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Author manuscript

Front Mar Sci. Author manuscript; available in PMC 2019 April 22.

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Published in final edited form as:

Front Mar Sci. 2018 ; 5: 293–. doi:10.3389/fmars.2018.00293.

A Framework for Understanding Marine Cosmopolitanism in the Anthropocene

John A. Darling^{1,*} and James T. Carlton^{2,3}

¹ United States Environmental Protection Agency, National Exposure Research Laboratory, Research Triangle Park, NC, United States

² Maritime Studies Program, Williams College-Mystic Seaport, Mystic, CT, United States

³ Department of Biology, Williams College, Williamstown, MA, United States

Abstract

Recent years have witnessed growing appreciation for the ways in which human-mediated species introductions have reshaped marine biogeography. Despite this we have yet to grapple fully with the scale and impact of anthropogenic dispersal in both creating and determining contemporary distributions of marine taxa. In particular, the past several decades of research on marine biological invasions have revealed that broad geographic distributions of coastal marine organisms—historically referred to simply as “cosmopolitanism”—may belie complex interplay of both natural and anthropogenic processes. Here we describe a framework for understanding contemporary cosmopolitanism, informed by a synthesis of the marine bioinvasion literature. Our framework defines several novel categories in an attempt to provide a unified terminology for discussing cosmopolitan distributions in the world’s oceans. We reserve the term *eucosmopolitan* to refer to those species for which data exist to support a true, natural, and prehistorically global (or extremely broad) distribution. While in the past this has been the default assumption for species observed to exhibit contemporary cosmopolitan distributions, we argue that given recent advances in marine invasion science this assignment should require positive evidence. In contrast, *neocosmopolitan* describes those species that have demonstrably achieved extensive geographic ranges only through historical anthropogenic dispersal, often facilitated over centuries of human maritime traffic. We discuss the history and human geography underpinning these neocosmopolitan distributions, and illustrate the extent to which these factors may have altered natural biogeographic patterns. We define the category *pseudocosmopolitan* to encompass taxa for which a broad distribution is determined (typically after molecular investigation) to reflect multiple, sometimes regionally endemic, lineages with uncertain taxonomic status; such species may remain cosmopolitan only so long as taxonomic uncertainty persists, after which they may

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*Correspondence: John A. Darling darling.john@epa.gov.

AUTHOR CONTRIBUTIONS

JD and JC both developed the conceptual framework, assembled appropriate literature, and wrote the manuscript.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

splinter into multiple geographically restricted species. We discuss the methods employed to identify such species and to resolve both their taxonomic status and their biogeographic histories. We argue that recognizing these different types of cosmopolitanism, and the important role that invasion science has played in understanding them, is critically important for the future study of both historical and modern marine biogeography, ecology, and biodiversity.

Keywords

introduced species; marine biogeography; cosmopolitanism; eucosmopolitan; pseudocosmopolitan; neocosmopolitan; provincial; invasion biology

“To trace the courses that Dennis, Barnstable, and Truro navigators pricked off between 1815 and 1850, would be to draw a network over all the oceans of the world.”

- Henry Kittredge, *Cape Cod, Its People and Their History* (1930, Houghton Mifflin)

THE NEED FOR A TYPOLOGY OF COSMOPOLITANISM

Students of marine biodiversity have long eyed the phenomenon of cosmopolitanism with some skepticism. Among the seeds of a fundamental shift in questioning the existence of cosmopolitan species were those planted by Grassle and Grassle (1976), who in a seminal paper announced that a classic example of a globally-distributed worm, *Capitella capitata*, in fact consisted of six sibling species in New England waters alone. Carlton (1975) commented that the “amazingly wide distributions of some marine organisms may reflect more the marvels of taxonomy than of nature.” And by the early 1980s polychaete systematist Mary Petersen was already referring to the “characteristic species disease” afflicting many polychaete taxa, a common ailment of what were misconstrued as single broadly distributed species, despite the fact that they often exhibited substantial variation throughout their ranges (Petersen, 1984). The paradigm of predominantly cosmopolitan distributions among marine annelids, in slow demise since the late 1970s, has now been partially supplanted by taxonomic descriptions of geographically restricted taxa (Hutchings and Kupriyanova, 2018), even as many polychaete species around the world still retain cosmopolitan nomenclature. Despite clear advances, the notion of cosmopolitanism among largely shallow water benthic marine species persists in many corners, in the face of growing apprehension that this may be a reflection less of biogeography than of taxonomic uncertainty. Observations ranging from “suspiciously cosmopolitan” algal species (Sherwood, 2007) to “implausible cosmopolitanism” of some bryozoan taxa (Harmelin et al., 2012) and “complexes of (pseudo-) cryptic species” among marine meiofauna (Van Steenkiste et al., 2018) all highlight the reluctance to shed a concept that has dominated thinking about marine biodiversity for nearly 200 years.

Mounting wariness of cosmopolitan distributions can be attributed to a number of factors, including increased and more internationally collaborative taxonomic efforts (Hutchings and Kupriyanova, 2018), recognition of overconservative systematics among many taxonomic

groups (Klautau et al., 1999), and the advent and rapidly expanding accessibility of molecular genetic data (Brasier et al., 2016; Leray and Knowlton, 2016). But of critical general importance has also been the emergence and maturation of marine invasion biology as a field of scientific inquiry. The burgeoning literature describing anthropogenic introductions of marine taxa, similarly nascent in the late 1970s, has paralleled increasing circumspection directed at the paradigm of marine cosmopolitanism. This relationship can in part be traced to two related but separable aspects of marine invasion biology, each of which has influenced thinking about cosmopolitan species in different ways.

First, the past several decades of research have laid bare the extensive influence that humans have had on the global distribution of marine species. This realization is rooted not only in recognition of the importance of contemporary anthropogenic vectors of biotic homogenization and the ongoing role humans play in reshaping marine biogeography (Bax et al., 2003; Carlton and Ruiz, 2015), but also—as suggested by the above epigraph—in acknowledgement that humans have been playing that role for many centuries, if not millennia (Carlton, 2003; Gollasch et al., 2009; Rick et al., 2013). The extent of marine species introductions in the Anthropocene—that geological era dominated by the influence of our own species (Capinha et al., 2015)—may dwarf current estimates based solely on historical observations of novel incursions outside of known native ranges, as many human-mediated distributional shifts may have preceded by centuries any concerted attempts to catalog marine biodiversity (Carlton, 2009). Acceptance of this fact weighs heavily against the default assumption that observed contemporary cosmopolitanism must reflect solely the effects of natural processes driving community assembly over ecological and evolutionary time.

Second, greater attention leveled at the phenomenon of anthropogenic introductions of marine species—either for the sake of informing management of costly invasions (Darling, 2015; Darling et al., 2017) or as unique “experiments” offering insight into fundamental processes in evolution and ecology (Rius et al., 2015)—has led to considerable investment in attempts to reconstruct invasion histories. These attempts, powered often by application of increasingly sophisticated molecular genetic tools (Cristescu, 2015; Viard et al., 2016), have frequently unearthed unexpected diversity among widespread introduced marine species, leading naturally to questions about their taxonomic and biogeographic status (Geller et al., 2010). Such observations have become so commonplace that the literature is rich with papers hypothesizing cryptic species-level diversity among introduced marine taxa; one may be tempted to stop using the term “unexpected” to describe the diversity revealed by these investigations. Similar revelations have derived from general studies of marine biodiversity, with genetic evidence indicating that some groups harbor truly astonishing levels of cryptic diversity (Brasier et al., 2016). These discoveries, demonstrating the power of the molecular hammer to shatter species into multiple lineages of uncertain status, have only further eroded confidence in the phenomenon of marine cosmopolitanism.

We describe here a framework for understanding cosmopolitanism in the context of lessons learned over three decades of marine invasion biology. This effort is motivated by the conviction that we are in need of both a unified language to discuss marine cosmopolitanism and a common understanding of how to resolve the status of broadly distributed marine

species. Our framework (Figure 1) thus comprises both a typology of cosmopolitanism and a structure for describing how changes in knowledge about marine species allow their categorization within this typology.

To accomplish our goals, we find it useful to re-introduce or propose several terms, which together constitute our typology (see Box 1 for a summary of definitions). We use the term **eucosmopolitan** to refer to a subset of those species previously referred to simply as “cosmopolitan,” but here restricted to species whose broad distribution in multiple oceans can clearly be attributed to natural processes acting over eco-evolutionary timescales. An important emphasis of our framework is thus that assignment of eucosmopolitan status requires positive evidence (below, and Scenario I in Figure 1), and should no longer be taken as the default assumption for broadly distributed species. This cautious approach signals a “once bitten, twice shy” attitude, an appreciation for the sheer repetitive force of innumerable studies in which presumed “natural” cosmopolitan distributions have been shown to reflect either recent anthropogenic spread or the global occurrence of multiple provincial species. In contrast, we define **neocosmopolitan** species as those that have demonstrably achieved cosmopolitan distributions through anthropogenic dispersal (Scenario II). We believe that this distinction is critical, as the two categories have markedly different implications for inferences about marine biogeographic theory and history and the ecological and evolutionary processes underlying community assembly, as we discuss further below.

Neocosmopolitan species are distinguished from eucosmopolitan species by a set of criteria that have been developed to differentiate non-native from native species (Carlton, 1979; Chapman and Carlton, 1994; Pocięcha et al., 2016). Neocosmopolitan species are thus recognized in a given region by their historical absence (including, if applicable, absence from the archeological and paleontological record), association with a human-mediated vector, a known or suspected region of origin, and for many (but by no means all) species, presence in a disturbed, anthropogenic habitat (such as artificial substrates in ports and harbors). In contrast, eucosmopolitan species could have evidence of historical, archeological, or paleontological presence predating any possible human influence on their distribution, would be unlikely to be commonly associated with or transported by human-mediated vectors, would not be associated with any particular region of endemism, and would not be frequently associated with anthropogenic habitats. In addition, eucosmopolitan species should possess dispersal capabilities (at some stage of their life cycle) that would suggest the capacity to sustain both transoceanic and interoceanic dispersal for months if not years on ocean currents (Hilario et al., 2015). In order to maintain a genetic structure suggestive of a single eucosmopolitan species, such dispersal would further have to be continuous in ecological time to prevent allopatric speciation in different ocean basins.

By definition, then, eucosmopolitan species would not include introduced species. This said, we recognize that under certain circumstances, such species could be engaged by a vector such as shipping (for example, a vessel ballasting in the open ocean taking in a pelagic species that would be released in another ocean). Such dispersal could in theory result in anomalous genetic exchange across unexpectedly large distances, or even in the appearance of the species beyond its known eucosmopolitan range.

Additional scenarios involve changes to the taxonomic status of broadly distributed marine species. Some of these changes may draw on novel morphological (or morphological and genetic) evidence, typically resulting in assignment of new (or resurrected) binomials for previously unresolved lineages (Scenario III). Cosmopolitan species may thus dissolve into complexes of endemic (or indigenous) or introduced regional species (Box 1); alternatively, one or more of the species in these complexes may still exhibit broad distributions across multiple oceans, requiring categorization as either eucosmopolitan or neocosmopolitan depending on biogeographic history (Figure 1, lower left dotted blue arrows). Species currently with invasions only within the same ocean where they are native (that is, introduced regional species), would become neocosmopolitan species if dispersed to another ocean.

Other changes in knowledge, most often provided by molecular genetic studies, frequently result in identification of evolutionary lineages sufficiently highly diverged to raise suspicions of the existence of multiple species (Scenario IV). In the absence of non-genetic corroboration of species-level distinctions, however, these lineages normally remain unnamed (Pante et al., 2015a), leaving us with a single accepted binomial describing a taxon with cosmopolitan distribution that we nevertheless suspect may represent a complex of multiple species—some or all of which may, in fact, be geographically restricted provincials. We define such taxa, now numerous in the literature, as **pseudocosmopolitan** to reflect the possibility that their current cosmopolitan status may be an illusory effect of overconservative taxonomy; that effect could be—and ultimately sometimes is—dispelled by future integrated taxonomic revision of the taxon.

Finally, we propose the term **unresolved cosmopolitanism** to describe what remains. We define this category as encompassing those species—perhaps the majority of species still described as “cosmopolitan”—which are said to exhibit a contemporary cosmopolitan distribution but have not yet been subjected to rigorous investigation into their taxonomic status and/or biogeographic history (Scenario V). In effect, taxa assigned unresolved cosmopolitan status are in a holding pattern, awaiting morphological, genetic, historical, and/or other analyses to resolve their status. We propose this category, then, as the new default. We feel such caution is warranted given what has been learned over the last several decades, and the suspicion with which marine biologists have grown to view the legacy of cosmopolitanism inherited largely from systematics of the 19th and 20th centuries.

These terms are not entirely new, but their usage in the past has been either obscure or inconsistent. Most notably, the two terms eucosmopolitan and neocosmopolitan were first proposed by Rapoport and Marino (1998) relative to terrestrial plant invasions. They used the terms much as we use them here, defining them simply as either “true or natural cosmopolitan species” or “human-transported cosmopolitans.” Gartner (1998), apparently independently, used eucosmopolitan to refer to what was thought to be a “circumglobal” mesopelagic (deep water) fish species; the term was repeated in the same sense by Rees et al. (2017). We have found no further use of the word neocosmopolitan prior to our current work, and the terms have clearly not attained broad usage in the literature. Pseudocosmopolitan was used by Fernald (1926) to refer to New Zealand flowering plants mis-identified as European species. Hoagstrom and Berry (2006) also used

pseudocosmopolitan in a restricted sense to refer to less-than-widespread distributions of fish within Great Plains drainage basins. Closer to our usage is that of Nikulina et al. (2007) who defined pseudocosmopolitans as “complexes of regionally restricted cryptic species” (we include native, introduced, and cryptogenic species within pseudocosmopolitanism), and Kuklinksi and Taylor (2008) who referred to pseudocosmopolitans as species with “seemingly cosmopolitan distribution(s) (that are) probably spurious.” By placing these sporadically used terms into a comprehensive framework we hope to confer upon them sufficient weight that they might be adopted more broadly to ground future discussion and investigation.

In the remainder of this review we provide evidence from the literature supporting this framework, identify examples illustrative of each of the scenarios described briefly above, and describe how various lines of evidence are brought to bear to elucidate the appropriate status of particular species. We focus largely on neocosmopolitan and pseudocosmopolitan species, primarily because these categories align most closely with the two ways in which marine invasion biology has influenced thinking about cosmopolitanism over the past several decades. On the one hand, growing understanding of the pervasive influence of maritime traffic on species distributions has led to identification of a large and growing number of neocosmopolitan species; on the other, increasing application of molecular genetic and other tools to understand invasion histories has resulted in a similar proliferation of pseudocosmopolitan taxa.

These categories thus capture important lines of evidence linking invasion biology to a broader understanding of marine biogeography. We intentionally exclude from our study a substantial literature investigating cosmopolitan taxa that lack a known history of anthropogenic introductions, in order to focus specifically on the indispensable role of invasion biology in informing our framework. We hope through this exploration to illustrate the significant influence that invasion biology has had on marine biodiversity studies, and more broadly to provide a systematic approach for interpreting cosmopolitan distributions of marine species in the Anthropocene.

NEOCOSMOPOLITANISM:HUMAN-MEDIATED SPREAD AND THE CREATION OF COSMOPOLITAN SPECIES

A vast literature accompanies the rapidly growing recognition since the 1980s of both the historic and modern-day scale of global dispersal of marine organisms by human activity. There are now many hundreds of papers that address the depth and breadth of the introduction of non-native marine and estuarine protists, invertebrates, fish, algae, seagrasses, and halophytes on most coastlines of the world. In contrast, Carlton (1979) was able to cite only one peer-reviewed paper (Lachner et al., 1970) that summarized selected examples of introduced marine species. This surge of modern literature reflects in part the vastly increased globalization of maritime trade since World War II that has led to a mushrooming of invasions, and in part to the realization that hundreds if not thousands of species invasions occurred prior to the 1900s that were simply never remarked on, mistaken for native species, or were members of poorly-studied taxa (Carlton, 2009).

The anthropogenic vectors that have historically transported, continue to move, or will persist in translocating marine species both within and between oceans have been reviewed in recent years (Carlton et al., 1995, 2017, 2018; Carlton, 2001; Minchin and Gollasch, 2002; Carlton and Ruiz, 2005; Minchin et al., 2005; Hewitt et al., 2007; Galil et al., 2015; Muirhead et al., 2015). These vectors have been or now include the extensive niche areas on or in ocean-going vessels that transport fouling, entangled, and ballasted organisms, sea level (such as the Suez) and lock (Panama) canals, mariculture (aquaculture), the aquarium and saltwater bait industries, and long-distance rafting on anthropogenic debris. Reviews of some marine bioinvasions successfully introduced via these mechanisms or corridors are available, for example, for *North America* (Cohen and Carlton, 1995; Ruiz et al., 2000, 2011, 2015), *Europe* (Wolff, 2005; Gollasch, 2006; Galil et al., 2014), the *Mediterranean* (Galil, 2009; Rilov and Galil, 2009; Ulman et al., 2017), the *Azores* (Cardigos et al., 2006) and *Madeira* (Canning-Clode et al., 2013), *South Africa* (Mead et al., 2011; Alexander et al., 2016), *Argentina* (Orensanz et al., 2002), *Brazil* (Ferreira et al., 2009); the Pacific coast of *Mexico* (Low-Pfeng and Peters-Recagno, 2012), *Chile* (Villasenor-Parada et al., 2017), the *Hawaiian Islands* (Carlton and Eldredge, 2009, 2015), *Japan* (Otani, 2006), *China* (Xiong et al., 2017), *Korea* (Park et al., 2017), *Australia* (Wyatt et al., 2005, and references therein; Sliwa et al., 2009), and *New Zealand* (Hayden et al., 2009). The majority of these introduced species—whether phytoplankton, foraminifera, other protists, invertebrates, fish, or plants—are recognized as neocosmopolitan taxa based upon morphological and other criteria noted above.

We remark here briefly on the extent and antiquity of ship-mediated transport of species, and how this antiquity may have led to an under-assessment of the scale of neocosmopolitanism. When humans first sailed significant distances within, across or between oceans such that biogeographic barriers were bridged, is not known (Erlandson, 2017; Lawler, 2018). Whatever the antiquity and range of early wooden craft, there is no doubt that marine animals and plants became attached to, burrowed into, or were accidentally drawn inside these vessels (Carlton, 1999, 2011). Within the past 1,000–500 years these craft became sufficiently advanced to permit long-distance ocean voyages, such that northern European cultures (including the Norse) explored North America, Chinese empires reached East Africa (discussed further below), and Polynesians reached the Hawaiian Archipelago, leading to a global web of voyages that eventually connected virtually all shores of the world (Woods Hole Oceanographic Institution (WHOI), 1952; Natkiel and Preston, 1986; Casson, 1995; Woodman, 1997; McGrail, 2015). As vessel size and technology continued to evolve, expanding fleets of vessels sailing out of Europe commencing largely in the 1500s roamed the “Seven Seas,” which in modern times constitute the North and South Atlantic Ocean, the North and South Pacific, the Indian Ocean, and Arctic and Antarctic waters. Within the Atlantic Ocean alone, for example, between the 1,500s and 1,800s, a staggering 36,000 sailing voyages have been recorded that transported over 10 million Africans into slavery to North and South America (Eltis, 2007).

That ancient voyages may have long confounded our understanding of marine biogeography is perhaps no better illustrated than by the distributions of many hundreds–thousands–of species that are believed to “naturally” occur over the vast distances from the Red Sea to the North Pacific Ocean (Carlton, 1987). A great many species of invertebrates and algae are

described as ranging from the Red or Arabian Seas throughout the Indian Ocean, across Indonesia north to the China and Philippine Seas and southern Japan, and, often, continuing on through all of Oceania (Melanesia, Micronesia, Polynesia, and Australasia), if not to the Hawaiian Archipelago. To explain such distributions, taxonomists, biogeographers, and ecologists typically infer either “rafting” or larval dispersal over distances exceeding 20,000 km, implying that such natural dispersal mechanisms effectively insure a remarkable level of gene flow sufficient to prevent speciation.

In contrast, if we look through the lens of maritime history coupled with its imperceptible boundary with the history of marine biodiversity, ancient ports are positioned throughout this vast Indo-West Pacific theater. As an example, the island state of Singapore, at the tip of the Malay Peninsula in Southeast Asia, has been a strategic entrepot since the 1,300s. While not without interruption in terms of scale and intensity, the Port of Singapore presumably has been a hub for the dispersal of marine animals and plants across a vast sweep of the Indian and Pacific Oceans for at least 700 years (Wang, 1339; Turnbull, 2009). As Turnbull (2009) has remarked, “... since time immemorial the Straits of Singapore lay at the heart of a rich trading region in which great Malay empires had flourished.”

Over the centuries, a maritime Silk Road (commencing centuries B.C.E. and continuing into the 1,400s), also known as the Porcelain Road, settled into place, connecting European ports with those of the Indo-West Pacific and Asia (Figure 2A; Rapoport and Marino, 1998; Lawler, 2014; Church, 2018). The famous Chinese mariner, Admiral Zheng He, departed Suzhou in the East China Sea in July 1405 with no fewer than 317 vessels to sail to Southeast Asia, India, and Africa (Levathes, 1996; Dreyer, 2006; Liu et al., 2014), the first of seven naval expeditions that lasted until 1,433. It gives pause to begin to imagine the diversity of marine fouling and boring organisms carried by these homogenizing fleets alone for more than a quarter century.

That vessels were plying many of these waters long before the 1,300s is without doubt. Since the 1,300s, hundreds of thousands of voyages crisscrossed the Indian and Western Pacific Oceans alone, marked by expeditions of exploration and colonization that were replaced by trade routes that endured for centuries (Figure 2B). Punctuating the development of commerce and supporting port systems were intense pulses of shipping related to perceived riches (such as the nineteenth century gold rushes of California and Australia) or to wars, all of which fundamentally both changed and expanded the hubs and spokes of the sea routes of empires. By the early Twentieth century, a new layer of global tourism on ocean-going cruise ships had developed as well (Figure 2C). Remarkable is how little reference to these centuries of global shipping is often made in the marine systematic, ecological, and biogeographic literature.

The continuous introductions and reintroductions of species along these routes may have created what today would be nearly undecipherable homogenized global gene pools, making the origin of many species difficult to determine. How many such species—ranging from foraminiferans, sponges, hydroids, flatworms, polychaetes, amphipods, and sea spiders to bryozoans and sea squirts—have become Flying Dutchmen, sailing the seas without a known home, we have as yet no idea. David et al. (2016) and David and Loveday (2017) refer to the

widespread dispersal of individuals by anthropogenic vectors as “cryptic dispersal.” Observing that human-mediated movement may be an important contributor to gene flow, they note that such movements may conceal or erode signals of past phylogeographic structure. “If cryptic dispersal has been occurring across long timescales” (as we suggest here for Flying Dutchmen), “even genetic patterns inferred from mtDNA may be obscured via reshuffling of ancient haplotypes due to past translocation events” (David and Loveday, 2017).

While a reliable estimate of the total number of marine species invasions worldwide is not available (the summary statistics in Ahyong et al., 2018 omit many species and include non-established species), the number may be considerably more than 2,000 taxa. Even this estimate, however, overlooks what may be at least the same number of species that remain unrecognized as invasions, a significant fraction of which may be microscopic species [a reflection of what is known as the “small rule of invasion ecology,” defined as the inverse correlation of body size with the probability of being recognized as a non-native species (Carlton, 2009)]. For example, Carlton (2009) noted while at least 500 distinct phytoplankton taxa are recognized in San Francisco Bay, California, and despite the 100 or more years of vectors that have released non-native diatoms, dinoflagellates, or other phytoprotists into the Bay, no phytoplankton are recognized there as introduced. Doubtless, however, the largest fraction of unrecognized invasions are what are now either classified as native or cryptogenic species, the classical default in biogeography, evolutionary biology and ecology being to regard the latter as the former.

In Table 1 we present a few (33 taxa in 9 phyla) examples of neocosmopolitan species for which robust morphological, or morphological and genetic, data suggest that a single species is involved. It remains unclear how many of the hundreds of presumed neocosmopolitan species discussed above would withstand such inquiry to retain their current taxonomic assignments. We maintain that this stringent condition for formal categorization as neocosmopolitan—that the taxon be subjected to rigorous examination of its taxonomic status throughout its cosmopolitan range—is indispensable given rapidly mounting evidence for morphologically cryptic provincial species disguised as cosmopolitans (see below). Indeed, even given such exacting investigation it would not be surprising if cryptic species remain undetected amongst those taxa where only morphological evidence is available to support probable conspecificity. A number of species listed as pseudocosmopolitan in Table 2 have been subjected to morphological analysis by researchers forearmed with information about cryptic lineages disclosed by genetic data; even in such cases, distinctive morphological traits separating those lineages may remain elusive (Lessios et al., 2001; Xavier et al., 2010; Perez-Portela et al., 2013; Knapp et al., 2015). Low-hanging fruit for future such investigations include those morphospecies said to occur (and reproduce) from cold temperate (including freezing conditions) to tropical latitudes, such as the sea anemone *Diadumene lineata* and the barnacles *Amphibalanus improvisus* (whose tropical populations were not studied by Wrange et al., 2016) and *Amphibalanus eburneus*.

NEOCOSMOPOLITAN AND EUCOSMOPOLITAN: A DISTINCTION WITH A DIFFERENCE

We conclude these brief thoughts by underscoring that to fail to distinguish natural (eucosmopolitan) from anthropogenically-created (neocosmopolitan) distributions undermines many of the core assumptions of evolutionary community ecology and biogeography. Classical ecosystem and community marine studies—such as those of rocky intertidal shores, soft-bottom benthos, and salt marshes—assume that the species assemblages under investigation, and the processes regulating such communities, including competition, predation, and disturbance, are the result of long-term evolutionary interactions. Thus it is that, unbeknownst to, or overlooked by the researchers at the time of their work, a number of definitive studies on the ecological interactions of presumed native species were in fact based upon one or more members of the community that were introduced. Steneck and Carlton (2001) have already remarked that fundamental studies on the regulatory role of the periwinkle snail *Littorina littorea* on New England intertidal shores do not mention that it arrived in North America in the 1,800s; as a result, what would be today regarded as iconic studies on the impact of a marine invader often go without mention in reviews of the effects of non-indigenous species. Of note is that Steneck and Carlton's chapter on human alterations of marine communities is found in an end-of-book section on "Conservation Issues," rather than under a leading section of "Processes influencing pattern in marine communities."

Many other studies seeking to elucidate natural patterns were also founded inadvertently on non-native species. Sutherland's (1974) classic work on "multiple stable points in natural communities" was based in part on the seasonal phenology of the ascidian *Styela plicata*, now known to be native to the Western Pacific Ocean (De Barros et al., 2009; Pineda et al., 2011; Carlton, unpublished, relative to its Asian origin). Harger's (1972a,b) work on the ecological interactions of two intertidal native mussels, *Mytilus edulis*, and *Mytilus californianus*, in southern California, we now know to be studies on the introduced mussel *Mytilus galloprovincialis* and the native species *M. californianus*. Eyebrow-raising is the resolution that the amphipod *Corophium volutator*, a species long known to be central to trophic dynamics and benthic processes in the Bay of Fundy, is in fact native to Europe (Einfeldt and Addison, 2015), having been introduced by shipping in the nineteenth century. Hair-raising is the discovery that the saltmarsh cordgrass *Spartina alterniflora*, a dominant member of the coastal marine flora of the Atlantic coast of North America, is also a nineteenth century invasion, leading to the conclusion that what were bare mudflats are now endless expanses of rooted vegetation that have led to "vast unrecorded and thus overlooked shifts in bird, fish and invertebrate biodiversity, and immense shifts in algal vs. detritus production, with the concomitant trophic cascades that these changes imply" (Bortolus et al., 2015).

These are only a few such examples. To our knowledge, few of these realizations that presumptive indigenous species are not native (thus leading to significant re-interpretations of the work conducted on the communities in question) are reflected in most broader (let alone textbook) treatments on the structure and function of marine ecosystems. This

illustrates the wider point, that failure to appropriately categorize taxa as either eu- or neocosmopolitan may guide researchers to inferences regarding community assembly, dispersal, and other critical ecological processes that rest on shifting sands. To continue to refer to all marine taxa with cosmopolitan distributions as merely “cosmopolitan” thus potentially obscures a conceptual distinction of critical importance.

PSEUDOCOSMOPOLITANISM: GENETIC EVIDENCE FOR CRYPTIC LINEAGES

The splintering of marine species into complexes of cryptic lineages is a common recent phenomenon, particularly among certain taxonomic groups (Nygren, 2014; Leray and Knowlton, 2016). Even when considering only the subset of species known to be anthropogenically introduced beyond their native ranges, examples abound of studies revealing previously unrecognized diversity. Table 2 provides a summary of over three dozen such studies; while not an exhaustive account, it represents a fair sampling of the breadth of evidence for cryptic diversity described in the invasion biology literature. Examples span 11 marine phyla, including both plants and animals, and are predictably dominated by groups well-known to harbor large numbers of introduced species.

Of the 38 species groups captured in Table 2, only 6 of them have been subjected to sufficiently rigorous integrated taxonomic analysis to allow resolution of cryptic status into multiple named species; these constitute examples of our Scenario III from Figure 1. The remainder, all investigated with molecular genetic approaches only (or including only superficial or limited non-genetic evidence), represent Scenario IV. As our collection has been neither exhaustive nor entirely systematic, it is difficult to say with confidence whether this ratio is representative of the state of the science or merely our own biased knowledge of the literature; however, we believe it likely that the literature is dominated largely by studies that introduce, rather than resolve, taxonomic uncertainty.

This pattern may be unsurprising, given the relative ease with which genetic data can be generated compared to the kind of information required to conduct integrated taxonomic revision of a species or species group. In the vast majority of cases, inference of multiple cryptic lineages from genetic data derives from one or very few standard genomic loci, most commonly those loci frequently adopted for DNA barcoding (Hajibabaei et al., 2007): mitochondrial loci such as cytochrome C oxidase subunit I (COI, 71% of cases in Table 2) and 16S (24%), the chloroplast marker RuBisCO (rbcL, 75% of plant taxa), or nuclear loci such as ribosomal 18S (13%), 28S (11%), or the internal transcribed spacer (ITS, 16%). Remarkably, over half of the taxa listed were investigated using only a single genetic marker, most often the “standard” animal barcode locus COI. This means that inference of evolutionary lineages perhaps deserving independent species status typically depends on one or very few lines of evidence, and almost universally on only two criteria: reciprocal monophyly (lineages form distinct branches with strong statistical support in phylogenetic trees) and average inter-lineage genetic distance greater than would be expected of intra-specific relationships.

These limitations may help explain the caution with which most molecular studies approach the task of declaring multiple cryptic species. Since the emergence of DNA barcoding as a powerful tool in molecular ecology and biodiversity studies, the connection between single-locus genetic divergence and species discovery has been fraught with controversy (Desalle et al., 2005). Most practitioners view such evidence as merely one small component of the much broader effort required to recognize novel species (Pante et al., 2015b). Nevertheless, information even from limited genetic surveys can sometimes be compelling. For instance, it is common practice to consider genetic divergence of approximately 3% at the COI locus to represent expected limits on intra-specific variation (Meyer and Paulay, 2005), despite some well-known exceptions (Huang et al., 2008). However, studies in Table 2 regularly report variation at the COI locus dramatically exceeding these limits: roughly 5% among specimens of the amphipod *Ampithoe valida* (Pilgrim and Darling, 2010), 8.4% in the sponge *Cliona celata* (Xavier et al., 2010), 12% for the hydroid *Cordylophora caspia* (Folino-Rorem et al., 2008), 18% in the ascidian *Botryllus schlosseri* (Yund et al., 2015), 20% in the ascidian *Diplosoma listerianum* (Perez-Portela et al., 2013), and 21% in the polychaete *Timarete punctata* (Seixas et al., 2017). For specimens ostensibly belonging to the same species these divergences range from the merely remarkable to the truly astounding. It is little wonder that they have been sufficient to raise the prospect of multiple species, notwithstanding evidence being limited in some cases to a single locus. Interestingly, in several of these cases additional, non-genetic lines of evidence have been shown to further support the hypothesis of multiple species. These cases inspire the suggestion that when multiple lineages are detected, reported lineage descriptions should include as many morphological, biological (reproductive, physiological, or other traits), or ecological characters as are known to the authors for each newly resolved lineage.

Still, in the absence of thorough taxonomic revision the preference has clearly been to maintain the observed cryptic entities as numbered or lettered lineages or clades, without attachment of binomial names. This is true even when data from multiple loci (derived, in many cases, from both mitochondrial and nuclear genomes) provide consistent evidence of evolutionarily divergent lineages.

WHAT'S IN A NAME? THE PROBLEM OF UNNAMED LINEAGES

This reluctance to attach names to cryptic lineages identified through molecular means alone is nearly universal. In some cases, practitioners of molecular genetic analysis—particularly those with appropriate systematic expertise within the groups being studied—may be bold enough to suggest outright the existence of unnamed new species (Mackie et al., 2006) or to refer genetic clades to previously existing species names (Teske et al., 2011). But in the vast majority of cases, molecular data result only in unresolved hypotheses of multiple species, particularly when associated morphological analysis was either not undertaken or failed to turn up any diagnostic features enabling more complete taxonomic revision. This creates a significant challenge for interpreting the cosmopolitan status of these species, now revealed to be potentially species complexes. The single species name persists, attached still to a distribution that is considered cosmopolitan. There is therefore no formal recognition of anything but a single cosmopolitan species, even though molecular data may suggest that the species actually represents a group of originally geographically restricted lineages (one or

more of which may then have been transported by human activity to other locations). This ambiguity—the lingering question of whether future analysis might provide sufficient data, morphological or otherwise, to resolve a cosmopolitan species into multiple species—leads us to characterize such species as pseudocosmopolitan, a designation reflecting the likelihood that the cosmopolitan distributions of these species are, at least in part, an artifact of overconservative taxonomy.

A number of the species cataloged in Table 2 provide especially compelling examples of this phenomenon. For example, analyses conducted by Bronstein et al. (2017) confirmed strong evidence of two largely geographically non-overlapping lineages of the widely distributed sea urchin *Diadema setosum*, “clade a” in the Indo-West Pacific and “clade b” in the Arabian Peninsula (with the latter introduced to the Mediterranean). These two clades exhibit sequence dissimilarity at the COI locus of approximately 8%, suggesting an estimated time of divergence 3–5 million years ago despite the lack of any as yet detected diagnostic morphological features (Lessios et al., 2001). Nevertheless, the species formally retains a distribution encompassing this entire range across multiple oceans. Figure 3 presents evidence from a particularly illustrative study revealing at least four genetic lineages of the globally distributed ascidian *Diplosoma listerianum* (Perez-Portela et al., 2013). One of these lineages, designated Clade A, exhibits a global distribution with a historical center in the British Isles (Figure 3A), and may represent a neocosmopolitan species. The remaining clades, however, have considerably more limited geographic ranges: Clades B and D apparently remain restricted to their native ranges in east Asia and the western Atlantic, respectively, while Clade C exhibits a disjunct distribution in South Africa and Panama. The hypothesis that these clades represent multiple species is supported by extraordinary genetic divergence, comparable with inter-specific distances observed in other colonial ascidians. Similar patterns of cosmopolitan “species” comprising provincial genetic lineages have been observed in isopods (Hurtado et al., 2018), polychaetes (Sun et al., 2017), and multiple hydrozoans (Miglietta et al., 2015; Govindarajan et al., 2017). In the absence of formal taxonomic revision, all of these species appear based on genetic evidence to harbor multiple lineages—possibly themselves all distinct species—that are most decidedly not cosmopolitan.

These examples reveal the importance of genetic data not only for identifying cryptic diversity, but also for attempting to disentangle complex invasion histories that are often very poorly documented in the historical record. Figure 1 registers these twin challenges associated with cryptic diversity—not only resolution of taxonomic identity, but also resolution of biogeographic history. The latter task can be extremely difficult depending on sample availability, marker resolution, and evolutionary history (Geller et al., 2010; Cristescu, 2015), resulting in many cases where biogeographic history may remain unsettled. For instance, the amphi-Atlantic distribution of *Diplosoma listerianum* Clade B could not be resolved based on existing genetic data, leaving unclear whether that lineage may be native to Panama or South Africa, or to neither of these locations (Perez-Portela et al., 2013); we note that a fourth choice, that Clade B may be native to both locations, is highly improbable, thus rendering this clade cryptogenic in its known locations.

Indeed, a large number of lineages identified across various efforts cataloged in Table 2 remain cryptogenic despite attempts to discern biogeographic patterns. Nevertheless, many studies have successfully resolved invasion histories for cryptic lineages emerging from genetic analysis. Sometimes a newly discovered lineage exhibits only a limited geographic distribution, in which case it is typically assumed to be a regional endemic (e.g., *D. listerianum* Clades B and D in Figure 3). However, often one or more novel lineages retains a cosmopolitan distribution, and the question then turns to the nature of that distribution, and whether it has been influenced by anthropogenic dispersal. As we have already noted, *D. listerianum* Clade A appears to be a globally distributed independent evolutionary lineage; similarly, Clade A of the polychaete *Hydroides dianthus* has been found in the northwest and southwest Atlantic, Mediterranean, and western Pacific (Sun et al., 2017); and Clade D of the isopod *Ligia exotica* may be native to East Asia but has been identified from South Africa, India, the western Atlantic, and Hawaii (Hurtado et al., 2018). In all cases, molecular genetic as well as historical evidence support the hypothesis that these clades represent as-yet unnamed neocosmopolitan species.

This clarity is obviously useful, but without taxonomic resolution these taxa should continue to be described formally as pseudocosmopolitan, given that demonstrably provincial lineages remain subsumed under the single accepted binomial. This categorization of these taxa is important for two reasons. First, attaching this category promotes much-needed transparency and broader recognition of the uncertainty concerning taxonomic status that now burdens numerous marine species. Adoption of a unified terminology to describe this condition may help us to better understand the extent to which it poses a challenge for marine biodiversity studies. Second, the pseudocosmopolitan label can serve as acknowledgement that even uncertainty may represent an improvement in our comprehension of marine biogeographic history. The conversion of “unknown unknowns” to “known unknowns” is progress, although it sometimes may not appear that way. In an ideal world, pseudocosmopolitan species do not remain in that category indefinitely.

SUCCESSFUL RESOLUTION OF TAXONOMIC UNCERTAINTY: A SUCCESS STORY AND A CAUTIONARY TALE

The fact that the uncertainty associated with pseudocosmopolitanism can be ultimately resolved by integrated taxonomic assessment is revealed by the existence of multiple species groups populating Scenario III. Of the six examples of such integrated assessments listed in Table 2, clearly the most exhaustive involves resolution of the globally introduced ascidian *Ciona intestinalis* into two sibling species, *C. intestinalis* and *C. robusta* (Figure 4). In addition to being recognized as a widely distributed marine pest with an extensive record of historical introductions, *C. intestinalis* has also long been embraced as a model organism due to its global availability, amenability to experimental manipulation, chordate body plan, and substantial molecular genetic resources, including a whole genome sequence completed in 2002 (Caputi et al., 2007). Early genomic analysis revealed unexpected divergence between individuals from Northern European and Pacific sources, suggestive of cryptic species (Suzuki et al., 2005). Ensuing genetic investigations based on multiple nuclear and mitochondrial markers as well as analysis of mitochondrial gene order further supported

recognition of two evolutionarily distinct lineages commonly labeled species A and species B (Caputi et al., 2007; Iannelli et al., 2007; Nydam and Harrison, 2007). Despite this wide-ranging and compelling molecular genetic evidence for multiple species, formal taxonomic revision of *C. intestinalis* failed to materialize until 2015. In that year, two publications thoroughly described morphological differences in both adult and larval specimens of sp. A and sp. B, and recognized diagnostic features previously associated with the Japanese species *C. robusta*, which had been synonymized with *C. intestinalis* (Brunetti et al., 2015; Pennati et al., 2015). The subsequent association of *C. robusta* with sp. A and *C. intestinalis* with sp. B completed the taxonomic resolution, and the acknowledged species-level distinction has since been further supported by experimental cross-breeding, although interspecific hybridization has been frequently observed (Malfant et al., 2018).

These extensive efforts undertaken to resolve taxonomic uncertainty have also been accompanied by comprehensive examination of introduction history for the two sibling species. Historical records suggest that *C. robusta*, the more broadly distributed species, has been introduced widely from its native range in east Asia to Australia and New Zealand, Europe (including the Mediterranean), South Africa, both coasts of South America, and western North America; *C. intestinalis* has been presumed native to the northeast Atlantic and either cryptogenic or introduced to the northwest Atlantic, and has also been introduced to China (Bouchemousse et al., 2016). The broad outlines of this historical picture have been roughly confirmed by genetic analysis. For *C. robusta*, observed patterns of genetic variation appear consistent with introductions to the northeast Pacific (including some evidence for multiple independent introductions), the southeast Pacific, and the northeast Atlantic (with genetic signatures of a more recent introduction to that region); populations from Australia and New Zealand were not examined in that study (Bouchemousse et al., 2016). The same study showed that for *C. intestinalis*, genetic evidence (though not unequivocal) was consistent with a natural amphi-Atlantic distribution of the species, with introduced populations in the Bohai and Yellow Seas. The current state of knowledge thus supports characterization of both *C. robusta* and *C. intestinalis* as neocosmopolitan species, i.e., taxa now occurring in multiple oceans. These results were consistent with an earlier 2010 study by Zhan et al. conducted prior to resurrection of *C. robusta* for sp. A. Interestingly, that earlier report suggested the existence of not only two, but rather four possible cryptic species, including a sp. D (apparent sister species to *C. robusta* and geographically restricted to the Black Sea) and sp. C (a rare and highly divergent lineage restricted to the Mediterranean). Thus, while the unambiguous association of sp. A with *C. robusta* and sp. B with *C. intestinalis* allows us to remove those species from the pseudocosmopolitan category, independent lineages C and D remain undescribed and attest to a measure of lingering uncertainty in this species group as a whole.

The case of *Ciona* is unusual in its comprehensiveness. But the considerable efforts devoted to disentangling the taxonomic and biogeographic mysteries of *C. intestinalis* offer a persuasive success story describing the resolution of pseudocosmopolitan status. They also sound an important cautionary note. It is significant that sp. A and sp. B did not receive proper names for a full decade after initial indications of likely cryptic species status. This was despite the fact that those 10 years witnessed proliferation of compelling genetic evidence for species-level divergence, driven in part by the availability of powerful

molecular resources. This plainly highlights the centrality of morphological evidence for resolving taxonomic uncertainty. Indeed, identification of diagnostic morphological traits traditionally remains the one principle requirement for erecting new species names, often even in the face of overwhelming non-morphological evidence for the existence of multiple species. This fact is convincingly revealed by those multiple species for which morphological examination could not identify such diagnostic features even when investigators were aware of divergent genetic lineages and thus knew where to look (Lessios et al., 2001; Xavier et al., 2010; Perez-Portela et al., 2013; Knapp et al., 2015); in such cases, the original single binomial has been universally retained. Not all taxa listed in Table 2 adhere to this narrative, as initial questions about cryptic diversity are not always broached by genetic studies. In many examples of Scenario III, for instance, genetic data are brought to bear in attempts to clarify relationships between previously observed morphotypes (Pfenninger et al., 2002; Vandepas et al., 2015; Tomioka et al., 2016). Nevertheless, the vast majority of our examples of pseudocosmopolitanism represent cases where genetic inference of cryptic lineages precedes availability of any suggestive morphological data.

With the growing accessibility of genetic data for non-model organisms and increasingly sophisticated methods for the analysis of such data, it is reasonable to suppose that even more studies in the future will uncover persuasive multilocus evidence for species-level distinctions. Given that the accessibility of expert morphological taxonomy may be on the reverse trajectory (Pearson et al., 2011; Carlton and Fowler, 2018), we anticipate a widening gulf between those taxa for which genetic evidence urges revision and those for which sufficient morphological data can be obtained to effect it. Indeed, this gulf is often reflected amongst ecologists, field biologists, and naturalists who shy away from working with taxa which have been discovered to be species complexes but are bereft of scientific names representing the distinct clades. We thus believe it important to raise the possibility of future efforts relying solely on genetic data to describe and name new species. Although this has a ring of heresy to it, the International Commission on Zoological Nomenclature has made it clear that “new species can be described on the basis of DNA,” with the caveat that the type specimen from which DNA is extracted should be retained and appropriately vouchered (International Commission on Zoological Nomenclature ICOZ, 2018). Recent studies have established precedent for erecting new species names based largely or entirely on genetic data, not only for microbial taxa known to resist morphological characterization (John et al., 2014) but also for large metazoan taxa (Leaché and Fujita, 2010; Jörger and Schrödl, 2013). While integrated taxonomic revision—incorporating genetics, morphology, ecology, and other lines of evidence (Sheth and Thaker, 2017)—ultimately remains the ideal for resolving the status of cryptic lineages, we feel that the sheer breadth of the challenge faced and the practical limitations on available data and expertise recommend consideration of all available solutions.

IMPLICATIONS FOR INCREASED RESOLUTION OF INTRODUCED AND CRYPTOGENIC SPECIES

As indicated in Figure 1, our changing knowledge of the taxonomic and biogeographic status of cosmopolitan taxa also has important implications for our general understanding of

introductions in marine systems. All possible outcomes of Scenario IV likely leave the number of known introduced species formally underestimated. Even when cryptic lineages can be convincingly identified as introduced in a region, the fact that they remain subsumed under a single original binomial masks the possibility that multiple introduced species exist where only one has been reported. This is true also of the case where taxonomy has been resolved, but biogeographic history—whether the species is native or introduced in a particular part of its range—remains uncertain. The abundance of such cryptogenic species has long been recognized as an indicator of our profound underestimation of human impacts on the composition of marine communities (Carlton, 1996), and more recent studies attest to the dramatic influence of cryptogenesis on our general understanding of coastal marine biogeography (Haydar, 2012).

The changing states of knowledge diagrammed in Figure 1 thus have implications not only for marine biodiversity studies, but also for management and policy related to marine bioinvasions. As biodiversity assessments including metrics reflecting the impacts of non-native species become more widely integrated into attempts to stay and reverse negative anthropogenic impacts on marine ecosystems (Darling et al., 2017), clear recognition of the uncertainties outlined in Figure 1—as well as approaches for their resolution—will no doubt become increasingly important.

ARE THERE ANY SHALLOW-WATER BENTHIC EUCOSMOPOLITAN SPECIES?

Marine taxa in at least three habitats are still commonly alleged to often include eucosmopolitanism species. Many *deep sea* species are held to be identical cosmotaxa in multiple ocean basins (Costello et al., 2017), an evolutionary outcome presumably driven by gene flow *via* global deep sea currents that serves to inhibit allopatric speciation. Similarly, species occurring in the *oceanic neustonic* habitat, including planktonic foraminifers (Darling et al., 2000) and pelagic invertebrates such as the gooseneck barnacle *Lepas anatifera*, the nudibranch *Fiona pinnata*, and the amphipod *Caprella andreae*, have long been held to be naturally cosmopolitan species. This said, genetic studies are now revealing that these neustonic taxa are species complexes (Cabezas et al., 2013; Schiffer and Herbig, 2016; Trickey et al., 2016), although other species of *Lepas*, including *L. anserifera* and *L. pectinata* “might represent true global species” (Schiffer and Herbig, 2016). For the latter, global homogenization over many centuries *via* vessel hull fouling may have contributed to what may in fact be neocosmopolitanism in these oceanic taxa (Carlton et al., 1995; Carlton, 2002). Finally, many species of *interstitial sandy beach meiofauna* were long considered cosmopolitan (Todaro et al., 1996; Curini-Galletti et al., 2012). Schmidt and Westheide (2000) concluded that the “cosmopolitan nature” of the meiofaunal polychaete *Hesionides arenaria* “has been confirmed at the DNA level,” being a single clade, while demonstrating that another presumably cosmopolitan worm, *Stygocapitella subterranea*, was composed of three distinct clades. However, the conclusion that *H. arenaria* is “cosmopolitan” was based upon the study of European and Washington USA populations, reflecting a well-known pattern of the apparently largely natural circumboreal distributions of many marine species in the North Pacific and North Atlantic. Gerlach (1977) has noted that the long history of

moving sand as ships' ballast around the world may have contributed to the perception of meiofauna cosmopolitanism; such taxa would now likely represent a broad mixture of introductions (neocosmopolitans) as well as pseudocosmopolitan and unresolved cosmopolitan species. These habitats aside, the question remains whether *any* shallow-water, benthic marine animal and plant, separated by continents and ocean basins, and in the absence of any data on their observed or potential for constant, consistent interoceanic rafting on natural materials, is eucosmopolitan. In this regard, for example, a very large number of what are said to be the same species of intertidal and shallow sublittoral algae (seaweeds) are reported from coastlines world-wide (<http://www.algaebase.org/>). None of these, to our knowledge, have been verified genetically as being eucosmopolitan.

This much, at least, is clear: it is far easier to find examples in the literature of neocosmopolitan and pseudocosmopolitan species than it is to find examples of presumed eucosmopolitan species that have withstood rigorous examination of their taxonomic and biogeographic status. There are two possible explanations for this observation. First, it may be that there is a bias among researchers (and possibly also editors) against publishing confirmation of eucosmopolitan status for species long assumed to be “natural” cosmopolitans. Under this hypothesis there may exist a large number of species for which considerable evidence exists supporting conspecificity across a cosmopolitan distribution, evidence that has not yet been made available in the peer-reviewed literature. If this is, indeed, the case, it is a problematic state of affairs in need of change. However, we find a second explanation much more likely: that most of the time, when workers take a closer look at a presumed eucosmopolitan species, it turns out either that it is a complex of evolutionary lineages masquerading as a single species, or that its broad distribution can be convincingly explained by anthropogenic dispersal.

We propose therefore, that there are likely no—or, at best, very few—eucosmopolitan neritic marine species. Rather, we predict that with morphological, genetic, historical, and related investigations (applying, in part, established criteria by which to distinguish native from non-native species as noted earlier) hundreds if not thousands of species of protists, invertebrates, and algae will prove to re-bin into neocosmopolitan, provincial, or pseudocosmopolitan categories. If the latter two, this is a further signal of the scale of underestimation of marine biodiversity. This hypothesis urges us, in the meantime, to describe what species remain as unresolved cosmopolitans. As noted previously, this category may encompass the vast majority of marine species to which are currently attributed cosmopolitan distributions.

THE WAY FORWARD

We offer here a framework that we believe accommodates most if not all circumstances that would explain why what are believed to be single species would occur in multiple oceans. Much work remains (see Box 2). Provincial (scenario III) species may yet be hidden within morphologically-determined neocosmopolitan (scenario II) taxa. Further resolution awaits a rapidly growing number of pseudocosmopolitan taxa; here, particularly pressing is that the proliferation of un-named lineages be steadily replaced with binomial nomenclature, with each named taxon delineated as clearly as possible by all available genetic, morphological,

ecological, and distribution data. Thousands of unresolved cosmopolitan species also await resolution. As new records of widespread species—both known invasions and those ostensibly “native”—are detected, and as undescribed widespread species are found, we urge that consideration be given to where such taxa fit into this new global framework. Assigning as many species (both fauna and flora) as possible in regional biotas into our five categories may reveal lacunae in our model. More importantly, from such regional work may arise a global understanding of the relative diversity—the weight, in a sense—of each scenario, and thus lead to a more sophisticated understanding of the past, present, and future of marine biodiversity.

ACKNOWLEDGMENTS

We are indebted to Agnese Marchini and Anna Occhipinti-Ambrogi for providing us this opportunity to synthesize and present our thoughts on cosmopolitan species in the ocean. We thank the American Association for the Advancement of Science for permission to reprint Figure 2A. We are grateful to three reviewers for comments that improved the manuscript. The United States Environmental Protection Agency, through its Office of Research and Development, supported the research described here. Though it has been subjected to Agency administrative review and approved for publication, its content does not necessarily reflect official Agency policy.

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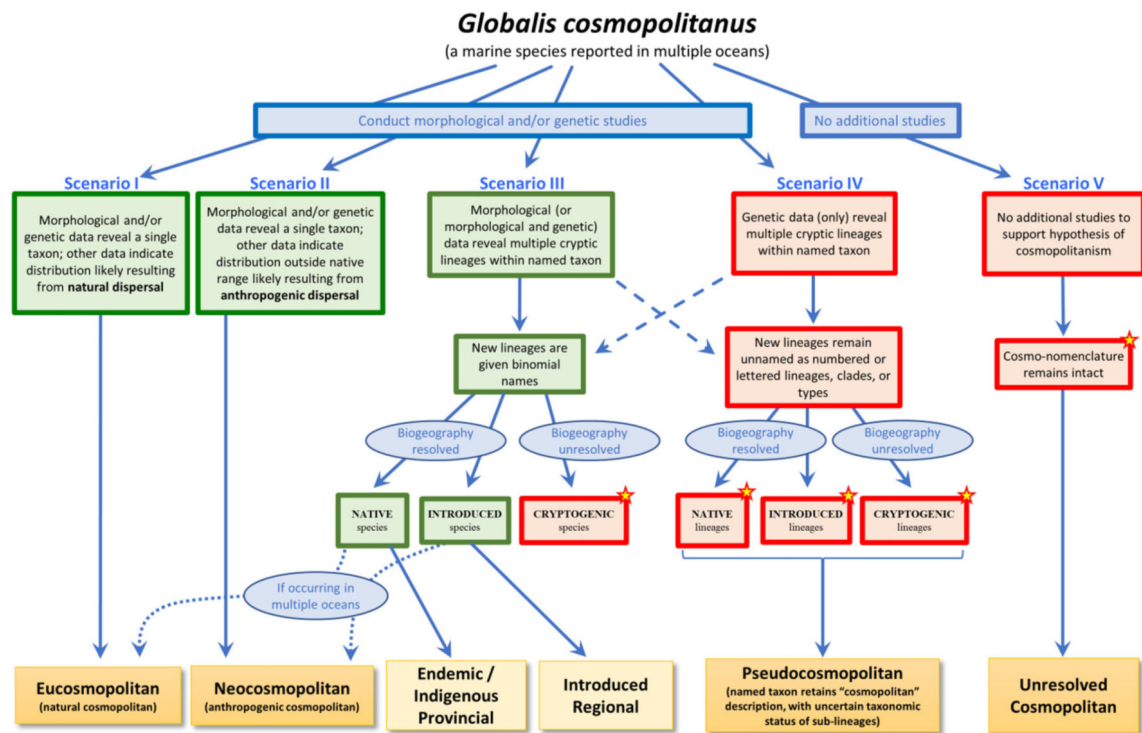
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BOX 1 |**Definitions.**

Term	Scenario (S), from Figure 1	Definition
Eucosmopolitan	S-I	Native species whose broad distribution in multiple oceans is attributed to natural processes acting over eco-evolutionary timescales
Neocosmopolitan	S-II	Introduced species that have achieved a widespread distribution in multiple oceans through anthropogenic (human-mediated) dispersal; an interoceanic invasion
Provincial	S-III	Native species either found nowhere else (endemic to, or in part of, a single province) or broadly distributed (indigenous; in one or more contiguous provinces); provinces as defined by (Spalding et al., 2007); (see also Pappalardo et al., 2015).
Introduced Regional	S-III	A species introduced outside of its native range but in the same ocean; an intraoceanic invasion
Pseudocosmopolitan	S-IV	A taxon composed of two or more lineages (which may be native, introduced, or cryptogenic) but retaining a single binomial name with an illusory “cosmopolitan” biogeographic status

BOX 2 |**Future research needs**

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- Investment in integrated taxonomic expertise, with emphasis on skillsets bridging morphological and genetic data generation and analysis
 - The development of novel criteria, and further elucidation of existing guidelines, for assignment of neocosmopolitan status based on history, distribution, association with anthropogenic vectors of introduction, etc.
 - Rigorous investigation of presumed neocosmopolitan species with suspicious distributions bridging cold temperate and deep tropical latitudes
 - Resolution of known pseudocosmopolitan taxa, replacing unnamed lineages with accepted binomials attached to diagnostic criteria accessible via morphological and/or genetic analysis
 - Investigation of methods for assigning species names to lineages determined solely by multilocus genetic evidence coupled with development of formally accepted protocols for making such assignments (including development of standard protocols for incorporating genetic evidence for divergent evolutionary lineages into widely accessible taxonomic descriptions)
 - Continued exploration of unresolved cosmopolitan species, with the aim of resolving taxonomic and biogeographic history sufficiently to assign provincial, neocosmopolitan, or eucosmopolitan status.
-

**FIGURE 1 |**

A framework for understanding the various types of cosmopolitanism. A species with an observed contemporary cosmopolitan distribution (the fictional *Globalis cosmopolitanus*, reported from multiple oceans) can fall into different categories depending on different trajectories of changing states of knowledge, represented by the five scenarios illustrated here. **Red boxes** indicate situations in which lineages are only identifiable by genetic means or otherwise remain unresolved either taxonomically or biogeographically; **green boxes** indicate situations in which lineages have binomial names and known biogeographic history. **Stars** identify those situations in which the number of introduced species is likely to be underestimated. **Dashed arrows** indicate the possibility that morphological and genetic data may not always result in new binomial names; similarly, genetic data alone may in rare cases be sufficient to erect new or resurrect old names. **Curved dotted arrows** reflect the possibility that newly identified species may still exhibit cosmopolitan distributions.

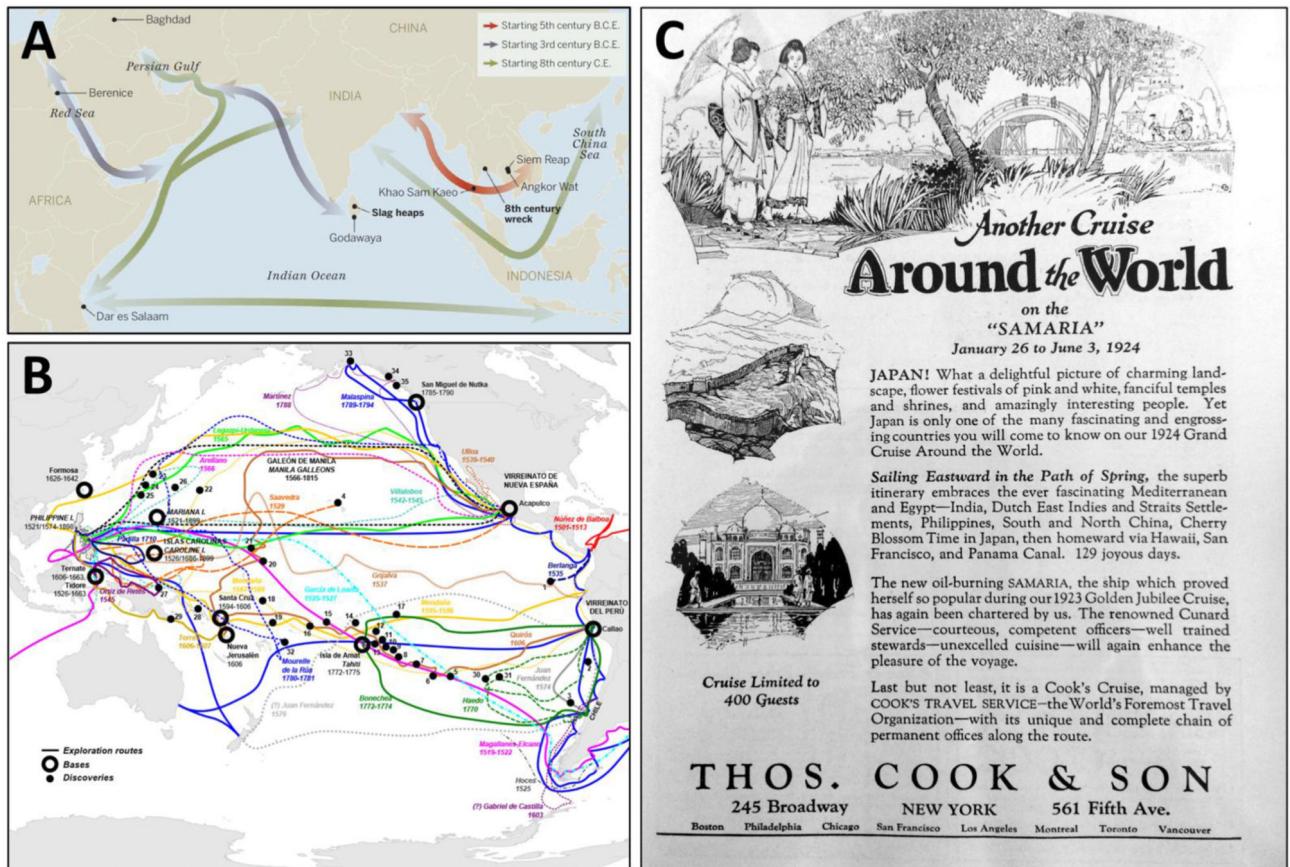


FIGURE 2 | (A) Shipping lanes of the “Maritime Silk Road,” starting in the fifth century B.C.E., connected the Red Sea to the South China Sea and beyond. From Lawler (2014); reprinted with permission from AAAS. (B) Spanish expeditionary routes and bases of exploration of the North and South Pacific Oceans over 240 years, touching virtually the entire Pacific rim from 1535 (to the Galapagos Islands) to 1775 (to the Alexander Archipelago, in what is now southeast Alaska). From <https://commons.wikimedia.org/wiki/File:SpanishPacific.svg>, open use without restriction through Wikimedia Commons (<https://creativecommons.org/licenses/by-sa/4.0>). (C) An advertisement for “Another cruise around the world” aboard the *Samaria* from January 26 to June 3, 1924 in “129 joyous days”: New York to the Mediterranean and Egypt through the Suez Canal to India, the Dutch East Indies and Straits Settlements (which included Singapore), Philippines, China, Japan, Hawaii, San Francisco, and then back to New York through the Panama Canal. From *National Geographic Magazine* 44(3), September 1923.

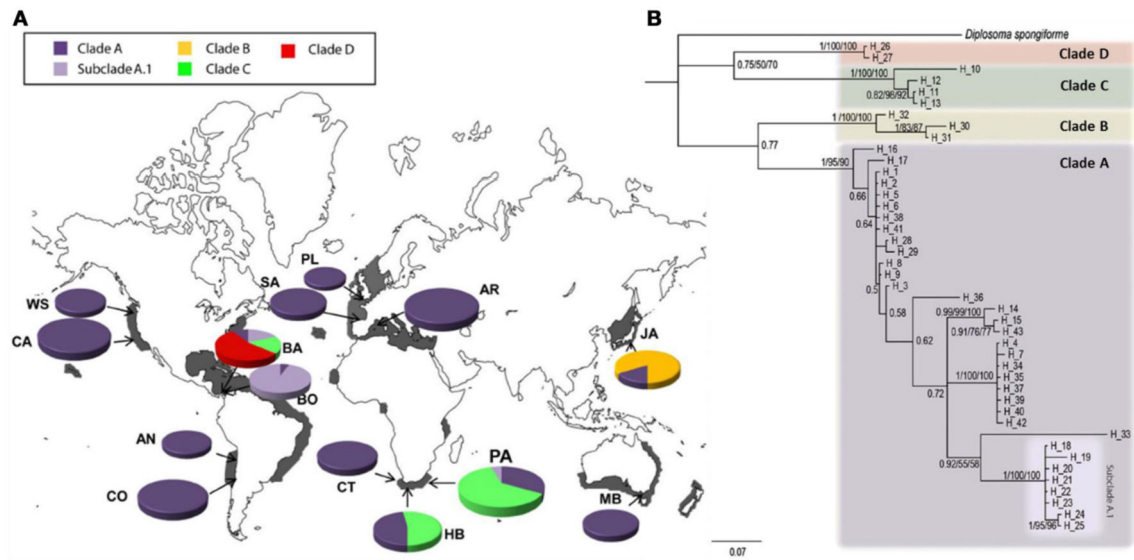
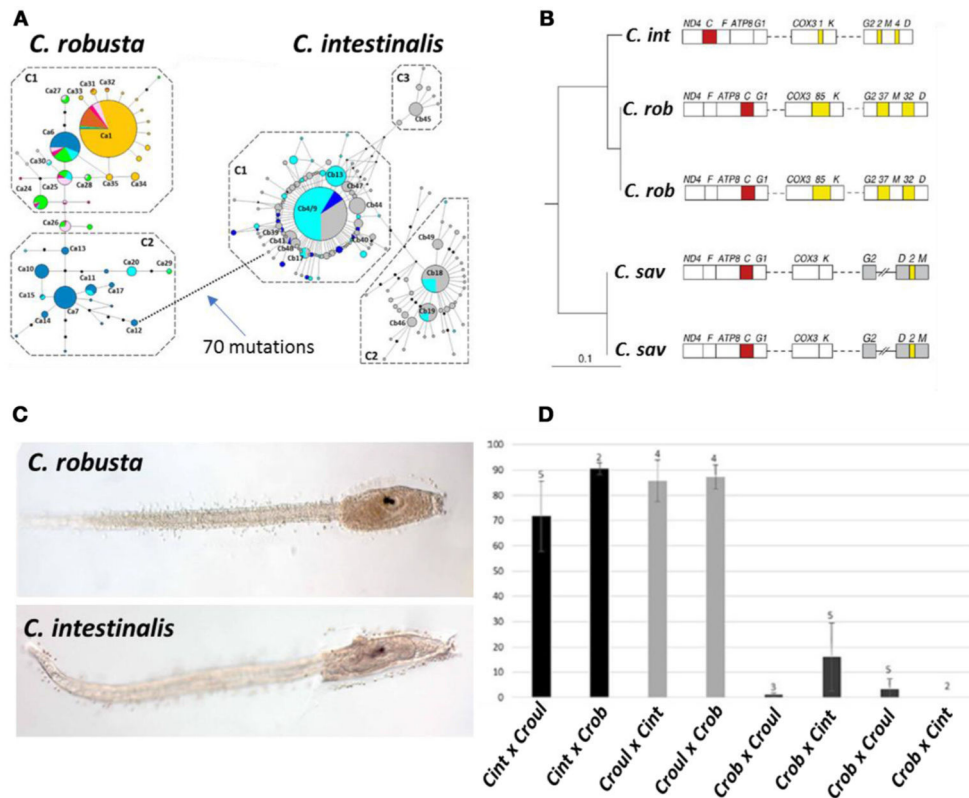


FIGURE 3 |

Geographic distributions of the multiple genetic lineages of the ascidian *Diplosoma listerianum*, from (Perez-Portela et al., 2013). **(A)** Global distributions of clades identified based on analysis of COI sequences. Clade A is widely dispersed, likely exhibiting a neocosmopolitan distribution, Clade B is cryptogenic, and Clades C and D display limited distributions consistent with provincial lineages. **(B)** Phylogenetic analysis revealing dramatic divergence between clades; interclade divergence was as great as 20% sequence dissimilarity at the COI locus, consistent with independent species status. Figures reprinted under the Creative Commons Attribution-Share Alike 4.0 International license.

**FIGURE 4 |**

Genetic, morphological, and reciprocal crossing evidence for species-level divergence between two lineages of the ascidian *Ciona intestinalis* (Type A and Type B). Figures are relabeled with the new names for these lineages, Type A = *C. robusta* and Type B = *C. intestinalis*. **(A)** Median-joining haplotype network based on COX3-ND1 sequences, showing 70 mutational steps between the two lineages; colors indicate geographic affinities, which are not shown (Bouchemousse et al., 2016). **(B)** Differences in gene order on the mitochondrial genomes of *C. intestinalis*, *C. robusta*, and *C. savigni* (Iannelli et al., 2007). **(C)** Larval morphology of the two species; a discriminant function obtained from larval measurements correctly classified >93% of larvae (Pennati et al., 2015). **(D)** Fertilization rate of heterospecific crosses between *C. intestinalis*, *C. roulei*, and *C. robusta*; homospecific crosses resulted in >80% fertilization rates for all species, but heterospecific crosses with *C. robusta* as the maternal lineage (listed first) showed extremely low success rates (Malfant et al., 2018). **(A,B,D)** Reprinted under the Creative Commons license (Attribution 4.0 International (CC BY 4.0)); **(C)** reprinted with permission.

TABLE 1 |

Examples of neocosmopolitan species fitting Scenario II from Figure 1.

Species group	Probable Origin	Morphological evidence for conspecificity?	Molecular evidence for conspecificity?	Molecular markers used	Citation(s)
ANNELIDA, POLYCHAETA (POLYCHAETE WORMS)					
<i>Polydora uncinata</i>	Unknown	✓	✓	ndNA (18S, 28S)	Sato-Okoshi et al., 2016
<i>Proscoplos cygnochaetus</i>	Unknown	✓	✓	ndNA (ITS)	Meyer et al., 2007
<i>Hydroides diramphus</i>	Western Atlantic?	✓			Carlton and Eldredge, 2009
<i>Myriamida pachycera</i>	Indo-West Pacific	✓	✓	Not specified	Nygren, 2004
ARTHROPODA, AMPHIPODA (AMPHIPODS)					
<i>Caprella mutica</i>	Northwest Pacific	✓	✓	mtDNA (COI)	Ashton et al., 2007, 2008; Boos et al., 2011
<i>Paracaprella pusilla</i>	Western Atlantic	✓			Ros et al., 2014
ARTHROPODA, CIRRIPIEDIA (BARNACLES)					
<i>Balanus glandula</i>	Northeast Pacific	✓	✓	mtDNA (COI), ndNA (EF1a)	Geller et al., 2008
<i>Amphibalanus improvisus</i>	Northwest Atlantic	✓	✓	mtDNA (COI), ndNA (msats)	Wrangle et al., 2016
<i>Amphibalanus eburneus</i>	Northwest Atlantic	✓			Carlton and Eldredge, 2009
ARTHROPODA, DECAPODA (CRABS AND SHRIMPS)					
<i>Carcinus maenas</i>	Northeast Atlantic	✓	✓	mtDNA (COI), ndNA (msats)	Darling et al., 2008
<i>Hemigrapsus sanguineus</i>	Northwest Pacific	✓	✓	mtDNA (COI), ndNA (msats)	Blakeslee et al., 2017
<i>Palaemon macrodactylus</i>	Northwest Pacific	✓	✓	mtDNA (COI)	Lejeune et al., 2014
ARTHROPODA, ISOPODA (ISOPODS)					
<i>Ianiropsis serricaudis</i>	Northwest Pacific	✓			Hobbs et al., 2015
<i>Sphaeroma walkeri</i>	Indian Ocean?	✓			Carlton and Iverson, 1981
<i>Paracerceis sculpta</i>	North Pacific Ocean?	✓			Marchini and Cardeccia, 2017
<i>Linnoria tripunctata</i>	Indo-Pacific?	✓			Carlton and Eldredge, 2009
BRYOZOA (BRYOZOANS)					
<i>Scopiadinipora costulata</i>	Unknown	✓			Hammelin et al., 2012
<i>Anathia verticillata</i>	Unknown	✓			McCann et al., 2015
CHLOROPHYTA (GREEN ALGAE)					
<i>Codium fragile fragile</i>	Northwest Pacific	✓	✓	cpDNA (msats and sequence markers)	Provan et al., 2005
CHORDATA, ASCIDIACEA (SEA SQUIRTS)					

Species group	Probable Origin	Morphological evidence for conspecificity?	Molecular evidence for conspecificity?	Molecular markers used	Citation(s)
<i>Botrylloides nigrum</i>	Atlantic Ocean	✓	✓	mtDNA (COI), nDNA (ANT)	Sheets et al., 2016
<i>Didemnum vexillum</i>	Northwest Pacific	✓	✓	mtDNA (COI), nDNA (tho2)	Stefaniak et al., 2009
<i>Molgula manhattensis</i>	Northwest Atlantic	✓	✓	mtDNA (COI)	Haydar et al., 2011
<i>Styela clava</i>	Northwest Pacific	✓	✓	mtDNA (COI)	Goldstien et al., 2011
CNIDARIA, ANTHOZOA (SEA ANEMONES)					
<i>Diadumene lineata</i>	Northwest Pacific	✓			Hancock et al., 2017
CNIDARIA, HYDROZOA (HYDROIDS)					
<i>Cladonema radiatum</i>	North Atlantic	✓			Carlton and Eldredge, 2009
<i>Bougainvillia muscus</i>	unknown	✓			Carlton and Eldredge, 2009 (but see Batisti and Gari 2015)
MOLLUSCA, BIVALVIA (OYSTERS, MUSSELS)					
<i>Crassostrea gigas</i>	Northwest Pacific	✓	✓	nDNA (msats)	Miller et al., 2012
<i>Musculista senhousia</i>	Northwest Pacific	✓	✓	mtDNA (COI)	Asif and Krug, 2012
MOLLUSCA, GASTROPODA (SNAILS)					
<i>Ocenebrellus inornatus</i>	Northwest Pacific	✓	✓	mtDNA (COI, 16S, 12S), allozymes	Martel et al., 2004
OCHROPHYTA (BROWN ALGAE)					
<i>Sargassum muticum</i>	Northwest Pacific	✓			Engelen et al., 2015
<i>Undaria pinnatifida</i>	Northwest Pacific	✓	✓	mtDNA (intergenic spacers)	Voisin et al., 2005; Uwai et al., 2006
RHODOPHYTA (RED ALGAE)					
<i>Gracilaria vermiculophylla</i>	Northwest Pacific	✓	✓	mtDNA (cox1), nDNA (msats, RAPDs)	Krueger-Hadfield et al., 2016
<i>Polysiphonia foetidissima</i>	unknown	✓	✓	cpDNA (rbcL)	D az-Tapia et al., 2013

Taxa are grouped and alphabetized at the phylum level; some phyla are broken into multiple groups at lower taxonomic levels. 33 species are listed across 9 marine phyla.

TABLE 2 |
 Examples of provincial native and regional introduced (Scenario III) and pseudocosmopolitan (Scenario IV) species.

Species group	Scenario	Morphological evidence of multiple lineages?	Molecular evidence of multiple lineages?	Molecular markers used	Taxonomic resolution?	Resolution of native/introduced status?	Citation(s)
ANNELIDA, CLITELLATA (CLITELLATE WORMS)							
<i>Tubificoides</i> spp.	IV	✓	✓	mtDNA A (COI, 16S, 12S), nDNA (28S, 18S, ITS)	Resolution of “phylogenetic species” including named species as well as 3 new cryptic lineages	Unknown native and introduced ranges; “overwhelming evidence that these taxa are ubiquitous, opportunistic worms that have become common in several coastal sediments”	Kvist et al., 2010
ANNELIDA, POLYCHAETA (POLYCHAETE WORMS)							
<i>Capitella teleta</i>	III	✓	✓	mtDNA (COI)	New name proposed for non-introduced lineage	Presumed native to northwest Pacific but introduced to Northwest Atlantic	Tomioka et al., 2016
<i>Eulalia clavigera</i>	IV	✓	✓	mtDNA (COI)	Second, undescribed lineage observed in the native Mediterranean range	Known introduction to Southwest Atlantic, presumed native to Mediterranean	Langeneck et al., 2018
<i>Ficopomatus enigmaticus</i>	IV	✓	✓	mtDNA (cytB), nDNA (iSSR)	Three lineages of <i>F. enigmaticus</i> identified, one with similarities to tropical <i>F. uschakovi</i>	Cryptogenic (previously presumed native) status of <i>F. enigmaticus</i> in Australia	Styan et al., 2017
<i>Hydroides dianthus</i>	IV	✓	✓	mtDNA (COI)	Second cryptic lineage of <i>H. dianthus</i> described	Native range in Atlantic North America, introduced broadly; second undescribed lineage native to Gulf of Mexico and introduced to Black Sea	Sun et al., 2017
<i>Marenzelleria viridis</i>	IV	✓	✓	mtDNA (16S)	Three cryptic lineages identified	All three lineages introduced to Europe from North America	Bastrop et al., 1998
<i>Timarete punctata</i>	IV	✓	✓	mtDNA (COI, 16S)	Two cryptic lineages identified; rough morphology suggests reference of Type A to Indo-Pacific material, Type B to Mediterranean	Broad global distribution of Type A and association with anthropogenic vectors leads to presumption of neocosmopolitan status, introduced in Atlantic from Indo-Pacific; unresolved status of Type B	Seixas et al., 2017
ARTHROPODA, AMPHIPODA (AMPHIPODS)							

Species group	Scenario	Morphological evidence of multiple lineages?	Molecular evidence of multiple lineages?	Molecular markers used	Taxonomic resolution?	Resolution of native/introduced status?	Citation(s)
<i>Ampithoe valida</i>	IV		✓	mtDNA (COI)	Three lettered clades identified	All clades presumed introduced to Pacific North America; unknown native source range, possibly NW Pacific or NW Atlantic	Pilgrim and Darling, 2010
<i>Grandidierella japonica</i>	IV		✓	mtDNA (COI)	Two lettered clades identified	Both clades presumed introduced to North America from native range in northwestern Pacific	Pilgrim et al., 2013
<i>Jassa marmorata</i>	IV		✓	mtDNA (COI)	Unnamed <i>Jassa</i> sp. identified	Unclear status of multiple species in northwest Atlantic; one lineage cryptogenic	Pilgrim and Darling, 2010
ARTHROPODA, CIRRIPIEDIA (BARNACLES)							
<i>Megalbalanus coccopoma</i>	IV		✓	mtDNA (COI, 16S)	Multiple lineages, including a second species introduced to US which remains unnamed	<i>Codylophora</i> caspiain northeast Pacific	Cohen et al., 2014
Arthropoda, Isopoda (isopods)							
<i>Ligia exotica</i>	IV		✓	mtDNA(16S), nDNA (12S, NaK)	Several highly divergent lettered lineages identified	Highest diversity observed in presumed native range in East and Southeast Asia; only one lineage has spread widely from that region	Hurtado et al., 2018
<i>Sphaeroma terebrans</i>	IV		✓	mtDNA (COI)	Multiple unnamed clades of <i>S. terebrans</i> , consistent with some observations of morphological differentiation	Limited sampling preclude strong inference of biogeography for different clades	Baratti et al., 2005
BRYOZOA (BRYOZOANS)							
<i>Membranipora membranacea</i>	IV		✓	mtDNA (COI)	Three unnamed clades in the northwest Pacific	Evidence for both ancient residence of some lineages and recent genetic mixing likely associated with human vectors; incomplete resolution of native/non-native status for all lineages	Schwaminger, 2008
<i>Bugula neritina</i>	IV		✓	mtDNA (COI, 16S), nDNA (DYN, VDAC)	Three lettered types identified, corresponding to unnamed separate species based solely on genetic evidence	North American native ranges of all three types identified; two appear to have spread broadly by anthropogenic means	Davidson and Haygood, 1999; Fehlauer-Ale et al., 2014

Species group	Scenario	Morphological evidence of multiple lineages?	Molecular evidence of multiple lineages?	Molecular markers used	Taxonomic resolution?	Resolution of native/introduced status?	Citation(s)
<i>Watersipora subtorquata</i>	IV		✓	mtDNA (COI)	Two lettered clades of <i>W. subtorquata</i> , as well as a new unnamed species	Native origins of unnamed <i>W. new sp. is unclear</i> ; presumed native range of <i>W. subtorquata</i> is Brazil, but that species appears to have been replaced in that range by another species and origins of unnamed clades are unknown	Mackie et al., 2006, 2012
CHLOROPHYTA (GREEN ALGAE)							
<i>Caulerpa taxifolia</i>	IV		✓	nDNA (ITS)	Two incipient species of <i>C. taxifolia</i> presumed (coastal and clear-water)	Multiple non-native aquarium strains identified and sourced to Australia, but native range presumed to be pan-tropical; unclear if native biogeography differs between unnamed lineages	Meunier et al., 2004
<i>Ulva spp.</i>	III	✓	✓	cpDNA (rbcL)	Identification of lineages with affinities to three different genera, morphological data alone insufficient to distinguish many species	At least five species likely introduced to New Zealand, others likely indigenous	Heesch et al., 2009
CHORDATA, ASCIDIACEA (SEA SQUIRITS)							
<i>Botryllus schlosseri</i>	IV		✓	mtDNA (COI)	Five lettered clades identified; clade A referred to <i>B. schlosseri</i> after designation and description of a Mediterranean neotype	Evidence of a clade native to the northwest Atlantic, where the species was previously described as introduced; evidence also of bi-directional introductions across the Atlantic	Yund et al., 2015; Brunetti et al., 2017
<i>Ciona intestinalis</i>	III	✓	✓	nDNA (ITS, Hox introns/exons), mtDNA (COI), microsatellites, mtDNA gene order	Two lettered types assigned to <i>C. intestinalis</i> and <i>C. robusta</i> based on morphological and genetic evidence as well as cross-breeding experiments	Neocosmopolitan distributions of <i>C. robusta</i> native to east Asia introduced to Australia/New Zealand, Europe, South Africa and South and North America, and of <i>C. intestinalis</i> native to Europe and introduced to China,	Suzuki et al., 2005; Caputi et al., 2007; Iannelli et al., 2007; Nydam and Harrison, 2007; Zhan et al., 2010; Brunetti et al., 2015; Pennati et al., 2015; Bouchemousse et al., 2016; Malfant et al., 2018
<i>Diplosoma listerianum</i>	IV		✓	mtDNA (COI)	Four lettered clades of <i>D. listerianum</i> identified; no diagnostic morphological features could be identified; clade A referred as <i>D. listerianum</i> , since this is the	Genetic data insufficient to identify native/introduced ranges for various clades	Perez-Portela et al., 2013

Species group	Scenario	Morphological evidence of multiple lineages?	Molecular evidence of multiple lineages?	Molecular markers used	Taxonomic resolution?	Resolution of native/introduced status?	Citation(s)
<i>Phaiusia nigra</i>	III	✓	✓	mtDNA (cox B), nDNA (18S)	only clade present in Europe and the type locality is Britain Genetic clades referred to existing names	Some presumed non-native occurrences of <i>P. nigra</i> shown to be mistaken, while <i>P. philippinensis</i> is widespread	Vandepas et al., 2015
<i>Pyura stolonifera</i>	IV		✓	mtDNA (COI), nDNA (18S, ATP synthase subunit alpha, Adenine Nucleotide Transporter)	Five distinct initially unnamed "species" identified from global material referred to <i>P. stolonifera</i> ; subsequently studied morphologically and given binomial names	Resolved lineages include endemic, introduced regional, and neocosmopolitan species	Rius and Teske, 2011, 2013; Teske et al., 2011
<i>Styela plicata</i>	IV		✓	mtDNA (COI)	One lineage of <i>S. plicata</i> identified as highly divergent	Hypothesized native range in northwest Pacific center of diversity	De Barros et al., 2009
CNIDARIA, ANTHOZOA (CORALS)							
<i>Carthoja riisei</i>	IV		✓	mtDNA (ND2, ND6), nDNA (SRP)	Genetic evidence for multiple unnamed lineages; "unresolved taxonomy likely plays a role in the broad reports of spread for <i>C. riisei</i> "	Introduction to Hawaii from Caribbean source contradicted by genetic data, but non-native status in Hawaii confirmed by historical evidence; origins of various lineages remain unclear	Concepcion et al., 2008
CNIDARIA, HYDROZOA (HYDROIDS)							
<i>Cordytophora caspia</i>	IV		✓	nDNA (28S), mtDNA (16S, COI)	Four numbered and lettered clades identified; possible reference of two major clades to <i>C. caspia</i> and <i>C. lacustris</i>	Poor sampling in presumed native range precludes strong inference of native range, but almost certainly introduced to North America	Folino-Rorem et al., 2008
<i>Gonionemus vertens</i>	IV		✓	mtDNA (COI)	Two widely divergent unnamed clades	Genetic data consistent with multiple possible biogeographic scenarios	Govindarajan et al., 2017
<i>Pennaria disticha</i>	IV		✓	mtDNA (16S)	Multiple divergent unnamed lineages, three in Hawaii	Three lineages in Hawaii rather than one introduced species; two likely introduced, one either introduced or eucosmopolitan; native sources of lineages unclear	Miglietta et al., 2015
CNIDARIA, SCYPHOZOA (JELLYFISH)							
<i>Cassiopeia</i> spp.	IV		✓	mtDNA (COI)	Multiple highly diverged lineages as well as shared haplotypes between putative	Multiple introductions to Hawaii suggested, but native/	Holland et al., 2004

Species group	Scenario	Morphological evidence of multiple lineages?	Molecular evidence of multiple lineages?	Molecular markers used	Taxonomic resolution?	Resolution of native/introduced status?	Citation(s)
ECHINODERMATA, ECHINOIDEA (SEA URCHINS)							
<i>Diadema setosum</i>	IV	✓	✓	mtDNA (COI), nDNA (LYS)	Evidence for two divergent lettered clades	Lineages have non-overlapping distributions, one in the Red Sea and Persian Gulf, likely introduced to Mediterranean via the Suez Canal	Bronstein et al., 2017
ECHINODERMATA, OPHIUROIDEA (BRITTLE STARS)							
<i>Ophiactis savignyi</i>	IV	✓	✓	mtDNA (COI)	Two divergent lettered lineages	Atlantic lineage A highly diverged from Pacific specimens, likely ancestral isolation by formation of isthmus of Panama; Atlantic lineage B more widespread and likely recently introduced from Pacific	Roy and Sponer, 2002
MOLLUSCA, BIVALVIA (CLAMS, MUSSELS)							
<i>Corbicula spp.</i>	III	✓	✓	mtDNA (COI), nDNA (ITS)	Two distinct genetic lineages with statistically distinguishable morphotypes identified	Precise geographical origin of lineages (all presumed Asian) remains unknown	Pfenninger et al., 2002
<i>Mytilus edulis</i>	III	✓	✓	mtDNA (16S), allozymes	Worldwide <i>M. edulis</i> split into three species, <i>M. edulis</i> , <i>M. trossulus</i> , <i>M. galloprovincialis</i>	<i>M. edulis</i> defined as North Atlantic native, <i>M. trossulus</i> as North Pacific native, <i>M. galloprovincialis</i> rooted in Mediterranean with neocosmopolitan distribution	McDonald and Koehn, 1988; Geller et al., 1994; Hilbish et al., 2000
OCHROPHYTA (DIATOMS)							
<i>Paralia spp.</i>	IV	✓	✓	nDNA(18S, ITS)	Genetic data separate two species, <i>P. guyana</i> and <i>P. marina</i> ; only some lineages of <i>P. guyana</i> could be distinguished morphologically from <i>P. marina</i> , so the species remain morphologically cryptic	<i>P. guyana</i> restricted to North America but present on both Pacific and Atlantic coasts, <i>P. marina</i> widespread globally; both species identified in ballast water samples; unknown native/introduced ranges	Macgillivray and Kaczmarek, 2015
PORIFERA (SPONGES)							

Species group	Scenario	Morphological evidence of multiple lineages?	Molecular evidence of multiple lineages?	Molecular markers used	Taxonomic resolution?	Resolution of native/introduced status?	Citation(s)
<i>Cliona celata</i>	IV		✓	mtDNA (COI, Atp8), nDNA (28S)	Evidence for four morphologically indistinct species	Evidence of indigenous status for multiple clades, but possibility that some may be introduced	Xavier et al., 2010
<i>Haliclona caerulea</i>	IV		✓	mtDNA (COI, COlex, rnl), nDNA(18S)	Morphologically indistinguishable specimens can be highly diverged, as many as 12 geographically restricted subclades	Evidence of contemporary introduction of one clade from Caribbean to Hawaii, but detailed invasion history unclear	Knapp et al., 2015
RHODOPHYTA (RED ALGAE)							
<i>Asparagopsis taxiformis</i>	IV		✓	nDNA (28S), cpDNA (rbcL), mtDNA (intergenic spacer)	Five lineages identified for <i>A. taxiformis</i> , and a new lineage reported for sister species <i>A. armata</i>	New <i>A. armata</i> clade has regionally restricted distribution in Australasia; new clade of <i>A. taxiformis</i> with restricted distribution in Southeast Asia; all other clades of <i>A. taxiformis</i> widespread	Andreakis et al., 2007; Sherwood, 2008; Dijoux et al., 2014
<i>Neosiphonia</i> spp.	IV		✓	mtDNA (COI), nDNA(ITS), and cpDNA(rbcL)	Identification of two species and resurrection of a third based solely on genetic data	<i>N. harveyi</i> identified as native and restricted to western Atlantic, <i>N. japonica</i> and resurrected <i>Polysiphonia akkeshiensis</i> introduced and occurring in multiple oceans (neocosmopolitan)	Savoie and Saunders, 2015

Taxa are grouped and alphabetized at the phylum level; some phyla are broken into multiple groups at lower taxonomic levels. 38 total species groups are listed across 11 marine phyla.