for many species, would it be expected that there would have been such searches. For example, a number of commensal and symbiotic ciliophorans were reported between the 1920 and 1940s from only introduced molluscan and crustacean hosts in San Francisco Bay, California (Carlton 1979), but there are no subsequent records. In this case, however, there is no evidence of absence, and as all the hosts in question remain in San Francisco Bay, there are no reasons to suspect that these potentially host-specific symbionts are absent.

We suggest that species that have not been specifically searched for again, and which are not likely to be encountered in sampling programs without a targeted search (accompanied by taxonomic expertise) be retained in invasion inventories (while noting that recent details of their distribution or population size are not known). This approach would both serve to restore species to lists and to potentially promote interest in focused searches. Environmental DNA (eDNA) or qPCR samples might serve to reveal the continued presence of certain non-native species not collected in recent years, although many cryptic and small taxa of concern may not have been sequenced.

VD. Type localities are not default native regions

A great many species of marine, freshwater, and terrestrial invaders were first described from a non-native region, with a number of these still remaining unknown elsewhere, but are nevertheless unquestionable introductions (Carlton 2009, and above in Section "III. Reassessment of the status of "native" species").

Table 6 presents 15 recent (since 2005) examples of new species recognized at the time of their description as probable non-native species. That awareness is now increasing that non-native species can be both undescribed and unknown in their native regions is perhaps indicative of the generally greater recognition of bioinvasions but also perhaps the unsurprising scale of increasing human-mediated dispersal. These examples capture Western Europe and the Mediterranean, regions with deep and robust baselines that permit detection of novel macroscopic species, as well as North and South America, the Hawaiian Islands, and the Indian Ocean, and taxa as diverse as flatworms, sponges, cnidarians, worms, bryozoans, fish, and seaweeds. Of these few examples, only 2 have yet to be discovered in their homeland. We suggest that the spectacular occurrence of the previously undescribed red seaweed *Chondria tumulosa* in the Hawaiian Archipelago, although initially categorized as cryptogenic (Sherwood et al. 2020), is certainly an invasion and is not native to the Islands. Similarly, although not shown in Table 6, the amphipod *Corophium urdaibaiense* (Marquiegui and Perez 2006) found in the Bay of Biscay, France in 2004, and described from (and still only known in) France, was very unlikely to be overlooked in a country with a very long history of extensive study on these small crustaceans.

VI. Methods for establishing the timing of invasion records, and the importance of not using publication dates

The resolution of the date of first collection or detection may appear to be a matter of generally minor concern. However, a good deal of attention in invasion science, as well as invasion management, is focused on the pattern and pulse of invasions over time, and whether invasions can be related to, for example, the history of a particular vector (its beginning, its peak, and, perhaps, its demise), to environmental or other changes in the donating or receiving environment (Carlton 1989), or to other phenomena and processes. For example, Byers et al. (2015) employed data on "time since introduction" to examine whether there was a positive relationship between time since arrival and current (as of 2012) range size of marine invaders, and whether distributional equilibrium had been reached.

Here we identify methods by which to establish when a species was first discovered in a given region. Faced with apparently no or few recourses, many studies simply use the *publication date* of a paper to mark the first record of a species in a given region. Such a demarcation date is to be avoided if at all possible. The publication date of a record is often a poor substitute to establish invasion chronology, if the goal is to correlate invasion patterns with vectors, environmental changes, and post-invasion range expansion. Instead, time and effort should be invested in discovering if data may be available by which to establish when the species was in fact first detected or collected.

We distinguish here resolving the *date of first collection* from when a species may have *first become established* as reproducing populations. Many species may have arrived and become established in a given region years or decades (and in some cases centuries) before being first collected. This said, the known timing of relevant vector activity may help establish potential invasion timing baselines. For example, Hartman (1936) made many of the first collections of Atlantic polychaete worms in San Francisco Bay, California in the 1930s, many of which species were likely introduced beginning in the 1870s with the importation of Atlantic oysters (Carlton 1979). In this case, the first detection of these species is an artifact of the arrival of a taxonomic specialist (see also discussion in Macan 1974), and thus Cohen and Carlton (1998) elected to not include Hartman's 1930s records of Atlantic worms in San Francisco Bay in calculating invasion rates of the Bay, since their introduction may have occurred as much as 50 or more years earlier. In some regions, the scale of collection biases may be difficult to detect: Robinson et al. (2020) note that only 4 non-native species were collected in South Africa prior to 1900 (none recognized at the time as introductions), whereas between 1900 and 2000 another 65 non-native species were recorded, although many of the latter (such as hydroids, polychaetes, isopods, amphipods, bryozoans, and others) may have arrived in the 1800s if not earlier. Thus the commensal folliculinid protist *Mirofolliculina limnoriae*, an established non-native species in South Africa whose host is the non-native wood-boring isopod *Limnoria tripunctata*, while first noticed in Cape Town Harbor in 2008, may well have arrived centuries ago. A disconnect between a probable era of introduction and the first date of detection appears not to be recognized or acknowledged in many studies.

VIA. Methods for determining earlier dates of collection or detection

We suggest several avenues, often low-hanging fruit, by which to avoid using publication dates as dates of first detection.

Accessing station data

Many species reports in taxonomic literature provide only a station number (of an expedition or a collector) with no collection date. Station data should then be sought in other sources, although these may require considerable mining to discover. For example, Osburn (1950, 1953) reported the Indo-West Pacific bryozoan *Synnotum aegyptiacum* and the North Atlantic bryozoan *Anguinella palmata*, respectively, from Peru based upon collections made at *Velero* station 847–38. Osburn did not provide a reference for obtaining station data details. *Velero* station data can be recovered from Fraser (1943), producing a **1938** collection date for this station.

Museum specimens and museum records

Museum specimens may provide unpublished collection data. We offer several compelling examples:

(1) The ascidian *Polyandrocarpa zorritensis* was described from Peru by Willard Van Name in **1931** (Van Name 1931), without a collection date; it is now regarded as introduced to South America (Carlton et al. 2019). The type material was deposited at the Yale University Peabody Museum of Natural History, whose on-line catalogue (accessed October 2021) provides a collection date of **1866**, setting the record **back 65 years**.

(2) The Australasian ascidian *Asterocarpa humilis* was reported as a new introduction in Chile in 2000, based upon **1997** collections (Clarke and Castilla 2000). However, a synonym of *A. humilis* is *Cnemidocarpa robinsoni* Hartmeyer, **1916** (Turon et al. 2016) described from Robinson Crusoe Island, Chile; the type material was said by Hartmeyer to be deposited in the Natural History Museum in Berlin. Inquiry of the Museum revealed that the specimens were still extant, but bore only a collector's name ("Plate") and no collection date or further data (Carsten Lüter, personal communication, 2021). Plate is the German zoologist Ludwig Hermann Plate who spent two months on Robinson Crusoe Island in **1894** (Plate 1896), setting the record for this ascidian **back 103 years** in Chile.

(3) The Western Pacific amphipod *Incisocalliope derzhavini* was first identified in San Francisco Bay, California in **1971** (Chapman 1988, as *Parapleustes derzhavini*). However, study of preserved hydroids collected in San Francisco Bay and held at the Smithsonian Institution and the Yale Peabody Museum of Natural History revealed that *I. derzhavini* had been in San Francisco Bay since at least **1904** (Chapman 1988), setting the record **back 67 years.**

(4) The North Atlantic amphipod *Monocorophium acherusicum* was first identified from Yaquina Bay, Oregon, in **1987** (Chapman 1988). Examination of epibiota on shells of the Atlantic oyster *Crassostrea virginica* from Yaquina Bay in the Smithsonian Institution (received from F. L. Washburn in **1905**, revealed the presence of (dried) specimens of *M. acherusicum* (Carlton 1979), setting the record **back 66 years**. Atlantic oysters were imported from the Atlantic coast and planted in Yaquina Bay between 1897 and 1899 (Washburn 1900).

Discussion

The study of marine bioinvasions is in its infancy: the field did not exist prior to the 1970s. This young field, much of which work began in earnest only in the 1990s, would thus not be expected to catch up quickly with more than 500 years of invasion history. We identify in this essay, and suggest means by which to address, critical gaps in the global resolution of the diversity and history of marine bioinvasions. These gaps have arisen in part by profound differences in the range of taxonomic groups covered in regional invasion assessments, and in part limited rare attempts to question the presumed nativeness of many species that may have been introduced over prior centuries. Coupled with this are largely coarse-grained attempts to establish invasion timing, such that frequently the date of publication of a paper is used as the first record, or the date of collection is taken as the date of introduction, even when evidence may be at hand that the latter is an artifact of specialized investigation of a particular taxonomic group.

As we posed at the start of this essay, without taking into account differential levels of exploration and study, it is difficult to address fundamental questions in invasion science such as whether the strikingly different numbers of marine invasions reported around the world reflect varying propagule pressures (as mediated by many pulsating vectors over time), the differential susceptibility or resistance of communities and habitats to the colonization of new species ("invasibility"), to the characteristics of the potentially invading species ("invasiveness"), or to some combinations of these.

We close this essay by exploring current approaches to understanding the scale of marine bioinvasions in tropical waters.

Wells and Bieler (2020) argue that the consistently low numbers of non-native marine species reported from Guam, Pilbara (Western Australia), Singapore, and southern Florida, as well as work comparing tropical and temperate Australian ports, "strongly suggests that the relative paucity of non-indigenous marine species in the studied environments is not due to a lack of study or inability to detect NIMS [non-indigenous marine species] caused by poor taxonomic knowledge, but rather by increased biological interactions in a biodiverse environment." The potentially lower number of marine invasions in tropical waters have been discussed for some years (Hutchings et al. 2002). Relative to the goals of this essay, we address this conclusion briefly, and specifically probe Singapore as a model system.

None of the studies noted by Wells and Bieler address the large number of marine taxa that have never been studied relative to their biogeographic history, nor do these studies attempt a re-assessment of the history of ostensible native species in well-known taxa, nor do they plumb the depths of the potential scale of cryptogenic taxa. For Singapore, Wells et al. (2019), in listing 22 non-native marine species, noted that there had been "no comprehensive non-indigenous marine survey in Singapore," but cited Jaafar et al. (2012) as an "extensive" study. In turn, Jaafar et al. (2012) state that they conducted "an exhaustive review to determine the status of marine and estuarine non-indigenous species in Singapore," which review produced the names of three non-native species (two bivalves and one worm); they did not question the native designations of thousands of marine species recorded for Singapore. Wells et al. (2019), while acknowledging that the suggestion of Yeo et al. (2011) that "part of the explanation (for the low numbers of non-native species) may be that species were introduced in centuries before marine studies began" was "soundly based," nevertheless reached the conclusion that there was "strong evidence" for the relatively lower numbers of non-native species in the Indo-West Pacific tropics, and that these numbers are "neither due to a lack of knowledge nor an absence of sampling."

The phylum Arthropoda is represented in the current non-native species list for Singapore (Wells et al. 2019) by one species of amphipod and two species of barnacles; the phylum Annelida is represented by one species of serpulid tubeworm. No Singapore hydroids, sponges, or ascidians, among many other taxonomic groups, are considered relative to their non-native status. The situation is reminiscent of Angola, where marine Arthropoda invasions are represented solely by two species of barnacles (Pestana et al. 2017), although certain taxonomic groups omitted in the Singapore treatment, including sponges, hydroids, and ascidians, are recognized as non-native in Angola. Critically, Yeo et al. (2011) listed 127 (*sic*) species of crabs in Singapore that were cryptogenic—i.e., that could not be confirmed as native. Wells et al. (2019) acknowledge that analyzing the histories of 127 crab species would require a good deal of work. Wells et al. (2019) further argued that "taxonomists would have been looking for non-indigenous marine species in their marine studies but have found very few."

In fact, taxonomists involved in survey work rarely if ever look for non-indigenous species: they seldom address the critical historical biogeographic consideration that now widespread species may in fact not have been so, prior to human activity in the oceans. Further, in our experience, taxonomists identifying species not previously recorded in a location often do not consider whether such taxa might be non-native, but default to concluding that a previously undetected species may have been overlooked, or rare, or misidentified earlier by non-specialists. Thus, taxonomists working in Singapore (and elsewhere in tropical waters) may be aware of non-native species that are newly reported but rarely retrospectively question the distributions of the species they identify, which distributions, for hundreds if not thousands of species, are often said to range from the Red Sea and East Africa to the South China Sea and southern Japan and to the Hawaiian Islands. This lack of questioning is influenced in part by the fundamental assumption that such distributions are natural, despite a thousand and more years of potential mixing by coastal vessels transporting hull fouling organisms and ballast through the South Seas, the Central Pacific, and the Indian Ocean.

Given the lack of historical perspective, given the large number of species-rich taxonomic groups remaining largely or entirely unstudied, and given the number of regions around the world remaining largely uninvestigated, producing global "heat maps" documenting the number of marine invasions by country and region may overestimate the quality of the available data. Seebens and Kaplan (2022), using filtered ("cleaned") data from GBIF (Global Biodiversity Information Facility) and OBIS (Ocean Biodiversity Information System), produced a color-coded global map of the number of "recorded alien taxa" for marine and brackish taxa, scaled from 0 to > 140 taxa in intervals of 20. Broad swaths of the globe are plotted as having 0–50 invasions, with Seebens and Kaplan (2022) acknowledging that "the distribution of records is highly biased toward a few well-sampled regions such as Europe, North America, Australia, and New Zealand." However, simply reporting *more* invasions than elsewhere does not mean that these regions are well-sampled or well-understood, suggesting that, at this time, global maps of marine invasions may be better presented as the relative scale of selective study of some non-native species, rather than as the "number of recorded" non-native species. Global maps can be interpreted or used for many purposes outside academia, and may have a strong influence in setting priorities in research, with funding agenda, or in management decisions. Global maps, if used at all, should be accompanied by strong cautions about weaknesses and the scale of missing data in order to avoid misinterpretations about the status of bioinvasions.

Thus, the reporting of more non-native species in some regions of the world than others should not be interpreted to mean that better-studied areas have addressed the lacunae identified here. While Seebens and Kaplan (2022) correctly commented that "distinctly higher numbers of marine alien taxa than reported can be expected for most marine ecoregions," we cannot yet state, as they do, "except for European and North American coastal waters"—waters that we judge to be critically undersampled for invasions in a vast array of taxa and over deeper historical time.

Without thorough and vetted assessments of the scale of invasions in marine ecosystems over time, our ability to look deep into marine community ecology and evolution and into both ecological and evolutionary biogeography is limited, as is our ability to frame robust invasion management plans. At the beginning of the twenty-first century, science and management may be better served by recognizing the scale of what we may be overlooking, rather than conclude that the data are sufficient to render strong conclusions about where invasions have or have not been successful. This approach may more powerfully set the stage for anticipating, if not predicting, the scale of future invasions in the world's oceans.

Table 1 Phyletic dversity to be considered for marine bioinvasions assessments

Taxon or group	Examples of non-native marine Species (Brackish to marine habitats; polar to tropical; including parasites, commensals, and symbionts)	References (examples)
Viruses	WSS, IHHN	Schwindt et al. (2020)
Bacteria	Cyanobacteria; *Aeromonas salmonicida*; host-specific bacteria in introduced hosts	Evans et al. (2017) (host-specific bacteria in introduced ascidian hosts)
Fungi	*Cystospora rhizophorae, Etheirophora blepharospora*, and additional manglicolous and lignicolous fungi	Alexandrov et al. (2007), Carlton and Eldredge (2009)
Chromista		
Cercozoa	*Haplosporidium, Bonamia, Gromia*	Renault et al. (2000)
Foraminifera	*Trochammina hadai, Haynesina germanica, Amphistegina lobifera*	Schwindt et al. (2020)
Ciliophora	"ciliates", *Zoothamnium, Vorticella,* Folliculinidae	Mead et al. (2011a, b)
Myzozoa	Dinoflagellata (many species in many regions), Protalveolata (*Perkinsus*)	Hewitt et al. (2004), Pettay et al. (2015)
Ochrophyta	Bacillariophyceae (diatoms, many species in many regions), Phaeophyceae (brown algae, many species in many regions)	Ruiz et al. (2000), Hewitt et al. (2004), Carlton and Eldredge (2009), Lee II and Reusser (2012), Chainho et al. (2015), Xiong et al. (2017), Carlton et al. (2019), Galil et al. (2020), Schwindt et al. (2020), Texeira and Creed (2020)
Plantae		
Rhodophyta	Red algae (many species in many regions)	Ruiz et al. (2000), Hewitt et al. (2004), Carlton and Eldredge (2009), Lee II and Reusser (2012), Chainho et al. (2015), Xiong et al. (2017), Carlton et al. (2019), Galil et al. (2020), Schwindt et al. (2020), Texeira and Creed (2020)
Chlorophyta	Green algae (many species in many regions)	Ruiz et al. (2000), Hewitt et al. (2004), Carlton and Eldredge (2009), Lee II and Reusser (2012), Chainho et al. (2015), Xiong et al. (2017), Carlton et al. (2019), Galil et al. (2020), Schwindt et al. (2020), Texeira and Creed (2020)
Tracheophyta	Seagrasses, salt-marsh halophytes, brackish-tolerant riparian and emergent plants	Williams (2007), Mead et al. (2011a, b), Bortolus et al. (2015), Wang et al. (2021)
Animalia		
Invertebrates	Thousands of species in many phyla, including (for example), **Porifera** (sponges), **Cnidaria** (hydroids, sea anemones, corals), **Ctenophora** (comb jellies), Platyhelminthes (flatworms), **Nemertea** (ribbon worms); **Rotifera**; **Nematoda** (round worms); **Kamptozoa** (nodding heads); **Annelida** (echiurans, sipunculans, "oligochaetes," polychaetes), **Arthropoda** (crustaceans, pycnogonids, mites, insects), **Mollusca**, **Brachiopoda, Bryozoa**, and **Echinodermata**	Ruiz et al. (2000), Hewitt et al. (2004), Carlton and Eldredge (2009), Lee II and Reusser (2012), Chainho et al. (2015), Pestana et al. (2017), Xiong et al. (2017), Carlton et al. (2019), Galil et al. (2020), Schwindt et al. (2020), Texeira and Creed (2020)

Table 1 (continued)

Taxon or group	Examples of non-native marine Species (Brackish to marine habitats; polar to tropical; including parasites, commensals, and symbionts)	References (examples)
Chordata	**Ascidiacea** (sea squirts) (many species in many regions)	Ruiz et al. (2000), Hewitt et al. (2004), Carlton and Eldredge (2009), Lee II and Reusser (2012), Chainho et al. (2015, 2020), Pestana et al. (2017), Xiong et al. (2017), Carlton et al. (2019), Galil et al. (2020), Schwindt et al. (2020), Texeira and Creed
	Pisces: Actinopterygii (fish) (many species in many regions)	Carlton and Eldredge (2009), Lee II and Reusser (2012), Xiong et al. (2017), Galil et al. (2020), Schwindt et al. (2020), Texeira and Creed (2020)
	Mammalia: Norway rat *Rattus norvegicus*; Arctic fox *Alopex lagopus* (in Alaska)	Carlton and Hodder (2003)
	Aves (birds): mute swan *Cygnus olor,* duck *Anas platyrhynchos*	Levings et al. (2002), Carlton and Eldredge (2015)

See Supplementary File S1 for References

Table 2 Habitat diversity to be considered for marine bioinvasions assessments

Habitat (*Bold face italics:* artificial habitat/anthropogenic structures)	Examples of Bioinvasions from Brackish to Marine Habitats, in Polar to Tropical Regions (taxon and examples of regions or countries invaded; many species occur in noted habitats in many other regions)	References (for Species × Habitat × Location)
Water column (marine and estuarine)		
Coastal (neritic) waters	Examples of zooplankton (holoplankton) (see also Bollens et al. 2002; Dexter and Bollens 2020)	
	Temora turbinata (Cp, Brazil)	Muxagata and Gloeden (1995)
	Acartia spinicauda (Cp, South Africa)	Jerling (2008)
	Eurytemora americana (Cp, Argentina)	Hoffmeyer et al. (2000)
	Mnemiopsis leidyi (Ct, Caspian Sea)	Aladin et al. (2002)
	Pleopis schmackeri (Cl, Brazil)	Marazzo (2002)
	Pseudodiaptomus inopinus (Cp, NE Pacific)	Bollens et al. (2002)
	Tortanus dextrilobatus (Cp, NE Pacific)	Bollens et al. (2002)
	Sinocalanus doerrii (Cp, NE Pacific)	Cordell et al. (2008)
	Limnoithona tetraspina (Cp, NE Pacific)	Cordell et al. (2008)
	Examples of phytoplankton:	
	Dinophysis acuminata (D, Argentina)	Fabro et al. (2018)
	Coscinodiscus wailesii (A, North Sea)	Reise et al. (2002)
	Alexandrium catenella (D, Western Australia)	Dias et al. (2015)
	Alexandrium minutum (D, South Africa)	Pitcher et al. (2007)
	Trieres chinensis (Di, North Sea)	Reise et al. (2002)
	Thalassiosira punctigera (Di, North Sea)	Dürselen and Rick (1999)
	Gymnodinium microreticulatum (D, Portugal)	Amorim et al. (2001)
	Examples of nekton:	
	Alepes djedaba (F, Sea of Marmara)	Artüz and Kubanç (2014)
	Oncorhynchus tshawytscha (F, Argentina)	Ciancio et al. (2005)
	Omobranchus punctatus (F, Brazil)	Soares et al. (2011)
	Lutjanus gibbus (F, Hawaii)	Carlton and Eldredge (2009)
	Oreochromis mossambicus (F, Palau)	Campbell et al. (2016)
	Fistularia commersonii (F, Eastern Mediterranean Sea)	Kalogirou et al. (2007)
	Palaemon macrodactylus (De-Sh, Argentina)	Vázquez et al. (2012)
	Morone saxatilis (F, NE Pacific)	Goertler et al. (2021)
	Phyllorhiza punctata (Sc, Gulf of Mexico)	Verity et al. (2011)
	Rhopilema nomadica (Sc, Gulf of Mexico)	Giallongo et al. (2021)
Oceanic neuston-pleuston (neopelagic)	*Aglaophenia pluma* (Hy, North Pacific Ocean)	Haram et al. (2021)
	Anthopleura sp. (An-Sa, North Pacific Ocean)	Haram et al. (2021)
	Stenothoe gallensis (Am, North Pacific Ocean)	Haram et al. (2021)

Table 2 (continued)

Habitat (*Bold face italics:* artificial habitat/anthropogenic structures)	Examples of Bioinvasions from Brackish to Marine Habitats, in Polar to Tropical Regions (taxon and examples of regions or countries invaded; many species occur in noted habitats in many other regions)	References (for Species × Habitat × Location)
Dunes, Supralittoral, and Intertidal (marine and estuarine)		
Maritime sand dunes	*Ammophila arenaria* (P, South Africa)	Hertling and Lubke (1999)
	Carex kobomugi (P, NW Atlantic (USA))	Charbonneau et al. (2020)
	Carpobrotus edulis (P, Spain)	Novoa et al. (2013)
	Tamarix ramosissima (P, Argentina)	Natale et al. (2010)
Supralittoral (strand zone)	*Anisolabis maritima* (I, NE Pacific (USA))*Cafius xantholoma* (I, South Africa)	Langston (1974)
	Littorophiloscia culebrae (Is, Hawaii)	Taiti and Ferrara (1986)
	Porcellio lamellatus (Is, Cuba)	Jass and Klausmeier (2006)
	Halophiloscia couchii (Is, Hawaii)	Taiti (1999)
	Cafius xantholoma (I, South Africa)	Stenton-Dozey and Griffiths (1983)
	Telmatogeton japonicus (I, North and Baltic Seas)	Brodin and Anderson (2009)
	Gyrohypnus angustatus (I, Atlantic Canada)	Majka et al. (2008)
	Philonthus varians (I, Atlantic Canada)	Majka et al. (2008)
	Cakile maritima (P, Uruguay)	Alonso Paz and Bassagoda (2003)
	Spergularia media (P, Australia)	Adams et al. (2008)
Maritime wharf	*Nacerdes melanura* (I, Tristan da Cunha)	Chown and Convey (2016)
	Ligia exotica (Is, Uruguay)	Giambiagi de Calabrese (1931)
Rocky intertidal (exposed coast) *See also:* Steneck and Carlton (2001) (New England, USA); Wasson et al. (2005), Zabin et al. (2018) (California, USA)	*Littorina littorea* (G, NW Atlantic (USA, Canada))	Petraitis (1989)
	Sargassum muticum (A, NE Atlantic (Spain))	Olabarria et al. (2009)
	Hemigrapsus sanguineus (De-Cr, NW Atlantic (USA))	Brousseau and Goldberg (2007)
	Carcinus maenas (De-Cr, NW Atlantic (USA))	Lohrer and Whitlatch (2002)
	Petrolisthes elongatus (De-Cr, Tasmania)	Gregory et al. (2012)
	Balanus glandula (Ci, Argentina)	Schwindt (2007)
	Chthamalus proteus (Ci, Central Pacific Ocean)	Zabin and Hadfield (2002)
	Mytilus galloprovincialis (B, South Africa)	Erlandsson et al. (2006)
	Codium fragile subsp. *fragile* (A, Norway)	Armitage et al. (2014)
	Grateloupia turuturu (A, Portugal)	Freitas et al. (2016)
	Pyura praeputialis (T, Chile)	Castilla et al. (2014)
	Botrylloides violaceus (T, NW Atlantic)	Eddy and Roman (2016)
	Isognomon bicolor (B, Brazil)	Breves-Ramos et al. (2010)
	Anemonia alicemartinae (T, Chile)	Häussermann and Försterra (2001)
	Watersipora spp. (Br, California)	Zabin et al. (2018)
	Eleutheria dichotoma (Hy, Australia)	Fraser et al. (2006)
	Istiblennius meleagris (F, Israel)	Rothman et al. (2020)

Table 2 (continued)

Habitat (*Bold face italics:* artificial habitat/anthropogenic structures)	Examples of Bioinvasions from Brackish to Marine Habitats, in Polar to Tropical Regions (taxon and examples of regions or countries invaded; many species occur in noted habitats in many other regions)	References (for Species × Habitat × Location)
Rocky intertidal (protected coasts and estuaries)	*Austrominius modestus* (Ci, Ireland)	Gallagher et al. (2016)
	Littorina saxatilis (G, California)	Carlton and Cohen (1998)
	Littorina littorea (G, NW Atlantic)	Steneck and Carlton (2001)
	Sphaeroma quoianum (Is, Oregon)	Davidson et al. (2007)
	Balanus glandula (Ci, Argentina)	Schwindt (2007)
	Hemigrapsus takanoi (De-Cr, Wadden Sea)	Landschoff et al. (2013)
Other hard-bottom intertidal (e.g. oyster reefs, serpulid tubeworm reefs)	*Crassostrea gigas* (B, Ireland)	Joyce et al. (2021)
	Mytilicola orientalis (Cp, NE Pacific)	Chew et al. (1965)
	Urosalpinx cinerea (G, England)	Cole (1942)
	Ocinebrellus inornatus (G, Denmark)	Lützen et al. (2012)
	Ficopomatus enigmaticus (Po, Baltic Sea)	Hille et al. (2021)
	Isognomon bicolor (B, Brazil)	López et al. (2014)
	Musculista senhousia (B, NE Atlantic)	Bachelet et al. (2009)
	Charybdis helleri (De-Cr, Brazil)	Frigotto and Serafim-Junior (2007)
	Petrolisthes armatus (De-Cr, NW Atlantic)	Hollebone and Hay (2007)
Soft-bottom intertidal (e.g. mudflats, sandflats, clay-peat banks, sandy beaches, mixed sediments) *See also*: Ruesink (2018)	*Batillaria attramentaria* (G, NE Pacific (California))	Byers (2000)
	Gracilaria vermiculophylla (A, NW Atlantic (South Carolina))	Byers et al. (2012)
	Mya arenaria (B, NE Pacific (Alaska))	Powers et al. (2006)
	Ruditapes philippinarum (B, Mediterranean Sea (Turkey))	Genez et al. (2015)
	Gemma gemma (B, NE Pacific)	Carlton (1992)
	Ensis leei (B, Wadden Sea)	Van der Heide et al. (2014)
	Carcinus maenas (De-Cr, NE Pacific (California))	Grosholz et al. (2000)
	Sphaeroma quoianum (Is, NE Pacific)	Davidson (2008)
	Ampithoe valida (Am, Portugal)	Cunha et al. (1999)
	Haynesina germanica (Fo, Argentina)	Calvo-Marcilese and Langer (2010)
	Corophium volutator (Am, Canada (Atlantic))	Barbeau et al. (2009)
	Musculista senhousia (B, New Zealand)	Creese et al. (1997)
	Crassostrea gigas (B, NE Pacific)	Ruesink (2018)
	Ficopomatus enigmaticus (Po, Argentina)	Schwindt et al. (2001)
	Spartina anglica (Pl, NE Pacific, USA)	Hacker et al. (2001)
Sandy beaches and surf zones (exposed coast)	*Attheya armata* (Di, NE Pacific)	Lewin and Norris (1970)
	Ensis leei (B, Western Europe)	Gollasch et al. (2015)

Table 2 (continued)

Habitat (*Bold face italics:* artificial habitat/anthropogenic structures)	Examples of Bioinvasions from Brackish to Marine Habitats, in Polar to Tropical Regions (taxon and examples of regions or countries invaded; many species occur in noted habitats in many other regions)	References (for Species × Habitat × Location)
Salt marshes *See also:* Byers (2009)	*Myosotella myosotis* (G, South Africa)	Herbert (2012)
	Assiminea parasitologica (G, NE Pacific)	Laferriere et al. (2010)
	Nematostella vectensis (An-Sa, England)	Reitzel et al. (2008)
	Spartina alterniflora (Pl, SW Atlantic)	Bortolus et al. (2015)
	Spartina patens (Pl, Spain)	SanLeón et al. (1999)
	Phragmites australis (Pl, North America)	Meyerson et al. (2000)
	Diadumene lineata (An-Sa, Argentina)	Molina et al. (2009)
	Batis maritima (Pl, Hawaii)	Carlton and Eldredge (2009)
	Crassostrea talonata (B, Argentina)	Cavaleiro et al. (2019)
	Spergularia marina (Pl, Australia)	Saintilan (2009)
	Nuttallia obscurata (B, British Columbia)	Chan and Bendell (2013)
	Balanus glandula (Ci, Argentina)	Schwindt et al. (2009)
Rocky salt marshes	*Balanus glandula* (Ci, Argentina)	Sueiro et al. (2011, 2012)
	Ampithoe valida (Am, Argentina)	Sueiro et al. (2011, 2012)
	Monocorophium insidiosum (Am, Argentina)	Sueiro et al. (2011, 2012)
	Melita palmata (Am, Argentina)	Sueiro et al. (2011, 2012)
Mangroves	*Rhizophora racemosa* (Pl, Hawaii)	Carlton and Eldredge (2009)
	Laguncularia racemosa (Pl, China)	Fazlioglu and Chen (2020)
	Sphaeroma terebrans (Is, Tropical Western Atlantic)	Brooks and Bell (2005)
	Phallusia nigra (T, Jamaica)	Goodbody (2003)
	Xylomyces rhizophorae (Fu, Hawaii)	Kohlmeyer and Volkmann-Kohlmeyer (1998)
	Kappaphycus alvarezii (A, Caribbean (Panamá))	Sellers et al. (2015)
	Cardisoma crassum (De-Cr, Galápagos Is.)	Carlton et al. (2019)
	Mayaheros urophthalmus (F, Florida (USA))	Lawson et al. (2017)
	Oreochromis mossambicus (F, Australia)	Adame et al. (2019)
	Beania klugei (Br, Galápagos Is.)	McCann et al. (2019)

Table 2 (continued)

Habitat (*Bold face italics:* artificial habitat/anthropogenic structures)	Examples of Bioinvasions from Brackish to Marine Habitats, in Polar to Tropical Regions (taxon and examples of regions or countries invaded; many species occur in noted habitats in many other regions)	References (for Species × Habitat × Location)
Coral reefs (intertidal) *See also*: Eldredge (1987)	*Charybdis helleri* (De-Cr, Caribbean region)	Felder et al. (2010)
	Eualetes tulipa (G, Singapore)	Tan et al. (2021)
	Gonodactylaceus falcatus (St, Hawaii)	Kinzie (1968)
	Phoronis hippocrepia (Ph, Hawaii)	Bailey-Brock and Emig (2000)
	Lutjanus fulvus (F, Hawaii)	Coles et al. (2006)
	Cephalopholis argus (F, Hawaii)	Carlton and Eldredge (2009)
	Hypnea musciformis (A, Hawaii)	Coles et al. (2006)
	Acanthophora spicifera (A, Hawaii)	Carlton and Eldredge (2009)
	Erythropodium caribaeorum (An-C, Brazil)	Carpinelli et al. (2020)
	Tubastraea spp. (An-C, Brazil)	Miranda et al. (2016)
	Rochia nilotica (G, SW Pacific islands)	Bour (1990)
Subtidal (Sublittoral)		
Fouling (intertidal and subtidal)	*Ciona robusta* (T, Chile)	Figueroa et al. (2021)
	Bugulina stolonifera (Br, Aegean Sea)	Koçak (2008)
	Bugula neritina (Br, Argentina)	Giachetti et al. (2020)
	Ectopleura crocea (Hy, East China Sea)	Lin Heshan et al. (2017)
	Amphibalanus amphitrite (Ci, Azores)	Torres et al. (2012)
	Jassa marmorata (Am, California)	Needles and Wendt (2013)
	Paracerceis sculpta (Is, Argentina)	Rumbold et al. (2018)
	Hydroides elegans (Po, Eastern Tropical Pacific)	Bastida-Zavala et al. (2016)
	Mytilus galloprovincialis (B, Eastern Russia)	Zvyaginstev et al. (2011)
	Ophiactis savignyi (Op, South Africa)	Peters et al. (2017)
	Ficopomatus enigmaticus (Po, NE Pacific)	Bastida-Zavala et al. (2017)
	Diadumene lineata (An-Sa, South Wales (UK))	Holmes and Callaway (2021)
	Tricellaria inopinata (Br, NW France)	Bishop et al. (2015)
	Caprella mutica (Am, NW Atlantic (Canada))	Collin and Johnson (2014)
	Styela clava (T, British Columbia, Canada)	Gartner et al. (2016)
	Botrylloides violaceus (T, Maine, USA)	Tyrrell and Byers (2007)

Table 2 (continued)

Habitat (*Bold face italics:* artificial habitat/anthropogenic structures)	Examples of Bioinvasions from Brackish to Marine Habitats, in Polar to Tropical Regions (taxon and examples of regions or countries invaded; many species occur in noted habitats in many other regions)	References (for Species × Habitat × Location)
Wood-borers, largely in, but not restricted to, harbors and ports	*Redekea* sp. (O, California, USA)	Carlton (1979)
	Taenioplana teredini (Pol, Hawaii)	Edmondson (1945)
	Mirofolliculina limnoriae (Cil, South Africa)	Mead et al. (2011a, b)
	Caecijaera horvathi (Is, Hawaii)	Cooke (1977)
	Limnoria tripunctata (Is, United Kingdom)	Jones (1963)
	Teredicola typica (Cp, New Zealand)	McKoy (1975)
	Teredo navalis (B, Japan)	Tsunoda (1979)
	Teredo bartschi (B, Turkey)	Borges et al. (2014)
	Teredo furcifera (B, Galápagos Is.)	Cruz (1996)
	Teredothyra dominicensis (B, E Mediterranean Sea)	Shipway et al. (2014)
	Lyrodus pedicellatus (B, SW Atlantic)	Balech (1972)
	Bankia gouldi (B, Galápagos Is.)	Cruz (1996)
	Martesia striata (B, Hawaii)	Carlton and Eldredge (2009)
Hard-bottom subtidal to shelf (including rocky, to 200 m) *See also*: Bumbeer and Rocha (2012, 2016) (Brazil)	*Codium fragile* subsp. *fragile* (A, NW Atlantic)	Harris and Jones (2005)
	Undaria pinnatifida (A, SW Atlantic)	Irigoyen et al. (2011)
	Pleurobranchaea maculata (G, SW Atlantic)	Battini et al. (2019)
	Pyromaia tuberculata (De-Cr, New Zealand)	McLay (2009)
	Ascidiella aspersa (T, Argentina)	Tatián et al. (2010)
	Styela clava (T, NW Atlantic)	Simkanin et al. (2012)
	Carijoa riisei (An-C, Tropical East Pacific)	Cárdenas-Calle et al. (2021)
	Balanus trigonus (Ci, NW Atlantic (Florida))	Werner (1967)
	Botrylloides violaceus (T, NE Pacific)	Simkanin et al. (2012)
	Chromonephthea braziliensis (An-C, Brazil)	Ferreira et al. (2009)
	Pennaria disticha (Hy, Galápagos Is.)	Calder et al. (2021)
	Watersipora subtorquata (Br, off southern California)	Goddard and Love (2010)

Table 2 (continued)

Habitat (*Bold face italics:* artificial habitat/anthropogenic structures)	Examples of Bioinvasions from Brackish to Marine Habitats, in Polar to Tropical Regions (taxon and examples of regions or countries invaded; many species occur in noted habitats in many other regions)	References (for Species × Habitat × Location)
Soft-bottom subtidal to shelf (mixed sediments, to 200 m) *See also*: Edelist et al. (2013) (Mediterranean)	*Philine auriformis* (G, NE Pacific)	Cadien and Ranasinghe (2003)
	Rapana venosa (G, Black Sea)	Shalovenkov (2017)
	Crepidula fornicata (G, west coast Great Britain)	Bohn et al. (2015)
	Callinectes sapidus (De-Cr, Turkey)	Daban et al. (2016)
	Caulerpa taxifolia (A, Mediterranean Sea)	Boudouresque et al. (1995)
	Codium fragile subsp. fragile (A, Tunisia)	Cherif et al. (2016)
	Ensis leei (B, North Sea)	Gollasch et al. (2015)
	Maoricolpus roseus (G, New Zealand)	Allmon (1988)
	Didemnum vexillum (T, NW Atlantic – Georges Bank)	Lengyel et al. (2009)
	Udotea argentea (A, Hawaii)	Bailey-Brock and Magalhães (2010)
	Marenzelleria arctia (Po, Baltic Sea)	Maximov (2011)
	Cryptocentrus steinhardti (F, Israel)	Goren and Stern (2021)
Seagrasses *See also:* Williams (2007)	*Halophila stipulacea* (Pl, Mediterranean Sea)	Cormaci et al. (1992)
	Zostera japonica (Pl, NE Pacific)	Baldwin and Lovvorn (1994)
	Sargassum muticum (A, NE Pacific)	White and Orr (2011)
	Gonionemus vertens (Hy, France)	Marchessaux et al. (2017)
	Mercenaria mercenaria (B, Great Britain)	Eno et al. (1997)
	Mya arenaria (B, Baltic Sea)	Boström and Bonsdorff (1997)
	Didemnum vexillum (T, NW Atlantic)	Carman and Grunden (2010)
	Botrylloides violaceus (T, Canada (east coast))	Wong and Vercaemer (2012)
	Streblospio benedicti (Po, NE Pacific)	Posey (1988)
	Ampithoe valida (Am, NE Pacific)	Posey (1988)
	Jassa slatteryi (Am, Korea)	Jeong et al. (2006)
	Charybdis helleri (De-Cr, Venezuela)	Bolaños et al. (2011)
Kelp beds	*Membranipora membranacea* (Br, NW Atlantic (Maine))	Harris and Tyrrell (2001)
	Hymeniacidon perlevis (Por, NE Pacific)	Turner (2020)
	Mytilus galloprovincialis (B, South Africa)	Lindberg et al. (2020)
	Codium fragile subsp. *fragile* (A, NW Atlantic (Maine))	Levin et al. (2002)
	Sargassum horneri (A, NE Pacific (California))	Sullaway and Edwards (2020)
	Ciona robusta (T, Chile)	Almanza et al. (2012)
	Colpomenia peregrina (A, NE Pacific (California))	Devinny and Kirkwood (1974)

Table 2 (continued)

Habitat (*Bold face italics:* artificial habitat/anthropogenic structures)	Examples of Bioinvasions from Brackish to Marine Habitats, in Polar to Tropical Regions (taxon and examples of regions or countries invaded; many species occur in noted habitats in many other regions)	References (for Species × Habitat × Location)
Coral reefs (subtidal)	*Pterois* spp. (F, Bahamas)	Albins (2015)
	Tubastraea spp. (An-C, Brazil)	Creed et al. (2017)
	Carijoa riisei (An-C, SE Pacific)	Cárdenas-Calle et al. (2021)
	Nemalecium lighti (Hy, Galápagos Is.)	Banks et al. (2009)
	Leiosolenus aristatus (B, Galápagos Is.)	Reaka-Kudla et al. (1996)
	Symbiodinium trenchii (D, Caribbean)	Pettay et al. (2021)
Deep Sea		
Deep Sea mixed bottoms (> 200 m)	*Paralithodes camtschaticus* (De-Cr, Barents Sea)	Jørgensen and Nilssen (2011)
	Chionoecetes opilio (De-Cr, Barents Sea)	Agnalt and Jørstad (2010)
	Etrumeus golanii (F, Mediterranean Sea)	Galil et al. (2020)
	Champsodon nudivittis (F, E Mediterranean Sea)	Galil et al. (2020)
	Nemipterus randalli (F, Mediterranean Sea)	Galil et al. (2020)
	Pterois spp. (F, Honduras)	Gress et al. (2017)
	Lutjanus kasmira (F, Hawaii)	Randall (1987)

See Supplementary File S1 for References

Listed are examples (generally up to 15 species) per habitat type, but this does not mean that all habitats are comparably invaded, nor that the same habitats are equally invaded in different areas of the world. Many species shown here occur in the same habitat around the world, and many of the species occur in multiple locations globally (we present only examples of species × habitat × location). Taxonomic Abbreviations: A: Alga, Am: Amphipod, An-C: Anthozoa-coral, An-Sa: Anthozoa-sea anemone, B: Bivalve, Br: Bryozoa, Ci: Cirripedia, Cil: Ciliate, Cl: Cladocera, Cp: Copepod, Ct: Ctenophore, D: Dinoflagellate, De-Cr: Decapod-Crab, De-Sh: Decapod-Shrimp, Di: Diatoms (Bacillariophyceae), F: Fish, Fo: Foraminifera, Fu: Fungi, G: Gastropod, Hy: Hydroid, I: Insect, Is: Isopod, M: Mysid, O: Ostracod, Op: Ophiuroid, Ph: Phoronid, Pl: Plant, Po: Polychaete, Pol: Polycladid, Por: Porifera (sponges) Py: Pycnogonid, Sc: Scyphozoa, St: Stomatopod, T: Tunicate (ascidian). See Supplementary File S1 for References

Table 3 Examples of non-native marine species inventories conducted largely since 2000, and whether the biogeographic status of "native" species was re-assessed

Country or region	Reference(s)	Biogeographic status of selected "native" species re-assessed?		Cryptogenic species mentioned from the literature	Number of non-native marine species reported in reference(s) cited
		Re-assigned to non-native status	Re-assigned to cryptogenic status		
Northeast Atlantic Ocean					
Britain	Minchin et al. (2013)	No	No	No	58
Mediterranean Sea	Galil (2009), Galil et al. (2020), Katsanevakis et al. (2020)	No	No	No	573
Macaronesia (Canary Islands, Azores, Madera, Cabo Verde)	Castro et al. (2022)	No	No	Yes	144
Northwest Atlantic Ocean					
Canada: Atlantic coast	Chapman et al. (2002)	No	No	No	17
United States: Atlantic coast	Ruiz et al. (2000)	No	Yes	Yes	108
Mexico: Atlantic coast	Leon-Gonzalez et al. (2021)	No	No	Yes	15
Venezuela	Pérez et al. (2007), Figueroa López and Brante (2020)	No	No	Yes	22
Southeast Atlantic Ocean					
Angola	Pestana et al. (2017)	Yes	Yes	No	29
South Africa	Mead et al. (2011a, b), Robinson et al. (2016, 2020)	Yes	Yes	Yes	80*
Southwest Atlantic Ocean					
Brazil	Teixeira and Creed (2020)	No	No	Yes	138
Argentina-Uruguay	Schwindt et al. (2020)	Yes	Yes	Yes	129
Northeast Pacific Ocean					
Canada: Pacific coast	Levings et al. (2002)	No	No	No	57
United States: Pacific coast	Ruiz et al. (2000)	No	Yes	Yes	187
Mexico: Pacific coast	León-González et al. (2021)	No	No	Yes	73
Hawaiian Islands	Carlton and Eldredge (2009, 2015)	Yes	Yes	Yes	333
Northwest Pacific Ocean					
Japan	Iwasaki (2006), Otani (2006), Doi et al. (2011), Lutaenko et al. (2013)	Yes*	Yes*	Yes	30
China and South China Sea	Xiong et al. (2017), Wang et al. (2021)	No	No	No	90
Singapore	Jaafar et al. (2012), Wells et al. (2019)	No	No	No	22

Table 3 (continued)

Country or region	Reference(s)	Biogeographic status of selected "native" species re-assessed?		Cryptogenic species mentioned from the literature	Number of non-native marine species reported in reference(s) cited
		Re-assigned to non-native status	Re-assigned to cryptogenic status		
Southwest Pacific Ocean					
Galapagos Islands	Carlton et al. (2019)	Yes	Yes	Yes	53
Chile	Castilla et al. (2005), Castilla et al. (2009)	No*	No	No	26
Southeast Pacific Ocean					
Australia	Hewitt (2002), Hewitt et al. (2004), Wyatt et al. (2005), Sliwa et al. (2009)	Yes	Yes	No	132*
New Zealand	Cranfield et al. (1998)	Yes	No	No	127*

See Supplementary File S1 for References

*Japan: Doi et al. (2011) (crustacea) only

*Chile: Castilla et al. (2005) suggest 7 species as non-native candidates but do not include these as introductions

*New Zealand: Hayden et al. (2009) note an additional 40 "suspected introduced marine species," citing unpublished data

*Australia: from Table 25.2 of Sliwa et al. (2009)

*South Africa: number of species calculated from data in Robinson et al. (2016) and (2020); not 56 as in van Wilgen et al. (2022)

Table 4 Examples of records of known or probable non-native species "hidden" in taxonomic or invasions literature

Species	Known or probable native region	Examples of introduced locations	References (with parenthetical citations, if such exist, of authors who have discovered and cited these records; parallel locations bold-faced in columns 3 and 4)
Taxonomic Literature with "Hidden" Invasion Records			
Jassa marmorata (amphipod)	Northwest Atlantic Ocean	*Norway *Germany *Spain *Iceland *Peru *Japan *South Korea	Beermann et al. (2020)
Jassa slatteryi (amphipod)	North Pacific Ocean	*Spain *North Africa *Chile *Peru	Beermann et al. (2020)
Myosotella myosotis (salt marsh snail)	Northeast Atlantic Ocean	***South Africa** *Bermuda *Peru	Martins (1996) (Herbert 2012, **South Africa**)
Invasion Literature with "Hidden" Invasion Records for Other Countries or Regions			
Mycale parishii (sponge)	Indo-Pacific	** Jamaica ** Brazil ** Pacific Panama	Carlton and Eldredge (2009)
Tripedalia cystophora (box jellyfish)	Tropical Western Atlantic Ocean	**Indonesia **Seychelles	Carlton and Eldredge (2015)
Cassiopea andromeda (jellyfish)	Indo-West Pacific	**Red Sea *Bermuda **Florida Keys	Carlton and Eldredge (2009)
Anemonia alicemartinae (sea anemone)	Indo-West Pacific or Atlantic Ocean	*Chile *Peru	Glon et al. (2020)
Diadumene leucolena (sea anemone)	Northwest Atlantic Ocean	*Morocco *Canary Islands *Senegal *Indian Ocean *Pacific Panama *Mexico (Gulf of California)	Glon et al. (2020)
Diadumene paranaensis (sea anemone)	Unknown	*California	Glon et al. (2020)
Exaiptasia pallida (sea anemone)	Atlantic Ocean	*California *Mexico *Pacific Panama ***Galápagos Islands** *Hawaiian Islands *Australia *Japan *Red Sea	Glon et al. (2020) (Carlton et al. 2019, **Galápagos**)
Leodora knightjonesi (spirorbid tube worm)	Indo-Pacific	**West Indies	Carlton and Eldredge (2009)
Amphibalanus amphitrite (barnacle)	Indo-Pacific	*Peru	Carlton et al. (2011)
Fistulobalanus pallidus (barnacle)	Atlantic Ocean	**Indian Ocean	Carlton et al. (2011)

Table 4 (continued)

Species	Known or probable native region	Examples of introduced locations	References (with parenthetical citations, if such exist, of authors who have discovered and cited these records; parallel locations bold-faced in columns 3 and 4)
Paralimnoria andrewsi (isopod)	Indo-Pacific	*Florida *Puerto Rico *Ghana	Carlton and Eldredge (2009)
Anoplodactylus erectus (sea spider)	Eastern North Pacific Ocean	**Korea	Carlton and Eldredge (2009)
Tanystylum rehderi (sea spider)	Indo-Pacific	**Guam	Carlton and Eldredge (2009)
Haplostomides hawaiiensis (parasitic copepod)	Indo-Pacific—Australia	**Mexico (Gulf of California)	Carlton and Eldredge (2015)
Dictyota flabellata (brown alga)	Northeast Pacific Ocean	**Japan **Pakistan	Carlton and Eldredge (2015)
Taxonomic Literature with "Hidden" Invasion Records Not Identified As Such in the Cited References			
Bugulina simplex (bryozoan)	Mediterranean Sea	***Peru	Ryland (1960) (re-identification *of B. flabellata* of Osburn 1950)
Anguinella palmata (bryozoan)	North Atlantic Ocean	***Peru	Osburn (1953)
Styela canopus (ascidian)	Northwest Pacific Ocean	***Ascension Id ***Mozambique ***Persian Gulf ***England ***Italy ***Bermuda	Kott (2005)
Styela plicata (ascidian)	Northwest Pacific Ocean	***Italy ***West Indies ***Philippines ***Australia	Kott (2005)
Janua heterostropha (spirorbid tubeworm)	Northeast Atlantic Ocean	***Brazil ***West Indies ***Mexico (Pacific) ***Australia ***New Zealand ***Tuamotu Islands ***Rapa Nui	Knight-Jones and Knight-Jones (1974), Knight-Jones et al. (1975, 1979)
Pentacoelum punctatum (flatworm)	Northeast Atlantic Ocean	***Louisiana	Sluys and Bush (1988)
Hydroides elegans (serpulid tubeworm)	Indo-Pacific	***Ghana	Bastida-Zavala and Ten Hove (2002)
Amphibalanus improvises (barnacle)	Northwest Atlantic Ocean	***Peru	Henry and McLaughlin (1975)

See Supplementary File S1 for References

[*] Indicated as introduced in the cited reference

[**] Newly hypothesized as introduced in the cited reference

[***] Newly suggested here as introduced species in the cited locations

Table 5 Criteria for recognizing non-native (introduced and range-expanding) species

Evidence (Criterion)	Definition	Comments	Examples
(1) Prior Absence: Absence from the Historical, Archeological, or Recent Fossil Record	The species can be shown from prior historical survey work, or, depending upon the taxon, archeological and recent fossil evidence, to have been absent prior to the first dates of collection or detection. This may include the absence of reference to the species in indigenous knowledge and languages	Criterion is limited for a great many taxa *with no prior sampling database* or *with no preservable hard parts* Alternative hypotheses include that a given taxon may have long been present in the region in question but was in very low background population numbers so as to evade sampling (but whose populations have now increased due to some environmental trigger or shift), or (b) existed as resting stages, which were not adequately historically sampled, but have now bloomed. Arguments against species being "rare background" native species include (Bortolus et al. 2015), (1) the unlikelihood that the taxon has never been sampled at any life stage for the entire history of biological investigation in an area, (2) the requirement that the species in question was uniformly historically undetectable everywhere within the area in question, and (3) environmental changes that cause a previously unknown native species to increase in abundance and/or range would likely not yield species-specific responses (i.e., broader biotic shifts should occur)	Most of the species in Table 3 match this criterion. Examples include, (a) The polychaete *Ficopomatus enigmaticus*, recognized as non-native at the same time it was described as a new species in an historically well-explored area in France (and thus the name "*enigmaticus*"; Fauvel 1923) (b) The Northeast Pacific Ocean barnacle *Balanus glandula*, detected in 1974 on Argentinean rocky shores that had long been studied (Orensanz et al. 2002) (c) The Western Atlantic barnacle *Chthamalus proteus* discovered in 1993 in O'ahu, albeit with a time gap of 20 years since prior shore barnacles survey did not detect it (Carlton and Eldredge 2009) (d) The introduced dinoflagellate *Gymnodinium catenatum*, absent from historical cores in Iberia (Amorim and Dale 2006) (e) The Indo-Pacific crab *Hyastenus spinosus*, first noted *circa* 1960s in the Hawaiian Islands, but absent from earlier historical accounts of the shallow-water crab fauna of the Archipelago (Carlton and Eldredge 2009)

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(2) Global Biogeography: Globally Disjunct Distributions	A species is reported broadly from one geographic region (potentially the native region), with isolated collections from distant continental margins in other oceans	Alternative hypotheses are that widespread reports of ostensibly the same species may be based on an unresolved species complex, or that isolated reports of a species far outside its known range may be based on misidentifications. Relative to the former, while species complexes may be involved, this does not preclude that one or more members of the complex have been introduced widely	Most of the species in Table 3 match this criterion. Examples include, (a) The black sea urchin *Tetrapygus niger*, widely distributed in its native area in the Southeastern Pacific from Peru to Chile, and then newly detected in South Africa (Mead et al. 2012) (b) The New Zealand and Australian sea slug *Pleurobranchaea maculata* first noticed in the Southwestern Atlantic in 2009 (Farias et al. 2016), the only location where it is reported outside of its native range (c) The sea spider *Anoplodactylus monotrema* occurring over a broad and presumably largely native range from Florida to Brazil, with a disjunct population in the Galápagos Islands, its only known Eastern Pacific location (Carlton et al. 2019) (d) The rocky shore barnacle *Balanus glandula*, widely distributed along the North American Pacific coast, and now occurring as isolated populations in Argentina, Japan, South Africa, and Belgium (Kado 2003; Schwindt 2007; Simon-Blecher et al. 2008; Kerckhof et al. 2018) (e) The Indo-West Pacific bryozoan *Triphyllozoon arcuatum* is found in (and introduced to) Todos os Santos Bay in Brazil *Triphyllozoon arcuatum* (Almeida et al. 2015)
(3) Global Biogeography and Temporal History	Species is historically known (all or most of the oldest available records) from one potentially native region, with later records from isolated and often distant locations	This criterion is distinct from the above: here, a careful, detailed history of the dates-of-first-collection of a species globally is constructed, to detect a possible pattern of spread over time. A caveat is that the invaded region may be historically the most explored, leaving the native region of a species undetected for a long period of time	The oldest records of the isopod *Sphaeroma walkeri* are anchored in the Indian Ocean, with a clear (but previously undetected) history of subsequent introductions around the world (Carlton and Iverson 1981)

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(4) Regional Biogeography: Highly Restricted Distribution	The species is found in only one restricted region (despite extensive searching elsewhere) on a continental margin or island in a geographic area not generally known to supported regional short-range endemics	Despite sampling efforts, the species may nevertheless in fact be widespread, due to being small or cryptic	(a) The 2.5 cm long isopod *Synidotea laticauda* was described from San Francisco Bay, California, in 1897, a location with no known endemic marine invertebrates. Carlton (1979) proposed that this isopod was therefore likely introduced, with its later identification as the Asian *S. laevidorsalis* (Chapman and Carlton 1991) (b) The seagrass *Halophila johnsonii* described from a restricted region of southeast Florida unknown to support endemic marine angiosperms, and considered an endangered species, is in fact the introduced Indo-Pacific seagrass *H. ovalis* (Waycott et al. 2021) (c) Additional examples are shown in Criterion 12 of taxa described from regions not known to harbor short-range regional endemics
(5) Regional Biogeography: History of Geographic Expansion	The species has a history of expansion along a coastal margin suggestive of an increasing post-introduction range matching the species' physiological breadth, rather than being related to climate change	Establishing the correct first collection dates of new populations may be difficult or impossible (see text) Species may experience considerable lag times (years to decades) before expanding from initial colonization sites The history of expansion of a species may be long forgotten, having been documented in much earlier but now overlooked literature, or a history of expansion may never have been recorded as such, with sequential reports of a species along a coastline going unnoticed as potential post-introduction expansions. This said, sequential reports that might suggest an expanding range must be distinguished from greater taxonomic scrutiny and expertise, especially for small, easily overlooked, and difficult to identify taxa	(a) The reconstructed history of the North American salt marsh plant *Spartina alterniflora* shows a northern and southern expansion along the Atlantic coast of South America from an initial colonization in Brazil (Bortolus et al. 2015) (b) the European snail *Littorina littorea* has a striking history of detection and expansion starting in the first half of the nineteenth century in the Gulf of St. Lawrence south to New England, with its Northeast Atlantic origin supported by ecological, molecular, and archeological evidence (Blakeslee et al. 2008)

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(6) Allochthonous (exotic) Evolutionary Origin	A taxon's morphology and/or genetics places it most closely with a clade or clades found on other continents or other ocean basins (i.e., its nearest likely evolutionary relatives), or a taxon's physiology suggests evolution under a different climatic regime than where it has now been found	Morphological evidence may at times be insufficient to establish evolutionary biogeographic roots, due to strikingly similar morphologies of co-occurring demonstrably native species	(a) The amphipod *Sinocorophium alienense,* described from San Francisco Bay, California (Chapman 1988), and now known from other harbors and embayments along the California coast, is related to species from the Western Pacific, not to the Northeast Pacific (Chapman 1988) (b) The closest relative to the commensal isopod *Iais floridana*, described from Florida USA, is the Indo-Pacific isopod *Iais singaporensis* (Carlton 2009) (c) *Spartina alterniflora*, established in South America, is considered to be a member of a clade of three hexaploid *Spartina* species considered to have evolved in the Northern Hemisphere (Bortolus et al. 2015) (d) The flatworm *Imogine necopinata*, described as a new species in The Netherlands, has its closest affinities with Asian species, and is thus considered non-native (Sluys et al. 2005) (e) A shrimp-associated goby, *Cryptocentrus steinhardti*, described as a new species in the Mediterranean, is related to Indian Ocean species, and is thus considered introduced (Goren and Stern 2021) (f) Knight-Jones et al. (1975) suggested that the spirorbid polychaete worm *Janua heterostropha* (as *J. pagenstecheri*), widely introduced around the world, was native to Europe due to the breadth of its physiological adaptations to the climatic regime of the Northeast Atlantic

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(7) Limited Natural Dispersal Potential for Transoceanic and Interoceanic Colonization	The species possesses insufficient active or passive natural dispersal mechanisms that could account for the observed distribution. Thus, species may have no planktonic larvae, or planktonic larval life is known to be only in hours, days, or weeks, too short for transoceanic or interoceanic crossings. For a marine plant, maximum floating duration may be too short to permit an ocean crossing	Rafting (historically on natural substrates) may permit distant movements of species with no, or no extended, early life stages in the water column, or no ability to survive floating on their own. For species with planktonic larvae rafting duration may be too long and exceed typical adult life span for successful dispersal. Rafting may be effective for species with direct development, thus passing through multiple generations at sea. Finally, rafting on anthropogenic substrates, such as long-lasting plastics, may significantly differ from natural rafting dispersal potential (Carlton et al. 2017)	Most of the species in Table 3 match this criterion
(8) Anthropogenic Dispersal Potential	The species (a) is, or is likely to be, associated with a human-mediated dispersal mechanism such as vessel hull fouling or ballast water, aquaculture, or other vectors, or (b) is known to have been intentionally introduced. Critically, vectors have changed over time, such that some vectors may have played a significant dispersal role in historical time that would be difficult to detect today. These include, for example, the transport of far greater fouling communities on ships' hulls prior to the advent of modern antifouling technology (WHOI 1952), or the probability of transporting species between bays and estuaries when some species may have been considerably more abundant before these habitats were severely extirpated	Even if known from port/harbor fouling communities, and thus suggestive of the potential to be associated with vessel fouling communities (although not recorded in vessel fouling), the species may not be capable of survival in transit during a vessel voyage Literature statements linking specific vectors to species are often repetitions of earlier suggestions, rather than reconsiderations or reanalysis of which vectors might have been probable at the time and places associated with a species introduction For some species, it may not be possible to distinguish between natural vectors and synanthropic vectors; such species are *cryptovectic* or *polyvectic* (Carlton and Ruiz 2005)	All of the species in Table 3 match this criterion

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(9) Invasion Founder Effect: Reduced Genetic Variation	Non-native populations may have significantly less genetic diversity than populations in the presumptive native range	Undersampling of populations in both introduced and native regions may lead to misinterpretations of species' history. Sampling modern populations to determine centers of highest genetic diversity (and thus presumptive native centers) may be compromised by loss of genetic diversity over time (due, for example, to metapopulation extinction (due to habitat destruction), to shifts in allele frequencies due to drift or selection (Hoss et al. 2010) or for other reasons). For example, the serpulid polychaete *Hydroides dianthus* appears to have higher genetic diversity in the Mediterranean Sea compared to populations in the North Western Atlantic, suggesting that the former area may be the native region (Sun et al. 2017), but it was known in the latter region long before being first found in the well-collected Mediterranean, and, critically, *Hydroides dianthus* is freezing tolerant, surviving in shallow water through extended New England winters, an attribute unlikely to have evolved in the Mediterranean Sea (see criterion 6)	(a) The snowflake octocoral *Carijoa riisei* is most genetically diverse in its native Indo-Pacific range compared to distant populations in the Caribbean and Hawaii (Concepcion et al. 2010) (b) The littoral isopod *Ligia exotica* described from the Mediterranean in 1828 (and at the time thought to be introduced by ships from South America) is most genetically diverse (including highly divergent lineages) in East and Southeast Asia, now regarded as the native region (Hurtado et al. 2018) (c) The wakame (brown alga) *Undaria pinnatifida* consists of at least 4 genetic and biogeographic clades in the Northwest Pacific; introduced populations worldwide are subsets of this genetic diversity (Uwai et al. 2006) (d) The European brown alga *Fucus serratus* exhibits low genetic diversity and a probable single introduction event in Iceland (Coyer et al. 2006)

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(10) Invasion Founder Effect: Reduced Morphological or Physiological Variation	Non-native populations may be demonstrate narrower morphological variation or physiological breadth compared to populations in presumptive native regions, implying reduced genetic variation	Environmental conditions in introduced region may constrain expression of potential biological variation	(a) The North American salt marsh plant *Spartina alterniflora* consists of the short-form in its introduced range in South America, whereas in the northern hemisphere *S. alterniflora* displays three distinct morphologies (short, medium, and tall); in addition, while in their full range in North America *S. alterniflora* is able to survive and reproduce from freezing to warm temperate conditions, South American populations are not cold-tolerant (Bortolus et al. 2015) (b) The sea anemone *Diadumene lineata* exhibits its highest morphological (color) variation in its native Asia (Ryan and Kubota 2018)
(11) Invasion Founder Effect: Reduced Variation in Reproductive Strategies	"If a plant reproduces entirely vegetatively it can legitimately be suspected of being an alien" (Webb 1985); "Due to random chance, particularly where the initial introduction size is small, only a single sex may be transferred to a new location as a 'founder effect.'" (Campbell et al. 2018)		(a) The Indo-Pacific seagrass *Halophila ovalis* is represented only by asexual populations in its introduced location in Florida (Campbell et al. 2018; Waycott et al. 2021) (b) For many decades the globally-introduced sea anemone *Diadumene lineata* was notable for having only asexual populations outside of Japan, although dioecious populations have now been reported out-of-Asia in recent years (Newcomer et al. 2019; Ryan and Miller 2019), perhaps reflective of the scale of increasing global trade and the modern-day export of sexual populations from Asia

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(12) Ecology: Predatory, Parasitic, Commensal, or Symbiotic Association with Non-Native Species	The species preys (as an herbivore or carnivore) solely on known non-native species, or is a symbiont, commensal, or parasite solely found with known non-native species	Alternative hypotheses are that native species may acquire new prey or hosts (although no demonstrably native marine species is known to rely solely on introduced species for prey or hosts)	(a) The sole host of the commensal isopod *Iais floridana*, described and known only from Florida, is the introduced Indian Ocean isopod *Sphaeroma walkeri* (Carlton 2009) (b) The predatory flatworm *Stylochoplana limnoriae,* described and known only from Los Angeles Harbor, California, preys only on the introduced isopod *Limnoria tripunctata* (Carlton 1979) (c) The commensal ostracod *Redekea californica* is known only from San Diego Bay, California, with its introduced host, also *Limnoria tripunctata* (Carlton 2009) (d) The parasitic copepod *Haplostomides hawaiiensis*, described from O ‘ahu, co-occurs with its introduced host ascidian *Polyclinum constellatum* in both Hawaii and Mexico (Tovar-Hernández et al. 2010, Carlton and Eldredge 2015). All of these associates are considered non-native in their type localities

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(13) Ecology: Prevalence in or Restriction to Disturbed, Anthropogenic Habitats (including Artificial Substrates), Often with Concentrations of Non-Native Species	A species may be primarily or only found in anthropogenically altered, disturbed (heavily modified) habitats, often on artificial substrates, and often in association with clusters of known non-native species; phrased as "indirect human agency" in Essl et al. (2018). Associated terminology includes synanthropic species and anthropofauna, terminology that embraces both native and non-native species	Introduced species are not restricted to such habitats, with many taxa in many regions having expanded (or been only introduced) into natural environments. In turn, many native species colonize new, artificial habitats in ports, harbors, and other disturbed habitats. While this "weeds live with weeds" concept is centered on the observation that non-native species are often found concentrated together (Lindroth 1957) in "man-made habitats" (Webb 1985), this criterion in and of itself may not distinguish a species as non-native (Cohen et al. 2005), and should not be used a priori as the sole criterion to classify species as native, introduced, or cryptogenic (Lambert 2003). Pociecha et al. (2016) suggested a corollary to this criterion: that the "earliest record(s) of the species in the assessed area are from "new or artificial environment(s)"	Many examples in Table 3 fit this criterion. Examples include, (a) The North Atlantic mud piddock *Barnea truncata*, occurring only in the highly disturbed Blanca Bay Estuary, one of the largest port systems of Argentina (Fiori et al. 2012) (b) 19 species of non-native ascidians were reported exclusively in port environments in Brazil (Marins et al. 2010) (c) The cryptogenic caprellids *Caprella penantis*, *C. equilibra* and *C. dilatata* are restricted to port fouling communities in Argentina (Rumbold et al. 2018)

Table 5 (continued)

Evidence (Criterion)	Definition	Comments	Examples
(14) Ecology: Rapid Increase in Population Size	A species has a rapid and often large increase in abundance in a restricted region, often linked to being unknown historically in the area	Native species may undergo a periodic increase in regional abundance for many reasons (see also Belmaker et al. 2021)	(a) The tunicate *Styela clava* was first detected in Argentina in 2013 and by 2014 its density was higher than reported in other invaded regions (Pereyra et al. 2015) (b) The sea slug *Pleurobranchaea maculata* was first noticed in Argentina in 2009, followed by its rapid increase in abundance and distribution (Farías et al. 2016) (c) The tubeworm *Ficopomatus enigmaticus* was first observed in an estuarine lagoon (Lake Merritt) in San Francisco Bay, California in 1920 followed by an explosive expansion which caught the attention of the public believing "coral reefs" had appeared in the Lake (Carlton 1979) (d) The blue mussel *Mytilus galloprovincialis* underwent an explosive population growth in the 1940s in southern California but its arrival was misinterpreted was resurgence of a native mussel (Geller 1999)

Noted are caveats and critiques for each criterion. For many species, the use of only one criterion is not sufficient to resolve a species as non-native (see text and, for example, criterion 13). Criteria summarized from Lindroth (1957), Carlton (1979), Webb (1985), Chapman and Carlton (1994), Essl et al. (2018) and Campbell et al. (2018). See Supplementary File S1 for References

Table 6 Recent examples of invertebrates recognized at the time of description as non-native, and therefore not native in their type localities

New species described as:	Type locality in:	Current status	References
Caulibugula arcasounensis (bryozoan)	Arcachon Bay, France	Remains unknown elsewhere	De Blauwe (2005)
Imogine necopinata (flatworm)	North Sea Canal, Netherlands	Remains unknown elsewhere	Sluys et al. (2005)
Celtodoryx girardae (sponge)	Gulf of Morbihan, France	Now recognized as *Celtodoryx ciocalyptoides*, native to Asia	Perez et al. (2006), Henkel and Janussen (2011), Gouillieux et al. (2022)
Biflustra perambulata (bryozoan)	Cochin Harbor, India	Since found in Singapore (Tilbrook and Gordon 2016) and in hull fouling on a vessel from the Ivory Coast intercepted in Spain (Cuesta et al. 2016)	Louis and Menon (2009), Louis et al. (2018)
Marivagia stellata (jellyfish)	Israel	Since found in the Indian Ocean	Galil et al. (2010), Galil et al. (2013)
Stragulum bicolor (soft coral)	Brazil	Remains unknown elsewhere	Van Ofwegen and Haddad (2011)
Mawai benovici (jellyfish)	Adriatic Sea	Since found elsewhere in the Mediterranean as well as in Senegal on the West Africa coast (Bayha et al. 2017)	Piraino et al. (2014), Avian et al. (2016)
Podocoryna loyola (hydroid)	Bahia de Paranagua, Brazil	Remains unknown elsewhere	Haddad et al. (2014)
Marphysa victori (polychaete)	Arcachon Bay, France	Now recognized as *Marphysa bulla* (Liu et al. 2018) (a junior synonym) native to China/Japan	Lavesque et al. (2020)
Arnoglossus nigrofilamentosus (fish)	Israel	Remains unknown elsewhere	Fricke et al. (2017)
Hazeus ingressus (fish)	Turkey	Remains unknown elsewhere	Engin et al. (2018)
Lissodendoryx littoralis (sponge)	Ladysmith Harbor, British Columbia, Canada	Remains unknown elsewhere	Ott et al. (2019)
Chondria tumulosa * (red seaweed)	Pearl and Hermes Atoll, Hawaiian Islands	Remains unknown elsewhere	Sherwood et al. (2020)
Cryptocentrus steinhardti (fish)	Israel	Remains unknown elsewhere	Goren and Stern (2021)
Aurelia pseudosolida (jellyfish)	Adriatic Sea	Remains unknown elsewhere	Garic and Batistic (2022)

See Supplementary File S1 for References

**Chondria tumulosa*: proposed as cryptogenic by Sherwood et al. (2020) but here recognized as non-native based upon criteria 1, 4, 6, 8, and 14. This macroscopic, conspicuous alga would not have been overlooked in the Hawaiian Archipelago in over 100 years of marine floristic exploration, even on Pearl and Hermes Atolls, where other marine bioinvasions have been present for many years

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Declarations

Conflict of interest The authors have no conflicts of interest to declare.

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