Research Article

A low number of introduced marine species at low latitudes: a case study from southern Florida with a special focus on Mollusca

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Abstract

The anthropogenic transfer of non-indigenous marine species (NIMS) into new areas of the oceans is a key issue. Despite increasing research effort in recent years many fundamental questions remain to be answered before we can effectively manage the issue. One question is whether the greater number of NIMS thus far documented in temperate waters is real or an artefact of fewer surveys being undertaken in tropical environments. Another one is whether poor taxonomic knowledge of the biodiverse tropics hides NIMS that actually occur there. Extensive taxonomic work in three Pacific localities (Guam, northern Western Australia and Singapore) has been collated in previous papers showing that there are relatively few NIMS in these biodiverse environments. The present paper replicates investigations for a low latitude environment in southern Florida in the Atlantic Ocean. The focus area includes the extensive Florida Keys coral reef environment, the southern margin of the Everglades on Florida Bay and the major PortMiami. Only 48 NIMS were identified in a literature-based compilation of 4,615 species; 15 species were represented by isolated records and have not established populations, leaving only 33 NIMS that are established or whose status is unknown. Records for Mollusca, the group with the most species (1,153) in the compilation, were individually researched and taxonomically verified. It is argued that the relative paucity of NIMS is not a straightforward temperature-driven tropical/temperate issue, but instead there are biological factor(s) restricting the ability of NIMS to colonise biodiverse environments compared to less diverse areas.

Key words: introduced marine pests, biotic resistance, artificial reefs, Florida Keys, biodiversity databases, molluscs

Introduction

The anthropogenic transfer of non-indigenous marine species (NIMS) from one part of the world's oceans to another is one of the key issues in protecting marine environmental diversity (Johnson and Chapman 2007; Molnar et al. 2008; Katsanevakis et al. 2014b; Crowe and Frid 2015). There has been growing concern about the increasing number of marine invasions reported and their perceived effects. For example, the recent introduction of the Indo-Pacific lionfish *Pterois volitans* and *P. miles* into Florida and the Caribbean Sea (Albins and Hixon 2008; Hackerott et al.

2013; Côté et al. 2013) has received extensive publicity. There are numerous anthropogenic mechanisms for species introductions. Shipping, either as biofouling (Hewitt 2002; Hewitt et al. 2004; Yeo and Chia 2010; Yeo et al. 2011; Jaafar et al. 2012) or in ballast water (Carlton 1985), is a dominant component in most areas. Construction of canals, particularly the Suez Canal, is another important cause. Deliberate introductions include aquaculture species and the release of unwanted aquarium species. Inadvertent introductions can include species attached to deliberate introductions, such as organisms adhering to introduced oysters (e.g., Lavesque et al. 2020).

The numbers of NIMS are truly staggering. Eight hundred twenty-one species are known to have been introduced to the Mediterranean Sea, largely a result of Lessepsian migration through the Suez Canal (Zenetos et al. 2017). A smaller number of species have migrated through the canal from the Mediterranean to the Red Sea; the numbers of NIMS in both areas continue to increase as new discoveries are made. A total of 343 NIMS has been recorded in Hawaii (Eldredge and Smith 2001). Fofonoff et al. (2018) provide data on 276 marine and estuarine NIMS in California, 190 of which are in San Francisco Bay alone (Foss 2008). A study published 15 years ago recorded 99 NIMS in Port Philip Bay, Melbourne, Australia (Hewitt et al. 2004) and undoubtedly there have been more introductions since then. In addition, there are many cryptogenic species whose native ranges cannot yet be determined, some of which may have been introduced through anthropogenic mechanisms.

NIMS can have various deleterious effects by disrupting native ecosystems, outcompeting local species, threatening commercial fisheries, introducing diseases and fouling industrial structures (Hayes et al. 2005; Wells et al. 2009). Fortunately, most of the NIMS have no apparent adverse effects; only a small proportion become marine pests (Hayes et al. 2005; Wells et al. 2009).

Most studies have reported fewer NIMS in tropical waters than in temperate environments (e.g., Coles and Eldredge 2002; Hewitt 2002; Hutchings et al. 2002; Huisman et al. 2008; Hewitt and Campbell 2010; Freestone et al. 2011, 2013). Several potential causes have been proposed for this, including an increase in biotic interactions such as predation and competition as a result of the higher tropical diversity making it more difficult for species to become established (Hewitt 2002). Alternatively, it has been suggested that the lower number of tropical NIMS is simply a result of fewer studies resulting in fewer detections, or our lack of taxonomic knowledge of the biodiverse tropics may result in NIMS remaining undetected (Hewitt 2002). The relative paucity of NIMS in tropical environments was specifically addressed by Hewitt (2002), who compared the results of four tropical and four temperate surveys of Australian ports conducted with the same techniques. Fifty-eight NIMS were detected; 48 in the temperate ports and only 28 in the tropical ports.

Wells (2018) investigated whether the apparent low number of tropical NIMS is real or an artefact of a lack of taxonomic knowledge along the 800 km long coast of the Pilbara region in northwestern Australia. The shallow water marine biota of the Pilbara has been extensively investigated, primarily by studies led by the Western Australian Museum, and identifications have been made of 5,532 species across a wide range of taxa. Prior to the development of an iron ore mining industry in the 1960s the Pilbara had been visited by relatively few vessels from overseas or interstate, limiting the opportunities for NIMS introductions. This changed in the early 2000s with the commencement of a ten-year boom in iron ore mining and liquefied natural gas construction projects. Strict marine quarantine procedures were instituted in the Pilbara to minimise the introduction of NIMS and extensive monitoring programs were undertaken to detect any species that had penetrated the quarantine barriers. Only 17 NIMS have been detected in the Pilbara, compared to 54 in southern Western Australia. Only one species (the ascidian *Didemnum perlucidum*) on the Australian national marine pest list of 55 species (NIMPCG 2009a, b) occurs in the Pilbara; it also occurs on the west and temperate south coast of Western Australia. In contrast 12 species on the Australian national marine pest list occur in southern Australia (DAWE 2020).

The Pilbara study was repeated in Singapore (Wells et al. 2019). In contrast to the relatively undisturbed Pilbara marine environment, international trade in Singapore goes back at least to the 1300s. European vessels first arrived in the 1500s, and vessel numbers increased rapidly in the early 1800s when Singapore became a British colony (Yeo et al. 2011). Singapore is now one of the busiest ports in the world and is connected to over 600 ports in 120 countries (MPA 2017). In 2016 there were 138,998 vessel arrivals involving a total of 593 million tonnes of cargo and a million passengers. Arrivals included a large number of high-risk vessels, such as barges, tugboats, dredges, oil rigs and similar vessels that remain in port areas for long periods (MPA 2017). Following the downturn in international shipping in 2008 associated with the global financial crisis many vessels remained in port for months, increasing the risk of biofouling and NIMS introductions (Floerl and Coutts 2009). Seebens et al. (2013) ranked Singapore as the number one port in the world for the risk of marine bioinvasions. The shallow water marine biota of Singapore has been extensively studied by the National University of Singapore, with 3,650 species recorded, but Wells et al. (2019) found only 22 NIMS in Singapore waters. Only three of these (the mussels *Brachidontes striatulus*, *Mytella strigata* and *Mytilopsis sallei*) were potential marine pests.

The present study replicates the Pilbara and Singapore studies in low latitude southern Florida. The location was chosen for several reasons. It is in a different ocean, the western North Atlantic. The coral cay archipelago of the Florida Keys is a large, coral reef marine environment that is biodiverse and well documented. Although the Keys are outside the tropics, the biota is tropical. The Florida Current originates in the South Atlantic and Caribbean Sea and carries warm, marine water from the Caribbean to the Keys (FKNMS 2020). Florida Bay, to the northeast of the Keys, is shallow water and abuts the ecologically important Florida Everglades, where the variety of invasive terrestrial and freshwater species is a considerable problem (Ferriter et al. 2006). Salinities in Florida Bay are highly variable. They reached a maximum of up to 70 PSU in the late 1980s. Monthly monitoring from 1998 to 2004 showed a range of 24 PSU in October 1999 just after Hurricane Irene to 42 in July 2001 after a drought (Kelble et al. 2007). The Miami area, which includes PortMiami, is situated just north of the Keys, on the east coast of Florida's peninsula. The port advertises itself as the cruise capital of the world, with 55 cruise ships operating from the port and visiting the Bahamas, Caribbean and Mexico. In 2019, 958 cargo ships entered the port, importing 5.7 million tons of cargo and exporting 4.4 million tons (PortMiami 2020). There were over 950,000 registered boats in Florida in 2018 (FHSMV 2020), many of which are trailered between locations and thus provide an additional mechanism for introductions.

Materials and methods

Separate literature and internet searches were undertaken of the shallow water benthic marine biota of southern Florida, including macroscopic invertebrates, fishes and marine plants. Marine birds, mammals, reptiles, parasites and microscopic species were excluded.

The literature search commenced by examining a major three volume work *Gulf of Mexico–Origins, Waters, and Biota* on the biota of the Gulf of Mexico edited by Felder and Camp (2009). Numerous chapters in the biodiversity volume provide information on specific taxonomic groups authored by specialists in the respective taxa. While there is a consistent format, there are some differences in the treatment of the different taxa. The Gulf for the purposes of that study was divided into four quadrants, with our study area falling into the border area of north-east and south-east quadrants. Few distributional point data are provided in that study, so the taxonomic chapters were used to develop an Excel database of Gulf of Mexico species in each taxon. Specific mentions of species occurring in the Florida Keys and data on NIMS in the Gulf of Mexico (provided in some chapters) were noted.

The literature search then built on the information sourced from Felder and Camp (2009). Relevant references were examined for marine species reported as occurring in the Florida Keys, Florida Bay and Biscayne Bay, where PortMiami (25.77°N; 80.17°W) is located. Miami Beach is on the north-eastern side of Biscayne Bay. Both the bay and seaward side of Miami

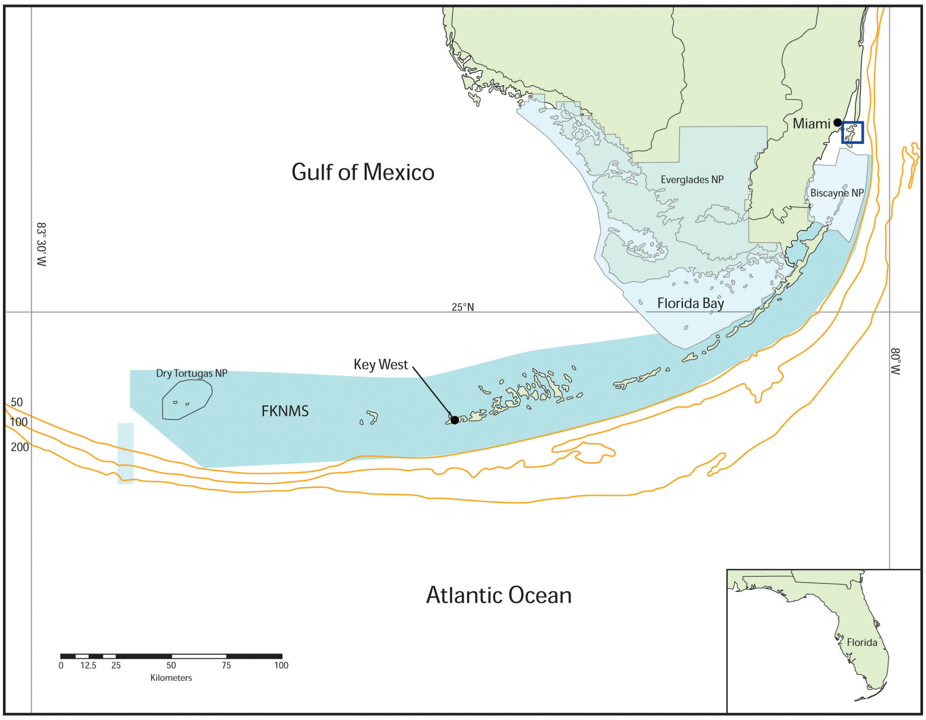

Figure 1. Project region at the southern tip of the State of Florida, encompassing several large federally protected areas, including the Florida Keys National Marine Sanctuary (FKNMS, dark blue) and three U.S. National Parks (Biscayne, Everglades, and Dry Tortugas). Two major cities, Miami in Miami-Dade County (with PortMiami indicated by a box) and Key West in Monroe County, are marked. 50, 100, and 200 m isobaths indicated.

Beach were included. The Florida Keys was broadly defined to include Dry Tortugas (24.63°N; 82.92°W) and Florida Strait to a depth of 300 m (Figure 1).

The University of Miami commenced publication of the *Bulletin of Marine Science of the Gulf and Caribbean* in 1951. Many early papers concentrated on the biota near the university laboratory at Virginia Key in Biscayne Bay. Over the years the geographical coverage of the journal broadened and it was renamed in 1965 as the *Bulletin of Marine Science*. Because of the regional relevance, all issues of the journal through 2019 were examined for additional occurrence data and mention of NIMS.

The internet searches used Google Scholar to search for taxonomic papers for the localities of Florida Keys, Florida Bay, Biscayne Bay, Miami, Dry Tortugas and Florida Strait. Each locality was searched individually for all of the taxa listed in Table 1 and also for general biotic surveys. We also analysed records in the study area for all of the taxa in Table 1 from GBIF (2019).

An Excel spreadsheet was constructed for each of the taxa in Table 1 showing species recorded for Florida Keys, Florida Bay and Biscayne Bay. Whereas the spreadsheets provided a wealth of distributional data, we are aware of quality control issues in such data compilations (e.g., as discussed by Ball-Damerow et al. 2019) and have, were possible, checked outliers against additional sources. In addition, it must be noted that the data capture and georeferencing of North American marine invertebrate collections lags

Table 1. Numbers of species recorded in various taxonomic groups in southern Florida and the primary sources of information.

Taxonomic group	Number of species	Primary sources of information
Multiple taxa		Voss and Voss (1955); Smith et al. (2007); NOAA (1995); FLDEP (2018), GBIF (2019)
Marine algae	544	Tabb and Manning (1961); Humm (1963, 1964); Ballantine (1996); Croley and Dawes (1970); Hine and Humm (1971); Mathieson and Dawes (1975); Zieman et al. (1989); Frankovich and Fourqureane (1997); Dawes et al. (1999); Cho and Fredericq (2006); Glardon et al. (2008); Fredericq et al. (2009); Burke et al. (2011)
Seagrasses	7	Zieman et al. (1989); Ley et al. (1994)
Mangroves	4	Ley et al. (1994); UF/IFAS (2019)
Sponges	112	Tabb and Manning (1961); Callahan (2005); Alvarez et al. (1998); Rützler et al. (2009); Stevely et al. (2010)
Corals	83	Wheaton and Jaap (1988); Jaap et al. (1989); Cairns (2000); Callahan (2005); Cairns et al. (2009)
Other cnidarians	111	Wallace (1909); Bayer (1961); den Hartog (1980); Wheaton and Jaap (1988); Jaap et al. (1989); Fautin and Daly (2009); Opresko (2009); Cairns and Bayer (2009); Calder and Cairns (2009)
Nemerteans	22	Correa (1961); Norenburg (2009)
Polychaetes	573	Treadwell (1911); Monro (1933); Hartman (1951, 1959); Taylor (1966); Ebbs (1966); Perkins (1979, 1980, 1981, 1984, 1985); San Martín (1991, 1992); Fauchald (1992); Rouse (1994); Fauchald et al. (2009); Bastida-Zavala et al. (2017)
Sipunculans	20	Rice (2009)
Bryozoans	122	McCann et al. (2007); Winston and Maturo (2009), Osburn (1914), Bastida-Zavala et al. (2017)
Crustaceans	813	Voss and Voss (1955); Provenzano (1959); Moore and McPherson (1963); Biffar (1971); Moore et al. (1974); Abele and Kim (1986); Griffith (1987); Holmquist et al. (1989); Thomas and Barnard (1992); Criales et al. (2000); Smith et al. (2007); Felder et al. (2009); Gittings (2009); Reaka et al. (2009); Schotte et al. (2009); Carlton et al. (2011), Tavares (2011).
Echinoderms	184	Thomas (1962, 1964); Kier and Grant (1965); Singletary (1971); Pawson et al. (2009)
Brachiopods	10	Santagata and Tunnell (2009)
Molluscs	1153	Clark (1994); Mikkelsen and Bieler (2000, 2004, 2007); Bieler and Mikkelsen (2003, 2004a, 2004b, *unpublished data*); Bieler et al. (2004); Lyons and Moretzsohn (2009); Rosenberg et al. (2009); Turgeon et al. (2009); Collins et al. (2019); NPS (2020)
Ascidians	23	Plough and Jones (1939); Cole and Lambert (2009); Rocha et al. (2012)
Fishes	834	Roessler (1970); Emery (1973); Jones and Thompson (1978); Sogard et al. (1989); Thayer and Chester (1989); Ley et al. (1994); Serafy et al. (2003); Wiley and Simpfendorfer (2007); McEachran (2009); Starck et al. (2017); Hepner (2017); Bannerot and Schmale (2002)
Total	4615	

behind those of vertebrates and flowering plants and the GBIF data holdings do not yet reflect the majority of actual collections-based records for many groups (e.g. Sierwald et al. 2018).

One of the authors of this paper (RB) has worked extensively over the last two decades on the molluscan diversity of the Florida Keys and Florida Bay (Bieler and Mikkelsen 2003, 2004a, b; Collins et al. 2019; Mikkelsen and Bieler 2000, 2004, 2007), with focus on non-native taxa (Bieler et al. 2004, 2017). This provided the opportunity to verify individual published records of NIMS for this phylum and to evaluate potential additions to that list. To better ascertain actual distribution data for molluscs, we analysed aggregated listings of museum collection records. For the region, there are several data aggregators providing such services, e.g. (in order of increasing taxonomic and geographic inclusiveness), InvertEBase (2020), IDigBio (2020), and GBIF. This information was used to update the molluscan species list for the present study. We disregarded unique records of shells that were likely discarded as food or decorative items; or were introduced to the region as part of beach nourishment projects.

To avoid double counting, only taxa identified to species were included. Those cited as tentatively identified (e.g., referred to family or genus sp. A, sp. 1, etc.) were not included as there was no way of determining species-level identity across studies and there was no mechanism for assessing whether or not the taxon was introduced to southern Florida.

Information was derived on NIMS during all of the above literature and database surveys. In addition, a specific internet search was undertaken using terms such as marine invasive species, introduced marine species, etc. coupled with the specific localities. Further, broader databases on introduced species in Florida and the United States were examined. In particular, the National Exotic Marine and Estuarine Species Information System (NEMESIS) (Fofonoff et al. 2018) was used to identify NIMS. Species recorded during this search were checked against the World Register of Marine Species (WoRMS 2019) and the names updated where appropriate. The WoRMS category "marine" was used to determine the habitat occupied by a species for inclusion on the NIMS species list. The World Register of Introduced Marine Species (WRiMS 2019) was also consulted. While WRiMS requires considerable work to verify the information contained, it is the most comprehensive resource available.

One of the problems is that the native ranges of many widespread species are not known; these species are referred to as cryptogenic. For example, Fauchald et al. (2009) list 854 polychaete species from the Gulf of Mexico, 181 of which are considered to be potential invaders (but these are not specified in the publication). In a study such as the present paper, with thousands of species across a wide range of taxa, it is not possible to accurately determine the published ranges of all species. We have adopted a very conservative approach of restricting the term cryptogenic to species listed as such by Fofonoff et al. (2018). Two molluscs reported as "potentially introduced" by Bieler et al. (2017) are also listed here as cryptogenic as they essentially used that phrase as equivalent to cryptogenic.

Results

A total of 4,615 taxa were identified in the study area (Table 1). The most diverse groups were molluscs (1,153 species), fishes (834), crustaceans (813), polychaetes (573) and marine algae (544). Apart from polychaetes, these are well known groups that tend to have large-bodied species. Ascidians, a group known to include marine invasive species, were not well represented in the study with only 23 species.

Forty-eight species are non-indigenous to the study area (Table 2); an additional 19 species are cryptogenic (Supplementary material Table S1).

Table 2. Non-indigenous marine species (NIMS) recorded in southern Florida. Abbreviations: Keys, Florida Keys; FB, Florida Bay; BB, Biscayne Bay; WoRMS, World Register of Marine Species; WRiMS, World Register of Introduced Marine Species.

Group/Species	Location	Presumed source	WRiMS	Established	Notes
MANGROVE					
Lumnitzera racemosa Willd.	BB	Botanical garden escape	No	Yes	Spread from cultivation at Fairchild Tropical Botanic Garden where trees had been planted in the late 1960s. Spread was discovered in 2008 and eradication is ongoing (UF/IFAS 2019). Recorded by GBIF (2019) from BB. The species closely resemble the native *Laguncularia racemosa* (L.) C.F. Gaertn.
CNIDARIANS					
Carijoa riisei (Duchassaing & Michelotti, 1860)	Keys, BB	Shipping	Yes	Presumed to be established.	Although described from the Virgin Islands, *Carijoa riisei* is an Indo-West Pacific species. It was first recorded from Dry Tortugas in 1869 and BB in 1947 (Fofonoff et al. 2018).
Diadumene lineata (Verrill, 1869)	Keys, BB	Shipping	Yes	Presumed to be established.	Native range from Hong Kong to Japan. Widely introduced to east and gulf coasts (Fofonoff et al. 2018). Recorded from the Keys and BB by GBIF (2019).
Tubastraea coccinea Lesson, 1829	Keys, BB	Shipping?	Yes	Yes	Indo-West Pacific species. Cairns (2000), Fenner & Banks (2004); Ferry (2009), Precht et al. (2014), Bieler et al. (2017), Fofonoff et al. (2018), GBIF (2019).
POLYCHAETES					
Ficopomatus uschakovi (Pillai, 1960)	BB	Shipping	Yes	Yes	An Indo-West Pacific species reported by Bastida-Zavala et al. (2017) and Fofonoff et al. (2018).
Hydroides elegans (Haswell, 1883)	Keys, BB	Shipping	Yes	Yes	Çinar (2013), Bastida-Zavala et al. (2017). The map provided by Fofonoff et al. (2018) shows Florida populations as cryptogenic, but the text states the species is thought to have originated in the Indo-Pacific and introduced in the western Atlantic.
Poecilochaetus johnsoni Hartman, 1939	Keys, BB	Shipping	No	Yes	Described from southern California. Taylor (1966) recorded the species in BB and other localities. Recorded from the Keys and BB by GBIF (2019).
Protula balboensis Monro, 1933	BB	Shipping	No	Rare	Thought to be an eastern Pacific species introduced to the western Atlantic, but possibly originated in the western Atlantic (Bastida-Zavala et al. 2017; Fofonoff et al. 2018).
CRUSTACEANS					
Amphibalanus amphitrite (Darwin, 1854)	Keys, BB	Shipping	Yes	Yes	Possibly native to the Indo-West Pacific. Carlton et al. (2011). Fofonoff et al. (2018) report that a single specimen from Dry Tortugas may have been from a ship's bottom. Moore and Frue (1974) from BB. GBIF (2019) records from both the Keys and BB.
Amphibalanus reticulatus (Utinomi, 1967)	Keys, BB	Shipping	Yes	Yes	Indo-West Pacific species. Carlton et al. (2011), Fofonoff et al. (2018).
Balanus trigonus Darwin, 1854	Keys, BB	Shipping	Yes	Yes	Broad Indo-West and eastern Pacific distribution (Fofonoff et al. 2018). Recorded in southern Florida by Carlton et al. (2011), Fofonoff et al. (2018), GBIF (2019).
Caprella scaura Templeton, 1836	BB	Shipping	Yes	Unknown	Described from Mauritius but origin is uncertain (Fofonoff et al. 2018). Recorded from BB (Fofonoff et al. 2018; GBIF 2019).
Charybdis hellerii (A. Milne-Edwards, 1867)	Keys	Shipping	Yes	Yes	Indo-West Pacific. Fofonoff et al. (2018) reported from Long Key, USGS (2019) from Monroe County, and two GBIF (2019) two records in the Keys.
Cyclograpsus integer H. Milne Edwards, 1837	Keys	Shipping	No	Yes	Eastern Atlantic. Rathbun (1918) listed from Key West and GBIF (2019) has several records.
Ligia exotica Roux, 1828	Keys, BB	Shipping	No	Yes	Fofonoff et al. (2018) recorded as an Indo-Pacific species found in Key West in 1883. Widely distributed on US east coast and Gulf of Mexico. GBIF (2019) records from both the Keys and BB.

Table 2. (continued).

Group/Species	Location	Presumed source	WRiMS	Established	Notes
Limnoria pfefferi Stebbing, 1904	BB	Shipping	No	Unknown	Indo-Pacific species recorded from Miami Beach. Assumed to be a viable population (Fofonoff et al. 2018).
Paradella dianae (Menzies, 1962)	Keys, BB	Shipping	Yes	Unknown	Native to west coast of North America, California to Mexico. Recorded from BB (Fofonoff et al. (2018). GBIF (2019) records from the Keys.
Penaeus monodon Fabricius, 1798	Keys, BB	Aquaculture release	Yes	Yes	Tavares (2011), Fofonoff et al. (2018), USGS (2019) and GBIF (2019) records from the Keys and BB.
Penaeus vannamei (Boone, 1931)	Keys, BB	Aquaculture release	Yes	No	Fofonoff et al. (2018) discuss the species in detail. Wild catches are thought to have been the result of escapes from aquaculture farms. No evidence of living populations. GBIF (2019) records from both the Keys and BB.
Pullosquilla litoralis (Michel & Manning, 1971)	Keys	Shipping, aquarium release or possibly scientific research.	Yes	No	Indo-Pacific species. Single individual collected at Key Largo in 1998 (Fofonoff et al. 2018).
Sphaeroma terebrans Bate, 1866	BB	Shipping	Yes	Unknown	Thought to be native to Indo-West Pacific but widespread in tropical waters (Fofonoff et al. 2018).
Sphaeroma walkeri Stebbing, 1905	BB	Shipping	Yes	Unknown	Native to Indian Ocean, recorded from BB (Fofonoff et al. 2018, GBIF 2019).
MOLLUSCS					
Eualetes tulipa (Rosseau in Chenu, 1843)	Keys, BB	Shipping	No	Yes	Eastern Pacific. Reported from southern Florida for the first time in this paper. Earlier record by Miller (1970) was misidentified as *Petaloconchus mcgintyi*, from Miami. Widely introduced elsewhere (e.g., Miloslavich 1995).
Hyotissa hyotis (Linnaeus, 1758)	Keys, BB	Shipping	Yes	Yes	Indo-West Pacific. Bieler et al. (2004), Rosenberg et al. (2009), Bieler et al. (2017). Apparently still limited to artificial reef structures. Recorded by GBIF (2019) in the Keys and BB.
Littorina littorea Linnaeus, 1758	Keys	Shipping	Yes	No	Eastern North Atlantic. A single specimen from Monroe County collected in 1952 (EDDSMapS 2020).
Pinctada margaritifera (Linnaeus, 1758)	BB	Shipping	Yes	No	Indo-West Pacific species. Fofonoff et al. (2018) provide several Florida records, including an undated specimen from off Key West.
Rapana venosa (Valenciennes, 1846)	Keys	Discard?	Yes	No	Western Pacific. Near Fiesta Key 1973 (single live-collected specimen), USGS (2019).
Thylacodes vandyensis Bieler, Rawlings & Collins, 2017	Keys	Shipping	No	Yes (single site)	Originally described from Keys shipwreck but Bieler et al. (2017) provided molecular evidence for a likely Pacific origin. Discussed as "potentially invasive" by the authors. South Florida (South Florida PBS 2018). Recorded by GBIF (2019) in the Keys and BB.
ASCIDIANS					
Ascidia sydneiensis Stimpson, 1855	BB	Shipping	Yes	Yes	Indo-West Pacific species reported by Fofonoff et al. (2018).
Botrylloides violaceus Oka, 1927	Keys, BB	Shipping	Yes		Northwestern Pacific species (Fofonoff et al. 2018). GBIF (2019) records from the Keys and BB.
Didemnum perlucidum Monniot, 1983	Keys	Shipping	Yes	Yes	Cryptogenic, but Florida populations are introduced (Fofonoff et al. 2018). Simkanin et al. (2016). GBIF (2019) records from the Keys.
Didemnum psammatodes (Sluiter, 1895)	Keys, BB	Shipping	Yes	Yes	Indo-West Pacific species recorded by Simkanin et al. (2016), Fofonoff et al. (2018). GBIF (2019) records from the Keys.
Diplosoma listerianum (Milne-Edwards, 1841)	Keys, BB	Shipping	Yes	Yes	A complex of species, but introduced in the northwest Atlantic (Fofonoff et al. 2018). Recorded from the Keys and BB by GBIF (2019).
Styela canopus (Savigny, 1816)	Keys, BB	Shipping	Yes	Yes	Indo-West Pacific species reported by Simkanin et al. (2016), Fofonoff et al. (2018), GBIF (2019) records from the Keys.
Styela plicata (Lesueur, 1823)	BB	Shipping	Yes	Yes	Possibly native to Northwest Pacific (Fofonoff et al. 2018). Weiss (1948), Simkanin et al. (2016). GBIF (2019) records from BB.

Table 2. (continued).

Group/Species	Location	Presumed source	WRiMS	Established	Notes
FISHES					
Acanthochromis polyacanthus (Bleeker, 1855)	BB	Aquarium release	No	No	Two individuals were removed from the Miami Beach Marina in 2017 (USGS 2019). Considered as of unknown status by Schofield & Akins (2019).
Cephalopholis argus Schneider, 1801	Keys	Aquarium release	Yes	No	Observed off Key West in 2006 (Schofield et al. 2009).
Cromileptes altivelis (Valenciennes, 1828)	Keys	Aquarium release	Yes	No	One specimen taken by spearfisherman off North Key Largo (Huffpost 2013). Previously recorded at several other Florida localities but considered to be extirpated (Mundy 2005, Schofield et al. 2009).
Dascyllus aruanus (Linnaeus, 1758)	Keys, BB	Aquarium release	No	No	One individual removed from Palm Beach County in 2009 and two were sighted in the Miami Beach Marina in 2017 (USGS 2019). GBIF (2019) records from the Keys.
Hypsoblennius invemar Smith-Vaniz & Acero, 1980	Keys, BB	Shipping	No	Yes	Native to Lesser Antilles and South America. Schofield et al. (2009), Schofield & Akins (2019). GBIF (2019) records from the Keys.
Naso lituratus (Forster in Bloch and Schneider, 1801)	Keys	Aquarium release	No	No	The species was sighted off Boca Raton in 2000 and 2001 and a single individual was removed from Molasses Reef, Florida Keys in 2018 (USGS 2019).
Platax orbicularis (Forsskål, 1775)	Keys	Aquarium release	Yes	No	Isolated specimens found off Keys and removed. Schofield et al. (2009), Florida Museum (2019), USGS (2019). GBIF (2019) records from Keys. Considered as of unknown status by Schofield & Akins (2019).
Pomacanthus imperator (Bloch, 1787)	BB	Aquarium release	Yes	No	Three sightings have been made in Florida, including one off North Miami Beach in 2002 (USGS 2019).
Pterois miles (Bennett, 1828)	Keys	Aquarium release	Yes	Yes	Widespread in southern Florida. Invasive (Schofield 2009).
Pterois volitans (Linnaeus, 1758)	Keys, BB	Aquarium release	Yes	Yes	Widespread in southern Florida. Invasive (Schofield 2009). GBIF (2019) records from the Keys and BB.
Zanclus cornutus (Linnaeus, 1758)	BB	Aquarium release	No	No	Three individuals have been found in Florida, including one in Biscayne National Park in 2018 (USGS 2019).
Zebrasoma flavescens (Bennett, 1828)	Keys	Aquarium release	Yes	No	Isolated individuals recorded from several Florida localities, including Marathon and Dry Rocks in the Keys (USGS 2019).
Zebrasoma veliferum (Bloch, 1795)	Keys	Aquarium release	Yes	No	Seen in three Florida localities from 2001 to 2003, including Key Largo (Schofield et al. 2009). GBIF (2019) records from the Keys.

Six records of potential NIMS are rejected (Table S2). The 48 non-indigenous species are dominated by crustaceans (14 species), fishes (13) and ascidians (7) (Table 2). Ten species of fishes, two crustaceans and three molluscs have not established populations, leaving 33 NIMS that are thought to have become established or whose status is uncertain. Twenty-four NIMS have been recorded from the Florida Keys and 28 from Biscayne Bay.

Twelve of the non-indigenous fish species are thought to have been introduced as aquarium releases. Specimens of the non-indigenous mangrove were planted in a botanical garden. The species was later discovered growing in a nearby stand of mangroves and has not yet been eliminated. Two crustacean species were aquaculture releases and one mollusc may have been discarded at the site where it was recorded. The likely introduction method of one species cannot be determined. Interestingly, 29 of the 33 species of NIMS are thought to have been introduced through shipping, but only one of the 13 fish species was introduced through shipping.

Discussion

Overview of NIMS in Southern Florida

Ferriter et al. (2006) list 129 priority introduced terrestrial species and 83 priority introduced freshwater species the Florida Everglades, Florida Bay and Florida Keys (non-priority taxa not listed). In contrast to the terrestrial and freshwater environments, only 48 of the 4,615 marine species we recorded in the southern Florida study area have been introduced, and only 33 are believed to have established populations or whose population status is uncertain. Twenty-four potentially established NIMS have been recorded from the Florida Keys and 28 from Biscayne Bay.

The question arises: How complete is the analysis of NIMS in southern Florida if there has been no specific survey for NIMS? However, even targeted NIMS surveys such as the eight reported by Hewitt (2002) are incomplete due to the limited extent of the surveys, absence of taxonomists to identify key groups and the large number of cryptogenic species. Bishop and Hutchings (2011) assessed the results of 46 NIMS surveys of Australian ports and concluded that surveys for targeted species may provide information on those species, but the surveys are not effective in a broader context. Most NIMS are molluscs and crustaceans (Ruiz et al. 2000). Data for these taxa in southern Florida are extensive, with 1153 species of molluscs and 813 crustaceans recorded, but only 3 molluscs and 12 crustaceans were NIMS with established populations. Two of the molluscs are apparently still limited to artificial reefs (the foam oyster *Hyotissa hyotis* and the worm-snail *Thylacodes vandyensis*). Only one species, the worm-snail *Eualetes tulipa*, is widely established. Likely of eastern Panamic origin, it was first reported in Miami by Miller (1970) as *Petaloconchus mcgintyi*, a misidentification. This species became tagged as a potential invasive in Hawaiian waters (Bieler in Carlton 1999: 449; as *Vermetus alii*). It is now known from many localities, including Venezuela (Miloslavich 2009), Brazil (Spotorno-Oliveira et al. 2018) and India (Jebakumar et al. 2015). Two other molluscs established in the Florida Keys (the pyramidelloidean snail *Cyclothyca pacei* and the foam oyster *Hyotissa mcgintyi*) are viewed as cryptogenic and need further study as to their geographic origin. Fishes, with 834 species are well known in southern Florida and NIMS have been closely monitored by Schofield and Akins (2019). Of the 13 species of fish recorded as possible NIMS, ten are not believed to have established populations (Table 2); only three are believed to be anthropogenic introductions that are living in natural environments.

Bryozoans can be a key component of NIMS (Wyatt et al. 2005). One hundred twenty-two species were recorded in the present study, none of which were NIMS. McCann et al. (2007) surveyed fouling communities of four bays in Florida, the southernmost of which were Tampa Bay and Indian River. Four bryozoan NIMS were detected; none of these were recorded in the present study of southern Florida. Polychaetes are a major gap. Although 573 species were recorded, their taxonomy and ranges are poorly known. Çinar (2013) reported that 292 species of polychaetes have been moved in world oceans by human transport and 180 have become established; how many of these species are in southern Florida is not known. Ascidians are another group with known NIMS. They are poorly represented in the southern Florida data with only 23 species, but 7 of these are NIMS. We conclude that, while incomplete, the data for southern Florida are consistent with the completeness of similar studies.

Key invasive species in southern Florida

The two lionfishes, *Pterois volitans* and *P. miles,* established in southern Florida (Schofield and Akins 2019), are having major impacts on native reef systems (e.g., Green et al. 2012). Having been recorded in low numbers along the Florida east coast since the 1980s, they were reported from the Florida Keys in 2009 and have rapidly expanded in numbers (Ruttenberg et al. 2012), especially along the reefs of the Florida Keys. Various efforts are underway to remove lionfish from Florida waters, including events for the general public (such as lionfish derbies and removal days) to collect the species (FFWCC 2020).

Potential NIMS not found in southern Florida

There are a number of potential NIMS species that could be introduced to southern Florida, that have not yet been recorded. It is interesting that none of the 544 species of macroalgae recorded from southern Florida are introduced despite the well-known invasives in the group and the presence of records of introduced *Caulerpa* in other parts of Florida. Approximately 150 marine algal species have been introduced to the Mediterranean Sea (Verlaque et al. 2004), with the genus *Caulerpa* attracting the most attention. A small patch of an aquarium strain of *C. taxifolia* was first detected off Monaco in 1984 (Meinesz et al. 1993). It became invasive and spread rapidly in the northern Mediterranean (Glardon et al. 2008). The strain was also reported from California (Jousson et al. 2000) and Australia (Wiedenmann et al. 2001; Millar 2004). A second variety of *C. taxifolia* discovered off southeastern Turkey (Cevik et al. 2007) spread westwards and has been reported from Sicily (Picciotto et al. 2016). A third invasive *Caulerpa*, *C. cylindracea,* has become widespread in the Mediterranean (Verlaque et al. 2000; Boudouresque and Verlaque 2002) and the Canary

Islands (Verlaque et al. 2004). Davidson et al. (2015) analyse the impacts of these and other algal species worldwide. Jacoby et al. (2004) reported the Indo-Pacific *Caulerpa brachypus* and native species becoming invasive in Palm Beach County and Broward County, Florida. As aquaria are a potential source of *Caulerpa*, Stam et al. (2006) examined the genetics of 256 individuals of *Caulerpa* being sold in aquarium shops and internet sites and in field locations in Florida (including the Florida Keys), the Bahamas, US Virgin Islands, and Honduras. Fourteen species were found. Only a single individual of an invasive strain of *C. racemosa* was detected, and this was in California.

The Asian green mussel *Perna viridis* is a highly successful invader (Rajagopal et al. 2006) due to its short life span, rapid growth rate, rapid sexual maturity, high fecundity, ability to colonise a wide range of habitats, wide physiological tolerances, gregarious behaviour, suspension feeding and ability to repopulate following a population crash (Morton 1997). It was first detected in Trinidad, West Indies in about 1991, spread to Venezuela by 1993 and now occurs widely in the Caribbean. The first detection in Florida was in Tampa Bay in 1999 (Ingrao et al. 2001; Barber et al. 2005). It has since been found at numerous localities on both the east and west coasts of Florida (McGuire and Stevely 2018), but has not been recorded in the Florida Keys. The absence of *P. viridis* in the Keys may simply be an artefact, but it parallels the situation in northern Australia where its absence may be due to oligotrophic water conditions (Huhn et al. 2017; Wells 2017).

The seagrass *Halophila stipulacea* was first detected in Grenada, West Indies, in 2001 (Ruiz and Ballantine 2004). It is now widespread in the Caribbean and is expected to continue its spread into the Gulf of Mexico (Ruiz et al. 2017) but has not yet been recorded from southern Florida.

The Indo-West Pacific orange cup coral *Tubastraea coccinea* is widespread in the Caribbean Sea and Gulf of Mexico, including the southern Florida study area (Fenner and Banks 2004; Figueroa et al. 2019). The congeneric *T. tagusensis* was recently detected at several sites, including in northern Florida. Further research may well record the species in southern Florida.

Methods of introductions

Apart from the apparent aquarium introductions of isolated individuals and aquaculture introductions it is very difficult to determine the methods of introduction of NIMS. As indicated above, biofouling (Hewitt 2002; Hewitt et al. 2004; Yeo and Chia 2010; Yeo et al. 2011; Jaafar et al. 2012) and ballast water (Carlton 1985) are the most important sources of NIMS in most regions.

Fifty-five cruise ships operate from PortMiami, near the northern end of Biscayne Bay. In 2018 the port also handled 1081 cargo vessels (PortMiami

2020). There were 4,016 ship arrivals, including operations by 40 cruise ships in 2019 in Port Everglades, 35 km north of PortMiami (Port Everglades 2020). Noting the difficulties in establishing introduction vectors discussed above, shipping is the most likely source of 29 of the 33 NIMS recorded in the study area (Table 2). Key West is only 200 km southwest of PortMiami in a straight line, so it would be relatively easy for vessels to secondarily disperse NIMS from either port to any location in the Keys.

Cruise ships have little requirement for ballast water. However, cargo vessels delivered 5.7 million tons of cargo to Miami in 2019 and 4.4 million tons were exported (PortMiami 2020). The ballast water associated with these cargoes provides a mechanism for the importation of NIMS into Miami, and also the export of species from the port. With the current Covid-19 crisis many of the cruise ships have remained for months in PortMiami with cruises suspended until 15 September (PortMiami 2020). This increases the risk of biofouling accumulations with potential NIMS species that could be exported to other ports once cruises resume (Floerl and Coutts 2009).

Commercial trading vessels, including cruise ships and cargo vessels, are regarded as low risk for the transfer of NIMS through biofouling as the vessels have antifouling coatings, remain in ports for short periods and move at relatively high speeds through the water. However, low risk does not mean no risk. There are a number of areas on commercial trading vessels where biofouling is likely to accumulate (Coutts and Taylor 2004; DoF 2009). An antifouling coating (AFC) cannot be applied to some structures, such as propellers and internal seawater systems. Vessels are supported on blocks during drydocking when the AFC is applied; AFC cannot be applied to the drydock support strips. All of these factors increase the risk of biofouling accumulation, potentially including NIMS, on the vessel.

Comparison of southern Florida with other geographical areas

The 33 NIMS in southern Florida is substantially fewer than 276 reported for California (Fofonoff et al. 2018), 190 in San Francisco Bay (Foss 2008) and 99 in Port Philip Bay, Melbourne, Australia (Hewitt et al. 2004). Teixeira and Creed (2020) recently recorded 119 NIMS along the 8,000 km coastline of Brazil. They demonstrated a generally increasing number of NIMS with latitude, though the pattern was complicated by concentrations of NIMS in areas where there were extensive maritime facilities. Even the brief surveys conducted in four temperate Australian ports by Hewitt (2002) reported more NIMS (58) than the present study. The low number of NIMS in southern Florida is consistent with the paucity of NIMS reported in other tropical studies: 85 in > 5,500 species recorded in Guam (Paulay et al. 2002); 17 NIMS of 5,532 species in the Pilbara, northwestern Australia (Huisman et al. 2008; Wells 2018); and 22 NIMS in 3,650 species in Singapore (Wells et al. 2019). These data support the contention that NIMS are more common in temperate than tropical marine environments.

Hawaii, with 343 NIMS (Eldredge and Smith 2001) is an exception to the low number of NIMS in the tropics. NIMS in Hawaii occur primarily in disturbed areas and relatively few are in open coastal areas (DeFelice et al. 2001). A rapid survey of 41 coral reef sites detected only 26 NIMS in 486 identified taxa; 17 were found at one or two sites and half of the sites had three or less NIMS (Coles et al. 2006). However, Hawaii is biogeographically isolated with a less diverse marine biota than other Indo-West Pacific localities (Hutchings et al. 2002), suggesting the issue is not one of tropical-temperate environments but instead an increased ability of NIMS to colonise environments that are less biologically diverse.

Another example of increased NIMS in a less biologically diverse environment is the Mediterranean Sea, which has a warm temperate biota. Zenetos et al. (2017) reported that 821 invasive alien species have been recorded in the Mediterranean. Katsanevakis et al. (2014a) divided the introduction mechanisms of each species in the eastern Mediterranean into four categories based on how well understood the introduction mechanism was. Four hundred twenty species in the two best understood categories were Lessepsian migrants through the Suez Canal, and additional Lessepsian migrants have subsequently been reported (e.g. Steger et al. 2018). While we could not find a species count, fewer anti Lessepsian migrations from the Mediterranean into the Red Sea, which has a tropical biota, are known (Rais Lasram et al. 2008). When the Suez Canal opened in 1869 two salinity barriers restricted movement between the Mediterranean Sea and Red Sea. The Bitter Lakes in the canal initially posed a high salinity barrier to movement of species through the canal, but over time the salinity decreased, removing the barrier. Also, the eastern Mediterranean had a lower salinity than the Red Sea. Construction of the Aswan Dam in 1965 restricted flow from the Nile River, increasing salinity in the eastern Mediterranean (Rais Lasram et al. 2008). Despite the salinity barriers, the Red Sea bivalve *Brachidontes pharaonis* was first detected at Port Said at the Mediterranean entrance to the canal in 1876 (Dogan et al. 2007). The greater number of Lessepsian species is not due entirely to a greater diversity of Red Sea biota as the dominant water flow in the Suez Canal is from south to north (Rais Lasram et al. 2008).

Studies in Guam (Paulay et al. 2002), Pilbara, Western Australia (Wells 2018), Singapore (Wells et al. 2019) and southern Florida (this paper) are all from biodiverse low latitude regions where the biota is relatively well known, yet all four reported relatively few NIMS. Hewitt (2002) examined four tropical and four temperate Australian ports using the same methodology and found more NIMS in the temperate ports. This strongly suggests that the relative paucity of NIMS in the studied environments is not due to a lack of study or inability to detect NIMS caused by poor taxonomic knowledge, but rather by increased biological interactions in a biodiverse environment (Hewitt 2002). One possible mechanism leading to a larger number of NIMS in a less biodiverse setting is physical separation, as was described by Zabin and Hadfield (2002), who found the Caribbean barnacle *Chthamalus proteus* higher on the Hawaiian intertidal shoreline than the native *Nesochthamalus intertextus*. Another approach was undertaken by Freestone et al. (2011, 2013), who demonstrated that increased predation could limit tropical invasions. Further study is required to confirm these and possible other biological interactions to explain the relative paucity of NIMS in diverse marine ecosystems.

Origin of NIMS in southern Florida

The presumed native ranges of 31 of the 33 NIMS recorded in southern Florida are shown on Table 2: 21 species are from the Indo-West Pacific, Northwestern Pacific or Indian Ocean; 1 (*Balanus trigonus*) has a broad distribution in the Indo-West Pacific and Eastern Pacific; 6 are from the Eastern Pacific; 2 are from the Eastern Atlantic; and 1 (the fish *Hypsoblennius invemar*) is from the Lesser Antilles and South America. It may have been introduced either naturally by currents or through shipping (Schofield and Akins 2019).

PortMiami (2020) reports that cruises from the port travel to the Bahamas, Caribbean and Mexico. Cargo trade is more widespread, with 46% with Latin America and the Caribbean, 37% to Asia and 16% to Europe.

The generally north flowing oceanic circulation pattern in the region provides a natural mechanism for the distribution of species from the Gulf of Mexico and Caribbean to southern Florida. This is well illustrated by the orange cup coral *Tubastraea coccinea* as discussed by Fenner and Banks (2004) and Creed et al. (2016). The species was described from Bora Bora in 1829 and was first recorded in the eastern Caribbean Sea in 1943. The most likely source of the first introduction was by ship. The expanding range of *T. coccinea* in the Caribbean and Gulf of Mexico follows the pattern of the die-off of the urchin *Diadema antillarum* which began in Panama in 1983–1984 and was spread by ocean currents. *Tubastraea coccinea* was first seen on a shipwreck in Florida in 1999 and has subsequently been found on a number of additional shipwrecks and other artificial habitats in southern Florida (Fenner and Banks 2004; Creed et al. 2016; Bieler et al. 2017). As described above, *Perna viridis* was first detected in Trinidad in about 1991 and since then has spread throughout the Caribbean and Gulf of Mexico to both coasts of Florida (McGuire and Stevely 2018).

It is possible that some of the presumed naturally widespread ranges of species known from the Caribbean, Gulf of Mexico and southern Florida have in resulted from vessel traffic in the past. Such a possibility has been discussed in detail in Singapore by Yeo et al. (2011).

The fact that NIMS in southern Florida have been introduced from other marine biogeographic regions rather than within the same region parallels the situation in the previous studies in Western Australia (Wells 2018) and Singapore (Wells et al. 2019). The recent distribution of *P. viridis* into eastern Indonesia (Huhn et al. 2017) is an exception.

It is noteworthy that many of the recognized NIMS and listed cryptogenic species in southern Florida are larger-bodied and/or colourful forms (foam oysters, orange cup corals, sea slugs, tropical fish) that are more readily noticed than small-bodied and cryptic members of their respective groups. However, in taxa where good data exist (e.g., molluscs), there is no indication that smaller-bodied NIMS have escaped detection.

It is also noted that the current list for southern Florida will be modified as additional information becomes available. Additional species are likely to be recorded, either as new records or revised taxonomy of existing known species. Alternatively, the number of NIMS in southern Florida may be reduced as understanding of the origins of individual species improves. For example, in the Mediterranean a group of experts in the taxonomy of various phyla (Zenetos et al. 2017) made major changes to a NIMS list published only a year earlier (Galil et al. 2016), excluding 72 species as being not-established or native, but adding a similar number of new records.

In particular, application of recent advantages in genetic techniques will enhance our understanding of NIMS, including those of southern Florida. For example, Sun et al. (2017) used genetic barcoding to investigate the status of the highly invasive serpulid polychaete *Hydroides dianthus*. Although the species was described from New England and is considered to be native to the east coast of North America, the genetic evidence suggests it may have originated in the Mediterranean. In addition, a distinct clade was detected in Texas that may represent separate species. Similarly, Dias et al. (2018) used genetic techniques to detect three clusters in the mytilid *Perna viridis*: (1) USA and Caribbean, (2) India and (3) Southeast Asia. Figueroa et al. (2019) used morphological analyses to demonstrate that there are three clades of the orange cup coral *Tubastraea* in the Gulf of Mexico: *T. coccinea, T. tagusensis* and an intermediate clade. The morphological results were confirmed by genetic analyses.

Thus, the present paper synthesizes our current understanding of NIMS patterns in the southern Florida study area. The details will undoubtedly change as more information is developed in future.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Cryptogenic marine species recorded in southern Florida.
Table S2. Doubtful and rejected records of non-indigenous marine species (NIMS) recorded in southern Florida.

This material is available as part of online article from:
http://www.reabic.net/journals/mbi/2020/Supplements/MBI_2020_Wells_Bieler_SupplementaryMaterials.xlsx