



Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective

Sarah A. Bailey¹ | Lyndsay Brown² | Marnie L. Campbell³ | João Canning-Clode^{4,5} | James T. Carlton⁶ | Nuno Castro⁴ | Paula Chainho⁷ | Farrah T. Chan¹ | Joel C. Creed⁸ | Amelia Curd⁹ | John Darling¹⁰ | Paul Fofonoff⁵ | Bella S. Galil¹¹ | Chad L. Hewitt¹² | Graeme J. Inglis¹³ | Inti Keith¹⁴ | Nicholas E. Mandrak¹⁵ | Agnese Marchini¹⁶ | Cynthia H. McKenzie¹⁷ | Anna Occhipinti-Ambrogi¹⁶ | Henn Ojaveer^{18,19} | Larissa M. Pires-Teixeira^{7,20} | Tamara B. Robinson²¹ | Gregory M. Ruiz¹⁰ | Kimberley Seaward¹³ | Evangelina Schwindt²² | Mikhail O. Son²³ | Thomas W. Therriault²⁴ | Aibin Zhan²⁵

¹Great Lakes Laboratory for Fisheries and Aquatic Sciences, Burlington, ON, Canada

²Marine Lab, Marine Scotland Sci, Aberdeen, UK

³School of Life and Environmental Science, Deakin University, Geelong, Vic., Australia

⁴MARE – Marine and Environmental Sciences Centre, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (ARDITI), Madeira Island, Portugal

⁵Smithsonian Environm Res Ctr, Edgewater, MD, USA

⁶Maritime Studies Program, Williams College – Mystic Seaport, Mystic, CT, USA

⁷Faculdade de Ciências, MARE – Marine and Environmental Sciences Centre, Universidade de Lisboa, Lisbon, Portugal

⁸Departamento de Ecologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

⁹Ifremer, DYNECO, Centre Ifremer de Bretagne, Plouzané, France

¹⁰Center for Environmental Measurement & Modeling, United States Environmental Protection Agency, Research Triangle Park, NC, USA

¹¹The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

¹²Harry Butler Institute, Murdoch University, Murdoch, 6150, Western Australia, Australia

¹³National Institute of Water & Atmospheric Research Ltd., Christchurch, New Zealand

¹⁴Charles Darwin Research Station, Charles Darwin Foundation, Santa Cruz, Galapagos, Ecuador

¹⁵University of Toronto Scarborough, Toronto, ON, Canada

¹⁶Department of Earth & Environmental Sciences, University of Pavia, Pavia, Italy

¹⁷Northwest Atlantic Fisheries Centre, Fisheries & Oceans Canada, St John's, NL, Canada

¹⁸Pärnu College, University of Tartu, Pärnu, Estonia

¹⁹National Institute of Aquatic Resources, Technical University of Denmark, Kgs. Lyngby, Denmark

²⁰Programa de Pós-Graduação em Ecologia e Evolução, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

²¹Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University, Stellenbosch, South Africa

²²Instituto de Biología de Organismos Marinos (IBIOMAR-CONICET), Puerto Madryn, Argentina

²³Institute of Marine Biology, NAS of Ukraine, Odessa, Ukraine

²⁴Pacific Biological Station, Fisheries & Oceans Canada, Nanaimo, BC, Canada

²⁵Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China

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Correspondence

Sarah A. Bailey, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries & Oceans Canada, 867 Lakeshore Road, Burlington, ON, L7S 1A1, Canada.
Email: sarah.bailey@dfo-mpo.gc.ca

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Abstract

Aim: The introduction of aquatic non-indigenous species (ANS) has become a major driver for global changes in species biogeography. We examined spatial patterns and temporal trends of ANS detections since 1965 to inform conservation policy and management.

Location: Global.

Methods: We assembled an extensive dataset of first records of detection of ANS (1965–2015) across 49 aquatic ecosystems, including the (a) year of first collection, (b) population status and (c) potential pathway(s) of introduction. Data were analysed at global and regional levels to assess patterns of detection rate, richness and transport pathways.

Results: An annual mean of 43 (± 16 SD) primary detections of ANS occurred—one new detection every 8.4 days for 50 years. The global rate of detections was relatively stable during 1965–1995, but increased rapidly after this time, peaking at roughly 66 primary detections per year during 2005–2010 and then declining marginally. Detection rates were variable within and across regions through time. Arthropods, molluscs and fishes were the most frequently reported ANS. Most ANS were likely introduced as stowaways in ships' ballast water or biofouling, although direct evidence is typically absent.

Main conclusions: This synthesis highlights the magnitude of recent ANS detections, yet almost certainly represents an underestimate as many ANS go unreported due to limited search effort and diminishing taxonomic expertise. Temporal rates of detection are also confounded by reporting lags, likely contributing to the lower detection rate observed in recent years. There is a critical need to implement standardized, repeated methods across regions and taxa to improve the quality of global-scale comparisons and sustain core measures over longer time-scales. It will be fundamental to fill in knowledge gaps given that invasion data representing broad regions of the world's oceans are not yet readily available and to maintain knowledge pipelines for adaptive management.

KEYWORDS

aquatic non-indigenous species, biological invasions, detection rate, inventory, long-term dataset, population status, richness, spatial patterns, temporal trends, transport pathways

1 | INTRODUCTION

Analyses of long-term datasets on species introductions can provide insights into past and future trends to inform conservation management (Seebens et al., 2017; van Kleunen et al., 2015), yet such studies are relatively rare, particularly for aquatic ecosystems where species introductions are often more difficult to detect and study (Ojaveer et al., 2015). A recent study examining more than 45,800 records of mainly terrestrial non-indigenous taxa showed a continuous rise in the rate of detection during the time period 1800–2000 and a strong correlation between detection rates and trade values for taxa associated with transport pathways (Seebens et al., 2017). Moreover, the growth of trade and worldwide transport of goods

by shipping is predicted to lead to a surge in the translocation of both terrestrial taxa (as stowaways in cargo and packing materials) and marine taxa (within ships' ballast water and biofouling) (Sardain et al., 2019). Despite the expected surge in species delivery to novel aquatic ecosystems, prior studies examining detection rates and/or pathways of aquatic non-indigenous species (ANS) have been conducted at local or regional scales (e.g. Galil, 2009; Katsanevakis et al., 2013; Ojaveer et al., 2017) and/or have focused on a single taxonomic group (e.g. Carlton, 2011; Darrigran et al., 2020). As introductions of many different ANS have occurred and continue to occur worldwide, studies are needed at a global scale to provide a robust understanding of invasion dynamics, identify needed management strategies and evaluate policy effectiveness in aquatic ecosystems.

The introduction of species across biogeographic barriers by human activities is a key component of global biodiversity loss and subsequent environmental change (Lewis & Maslin, 2015; Pyšek et al., 2020; Simberloff et al., 2013). The importance of coastal marine diversity was highlighted as part of the Convention on Biological Diversity (CBD) Ministerial Statement at the Conference of the Parties meeting in Jakarta in 1995 (the Jakarta Mandate) (UNEP, 2000). It is widely accepted that management of non-indigenous species introductions should be based on the precautionary approach and focus primarily on management of invasion pathways (e.g. Finnoff et al., 2007; Hewitt, Willing, et al., 2004; Lodge et al., 2016). In recognition of the urgent need to address the impacts of non-indigenous species, the CBD states that each contracting party shall, as far as possible and as appropriate, “prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species” (UNEP, 1994). The CBD revised Strategic Plan for 2011–2020 proposes that “By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment” (UNEP, 2011). New goals for 2021–2030 are currently being drafted, with prevention and pathway management likely to remain important components of the strategy.

Despite efforts to establish reporting mechanisms (e.g. Pagad et al., 2018), reliable inventories worldwide of non-indigenous species and their pathways are still relatively few in the published literature, especially for aquatic environments. Here, we assembled an extensive dataset of first records of detection of ANS to assess patterns of detection rate, richness, population status and transport pathways during a 50-year time period across 49 global ecosystems, including marine and estuarine habitats as well as the freshwater Laurentian Great Lakes. This synthesis is intended to provide a baseline of current knowledge, a baseline largely built on a multi-decade and perhaps in some cases a century or more, backlog of undetected invasions, to identify and support prioritization of pathways and to guide recommendations for policy and management in support of biological conservation objectives.

2 | METHODS

We assembled an extensive dataset of primary detection events of ANS (i.e. the first recorded collection of each species in each region) across global (primarily coastal marine, but also estuarine and freshwater) aquatic ecosystems for the period 1965–2015 using online ANS databases as primary data sources, including AquaNIS (<http://www.corpi.ku.lt/databases/index.php/aquanis/>), GLANSIS (<https://www.glerl.noaa.gov/glansis/>), Marine Biosecurity Porthole (<https://www.marinebiosecurity.org.nz/>) and NEMESIS (<http://invasions.si.edu/nemesis/>). In addition, we conducted a literature search using the Web of Science to locate published datasets not available online, using the search terms “nonindigenous” or “non-indigenous” or “nonnative” or “non-native” or “alien” AND “aquatic” or “marine”

AND “database” or “dataset” or “list” or “inventory”. Datasets were included only if dedicated, expert research on ANS had been conducted such that an up-to-date comprehensive and reliable inventory exists; datasets comprised of only a single taxonomic group, or not listing dates of first collection, or covering a shorter time period than this analysis were not included. As the geographic scale of different studies varied, we compiled data at the scale of Large Marine Ecosystem (Sherman, 1991; <http://lme.edc.uri.edu>), but also included available data for smaller marine ecosystems (i.e. Galápagos Islands and Madeira Archipelago). We excluded records from inland or freshwater habitats but included the Laurentian Great Lakes as a large freshwater ecosystem accessible to global shipping (Pagnucco et al., 2015).

At least one co-author with extensive regional knowledge of ANS carefully reviewed and edited each regional dataset for accuracy, checking scientific peer-reviewed publications, reports, books and personal collections to confirm: (a) year of first collection; (b) current population status and; (c) potential pathway(s) of introduction (as known up to July 15, 2020; Table 1). Records were compiled only for ANS collected from the natural environment while those reported exclusively on or within pathways were excluded (e.g. taxa sampled during surveys of ships’ ballast water and biofouling, tsunami debris and other marine litter). Only species considered fully aquatic were counted, including marine stenohaline, marine euryhaline, diadromous and freshwater euryhaline species, but excluding, for example, shoreline plants and aquatic birds. Freshwater stenohaline species were included for the Laurentian Great Lakes and Baltic Sea but excluded from all other estuarine and marine ecosystems as being “inland” introductions. We also excluded records for cryptogenic species (whose status as indigenous or non-indigenous is unresolved) and taxa poorly studied or otherwise presenting challenges for taxonomic identification and assessment of historical biogeographic origin (e.g. fungi, protists, parasitic and free-living flatworms, viruses and microbes). Scientific names of ANS were standardized according to the Integrated Taxonomic Information System (www.itis.gov), the World Register of Marine Species (www.marinespecies.org) or AlgaeBase (www.algaebase.org), or more recent literature when available.

We acknowledge that the date of first collection is likely to lag behind the actual date of introduction and that we do not know for most of these species when the introduction occurred nor when a reproducing population became established. The majority of the records analysed here resulted from the onset of ANS inventories that by and large did not commence worldwide until the last decades of the 20th century, thus resulting in first reports of species that may have been present much earlier. For example, of the 141 ANS species reported from Hawaii between 1965 and 2015, at least 101 may have been present prior to World War II, and many could have arrived in the 19th century; more than half of the remaining 40 species likely arrived after WWII but prior to 1965 (J. T. Carlton, Williams College—Mystic Seaport, personal communication). We thus take a conservative approach and define the date of first record as the *date of detection*, thus yielding a *detection rate*, rather than an introduction

TABLE 1 Categories and definitions of population status and pathways utilized in the analyses

Population Status ^a	Definition	
Established	Species has been repeatedly collected and/or there is evidence of successful reproduction (found in two separate locations or in two collections in separate years in the same location)	
Extinct	Reproducing populations appear to have existed in a location for a length of time but appear to have subsequently died out	
Failed	Species was introduced to a location, but there was no evidence of any prolonged survival or reproduction	
Unknown	Insufficient data to assign to one of the above three categories	
Pathways ^b	Sub-pathways ^b	Description
Corridor	Interconnected Waterways/ Basins/Seas	Species spreading to new regions along infrastructure such as canals or other artificial waterways interconnecting previously unconnected water bodies, basins and seas
Escape from confinement	Aquaculture/Mariculture	Species that have escaped from confinement or controlled situations in either freshwater or marine environments to produce food or other agricultural type products including bioenergy products
	Botanical garden/zoo/aquaria	Species that have escaped from confinement and that were kept for public display, public education or conservation breeding programmes
	Horticulture	Species that have escaped from confined or controlled environments where they were commercially cultivated for purposes other than aquaculture/mariculture
	Live food and live bait	Species that have escaped from confinement or controlled environments where they were kept and/or transported as live food or live bait
	Ornamental	Species that have escaped from confined or controlled environments where they were introduced for decorative or ornamental reasons excluding commercial horticulture
	Pet/Aquarium Species	Species that have escaped confinement or controlled environments where they were kept by private collectors or hobbyists for recreation
	Research	Species that have escaped confinement or controlled environments where they were kept and/or bred for use in research
Release in nature	Biological Control	Species released into the (semi)natural environment with the purpose of controlling the population(s) of one or more organisms
	Erosion Control	Species released into the (semi)natural environment to control the environment or to act as physical barriers
	Fishery in the Wild	Fish and other aquatic animals (e.g. invertebrates) released into the (semi)natural environment to provide additional or alternative subsistence and/or commercial or recreational fishing opportunities
	Other Intentional Release	Species released into the natural environment for reasons other than those covered in any other release in nature pathways
Transport (Contaminant)	Contaminant on Animals	Species introduced unintentionally as contaminants on animals transported through human related activities (e.g. aquaculture)
	Contaminant on Plants	Species introduced unintentionally as contaminants on plants or plant products transported through human related activities
	Contaminated Bait	Species introduced unintentionally as contaminants in/of bait
	Parasites on Animals	Unintentional introduction of parasitic species transported by a host animal or an animal that acts as a vector
Transport (Stowaway)	Angling/Fishing Gear	Species introduced unintentionally as stowaways on equipment used by recreational anglers or commercial/professional fishermen, including aquaculture gear
	Ballast Water	Species that have been introduced unintentionally via the ballast tanks of ships and boats, within ballast water, ballast sediments or solid ballast materials
	Container/Bulk	Species introduced as accidental stowaways in or on shipping containers and bulk cargo
	Hitchhikers on Plane	Species that have been introduced unintentionally by being a hitchhiker in or on airplanes and other aircraft

(Continues)

TABLE 1 (Continued)

Pathways ^b	Sub-pathways ^b	Description
	Hitchhikers on Ship	Species that have been introduced unintentionally by being a hitchhiker in or on ships, boats or other watercraft but excluding species transported in ballast tanks or via ship fouling
	Organic packaging material	Species that have been introduced unintentionally by being a stowaway in or on packing materials such as wooden pallets
	Ship Fouling	Species that have been introduced unintentionally as biofouling organisms on underwater surfaces of ships including the hull and niche areas
Unaided	Rafting on Anthropogenic Debris	Species that spread to new regions attached to marine litter and other anthropogenic materials drifting in natural water currents

^aAdapted from Fofonoff et al. (2018).

^bAdapted from Harrower et al. (2018).

rate. This date encompasses the relatively few cases where a species is known to have been intentionally planted or released; such cases are rare after the 1960s, as there was rapid growth in environmental awareness about the potential negative outcomes of deliberate introductions. Distinguishing between a date of detection and a date of introduction is critical. We emphasize that there should be no confusion between our use of detection and the concept of the rate of species discovery resulting from a given effort or type of sampling (which in classical community diversity studies is used to establish a probable species discovery asymptote).

We chose the timeframe 1965–2015 with the assumption that there has been increasing awareness and more comprehensive reporting since 1965, with time-lags presumably being smaller compared to reports prior to 1965. In cases of multiple records of the same ANS, the first record within each region was used. The year of first collection was typically recorded as a single year, but when only time ranges were provided (e.g. “2012–2015”), the first year of the range was taken as the earliest possible date. For a small number of records (<0.01%), the year of first report (the year of publication) was recorded when the date of collection was not provided. Population status was recorded for each introduced species as “established,” “extinct,” “failed” or “unknown” following definitions used by the NEMESIS database (see Table 1) which account for uncertainty associated with limited search effort. We acknowledge that established populations are more likely to be observed and documented and that, without regular surveillance programmes, many detections are recorded only as single records and the population status may be highly uncertain. Seven ANS populations were successfully eradicated after detection—these were labelled with the population status observed prior to eradication efforts.

We assigned pathways of introduction using categories and sub-categories proposed as part of the Convention on Biological Diversity following guidance in Harrower et al. (2018), with small modifications (Table 1). Ship fouling (rather than the more limited “hull” fouling) included organisms attached or associated with any underwater surfaces of ships (defined as a vessel of any type operating

in the aquatic environment, including fixed or floating platforms) including the hull and niche areas (e.g. sea chests, seawater inlets and inlet grates, anchors and anchor chain) (as per IMO, 2011). Ships’ ballast water also included stowaways within ballast sediments as well as solid ballast materials used historically. We considered aquaculture equipment as angling/fishing equipment.

Pathway information was initially taken from source online databases and published literature, if stated, and was then critically evaluated for completeness and standardization across regions/data sources based on our own expertise and knowledge. Many references implicate commercial shipping as a possible mechanism of introduction without assessing specific pathways. Therefore, we designated shipping pathways primarily based on our own prior biological surveys of ballast water and ship fouling combined with knowledge of life history characteristics of the species. Ballast water can be a possible transport pathway for a wide variety of aquatic species, not only those with pelagic life stages, as virtually any sessile organism may be drawn into ballast tanks (or floodable cargo holds) on floating pieces of debris, wood chips, algae or seagrass bearing a biofouling community of attached species. While this aspect of ballast-able biota is rarely studied, the potential for species associated with floating material to be taken into ballast tanks was suggested as early as the 1920s (Carlton, 1985). Conversely, ship fouling can be a possible transport pathway not only for encrusting or fouling species on a ships’ main hull, but also for sedentary and mobile species associated with more protected underwater niche areas such as sea chests (Coutts & Dodgshun, 2007). As a result, both ballast water and ship fouling were assigned as potential pathways for the majority of taxa, excepting purely pelagic free-swimming taxa (such as shrimps, planktonic copepods and ctenophores) associated only with ballast water. We standardized the assignment of shipping pathways for related taxa across regions, typically at the level of Family or Order, except where there was no geographic correlation between shipping activity and the site of first collection (e.g. where pathways such as aquaculture were more likely). As there is uncertainty associated with all pathway assignments, we tallied records where documented or direct evidence existed (e.g. species was observed within a pathway at the time of introduction to a particular location).

When a single detection was linked to multiple possible pathways of introduction, we tallied each pathway using an unweighted approach to identify the maximum number of detection events per pathway (as in Williams et al., 2013). In this analysis, canals, such as the Suez Canal, were evaluated both as a pathway through which ANS may move naturally (i.e. as species with pelagic life stages) and as a route used by ships. In cases where species have pelagic behaviour and are possibly associated with shipping, they were assigned multiple pathways. Although unassisted pathways, such as water currents, can be an important pathway for the movement of ANS (see Discussion), if the first report of an ANS within an ecosystem was considered solely due to natural spread from a neighbouring ecosystem (e.g. range expansion or range shift), it was excluded from this analysis because unassisted movement was not documented consistently across regional datasets. Transport associated with anthropogenic debris, however, was included (considering Carlton et al., 2017).

Data were analysed at global and regional levels to explore trends in the rate of detection, ANS richness, population status and pathways of introduction. A ten-year moving average was used in temporal plots to decrease variability across years due to inconsistent search effort (see Discussion).

3 | RESULTS

3.1 | Global patterns

The assembled comprehensive dataset comprises 2209 records of primary detections of ANS (1442 unique species belonging to 17 phyla) across 49 aquatic ecosystems, including ten ecosystems found to have zero confirmed records during the period of study (Figure 1; Table S1). Considering all regions combined, an annual mean of 43 (± 16 SD) primary ANS detections occurred. This translates to roughly one new detection every 8.4 days for this 50-year era. The rate of detections was relatively stable during 1965–1995, with a ten-year mean detection rate of about 32 ANS per year (Figure 2a). After this time, the rate increased, reaching 51 primary detections of ANS annually by the year 2000 and peaking at roughly 66 primary detections of ANS per year during 2005–2010. In the last five years, the rate of detection declined marginally, with about 59 primary detections per year.

A variety of ANS taxa were reported, with Arthropoda ($n = 522$, 23.6% of total), Mollusca ($n = 373$, 16.9%) and Chordata (Pisces) ($n = 279$, 12.6%) being most frequent, followed by Rhodophyta ($n = 209$, 9.5%), Annelida ($n = 200$, 9.1%), Chordata (Tunicata)

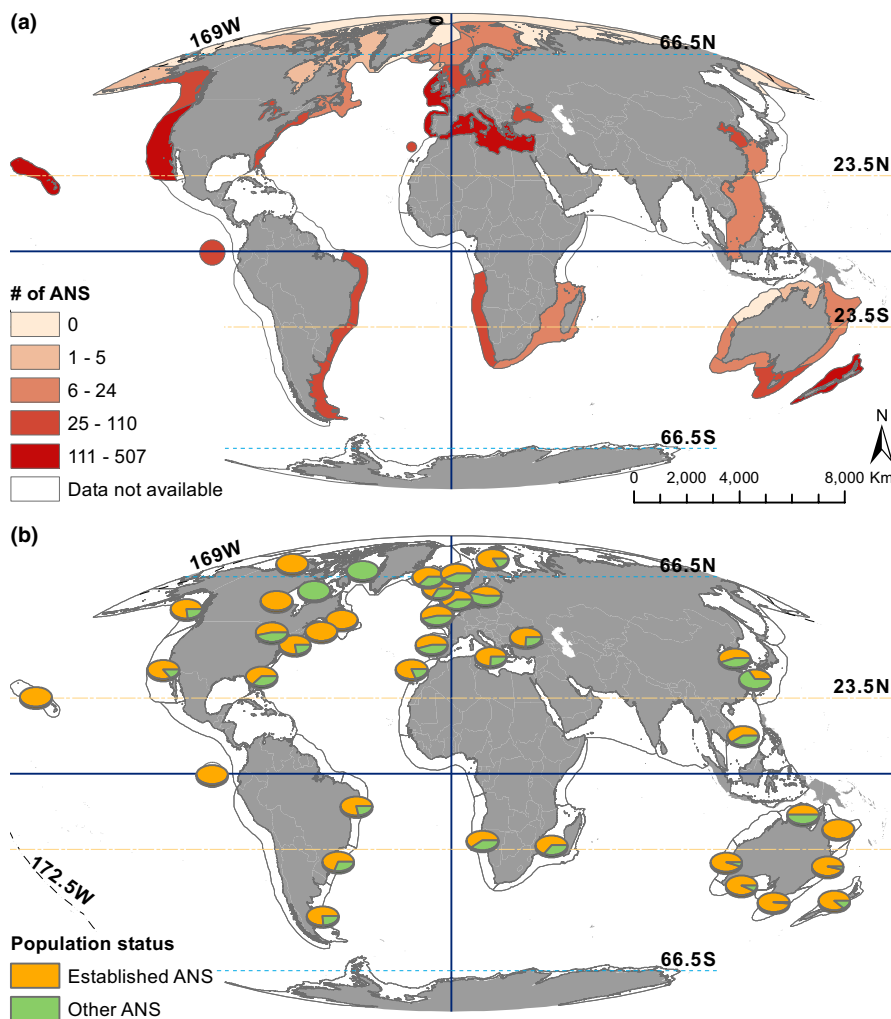
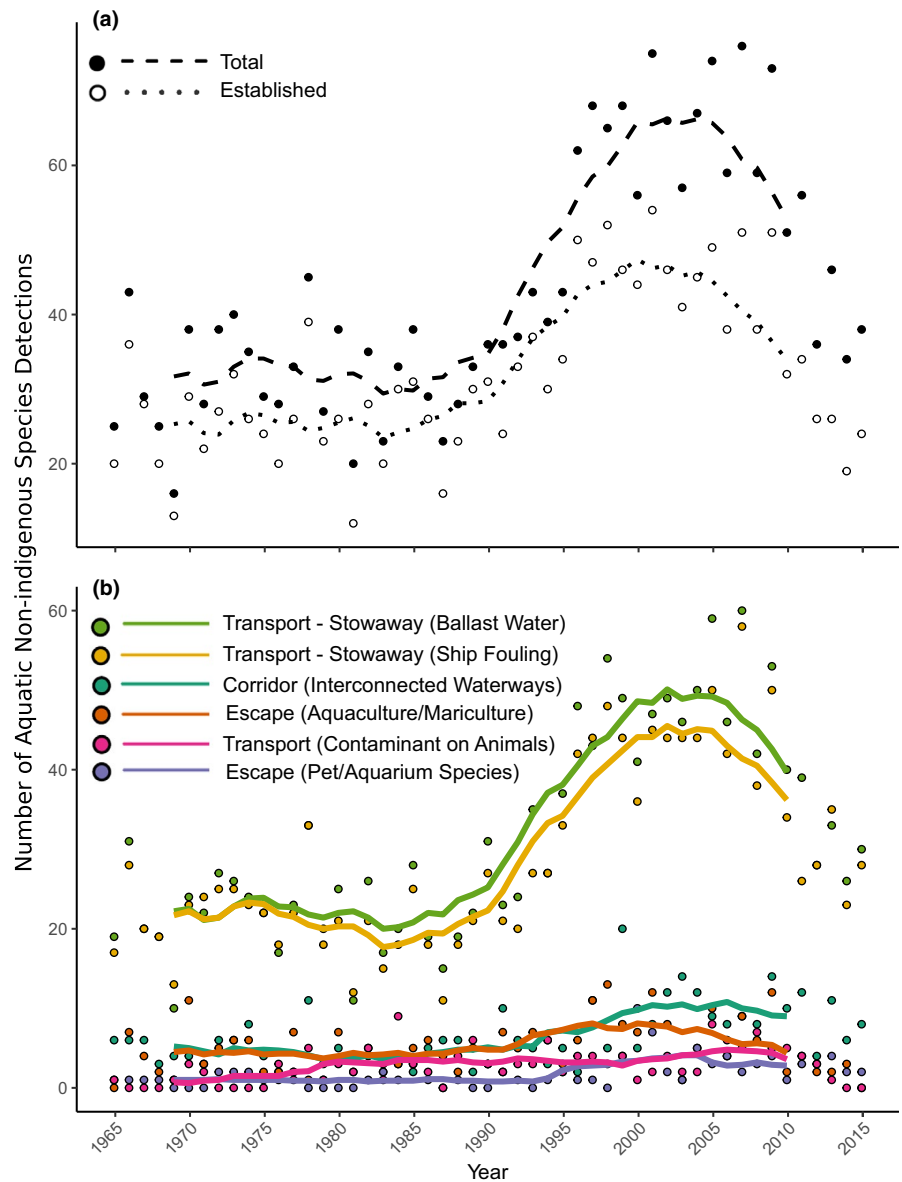


FIGURE 1 Records of primary detections of aquatic non-indigenous species (ANS) between 1965 and 2015 in each of 49 coastal marine, estuarine and freshwater ecosystems. Panels (a) and (b) show total number of detections and proportion of populations with established status, respectively. Comparable data were not available for regions in white, though ANS may be present, and are documented from a number of these regions

FIGURE 2 Chronology of primary detection events of aquatic non-indigenous species (ANS) across 49 coastal marine, estuarine and freshwater ecosystems during 1965–2015. Panel (a) shows trends by population status, where the dashed and dotted lines denote the ten-year moving averages for the annual number of detection events for total and established populations, respectively. Panel (b) shows trends in the number of primary detection events of ANS by pathway, for the top six pathways (96% of records)



($n = 160$, 7.2%), Bryozoa ($n = 148$, 6.7%) and Cnidaria ($n = 131$, 5.9%) (Table S2). Ochrophyta ($n = 57$, 2.6%), Chlorophyta ($n = 51$, 2.3%) and Porifera ($n = 26$, 1.2%) were reported relatively infrequently, while Tracheophyta, Echinodermata, Ctenophora, Kamptozoa, other Chordates (e.g. Amphibia and Reptilia), Phoronida, Brachiopoda and Charophyta were seldom reported (each having fewer than 20 detection events, cumulatively representing 2.4% of all records).

Most ANS were reported as having established (74.2%) or unknown population status (19.9%)—few records exist for ANS with failed (5.4%) or extinct (0.5%) populations (Table S1). Most ANS were likely introduced as stowaways in ships' ballast water or biofouling, although direct evidence is typically absent, particularly for ballast water (direct evidence cited for 42/1468 ship fouling vs. 4/1595 ballast water records, respectively). The temporal trends for these two pathways were similar to or are largely responsible for the overall pattern of detections through time (Figure 2b). Escape of aquaculture/mariculture species follows a similar pattern, although much

lower in magnitude, while the corridor pathway and escape of pet/aquarium species seem to have increased in importance/rate since the late 1990s. Nearly one-third of ANS primary detections were associated with a single pathway (32.7%), while most were associated with at least two (52.6%) or three (14.1%) pathways. Movement through connected waterways/seas/basins (193 records), stowaways in ballast water (162 records) and escape of aquaculture/mariculture species (144 records) were the most important pathways for single-pathway primary detection events. When two pathways were possible, stowaway as ship fouling and/or in ballast water were overwhelmingly implicated (91.5% of two-pathway events).

3.2 | Regional patterns

Patterns of primary detection were variable across regions, as would be expected due to differences in pathway strength (i.e. introduction

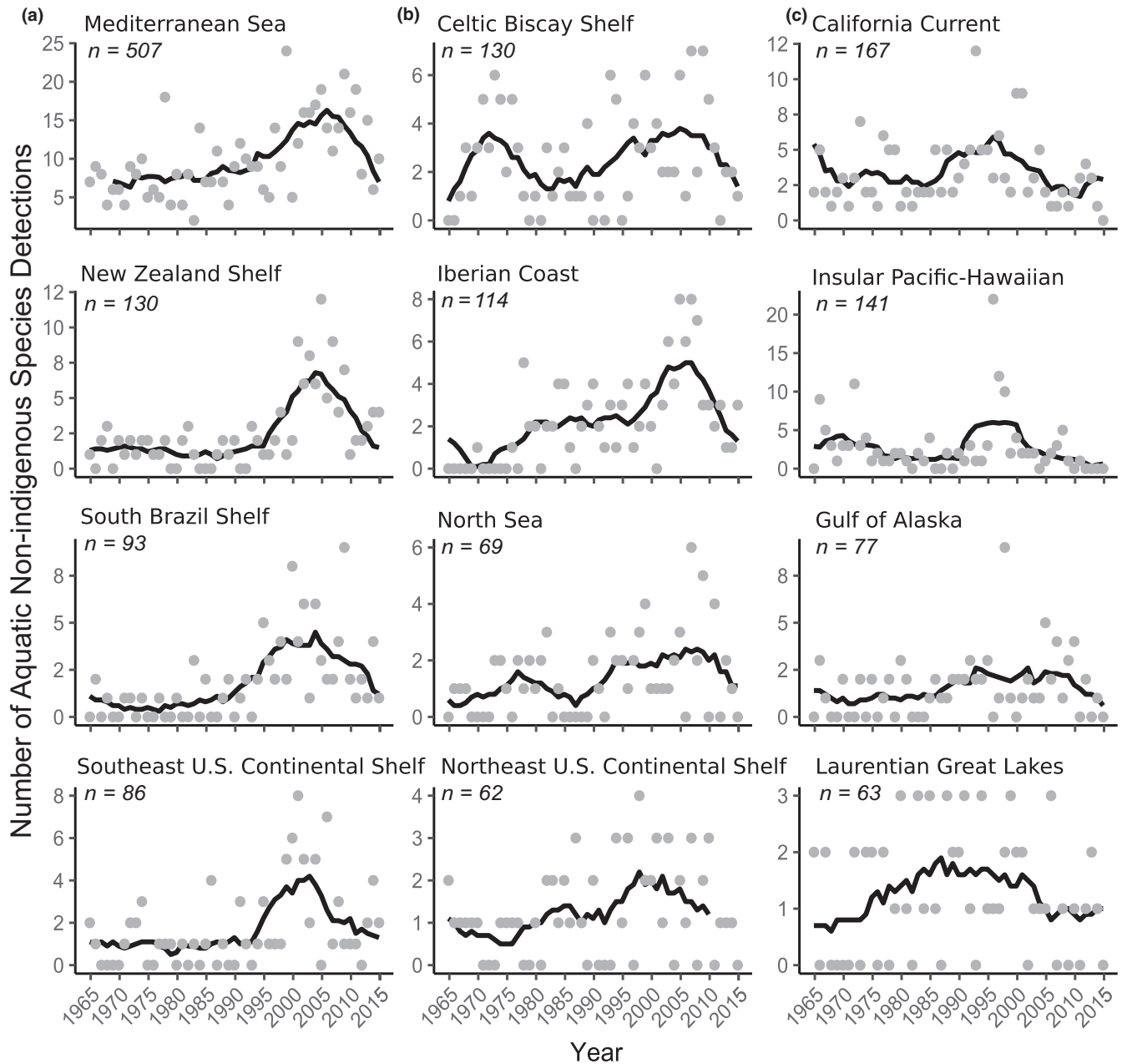


FIGURE 3 Temporal trends in primary detections of aquatic non-indigenous species across the top 12 ecosystems studied. Trend lines show ten-year moving average of the annual number (dots) of detections. Plots are arranged in columns to show (a) ecosystems having a strong peak in detections between 1995 and 2015; (b) ecosystems having an overall trend of increased rate of detections through time; and (c) ecosystems having relatively stable detection rate through time. Note differences in scale of y-axes across plots

effort), environmental conditions, ecosystem size, survey effort and taxonomic expertise. The cumulative number of primary detection events during the 50-year period ranged from zero to more than 500 per ecosystem, with variable levels of population establishment success across regions (Figure 1, Table S1). Inter-regional temporal trends varied with three patterns being typical: a distinct peak of ANS primary detections in the 1995–2015 timeframe, an overall trend (positive slope) of increased detections through time or a relatively stable rate of detections (Figure 3).

A majority (76.6%) of the 1442 unique ANS records were reported from a single ecosystem, while the 25 most reported ANS were reported from at least seven different ecosystems (Table 2). Regions having at least 10 primary detection records during the study period exhibited a diverse assemblage of ANS from at least five phyla, with any one phylum typically comprising no more than 30% of species within a location (exceptions being Arthropods and Pisces, which comprised 40%–50% of ANS in some regions) (Figure 4, Table S2).

TABLE 2 List of the 25 most common aquatic non-indigenous species reported as new primary detections across the studied ecosystems during 1965–2015

Species Name	Ecosystems	Potential Pathways of Introduction
<i>Caprella mutica</i>	13	BW, SF, AFG
<i>Botrylloides violaceus</i>	10	BW, SF, AFG, EAM, TCA
<i>Palaemon macrodactylus</i>	10	BW, EAM, CIW
<i>Styela clava</i>	10	BW, SF, EAM, AFG, TCA
<i>Agarophyton vermiculophyllum</i>	9	BW, SF, EAM, TCA
<i>Grateloupia turuturu</i>	9	BW, SF, EAM, TCA, OPM
<i>Mytilus galloprovincialis</i>	9	BW, SF, EAM
<i>Amphibalanus amphitrite</i>	8	BW, SF
<i>Antithamnionella spirographidis</i>	8	BW, SF, TCA, UAD
<i>Carcinus maenas</i>	8	BW, SF, AFG, TCB, ELF
<i>Crassostrea gigas</i>	8	EAM, SF
<i>Dasysiphonia japonica</i>	8	BW, SF, AFG, TCA
<i>Didemnum vexillum</i>	8	BW, SF, EAM, AFG, TCA, CIW
<i>Molgula manhattensis</i>	8	BW, SF, EAM
<i>Paracerceis sculpta</i>	8	BW, SF
<i>Pseudopolydora paucibranchiata</i>	8	BW, SF, EAM, TCA
<i>Boccardia proboscidea</i>	7	BW, SF, TCA
<i>Grandidierella japonica</i>	7	BW, SF, EAM
<i>Diadumene lineata</i>	7	SF, EAM
<i>Polyandrocarpa zorritensis</i>	7	BW, SF
<i>Polycera hedgpethi</i>	7	BW, SF, TCA
<i>Ruditapes philippinarum</i>	7	EAM, RFW
<i>Ulva australis</i>	7	BW, SF, TCA
<i>Undaria pinnatifida</i>	7	BW, SF, TCA, EAM OPM
<i>Watersipora subtorquata</i> complex	7	BW, SF

Note: The number of studied ecosystems reporting the species is given, as well as a cumulative list of possible pathways of introduction (pathways may differ for the same species introduced to different regions).

Abbreviations: AFG, Transport stowaway in angling/fishing gear; BW, Transport stowaway in ballast water, sediments or solid ballast; CIW, Corridor through interconnected waterways; EAM, Escape from aquaculture/mariculture; ELF, Escape of live food/live bait; OPM, Transport stowaway in organic packing materials; RFW, Release for fishery in the wild; SF, Transport stowaway in ship biofouling; TCA, Transport contaminant on animals; TCB, Transport contaminant in bait; UAD, Unaided rafting on anthropogenic debris.

Transport stowaway in ship fouling and ballast water tended to be the dominant pathways in most regions, typically responsible for at least 40% of primary detection events (Figure 5). Exceptions are the corridor pathway (Suez Canal) in the Mediterranean Sea and escape of aquaculture/mariculture species in the East China, South China and Yellow Seas (Table S3).

4 | DISCUSSION

Our analyses identified 2209 primary detection events of 1442 unique ANS over the past 50 years which, although confounded by time-lags between actual introduction and detection, likely is an underestimate of the actual number of introductions during this time period. It is widely recognized that ANS are frequently under-reported due to limited search effort, uncertainty about historical biogeography and an insufficiency of taxonomic expertise (Carlton & Fowler, 2018; Ojaveer et al., 2017), especially for smaller-bodied organisms (Carlton, 2009; Lohan et al., 2020). Our study also does not consider secondary introductions (spread) of ANS neither within an ecosystem nor between ecosystems, which will further contribute to this underestimation. Although our dataset represents an extensive collection of global detection records, it includes only ~73% of the world's large marine ecosystems, with very limited coverage of Africa, Central and South America and Asia. Introductions of ANS have undoubtedly occurred in these areas; the cost of ANS surveys can be prohibitive in regions with limited resources and a dearth of expertise across many taxa, which could explain why data were not accessible for this study.

The results of this study highlight a possible under-representation of taxa in global datasets of non-indigenous species: the 1442 unique species recorded here is more than ten-fold lower than the number of non-indigenous species (vascular plants, mammals, insects, birds, molluscs and fishes) observed in terrestrial ecosystems (Seebens et al., 2017). While land biodiversity is vastly higher than both marine and aquatic diversity combined (Grosberg et al., 2012; Vermeij & Grosberg, 2010), and thus more NIS would be proportionally expected in terrestrial systems, the documentation of the diversity of invasions in marine, estuarine and freshwater habitats has significantly lagged behind similar research on land. For example, extensive documentation of terrestrial invasions in the Hawaiian Islands and the Galápagos Islands commenced decades before the first investigations of marine invasions in those archipelagos (Carlton, & Eldridge, 2009, 2015; Carlton et al., 2019). We thus suspect that we may be at the tip of an invasion iceberg in understanding the scale of introductions in coastal environments (see also Byers et al., 2015).

Cumulatively, over the past 50 years, one ANS was reported as a primary detection within the evaluated ecosystems every 8.4 days (on average), and the rate of detection exhibits changes across years both within and across regions. While changes in the rate of ANS primary detections through time may reflect the actual introduction rate, this relationship is uncertain and confounded by variable survey effort and species detectability (Hewitt, Campbell, et al., 2004; Hewitt, Willing, et al., 2004; Ruiz et al., 2000). The rate of ANS primary detections appeared to increase in the 1990s and 2000s, possibly related to increased global trade (e.g. Sardain et al., 2019), but it is also likely influenced by increasing scientific, government and public awareness, and increased funding for surveys, monitoring and other assessments. For example, peaks in detection rate for Insular Pacific-Hawaii, New Zealand and Southeast

Proportions of Introductions by Taxon

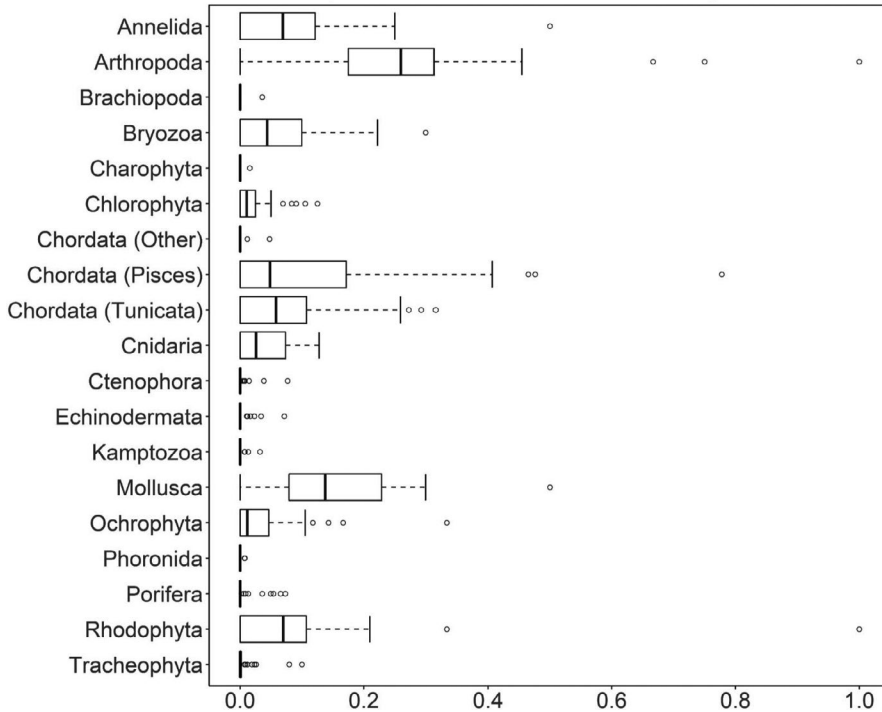


FIGURE 4 Relative importance of taxonomic groups (as a proportion of total primary detections) for aquatic non-indigenous species detected across 49 coastal marine, estuarine and freshwater ecosystems, from 1965 to 2015. In the box plots, the boundary of the box closest to zero indicates the 25th percentile, the black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points left and right of the whiskers indicate outliers outside the 10th and 90th percentiles

Proportions of Introductions by Pathway

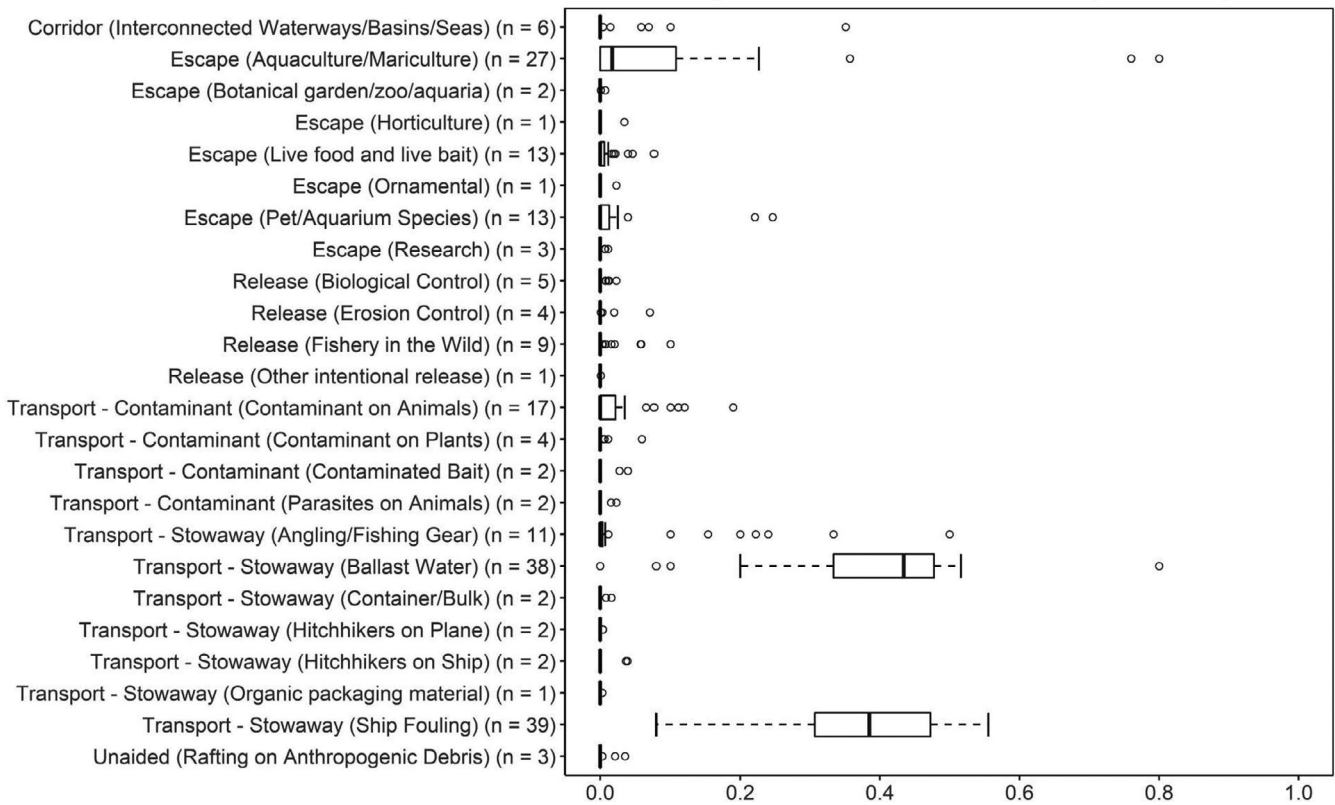


FIGURE 5 Relative importance of introduction pathways (as a proportion of total pathway records) associated with aquatic non-indigenous species detected across 49 coastal marine, estuarine and freshwater ecosystems, from 1965 to 2015. In the box plots, the boundary of the box closest to zero indicates the 25th percentile, the black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points left and right of the whiskers indicate outliers outside the 10th and 90th percentiles

Australian Shelf correspond with dedicated scientific surveys aiming to document ANS beginning in the 1990s (Carlton & Eldridge, 2009; Hewitt, 2002; Hewitt, Campbell, et al., 2004) and in the 2000s (Inglis & Seaward, 2016). Comparatively, these areas receive just a small proportion of global shipping but account for much greater numbers of recorded ANS than regions that are global centres for shipping (e.g. China, SE Asia, Japan, NW Atlantic), appearing to challenge predictions that invasion hot spots should be strongly correlated with modern shipping activity (Kaluza et al., 2010; Sardain et al., 2019; Seebens et al., 2016). In fact, for Hawaii (and for many of the regions reviewed here), the majority of introductions may have occurred long before the first reports. Similarly, regions with apparent increasing rate of primary detections since the 1990s (Patagonian Shelf, East Brazil Shelf and Madeira Archipelago) are likely reflective of recent, dedicated research (Canning-Clode et al., 2013; Schwindt et al., 2020; Teixeira & Creed, 2020).

The apparent decline in primary detections of ANS since 2005 in many regions may correspond with preventative measures implemented to reduce biological introductions, such as requirements to manage ships' ballast water (e.g. Hayes et al., 2019), and to diminish the risks associated with the intentional introduction and transfer of aquatic organisms via aquaculture and fisheries (e.g. Cook et al., 2008; Hewitt et al., 2006). However, given uncertainty due to inconsistent and often insufficient search effort leading to time-lags between introduction and first collection, any inferences about ANS introduction rate based on collection dates must be made cautiously and, ideally, consider multiple lines of evidence (see Costello & Solow, 2003). For example, Bailey et al. (2011) inferred that a declining rate of ANS detections in the Great Lakes could be due to management efforts (i.e. new ballast-tank flushing regulations) only after reviewing direct cause-and-effect studies of the management technique and evaluating compliance rates by the shipping industry. Even after such detailed analysis, the relative contribution of management versus search effort is not clear. Seebens et al. (2017) found similar declines in records of recent detections of terrestrial taxa and fishes consistent with a decline in deliberate introductions due to increasing awareness of impacts of biological introductions, but also cautioned that data collected after the year 2000 may be incomplete due to time-lags. We therefore suggest that future assessments should consider long-term averages and associated levels of search effort to evaluate invasion dynamics of ANS.

Most regions do not have regular surveillance programmes with consistent long-term funding or are pursuing generalized surveys to generate baseline inventories rather than targeted early detection of ANS. In the absence of standardized, targeted and repeated methods for surveillance, the true date of introduction could be years or even decades earlier than the date of first detection (e.g. Galil, 2008; Hewitt, Campbell, et al., 2004; Zenetos et al., 2019). One example of time-lags within these data is the collection and reporting of four beach-dwelling isopods from Hawaii between the 1970s and 1990s (*Halophiloscia couchii* (Kinahan, 1858), *Littorophiloscia culabrae* (H. F. Moore, 1901), *Porcellio lamellatus* (Budde-Lund, 1885) and *Armadilloniscus ellipticus* (Harger, 1878)), thought to have been

introduced in solid ballast materials such as rock and sand (Carlton & Eldridge, 2009); as solid ballast was phased out of use in the 1800s (National Research Council, 1996), these isopods may have been introduced one hundred years (or more) prior to their published collection date.

Where surveillance is designed specifically to detect targeted taxa and is implemented regularly, ANS can be detected at relatively small population sizes, reducing time-lags between introduction and detection (Hayes et al., 2019). More often, ANS are collected as "by-catch" during non-surveillance research activities (Ruiz et al., 2000). Additional lags then occur because time is required to detect, positively identify and report new species once collected in a sample (Azzurro et al., 2016; Stanislawczyk et al., 2018). A lack of taxonomic expertise can cause significant delays in reporting, particularly if individuals are first misidentified as native species (Campbell et al., 2007; Carlton, 2009; Mienis, 1992). Furthermore, without standardized and targeted surveillance programmes in place, many years may pass before a new ANS is collected because introduced populations are likely to be rare (both in spatial coverage and abundance) until several generations contribute to population growth and spread (Azzurro et al., 2016; Harvey et al., 2009). Similarly, it is difficult to ascertain the population status (established, failed or extinct) without repeated surveys in the location of introduction, and many introductions are likely to occur unnoticed if populations fail or go extinct within a short time-scale. The high proportion of records with unknown population status (19.9%) and low number of "failed" populations (5.4%) in this study indicate a need to better design or implement surveillance programmes with repeated measures.

Most detection events in this dataset are comprised of Arthropoda, Mollusca and Pisces. The reporting of certain taxa (such as Annelida, Rhodophyta, Bryozoa, Cnidaria and Tunicata) in only a subset of the studied ecosystems may reflect different active pathways (anthropogenic transport mechanisms and source regions of ANS) and species adaptations to different recipient conditions (Cardeccia et al., 2018). However, it is likely that the pattern is also heavily influenced by the availability of taxonomic specialists focusing on these groups and the different sampling methods used across studies. Interestingly, Echinodermata comprise only 12 ANS reported in six of the 49 estuarine and marine ecosystems studied. Given that this phylum is globally well studied, abundant and widely distributed (e.g. Lebrato et al., 2010), it is unlikely that the low number of echinoderm invasions can be attributed solely to the group's prevalence or to lack of taxonomic expertise, suggesting other factors also influence the frequency of ANS reports. Further, many experts argue that the biogeography and taxonomy of microscopic species in the Chlorophyta and Ochrophyta are so poorly understood that new reports of these taxa should be considered cryptogenic (sensu Carlton, 1996; see also De Clerck et al., 2013; Gómez, 2008, 2019) with few exceptions where forensic assessment clearly demonstrates introduction of ANS (e.g. Bolch & Hallegraeff, 1990; Hallegraeff et al., 1988).

The true rate of recent introductions (since 1965) is undoubtedly much greater than documented here for many small-bodied taxa.

More specifically, the magnitude of organism transfer (both in abundance and species richness) is inversely proportional to body size, yet relatively few ANS are recognized for fungi, protists, parasitic and free-living flatworms, viruses and microbes, likely reflecting high uncertainty in taxonomic identification and geographic origin (Lohan et al., 2020). The investigation of lesser-studied and cryptogenic taxa will be a fruitful avenue of future research, particularly as molecular tools, reference databases and museum collections advance (e.g. Darling et al., 2017), noting that both conventional and molecular biological surveys are dependent on taxonomic expertise—a skill set rapidly diminishing without dedicated funding and training programmes (Bik, 2017; Coleman, 2015; Costello et al., 2010; Kim & Byrne, 2006).

Assessment of the pathways of introduction of ANS is fundamental for biological invasion risk assessments and for prioritizing management, monitoring and surveillance activities (Barry et al., 2008; Essl et al., 2015). For many non-indigenous species, more than one introduction pathway is possible based on human activities occurring in or near the locality of first collection; hence, the assignment of the responsible pathway is uncertain (Ojaveer et al., 2018). As a result, many studies report only “commercial shipping” as the mechanism of introduction, without differentiating between the various pathways associated with this activity (e.g. ballast water and biofouling of underwater surfaces), making it difficult to quantify introduction likelihood and evaluate the efficacy of pathway-based management actions. Our study also indicates that commercial shipping activities are often inferred as the responsible pathway(s) of introduction without direct evidence (nor critical examination of alternate possibilities). Research examining commonly neglected or understudied pathways, such as the aquarium and bait trades, Internet commerce and anthropogenic marine litter (e.g. Campbell et al., 2017; Carlton et al., 2017; Chan et al., 2020; Fowler et al., 2015; Lenda et al., 2014), could lead to new insights and priorities for management of ANS. It is vital that future work transparently consider uncertainties in pathway assignments, describe the level of confidence and critically evaluate all possible pathways (Essl et al., 2015; Ojaveer et al., 2018).

National regulations requiring ballast water to be exchanged mid-ocean, thereby purging coastal species for presumably less harmful oceanic species and reducing viability of remaining coastal species via osmotic shock, have been implemented in multiple locations around the world since the early 1990s (Bailey, 2015). While there is evidence that ballast water exchange has effectively reduced ballast-mediated introductions to the Laurentian Great Lakes where there is a high level of enforcement (Bailey et al., 2011), there is greater uncertainty about the degree of protection offered to coastal marine ports (e.g. Casas-Monroy et al., 2015; Scriven et al., 2015) and locations lacking performance measures. For some marine ports, there have been trade-driven compensatory changes in the total ballast water and organism delivery (Carney et al., 2017), and biofouling remains a largely unmanaged source of ANS (Williams et al., 2013). It is notable that the declining trend in detections associated with ship fouling occurs after the entry-into-force of the International Convention on the Control of Harmful Anti-Fouling

Systems on Ships (IMO, 2001) in 2008 which banned the use of the anti-fouling compound tributyltin (TBT). This ban raised concerns that in the absence of effective replacements for TBT, introductions via ship fouling would escalate (Drake & Lodge, 2007; Faasse & Lighthart, 2007; Lewis et al., 2004); however, there is no evidence of this in our study. Further research is needed to disentangle the risk associated with ballast water versus biofouling and to evaluate if international measures (IMO, 2004, 2011) intended to curtail introductions by these pathways are effective or if additional measures are needed (ICES, 2019).

When species are introduced and become established in a new geographic region, they often spread beyond the initial site of invasion, expanding the area occupied and increasing the potential magnitude of impacts (Parker et al., 1999). Such secondary spread beyond the initial site of introduction results from a combination of natural processes (e.g. active swimming, passive larval transport or drifting) and human-mediated dispersal mechanisms (e.g. recreational vessels, aquaculture, fishing and restoration). Although excluded from this study due to a lack of consistent data across studied regions, secondary spread is known to be a very important component of invasion dynamics, at multiple scales within and among adjacent ecosystems. For example, the Japanese wireweed, *Sargassum muticum* (Yendo) Fensholt, is believed to have been introduced initially to the coasts of northern France through oyster aquaculture activities and to have subsequently spread via drifting plants to the English south coast and the Netherlands. It has now spread to most coastal countries in Europe, likely through a combination of natural dispersal, ships' ballast water or biofouling and oyster aquaculture activities (Gollasch et al., 2009).

A recently published study on the Baltic Sea indicates that secondary spread of ANS from the adjacent North Sea is responsible for around 50% of introductions when both natural dispersal and human-mediated pathways are considered (Ojaveer et al., 2017). In a previous analysis of 257 ANS established in California, 57% of these species were known from multiple bays along the coast with some occurring all the way to Alaska, suggesting secondary spread attributed primarily to shipping (ballast water and/or ship fouling) and aquaculture (Ruiz et al., 2011). There is mounting evidence that global warming has enabled ANS to expand into regions where previously they were not able to survive and reproduce (Canning-Clode & Carlton, 2017; Occhipinti-Ambrogi, 2007; Walther et al., 2009). Given the impressive rates of dispersal of ANS, it is likely that the unaided pathway is significantly underestimated (Hulme et al., 2008). This stresses the need for regional cooperation, as unaided spread is an important pathway to grasp both from a management perspective and in terms of fundamental invasion ecology (Faulkner et al., 2020; Schwindt & Bortolus, 2017).

This study indicates that introductions of ANS have occurred at an alarming rate on a global scale for the past 50 years. Coordinated actions are urgently needed to prevent new introductions and further spread of ANS, one of the top drivers of biodiversity change (IPBES, 2019; IUCN, 2017). While there have been significant advances over the past 30 years in policies to reduce

ballast water-mediated invasions, including those by the International Maritime Organization and regulations in several nations (e.g. Government of Canada, 2006; U.S. Coast Guard, 1998), these are still being implemented, and ship fouling is largely unregulated but gaining increased attention (e.g. Department of Agriculture and Water Resources, 2019; Georgiades et al., 2020; Ulman et al., 2019). Further regional actions, such as those to address introductions via the Suez Canal, will have substantial benefits for the Mediterranean Sea and across associated global trade networks (Galil et al., 2017).

Despite the good intentions of the CBD to evaluate non-indigenous species as a key indicator and recent efforts to establish a mechanism for reporting (Pagad et al., 2018), this is still at an early stage for aquatic and marine species, and synthetic inventories of ANS and associated invasion pathways are still very limited, inhibiting prioritization and control activities in aquatic environments. While numerous policies and strategies have been put in place that aim to reduce the introduction and spread of non-indigenous species as conservation measures, the coverage is piecemeal, taxonomically biased and focused only on a subset of pathways—implementation and enforcement is often lacking (see Ojaveer et al., 2018) and international treaties may be in conflict (Campbell et al., 2009). For example, the CBD and the World Trade Organization's General Agreement on Tariffs and Trade 1994 (GATT) apply the precautionary approach from different contexts, with the GATT able to utilize "gateway" provisions (Campbell et al., 2009). The end result is that Sanitary and Phytosanitary Measures may be cancelled out by the World Trade Organization if trade is blocked as a result of ANS. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services recently reported that, based on past and ongoing rapid declines in biodiversity, goals for conserving nature and achieving sustainability cannot be met without urgent and concerted efforts fostering transformative change to reduce drivers of biodiversity loss (IPBES, 2019). In our view, this requires robust and reliable inventories of ANS introductions and their introduction pathways, needed to both evaluate performance of management measures and accelerate the rate of adaptive management to achieve desired outcomes.

Studies such as this one, based on national and/or regional inventories of non-indigenous species, are only reliable if local experts can maintain and continually update lists considering new records, range expansions and evolving knowledge of nomenclature, population status and responsible pathways (Marchini et al., 2015). It is vital to continue and to expand research and survey efforts across marine, estuarine and large freshwater ecosystems to better inform both regional and global policy development and management activities, such as the European Water Framework Directive (Cardoso & Free, 2008). Inventories of ANS frequently suffer from a number of uncertainties in species identification (taxonomic uncertainty) and inferred pathways of introduction, inconsistent or uneven search effort (leading to low spatial, temporal and taxonomic resolution), poor documentation of data and knowledge and inadequate baseline information (Marchini & Cardeccia, 2017; McGeoch et al., 2012). These are all critical gaps that impair our ability to fully understand invasion

dynamics, their drivers and performance of policies and management actions. Addressing these gaps requires standardized and repeated measures for detection, in order to improve the core data quality and inferences that can be drawn (e.g. Ruiz & Hewitt, 2002). While this need is well recognized and several research groups have sought to advance this within their region, it is also the case that: (a) somewhat different methods and approaches are used among regions and (b) such efforts are usually short-term and limited by funding available to an individual researcher or group.

We call for standardized, targeted and repeated methods across regions in order to improve the quality of global-scale comparisons and sustain core measures over longer time-scales. Future studies should include key human activities/pressure trends over time in helping to interpret the temporal dynamics of new introductions. It will be fundamental to fill in existing knowledge gaps given that invasion data representing broad regions of the world's oceans are not yet readily available and to maintain knowledge pipelines for adaptive management. We hope that the baseline provided here will be updated in the future as pathway management is implemented and, ideally, becomes evidence of associated positive changes (fewer introductions of ANS).

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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13167>.

DATA AVAILABILITY STATEMENT

The full dataset of primary detection events of aquatic non-indigenous species collected for this study (and associated references) is available at <https://doi.org/10.5061/dryad.msbcc2fwk>.

ORCID

Sarah A. Bailey  <https://orcid.org/0000-0003-3635-919X>
 João Canning-Clode  <https://orcid.org/0000-0003-2143-6535>
 James T. Carlton  <https://orcid.org/0000-0002-3748-8893>
 Nuno Castro  <https://orcid.org/0000-0002-1051-4131>
 Farrah T. Chan  <https://orcid.org/0000-0002-1062-6707>
 Amelia Curd  <https://orcid.org/0000-0003-3260-7192>
 John Darling  <https://orcid.org/0000-0002-4776-9533>
 Bella S. Galil  <https://orcid.org/0000-0002-9268-7211>
 Chad L. Hewitt  <https://orcid.org/0000-0002-6859-6512>
 Inti Keith  <https://orcid.org/0000-0001-9313-833X>
 Agnese Marchini  <https://orcid.org/0000-0003-4580-0522>
 Cynthia H. McKenzie  <https://orcid.org/0000-0001-6421-0603>
 Henn Ojaveer  <https://orcid.org/0000-0003-2742-6063>
 Tamara B. Robinson  <https://orcid.org/0000-0001-5515-1445>
 Aibin Zhan  <https://orcid.org/0000-0003-1416-1238>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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BIOSKETCH

Sarah Bailey is a research scientist with Fisheries and Oceans Canada, where she provides science advice to policymakers concerning aquatic non-indigenous species transported by shipping pathways. Interests and expertise of the group of authors include invasion ecology, marine ecology, conservation biology and/or evolution, focusing on a variety of taxa from freshwater fishes to marine phytoplankton. The authors conduct independent and collaborative research on the patterns, mechanisms, management and/or consequences of species introductions to aquatic environments at multiple spatial and temporal scales, regularly informing policy development at national and international fora.

Author contributions: S.B. conceived the study, led data analysis and drafting of the manuscript. All authors compiled and critically reviewed data. S.B., J.T.C and P.F. conducted final standardization of data including pathway assignments. A.C., F.C. and J.D. contributed to data analysis. J.T.C., J.D., B.G., G.I., H.O. and G.R. made significant contributions to early drafts of the manuscript. All authors contributed to editing the final manuscript.