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Research Article

Assessing marine bioinvasions in the Galápagos Islands: implications for conservation biology and marine protected areas

James T. Carlton[1,*], Inti Keith[2,*] and Gregory M. Ruiz[3]

[1]*Williams College – Mystic Seaport Maritime Studies Program, 75 Greenmanville Ave., Mystic, Connecticut 96355, USA*
[2]*Charles Darwin Research Station, Marine Science Department, Puerto Ayora, Santa Cruz Island, Galápagos, Ecuador*
[3]*Smithsonian Environmental Research Center, Edgewater, Maryland 21037, USA*

Author e-mails: *james.t.carlton@williams.edu (JTC), inti.keith@fcdarwin.org.ec (IK), ruizg@si.edu (GMR)*

**Corresponding author*

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Abstract

The Galápagos Islands are recognized for their unique biota and are one of the world's largest marine protected areas. While invasions by non-indigenous species are common and recognized as a significant conservation threat in terrestrial habitats of the Archipelago, little is known about the magnitude of invasions in its coastal marine waters. Based upon recent field surveys, available literature, and analysis of the biogeographic status of previously reported taxa, we report 53 non-indigenous species of marine invertebrates in the Galápagos Islands. Forty-eight (90.6%) of these species are newly reported or newly recognized as introduced, a nearly ten-fold increase from the five species previously recognized as non-indigenous. Of these 48 species, 30 (62.5%) were newly discovered in surveys commenced in 2015. Ascidians (11 species), bryozoans (10), polychaetes (9), and hydroids (8) account for 38 (71.7%) of the introduced species. Our analyses further detected 33 cryptogenic invertebrate and algal species and one littoral vascular plant. Most taxonomic groups remain to be assessed for the presence of non-indigenous species. Importantly, the recent field surveys were restricted predominantly to one habitat (harbor biofouling) on two islands, further suggesting that introduced species richness for the Galápagos Islands may be considerably higher. Most of the introduced species treated here were likely brought to the Galápagos by ships. While we presume that most if not all of the many thousands of vessels arriving in the Galápagos Islands since the 1500s had marine animals and plants attached to their hulls, we hypothesize that the general absence in the Islands of extensive shoreline structures (in the form of wharves, docks, pilings, and buoys) until the last half of the 20th century may have constrained extensive colonization by fouling species. The proliferation of shoreline structures may have both provided expanded habitat for non-indigenous species that had earlier colonized natural substrates, as well as having facilitated a 20th and 21st century wave of new invasions in the Galápagos Islands. Our results represent the greatest reported increase in the recognition of the number of invasions for any tropical marine environment in the world. This work suggests that the number and potential ecological impacts of non-indigenous species in tropical marine and maritime habitats may be substantially underestimated in other regions of the world. Our study demonstrates that tropical marine invasions deserve significant attention, not only in a biogeographical, historical, and ecological context, but also from a management perspective, especially in the Galápagos and other high-value conservation areas.

Key words: cryptogenic, Eastern Tropical Pacific, dispersal vectors, ships, fouling, boring species, ballast

Introduction

The equatorial Galápagos Islands (Archipiélago de Colón), consisting of 18 major islands and several smaller islands and islets, occupy a sea area of 45,000 km^2 in the Eastern Pacific Ocean 900 km west of Ecuador. The Galápagos are recognized for their iconic biodiversity: they are a UNESCO World Heritage Site as well as a Biosphere Reserve. The Galápagos Marine Reserve of 138,000 km^2 is the largest reserve in the Eastern Tropical Pacific and one of the largest marine reserves in the world (Denkinger and Vinueza 2014). The Islands are thus of very high conservation priority for Ecuador as well as globally. This recognition of the unique, rich nature of the Galápagos Islands has led to significant attention on biosecurity, including some of the most advanced programs globally (Walsh and Mena 2013) that aim to prevent further invasions and reduce the number and impact of non-indigenous species on the Galápagos ecosystem.

First visited by Europeans in the 1500s and with colonization beginning in the 1800s, the history of discovery and exploration of the Galápagos has been well studied (Slevin 1959; Perry 1984; Larson 2010). Prior to World War II contact was by vessels arriving from the South American mainland or from overseas. That these vessels would likely have arrived with numerous fouling and (in wooden ships) boring species, as well as species transported in ballast, has been extensively documented (Carlton 1999, 2003; Keith et al. 2016; Ojaveer et al. 2018). Many of the thousands of vessels on international routes arriving in the Galápagos Islands over the centuries would have visited numerous ports en route, leading to the potential for the accumulation of species from multiple locations (Carlton and Hodder 1995). For example, the H.M.S. *Beagle* had stopped at 15 sites in the Atlantic and Pacific Oceans from 1831 to 1835, including the Canary Islands, Cape Verde Islands, Brazil, Uruguay, Argentina, Chile, and Peru, before reaching the Galápagos (Lipps 2010). A long history, commencing in the 19th century, of commercial exports of sulfur, timber, hides, and salt from the Islands (Wiggins and Porter 1971; Perry 1984; Fitter et al. 2000; Grenier 2009) meant that the vessels arriving to load these cargos discharged ballast – primarily solid ballast (rocks, sand, or other shore materials) prior to the 1900s and water ballast thereafter (Carlton 1985, 2007, 2011; Ojaveer et al. 2018). By 1920, for example, over 13,600 kg of sugar were exported monthly from San Cristobal Island (Hydrographic Office, United States Navy 1920). Occupation and visitation to the Islands have steadily grown, accompanied by a concomitant increase in sea (and eventually air) traffic. In 1938, 705 people lived in the Galápagos Islands (Grenier 2009). By the late 1960s, 2000–3000 people lived on the Islands (Wiggins and Porter 1971); by the early 1980s, 5000–6000 people were present (Perry 1984), and a 2010 census reported more than 25,000 inhabiting the five islands of Baltra, Floreana, Isabela, San Cristóbal and Santa Cruz (INEC 2010). In 2017 tourist visitation approached one-quarter million people per year (DPNG 2018).

Nearly 500 years of human contact between the Galápagos, South America, and the rest of the world inevitably led to numerous introductions of terrestrial animals and plants (Wiggins and Porter 1971; Peck et al. 1998; Causton et al. 2006; Phillips et al. 2012; Walsh and Mena 2013; Toral-Granda et al. 2017; Torres and Mena 2018). Despite this awareness of archipelago-wide human-mediated invasions, remarkably little attention was paid to the possibility of invasions in the Galápagos marine environment. Carlton (1988) presented the first discussion of the potential for marine introductions in the Galápagos Islands. Shortly thereafter, Banta (1991) suggested that the bryozoan *Bugula neritina* (Linnaeus, 1758) in Galápagos fouling communities was a probable introduction, and Zullo (1991) noted the introduction of the fouling barnacle *Megabalanus coccopoma* (Darwin, 1854). Peck et al. (1998) added two introduced shore flies to the maritime fauna. Hickman and Zimmerman (2000) reported the introduction of the mangrove crab *Cardisoma crassum* Smith, 1870. By the turn of the 21st century, five marine and maritime species had been documented as introductions to the Galápagos.

In 2015 we and colleagues initiated this study to test whether non-indigenous species richness is underestimated in the coastal marine communities of the Galápagos Islands, using field surveys and literature analyses that focused primarily on one habitat (harbor biofouling) and select taxonomic groups on two islands. In particular, we concentrated on the fouling community on artificial habitats as a model system, because these are hotspots for biological invasions in coastal habitats around the world (Glasby et al. 2007; Dafforn et al. 2009; Ruiz et al. 2009). Prior to our study, few investigators had examined Galápagos fouling communities. Before World War II maritime structures, such as wharves, docks, piers, and pilings, were rare in the Galápagos Islands. No wharves or docks appear to have been present prior to the 20th century (Hydrographic Office, United States Navy 1896), but by 1920 a 137-meter long pier had been built in Wreck Bay on San Cristobal Island (Hydrographic Office, United States Navy 1920). This pier (Figure 1) remained the sole maritime shore structure in the Galápagos Islands (Fraser 1943) until docks were built on Baltra Island in World War II to support a United States military installation. The dearth of anthropogenic structures on the Galápagos shoreline until the mid-20th century stands in remarkable contrast to the situation today (Figure 2).

Both before and after the War, most marine expeditions to the Galápagos Islands focused on shore and sublittoral sampling. The only three prior biofouling samples known to us are (1) a 1966 collection of the barnacle *Megabalanus coccopoma* from pilings at Baltra by Robert Rofen during an *Anton Dohrn* expedition (Supplementary material Table S1),

Figure 1. Wreck Bay, San Cristobal Island, 1930s, showing the only wharf then in existence in the Galápagos Islands and "the only port of call for vessels coming to the islands from Guayaquil" (Fraser 1943).

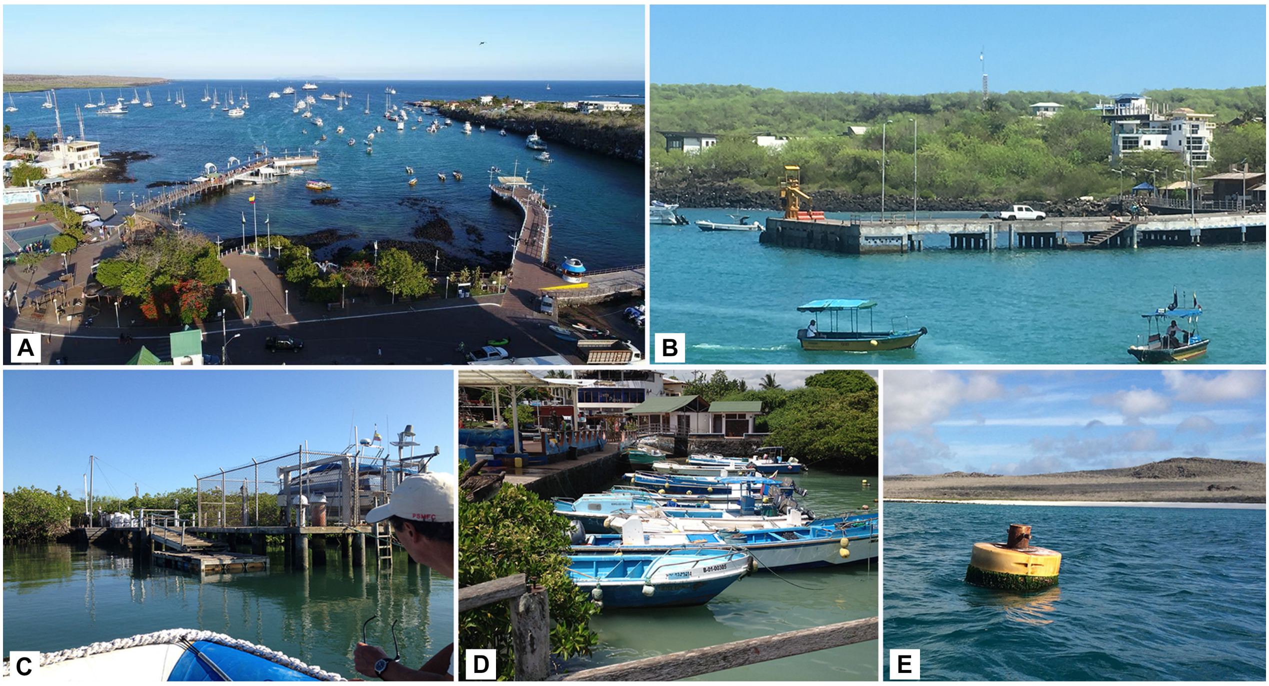

Figure 2. Modern day maritime structures in the Galápagos Islands. (A) Puerto Ayora, Santa Cruz Island, 2017; (B) Cargo dock, San Cristobal Island, 2018; (C) Franklin Bay, Puerto Ayora, February 2015; (D) seawall, pier, and docks, Puerto Ayora, February 2015; (E) Buoy, Espanola Island, July 2016. A, photograph by H. Cabrera; B, photograph by I. Keith; C–E, photographs by J. T. Carlton

(2) fouling bryozoans collected in 1980 in Academy Bay by William C. Banta (Banta and Redden 1990; Banta 1991), and (3) collections in 1987 by the first author from the hull of a resident vessel in Puerto Ayora. In addition, in 1964 Robert C. Miller visited the Galápagos as part of a scientific expedition and searched for and found wood-boring shipworms and isopods on the shores of Academy Bay (Miller 1966).

Materials and methods

Literature review and museum collections

Over the past 35 years, we maintained records of species mentioned in published Galápagos studies for selected groups of taxa that we knew (although often not noted by the authors of these studies) to potentially include (1) introductions or cryptogens in other tropical or subtropical regions of the Eastern or Central Pacific Ocean (for example, in the Hawaiian Islands (Carlton and Eldredge 2009, 2015) and on the Pacific coast of Mexico (Low-Pfeng and Peters Recagno 2012)), and (2) introduced species known to have been dispersed globally throughout maritime history. We took under consideration species said to occur, for example, widely throughout the Western Atlantic Ocean but whose only known Pacific (or Eastern Pacific) records were the Galápagos Islands or a few additional locations on the Pacific coasts of Central or South America. We did not assume that all such records represented human-mediated invasions from the Atlantic to the Pacific, noting that many species described as pantropical may represent species complexes (Darling and Carlton 2018). Commencing in the 1980s we compiled records of marine species (noted above) that workers had suggested as possibly introduced to the Galápagos. To further refine and expand our understanding of introduced and cryptogenic species we corresponded with many systematists, and examined museum material (Table S1 and Acknowledgments).

Much of the extensive literature of Galápagos marine and maritime protists, invertebrates, algae, fungi, and halophytes remains, however, to be sieved for records of species which have highly disjunct or anomalous distributions. Similarly, the early collection history of many taxa in the tropical Eastern Pacific Ocean remains to be worked out, such that many species introduced by ships since the 19th century (or earlier) may have gone undetected. Many scores of species came under our consideration as cryptogenic candidates; such cryptogens treated here are thus examples only.

Biofouling community and field surveys

Field surveys and deployment of experimental fouling panel arrays in the Galápagos commenced in 2015. Polyvinylchloride settlement plates were set out in February 2015 and January 2016 at three stations: (1) Puerto Ayora's Main Passenger Dock (latitude 0°44′52.04″S; longitude 90°18′44.98″W), (2) a private dock in Franklin Bay (0°45′18.72″S; 90°18′45.56″W), both on Santa Cruz Island, and (3) a floating dock of the Ecuadorian Navy on adjacent Baltra Island (0°26′9.52″S; 90°17′5.29″W). The plates serve as standardized passive collectors which are colonized by a wide diversity of benthic invertebrates (Marraffini et al. 2017; Chang et al. 2017). Plates were suspended at 1-meter depth with the plate oriented horizontally (facing downward and parallel to the bottom). Some plates were enclosed in 0.635 cm Vexar mesh cages to exclude predators, and we sampled at least five caged and five uncaged plates for each of the three locations. The plates were retrieved in April 2016 (thus 14 months from the February 2015 deployment and 3 months after January 2016) and transported in seawater to the Charles Darwin Research Station marine biological laboratory for immediate live analyses.

Although our primary focus was the biofouling communities of deployed panels, in February 2015 and in April 2016 additional biological samples were collected from mangrove roots, decayed mangrove wood debris, and other substrates in Tortuga Bay, from dock pilings in Academy Bay, and from floating docks on Baltra Island. In August 2016 we (1) deployed nocturnal pitfall traps on several beaches on Santa Cruz Island to sample supralittoral arthropods, (2) sampled wood boring communities (including those of teredinid bivalves (shipworms) and limnoriid isopods (gribbles)) in resident confiscated Galápagos vessels stored in Puerto Ayora at the Galápagos National Park Directorate (GNPD), and (3) sampled wood borers in natural driftwood retrieved on Santa Cruz and Isabela Islands.

In this paper, we provide a synthesis of non-indigenous and cryptogenic species detected in our field studies, as well as species formerly known from the Islands, many of which were not previously recognized as non-indigenous or potentially non-indigenous. As part of our current work, detailed taxonomic accounts are provided for hydroids by Calder et al. (2019), polychaetes (Keppel et al. 2019), bryozoans (McCann et al. 2019) and ascidians (Lambert 2019). Additional taxonomic groups are under study. Abundance and diversity patterns in exposed versus caged experimental panels will be reported elsewhere.

Results

Species diversity and phyletic and habitat breadth of introduced and cryptogenic species

We report 53 introduced marine invertebrates and 33 cryptogenic invertebrates, algae, and halophytes in the Galápagos Islands (Table 1, Table S1, Figure 3). Forty-eight, or 90.6%, of the introduced species are newly reported or newly recognized as non-indigenous, an increase by a factor of nearly 10 from the five marine species previously recognized as non-native. Of these 48 species, 30 (62.5%) were newly discovered in the present survey. Seventeen species were already known but previously regarded as native in the Galápagos, but are now treated as introductions. Four of these species are reported in the accompanying papers: the hydroids *Clytia hummelincki* (Leloup, 1935) and *Nemalecium lighti* (Hargitt, 1924) (Calder et al. 2019) and the ascidians *Didemnum perlucidum* Monniot, 1983

Table 1. The Introduced and Cryptogenic Marine and Maritime Animals and Plants of the Galápagos Islands. See Supplementary material Table S1 for first collection dates, vectors, possible origins, detailed remarks, and references. * _Introduced species_; unmarked taxa are cryptogenic.

Cnidaria: Hydrozoa (hydroids)
- *_Bougainvillia muscus_ (Allman, 1863)
- _Bimeria vestita_ Wright, 1859
- _Cirrholovenia tetranema_ Kramp, 1959
- *_Clytia elongata_ Marktanner-Turneretscher, 1890
- *_Clytia thornelyi_ (Nutting, 1927)
- *_Clytia hummelincki_ (Leloup, 1935)
- _Obelia dichotoma_ (Linnaeus, 1758)
- *_Obelia oxydentata_ Stechow, 1914
- *_Halecium labiatum_ Billard, 1933
- *_Nemalecium lighti_ (Hargitt, 1924)
- _Pennaria disticha_ Goldfuss, 1820
- _Ventromma halecioides_ (Alder, 1859)
- *_Halopteris alternata_ (Nutting, 1900)

Cnidaria: Anthozoa (corals, sea anemones)
- _Tubastraea coccinea_ Lesson, 1829
- _Exaiptasia diaphana_ (Rapp, 1829)

Annelida: Polychaeta (polychaete worms)
- _Capitella_ sp.
- *_Myrianida pachycera_ (Augener, 1913)
- *_Naineris setosa_ (Verrill, 1900)
- *_Branchiomma bairdi_ (McIntosh, 1885)
- *_Branchiomma_ sp.
- *_Pseudobranchiomma schizogenica_ Tovar-Hernández and Dean, 2014
- *_Dipolydora armata_ (Langerhans, 1880)
- *_Hydroides elegans_ (Haswell, 1883)
- *_Hydroides sanctaecrucis_ Krøyer in Mörch, 1863
- *_Janua heterostropha_ (Montagu, 1803)
- _Simplaria pseudomilitaris_ (Thiriot-Quievreux, 1965)
- _Protolaeospira capensis_ (Day, 1961)

Mollusca: Bivalvia (mussels, shipworms)
- *_Leiosolenus aristatus_ (Dillwyn, 1817)
- *_Bankia gouldi_ (Bartsch, 1908)
- *_Bankia carinata_ (Gray, 1827)
- *_Lyrodus medilobatus_ (Edmondson, 1942)
- *_Lyrodus pedicellatus_ (Quatrefages, 1847)
- *_Teredo bartschi_ Clapp, 1923
- *_Teredo furcifera_ (von Martens, 1894)
- *_Teredo triangularis_ (Edmondson, 1942)

Crustacea: Ostracoda (ostracods)
- _Xestoleberis setouchiensis_ Okubo, 1979

Crustacea: Cirripedia (barnacles)
- *_Megabalanus coccopoma_ (Darwin, 1854)

Crustacea: Isopoda (isopods)
- _Ligia baudiniana_ Milne Edwards, 1840
- *_Limnoria tripunctata_ Menzies, 1951

Crustacea: Decapoda: Brachyura (crabs)
- *_Cardisoma crassum_ Smith, 1870

Pycnogonida (sea spiders)
- *_Anoplodactylus monotrema_ Stock, 1979

Arachnida: Acari (mites)
- _Polyxylobates diversiporosus_ Hammer, 1973
- _Issaniella mograbin_ Grandjean, 1962

Collembola (spring tails)
- _Axelsonia littoralis_ (Moniez, 1890)

Insecta: Diptera (flies)
- _Atissa luteipes_ Cresson, 1944
- *_Hecamede brasiliensis_ Cresson, 1938
- *_Clasiopella uncinata_ Hendel, 1914
- _Psilopa girschneri_ Von Roder, 1889

Insecta: Dermaptera (earwigs)
- *_Anisolabis maritima_ (Bonelli, 1832)

Insecta: Hemiptera (bugs)
- _Pentacora sphacelata_ (Uhler, 1877)

Bryozoa (bryozoans)
- _Aetea curta_ Jullien, 1888
- *_Beania klugei_ Cook, 1968
- *_Bugula neritina_ (Linnaeus, 1758)
- *_Bugulina stolonifera_ (Ryland, 1960)
- *_Caulibugula cf. dendrograpta_ (Waters, 1913)
- *_Hippopodina tahitiensis_ (Leca and d'Hondt, 1993)
- *_Celleporaria inaudita_ Tilbrook, Hayward and Gordon 2001
- *_Biflustra irregulata_ (Liu, 1991)
- _Savignyella lafontii_ (Audouin, 1826)
- *_Schizoporella pungens_ (Canu and Bassler, 1928)
- *_Watersipora subtorquata_ (d'Orbigny, 1852)
- _Nolella stipata_ Gosse, 1855
- *_Amathia verticillata_ (delle Chiaje, 1822)

Chordata: Ascidiacea (seasquirts)
- *_Didemnum perlucidum_ Monniot, 1983
- _Didemnum cineraceum_ (Sluiter, 1898)
- *_Diplosoma listerianum_ (Milne-Edwards, 1841)
- *_Polyclinum constellatum_ (Savigny, 1816)
- _Aplidium californicum_ (Ritter and Forsyth, 1917)
- _Aplidium solidum_ (Ritter and Forsyth, 1917)
- _Cystodytes dellechiajei_ (Della Valle, 1877)
- _Ascidia ceratodes_ (Huntsman, 1912)
- *_Ascidia sydneiensis_ Stimpson, 1855
- *_Botrylloides giganteus_ (Pérès, 1949)
- *_Botrylloides niger_ Herdman, 1886
- _Botryllus tuberatus_ Ritter and Forsyth, 1917
- *_Polyandrocarpa zorritensis_ (Van Name, 1931)
- *_Styela canopus_ (Savigny, 1816)
- *_Symplegma brakenhielmi_ (Michaelsen, 1904)
- *_Symplegma rubra_ Monniot, 1972
- _Halocynthia dumosa_ (Stimpson, 1855)
- *_Microcosmus exasperatus_ Heller, 1878
- _Pyura haustor_ (Stimpson, 1864)

Algae (seaweeds)
- _Caulerpa chemnitzia_ (Esper) J.V. Lamouroux 1809
- _Caulerpa racemosa_ (Forsskål) J. Agardh, 1873
- _Asparagopsis "taxiformis"_ of authors

Tracheophyta: Magnoliopsida (flowering plants)
- _Batis maritima_ Linnaeus, 1759

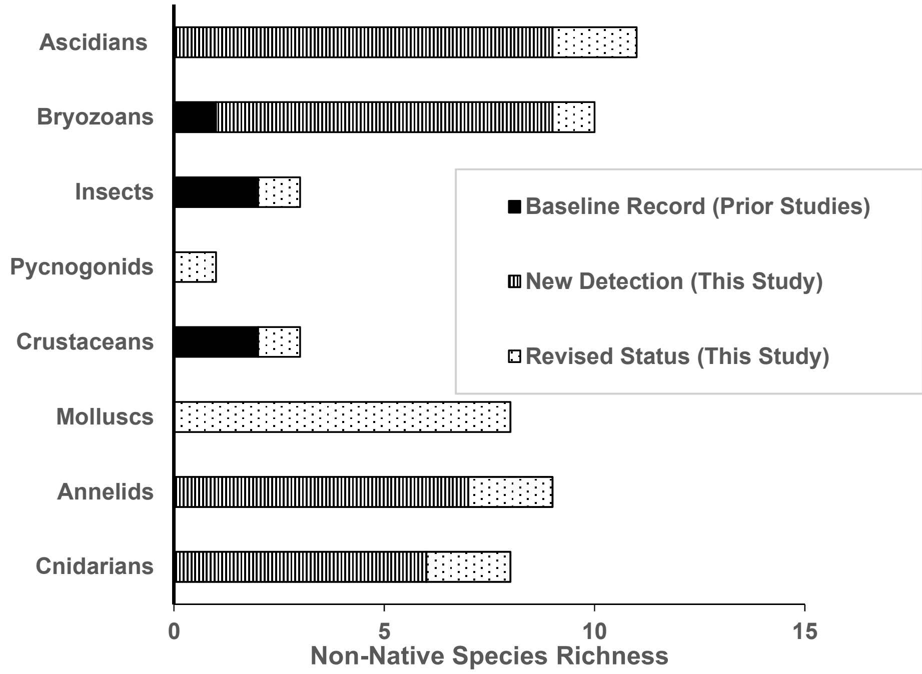

Figure 3. Documented number of non-indigenous marine invertebrates species in Galápagos Islands. Shown are the number of marine species per taxonomic group recognized as introduced, including the previous baseline of five species of recognized introductions (*black*), new detections from 2015–2016 field surveys (*vertical lines*), and species previously known from the Galápagos but newly recognized in the present studies as introduced (*dots*).

and *Diplosoma listerianum* (Milne Edwards, 1841) (Lambert 2019). The remaining 13 species are newly recognized in the present paper as introduced. The bryozoan *Watersipora subtorquata* (d'Orbigny, 1852) is newly reported in our studies, based upon both 1987 material and populations collected in the present work.

Six phyla (Cnidaria, Annelida, Mollusca, Arthropoda, Bryozoa, and Chordata) are represented in our current treatment. Ascidians (11 species), bryozoans (10), polychaetes (9), and hydroids (8) account for 38 (71.7%) of the 53 introduced species, which are, not coincidentally, the same groups treated in the accompanying accounts of the introduced marine fauna of the Galápagos (Lambert 2019; McCann et al. 2019; Keppel et al. 2019; Calder et al. 2019). Taxa unique to the cryptogenic category include a cup coral, a sea anemone, an ostracod, several arthropod groups (marine mites, spring tails, shore bugs), and one maritime flowering plant. Many taxa (including subgroups of these phyla) remain to be assessed for the presence of non-indigenous species.

Most of the species treated here are found (by virtue of our sampling strategies) in subtidal epibenthic biofouling communities on pilings, wharves, and docks, or boring into wood substrates. We discuss below the expansion of these species into non-anthropogenic habitats in the Galápagos Islands. Introduced species also occur in the maritime supralittoral habitat, including two species of shore flies, and a maritime earwig. Cryptogenic species in this strand habitat include additional arthropods and one littoral halophyte.

Dispersal vectors

At least 92.6% of the introduced species treated here were likely brought to the Galápagos Islands by ships (Table S1). The distinction between species transported in fouling or in ballast is often difficult to assess (Fofonoff et al. 2003). Nine species (seven shipworms, a wood-boring mussel and a wood-boring isopod) may have arrived in the days of wooden sailing ships; the mussel, *Leiosolenus aristatus* (Dillwyn, 1817), is also a biofouling nestler. Two halophilic flies and an earwig may have been entrained with cargo stored or staged near shore or transported on vessel decks, or, since World War II, accidentally entrained in airplane cabins or cargo holds. Only one species, the mangrove crab *Cardisoma crassum*, is a known direct release in the Galápagos Islands (Table S1). The relatively few cryptogenic species treated here may have arrived with ship-associated vectors as well.

Biogeographic origins

Introduced marine species in the Galápagos Islands originate from the Atlantic Ocean (and primarily from the tropical Western Atlantic) and from the Western or Indo-West Pacific Ocean (Table S1). Species origins are relatively evenly split between the Atlantic (28.3% [15 species] and Pacific (37.7% [20 species]). Fifteen species (27.8%) cannot be resolved at this time as from one or the other ocean. Of interest (and with implications for our historical understanding of dispersal vectors, as discussed below) is the introduction of two species, the barnacle *Megabalanus coccopoma* and the crab *Cardisoma crassum*, from the adjacent South American mainland.

Invasion chronology

The dates of arrival of almost all of the 53 introduced species documented here are not known, and thus temporal patterns of colonization of the Islands by non-indigenous species are difficult to discern. For only two species, the barnacle *Megabalanus coccopoma* (which likely arrived between 1964 and 1966) and the crab *Cardisoma crassum* (released in 1973) are dates of introduction known. The earliest marine invasions currently known in the Galápagos are the date mussel *Leiosolenus aristatus* collected in 1898 and the maritime earwig *Anisolabis maritima* (Bonelli, 1832) collected in 1905; we emphasize that these are the dates of first collection, and not necessarily the approximate dates of first arrival. The sea spider *Anoplodactylus monotrema* (Stock, 1979) was then collected in 1934**.** A long gap then ensues before the collections of several more introduced species in the 1960s (the isopod *Limnoria tripunctata* (Menzies, 1951), the barnacle *M. coccopoma*, the polychaetes *Janua heterostropha* (Montagu, 1803) and *Naineris setosa* (Verrill, 1900) and the shipworm *Teredo bartschi* Clapp, 1923). All other invasions are first recorded in the 1980s or later, although many of these species may have been present earlier.

The collection by Charles Darwin in the Galápagos of the Indo-Pacific coral *Tubastraea coccinea* (Lesson, 1829) (Table S1), regarded as cryptogenic by Creed et al. (2017), is compelling. As Creed et al. (2017) remarked, "*Tubastraea* are known to be hull fouling organisms and the history of shipping around the world is ancient. Darwin collected *T. coccinea* in the Galápagos in 1835—by which time long-distance (transoceanic) foreign vessels had been visiting the Islands for 300 years." Two other cryptogenic species were also present by the 19th century: the shore plant *Batis maritima* (Linnaeus, 1759) (collected in 1898) and the shore bug *Pentacora sphacelata* (Uhler, 1877) (1899), both of which, if introduced, may also have been in the Galápagos long before these dates.

Discussion

Our study identified more than 50 introduced species in marine and maritime habitats of the Galápagos Islands, representing a 90% increase in the previous number known. This is the greatest percent increase reported in a singe study, relative to the recognition of the number of invasions for any tropical marine environment in the world. We expect, as discussed below, that this number will grow significantly as work continues, especially as this initial survey was limited in scope and duration primarily to one habitat type at three sites on two islands, constrained to a relatively short time and small number of samples. The detection of far more introductions than previously reported is in concert with, but significantly exceeds, those resolved in other recent studies, such as in the Hawaiian Islands (Carlton and Eldredge 2009, 2015) and in South Africa (Mead et al. 2011a, b). In addition to the significance of these results for the Galápagos Islands, our work further suggests that the number of invasions in tropical marine and maritime habitats may be substantially underestimated in other regions of the world.

Introduced species diversity

Invasion diversity is often underestimated (Carlton 1999). Species are frequently assumed to be native rather than cryptogenic, the latter a concept (Carlton 1996) that has rarely been applied to the marine or maritime biota in the Galápagos Islands by other than us. New introduced species may be mistakenly described as endemic but were in fact already named in their native region. Several such known or possible pseudoendemic species have now been detected in the Galápagos, including the introduced tubeworm *Janua heterostropha* and several cryptogenic species (two additional spirorbid tubeworms, one ostracod, and one shore bug). Biogeographic assumptions of natural dispersal have played a large role in overlooking many invasions around the world, and these assumptions are well reflected in the literature of the Galápagos Islands. Species occurring both on the Islands and on the adjacent South American mainland have been, with rare exception, assumed to be the result of planktonic dispersal or rafting (James 1991). El Niño – Southern Oscillation (ENSO) events, or long-term rafting, independent of ENSO phenomena, are invoked to explain the presence of Western Pacific species in the Eastern Pacific (James 1991). A broad overarching pattern is the description of many Galápagos plant and animal species (terrestrial, freshwater and marine) as naturally cosmopolitan. Terms used to describe such species in the Galápagos include Pan-American (Banta and Redden 1990), pantropical (Barnard 1979; Zullo 1991) and tropicopolitan (Barnard 1979). The reality of the same species being found naturally in multiple oceans has been increasingly called into question (Darling and Carlton 2018).

This said, the largest gap in our understanding of marine bioinvasions in the Galápagos—and in almost all tropical regions of the world—is the lack of detailed study of the historical biogeography of most taxonomic groups. Based upon our knowledge of the Galápagos marine biota, we judge that only two groups—barnacles and fish—have been sufficiently studied to assess the probable absence of non-indigenous species at this time. Shallow-water Galápagos barnacles were considered by Zullo (1966, 1986, 1991) and by us in our present work. The Galápagos fish fauna has been the subject of long-term investigation (Grove and Lavenberg 1997). Thus, although we provide examples here of more than 50 non-indigenous marine species in the Galápagos, many groups remain to be thoroughly vetted for the presence of invasions. Particularly likely to harbor introductions—or far more introductions than reported here—are foraminiferans, sponges, hydroids, flatworms, nemerteans, polychaetes, oligochaetes, mollusks, many groups of crustaceans (especially amphipods and isopods), bryozoans, kamptozoans, marine mites, ascidians, algae, and marine fungi.

Dispersal vectors and the role of the Panama Canal

While we presume that most if not all of the many thousands of vessels arriving in the Galápagos Islands since the 1500s had marine animals and plants attached to their hulls (potentially accumulated, as noted above, from many different regions), the general absence in the Islands of extensive shoreline structures (in the form of wharves, docks, pilings, and buoys) until the last half of the 20th century, may have inhibited extensive colonization of the Islands by fouling species that had been distributed for centuries by international shipping. Shoreline structures have long been widely regarded as primary initial colonization sites for introduced species (Chapman and Carlton 1991; Glasby et al. 2007; Dafforn et al. 2009; Ruiz et al. 2009).

This said, we know little about the historical colonization in the Galápagos by introduced, ship-transported species on natural substrates, including mangroves, rocky shores, and the nearshore sublittoral, habitats also known to be susceptible to invasions (Carlton 2002). While non-indigenous

Table 2. Examples of introduced species found in natural habitats in the Galápagos Islands

Taxon (species authors and dates are shown in Table S1)	Habitat	Island and date	Reference
Cnidaria: Hydrozoa (hydroids)			
Clytia hummelincki	on hydroid *Pennaria disticha*	San Cristobal (1992)	Calder et al. (2003)
	on coral *Pavona*	Wolf (2000)	Calder et al. (2003)
Nemalecium lighti	subtidal coral and algal benthos, 6 and 15 m	Wolf, Darwin, Marchena (2005–2007)	Banks et al. (2009)
Annelida: Polychaeta (worms)			
Naineris setosa	rock tidepool	Santa Cruz (1966)	Blake and Giangrande (2011); Table S1 herein
Janua heterostropha	rock chippings, “crawfish” [lobster] carapace	Santa Cruz (1965–66)	Bailey and Harris (1968)
Mollusca: Bivalvia (mussels and shipworms)			
Leiosolenus aristatus	boring into live coral *Porites lobata*	Champion (1989–1990)	Reaka-Kudla et al. (1996)
Teredo triangularis	drift logs and branches	Santa Cruz (2015)	herein; Miller (1966) noted unidentified Teredinidae (likely one or more of the species treated here) in “dead mangrove stems” in Tortuga Bay on Santa Cruz Island.
Crustacea: Decapoda (crabs)			
Cardisoma crassum	mangroves	Santa Cruz (1973)	Hickman and Zimmerman (2000); herein
Pycnogonida (sea spiders)			
Anoplodactylus monotrema	dredged 0–3 m	Floreana (1934)	Child and Hedgpeth 1971
	intertidal rubble	Floreana (1934)	Child 1992
	washings of algal turf	Santa Cruz (1962)	Child and Hedgpeth 1971
	intertidal	Marchena (1966)	Child 1992
Bryozoa (bryozoans)			
Amathia verticillata	mangroves	Santa Cruz (2015)	McCann et al. 2015
	adrift in surf zone	Santa Cruz (2016)	J.T. Carlton, *field observations*
Beania klugei	mangroves	Santa Cruz (2016)	McCann et al. 2019
Chordata: Ascidiacea (seasquirts)			
Didemnum perlucidum	rock wall subtidal (12 m)	Rocas Gordon (1999)	Witman and Smith (2003)
Diplosoma listerianum	rock wall subtidal (12 m)	Rocas Gordon (1999)	Witman and Smith (2003)

marine species have successfully utilized these environments in the Galápagos (Table 2, and discussed further below), both retrospective study of earlier collections and extensive modern-day explorations, particularly of the mangrove habitat, have yet to be undertaken. It is nevertheless compelling to hypothesize that the proliferation of shoreline structures may have provided expanded habitat for non-indigenous species that had earlier colonized natural substrates, as well as having facilitated a 20th and 21st century wave of new invasions in the Galápagos Islands, providing a possible beachhead for colonization and potential spread to other habitats.

Of particular interest relative to the history of anthropogenic vectors is the introduction of the barnacle *Megabalanus coccopoma* and the mangrove crab *Cardisoma crassum*. Both species are native to the adjacent South American mainland. The ability to recognize these species as having been introduced in the 1960s and 1970s, respectively, by human-mediated vectors is due to our fine-grained knowledge of their taxonomy and biogeography. A key conclusion, however, is that had these species arrived earlier—prior to the 1960s for barnacle surveys, and prior to the 1930s for crab surveys—we would assume that both were indigenous to the Galápagos. Anthropogenic movements of marine species from South America to the Galápagos are doubtless underestimated, as it would appear unlikely that the only two marine species to be transported accidentally or intentionally from the mainland to the Archipelago happen to be species that arrived since the 1950s. The gap between the mainland and the Islands, albeit less than 1000 km, may in fact exceed the dispersal capabilities (either by larval dispersal or by rafting) of many species.

The opening of the Panama Canal in 1914 as a direct corridor for species from the tropical Western Atlantic Ocean to the tropical Eastern Pacific Ocean remains to be investigated relative to whether a new wave of invasions arrived in the Galápagos in the 20th century. While widely perceived as being a barrier to the interoceanic dispersal of marine species, due to the presence of a large freshwater lake and freshwater locks that vessels must pass through, the survival of species that could be (Menzies 1968) or were (Davidson et al. 2008) transported on the hulls of ships through the Canal has been established. Moreover, marine species carried inside ships, in water or solid ballast, would of course not be exposed to the freshwater of the Panama Canal. Carlton (1985) and Cohen (2006) have explored the role of the Panama Canal as an interoceanic corridor. Multiple species of shipworms in the genus *Bankia* were speculated by Carlton (1985) as candidates for dispersal through the Canal in ballast water due to their possession of planktotrophic larvae. The Atlantic *Bankia gouldi* (Bartsch, 1908), considered here as introduced to the Galápagos Islands, was however present in the Eastern Pacific no later than 1907 (Carlton 1985), making it a likely candidate for introduction by wooden ships going around Cape Horn prior to the 20th century (although additional populations may have been introduced through the Canal after 1914). We discuss below the recent 2015 expansion of the Panama Canal relative to the potential for future invasions in the Galápagos Islands.

Marine bioinvasion impacts, management, and future invasions in the Galápagos Islands

Our discovery that invasion diversity in the Galápagos Islands is far greater than previously understood sets the stage for research on ecological, environmental, economic and other societal impacts. Notable introduced biofouling species now present in the Islands include the ascidians *Didemnum perlucidum, Diplosoma listerianum, Ascidia sydneiensis* (Stimpson, 1855), *Botrylloides* spp. and *Microcosmus exasperatus* (Heller, 1878) (Lambert 2019), the bryozoans *Amathia verticillata* (delle Chiaje, 1822), *Bugula neritina*, and *Watersipora subtorquata* (McCann et al. 2019) and tubeworms *Hydroides* spp. (Keppel et al. 2019). The bryozoan *Amathia verticillata*, first detected in 2015, is in particular a well-known species fouling pipes and commercial fishing gear, as well as causing seagrass mortality (McCann et al. 2015). Introduced wood borers include seven species of shipworms and the gribble *Limnoria tripunctata* (Table S1). The introduced date mussel *Leiosolenus aristatus* has been found to be abundant boring into coral in the Galápagos Islands (Reaka-Kudla et al. 1996). We further note that a wide range of introduced species, including hydroids, polychaete worms, bivalve mollusks, bryozoans, ascidians, and other species, have invaded natural habitats in the Galápagos (Table 2). For all of these species, and for all of the rest now recognized as present in the Islands, we lack quantitative and experimental data on their roles and impacts in the Galápagos. Recognizing the scale of invasions in the Galápagos is further fundamental to our understanding of community ecology, relative to distinguishing long-term evolutionary processes from shifts caused in ecological time due to invasions. Given that our present account likely reflects only a fraction of the actual total number of marine bioinvasions, the establishment of dedicated research programs in the Galápagos to understand the past, present, and future impacts of invasions is critical (Campbell et al. 2015; Keith et al. 2016).

As tourism, trade and transport increase in the Galápagos, the amount of arriving marine traffic has increased as well. Cargo ships, private yachts, research vessels, patrol boats and illegal fishing boats are the primary examples of the types of vessels that now regularly enter the Galápagos. The marine traffic traveling between continental Ecuador and the archipelago is composed mainly of cargo ships. The increase in population, combined with the increase in tourism, has put a concomitant demand on the amount of cargo that must be shipped to the islands and thus the number of arriving vessels. Additional vessels that arrive in the Islands are Ecuadorian navy patrol boats and research vessels from the Oceanographic Institute of the Ecuadorian Navy (INOCAR, the Instituto Oceanográfico de la Armada) as well as tourist cruise boats that are largely resident in the Galápagos but undergo maintenance dry docking on the mainland every two years. The bulk of international marine traffic that the archipelago hosts are private yachts; as recreational sailing has increased over the decades, Galápagos ports have become an important stopover for yachts on passage to and from the South Pacific. Private yachts enter the Galápagos year round, with the majority arriving between December and June. The majority report Panama as their last port of call.

Current Ecuadorian management requires that international vessels entering the Galápagos Marine Reserve may only anchor in one of the official main ports of the archipelago. Upon arrival vessels are inspected by local authorities, including the ABG (the Ecuadorian Biosecurity Agency, the Agencia de Regulación y Control de la Bioseguridad y Cuarentena para Galápagos), the GNPD (Galápagos National Park Directorate), the CCREG

(Consejo de Gobierno del Regimen Especial de Galápagos), and the Ecuadorian Navy. Divers from the ABG marine unit inspect vessels that come into the Islands from international destinations and record the last port of entry. If a vessel is found to be transporting fouling species, the ABG reports this information to the GNPD which can then request the vessel to leave the Islands and return for a second inspection once the hull has been cleaned. As of 2019, little to no ballast water is discharged in the Galápagos Islands. This said, it always remains possible that not all biofouling (such as in difficult to inspect hull niche areas, or newly-settled recruits) could be detected.

The role of artificial habitats as a receiving system and reservoir for non-indigenous species has critical implications for marine invasion management for Marine Protected Areas and more broadly. While there is a rigorous program in Galápagos and other protected areas to limit propagule supply, especially associated with vessel arrivals, the urbanization of coastal areas and the expansion of artificial substrates may serve to increase susceptibility to invasions. Thus, managing both propagule supply and urbanization (especially the creation of artificial structures) may need to be developed in concert to achieve biosecurity and conservation goals (Dafforn 2017).

At the beginning of the 21st century, even as we continue to assess the number of non-indigenous marine and maritime species that have already arrived in the Galápagos, a number of new invasions are poised for imminent arrival. Notable among these is the biofouling Indo-Pacific "snowflake coral" *Carijoa riisei* (Duchassaing and Michelotti, 1860) which was first detected in the Eastern Pacific in about 2000, and has now spread to the Port of Manzanillo on the Mexican Pacific coast (Sanchez and Ballesteros 2014; Galvan-Villa and Rios-Jara 2018). In Colombia, massive mortalities of the native octocorals *Pacifigorgia* spp. and *Muricea* spp. have been documented due to *Carijoa* overgrowth (Quintanilla et al. 2017). The Atlantic skeleton shrimp *Paracaprella pusilla* (Mayer, 1890) was found in 2004 at the Pacific entrance to the Panama Canal (Ros et al. 2014) and has now been found on the Pacific coasts of Mexico and Costa Rica (Alarcon-Ortega et al. 2015; Alfaro-Montoya and Ramirez-Alvarado 2018). Overarching the presence of already established invasions on the Pacific coasts of Mexico and Central America is the expansion of the Panama Canal in 2015, which may lead to a significant increase in the number of new invasions in the Eastern Pacific (Muirhead et al. 2015), including the potential introduction of the lionfish *Pterois volitans* (Linnaeus, 1758) and *Pterois miles* (Bennett, 1828), carried in ballast water from the Caribbean through the Canal to the Pacific coast of Panama. MacIsaac et al. (2016) rank the probability of successful establishment of lionfish as very high, should they arrive, in the Galápagos.

Finally, in addition to vessel traffic, two modern-day drivers of marine biological invasions that may play a critical role in the future of the

Galápagos marine ecosystem are climate change (Sorte et al. 2010; Bates et al. 2014; Poloczanska et al. 2013; Keith et al. 2016) and the rafting of non-indigenous species on marine debris (Keith et al. 2016; Carlton et al. 2017, 2018). What these drivers, and what the continued ship-mediated arrival of non-indigenous species due to growing global maritime trade networks, will mean as emerging concerns for the conservation and preservation of Galápagos seas (Alava et al. 2014), and for the biosecurity of the Galápagos Marine Reserve in particular (Denkinger and Vinueza 2014) remains paramount on the environmental agenda of the Galápagos Islands.

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Supplementary material

The following supplementary material is available for this article:

Table S1. The Introduced (I) and Cryptogenic (C) Marine and Maritime Animals and Plants of the Galápagos Islands.
Appendix 1. List of References for Table S1.

This material is available as part of online article from:
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