

# Asymmetry of marine invasions across tropical oceans

MARK E. TORCHIN <sup>1,5</sup>, AMY L. FREESTONE <sup>1,2,3</sup>, LINDA McCANN,<sup>4</sup> KRISTEN LARSON,<sup>3</sup> CARMEN SCHLÖDER,<sup>1</sup>  
BRIAN P. STEVES,<sup>3</sup> PAUL FOFONOFF,<sup>3</sup> MICHELE F. REPETTO,<sup>1,2,3</sup> AND GREGORY M. RUIZ<sup>3</sup>

<sup>1</sup>Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama

<sup>2</sup>Department of Biology, Temple University, Philadelphia, Pennsylvania 19122 USA

<sup>3</sup>Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, Maryland 21037 USA

<sup>4</sup>Smithsonian Environmental Research Center, 3150 Paradise Drive, Tiburon, California 94920 USA

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**Abstract.** Understanding the mechanisms of spatial variation of biological invasions, across local-to-global scales, has been a major challenge. The importance of evolutionary history for invasion dynamics was noted by Darwin, and several studies have since considered how biodiversity of source and recipient regions can influence the probability of invasions. For over a century, the Panama Canal has connected water bodies and biotas with different evolutionary histories, and created a global shipping hot spot, providing unique opportunities to test mechanisms that affect invasion patterns. Here, we test for asymmetry in both the extent of invasions and predation effects, a possible mechanism of biotic resistance, between two tropical oceans at similar latitudes. We estimated nonnative species (NNS) richness for sessile marine invertebrates, using standardized field surveys and literature synthesis, to examine whether invasions are asymmetrical, with more NNS present in the less diverse Pacific compared to the Atlantic. We also experimentally tested whether predation differentially limits the abundance and distribution of these invertebrates between oceans. In standardized surveys, observed total NNS richness was higher in the Pacific (18 NNS, 30% of all Pacific species) than the Atlantic (11 NNS, 13% of all Atlantic species). Similarly, literature-based records also display this asymmetry between coasts. When considering only the reciprocal exchange of NNS between Atlantic and Pacific biotas, NNS exchange from Atlantic to Pacific was eightfold higher than the opposite direction, exceeding the asymmetry predicted by random exchange based simply on differences of overall diversity per region. Predation substantially reduced biomass and changed NNS composition in the Pacific, but no such effects were detected on the Atlantic coast. Specifically, some dominant NNS were particularly susceptible to predation in the Pacific, supporting the hypothesis that predation may reduce the abundance of certain NNS here. These results are consistent with predictions that high diversity in source regions, and species interactions in recipient regions, shape marine invasion patterns. Our comparisons and experiments across two tropical ocean basins, suggest that global invasion dynamics are likely driven by both ecological and evolutionary factors that shape susceptibility to and directionality of invasions across biogeographic scales.

**Key words:** biotic interactions; evolutionary history; evolutionary imbalance hypothesis; invertebrates; marine invasions; nonnative species; Panama; predation; tropical.

## INTRODUCTION

Considerable geographic variation exists in the extent of biological invasions, across local to global scales. Significant research emphasis surrounds the relationship of native biodiversity and the invasion of nonnative species (NNS), and a large body of theoretical and empirical work seeks to explain the underlying mechanisms (see Fridley et al. 2007). While this literature demonstrates that a diverse range of mechanisms contribute to the

observed patterns, these fall under three broad categories; ecological processes, evolutionary history, and propagule supply, which yield somewhat different predictions.

Elton (1958) advanced the importance of ecological processes in invasions, suggesting that species-rich communities are better able to resist invasions compared to less diverse communities, due to stronger biotic interactions. Conceptually, a more diverse array of competitors in the recipient community should reduce the available niches for colonization (MacArthur 1969), and a diverse suite of consumers could limit prey and hosts (Naem and Li 1997, 1998) relative to less diverse communities, forming the basis of the “biotic resistance hypothesis” (BRH). In support of the BRH, many experimental,

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<sup>5</sup>E-mail: torchinm@si.edu

theoretical, and correlative studies suggest that higher native species diversity reduces invasions compared to less diverse communities (Tilman 1997, Stachowicz et al. 1999, Levine 2000, Naeem et al. 2000, Fargione et al. 2003). However, such effects among studies are variable and often scale-dependent, and environmental heterogeneity, stochasticity, and disturbance can mask these local effects at larger scales (Levine 2000, Byers and Noonburg 2003, Stohlgren et al. 2003, Fridley et al. 2007).

Another conceptual approach has focused on the importance of evolutionary history, including where introduced species evolved and how biotic interactions in the new range might differ. While the importance of evolutionary history for invasion was noted by Darwin (1859), only recently have studies considered how conditions in the donor regions themselves influence the probability of invasions (Vermeij 2005). Fridley and Sax (2014) expanded upon this earlier work to propose the “evolutionary imbalance hypothesis” (EIH), positing that species that evolved in diverse donor communities with “high genetic potential” are stronger competitors and more effective invaders in lower diversity recipient regions than species that evolved in less diverse communities. The EIH predicts global invasion patterns using differences in phylogenetic diversity among biotic regions as a proxy for “genetic potential” (Fridley and Sax 2014). Thus, the relative phylogenetic diversity between regions should enable predicting which regions are more susceptible to invasion.

Differences in the magnitude of propagule supply among regions have also received attention as an important mechanism in explaining geographic variation in invasions. Theoretical and empirical work highlights the positive relationship between propagule supply, including both propagule number and frequency of inoculation, and probability of establishment across taxa and ecosystems (Simberloff 2009). There is no doubt that propagule supply plays a key role in human-mediated invasion dynamics, such that reducing propagule delivery is a major underpinning of biosecurity management and policy around the globe. However, the relative importance and interaction of propagule supply, ecological processes, and evolutionary history in geographic invasion dynamics are poorly resolved, as it is not possible to control for these factors at large spatial scales (see Fridley et al. 2007).

Pairwise comparisons of biotic interchange between regions have been used to gain insight about invasion biogeography and underlying mechanisms, whether in recent or geological time. For example, Vermeij (1991*b*) demonstrated asymmetry in the trans-Arctic faunal interchange of marine mollusks during the early Pliocene, resulting from a predominance of Pacific species invading the Atlantic. Similarly, dispersal of multiple taxa over geologic time from the Indo-West Pacific has strongly contributed to the diversity of the Tropical Eastern Pacific, with little reciprocal exchange (Vermeij

1991*b*, Bowen et al. 2013, Leigh et al. 2014). In these cases, the net direction of invasion export was from higher to lower diversity, which is consistent with the general predictions of both ecological and evolutionary mechanisms. In addition, this may also reflect differences in propagule supply among species-rich and species-poor regions (Vermeij 2005, Fridley and Sax 2014), in which areas of high species diversity would contribute more invaders just by chance. Fridley and Sax (2014) correct for this variation by estimating the relative size of “exchange pools,” which are the total number of species in each region minus the species that are shared between the regions being compared. Studies of asymmetrical exchange exist for both natural faunal dispersals as well as human-mediated invasions, representing the same general mechanisms but encompassing somewhat different processes, details, and time scales.

As such, paired bodies of water connected in recent time by canals can provide a strong comparative framework for testing mechanisms that affect susceptibility and patterns of invasions, including both the EIH and BRH. For example, the estimated faunal exchange through the sea-level Suez Canal has been overwhelmingly asymmetrical, both in total species number (Por 1978, Vermeij 1991*b*, Galil 2006, Galil et al. 2014) and proportion of each species pool exchanged between regions. In general, such directional movement of species from the Red Sea has been used as evidence that less diverse temperate marine communities in the Mediterranean are more susceptible to invasion than more diverse tropical communities of the Red Sea (Por 1978, Vermeij 2005, Galil 2006, Fridley and Sax 2014). However, it is also thought that environmental conditions and the tropicalization of the eastern Mediterranean Sea may favor northward expansion of the tropical Red Sea biota (Galil et al. 2014, Cramer et al. 2018).

Expanding on this approach, Panama provides a unique opportunity to test for invasion asymmetry in biotic exchange across two tropical ocean coastlines at similar latitudes. Once connected by the Central American Seaway, the tropical western Atlantic and eastern Pacific have been separated by the emergent Isthmus of Panama for at least 3 million years (Woodring 1966, Leigh et al. 2014, Montes et al. 2015, O’Dea et al. 2016). These two coastal marine communities isolated by a mere 60 km wide isthmus have evolved in isolation under very different biotic and abiotic conditions (Leigh et al. 2014). In general, marine invertebrate species richness is higher in the Caribbean compared to the eastern Pacific, and the Caribbean region is characterized by slower growing and more competitive species (Briggs 1968, Leigh et al. 2014). In contrast, high productivity and strong consumer pressure characterize the less diverse Pacific (Vermeij 1976, Bertness et al. 1981, Hay and Gaines 1984, Lubchenco et al. 1984, Leigh et al. 2014). However, consumer pressure can be high in the Caribbean as well (Freestone et al. 2013), and rigorous comparisons of predation intensity across the two

oceans remain limited (but see Birkeland 1977, Hay and Gaines 1984). Panama's historic significance as a hub of world trade since the fifteenth century expanded with the opening of the Panama Canal in 1914. This created an aquatic corridor and new shipping route through the isthmus, once again connecting the Atlantic and Pacific basins. Unlike the Suez Canal, it is important to note that the Panama Canal is not a sea level canal and is freshwater, which limits unaided dispersal of marine organisms between oceans. However, the large flux of commercial ships transiting in equal proportions in both directions over the past century suggests that Panama may be a region experiencing a high frequency of tropical marine invasions (Ruiz et al. 2009, Seebens et al. 2013) and can provide insight into the ecological and evolutionary mechanisms shaping patterns of invasions.

We used the areas adjacent to the marine entrances of the Panama Canal to examine the hypothesis that invasions across two tropical oceans that differ in ecological and evolutionary context will be asymmetrical. We used standardized quantitative comparisons of sessile marine invertebrates, supplemented with literature synthesis, to examine whether (1) the proportion of introduced vs. native species is higher in the less diverse Pacific compared to the Atlantic as predicted by the BRH, and (2) the number of species introduced from the Atlantic to the Pacific is higher than that from the Pacific to Atlantic as predicted by EIH (Fridley and Sax 2014). We also use a manipulative field experiment to test whether (3) predation pressure on sessile invertebrate communities is stronger in the Atlantic than the less diverse Pacific, as predicted by the BRH, despite evidence of strong consumer pressure in the Pacific. Here, we provide the most comprehensive analysis of invasions for marine communities surrounding the marine entrances of the Panama Canal to date, yielding insights into the biogeographic patterns of invasion across two tropical oceans and the mechanisms that underlie these patterns.

## METHODS

### *Study system*

We focused primarily on sessile marine invertebrate communities to test for asymmetry of invasion between Atlantic and Pacific coasts of Panama for three key reasons. First, a large fraction of NNS in coastal marine ecosystems worldwide are associated with hard substrate communities (Ruiz et al. 2009a). Second, sessile marine invertebrate or "fouling" species are readily dispersed by ships. Due to intense shipping activity through the Panama Canal (Ruiz et al. 2009b), and the major role of shipping in the transport of marine NNS, Panama may be particularly prone to invasions from ships. Moreover, ships deliver NNS to both coasts and often transit the Panama Canal, providing a mechanism to transfer species across the Isthmus of Panama (Schlöder et al. 2013). Although propagule supply associated with these ships is

not quantified, the relative number of vessels transiting to Pacific and Atlantic sides of the Panama Canal have been similar over time (Ruiz et al. 2009b), making Panama particularly useful for testing hypotheses about asymmetry of invasion while trying to control for gross differences in propagule supply. Third, many sessile marine invertebrates produce larvae, which readily settle on artificial substrate, making them especially conducive for standardized sampling to measure and compare species occurrence as well as manipulative experiments to evaluate biotic interactions (Freestone et al. 2011). Thus, we combined field-based comparisons and experiments on sessile invertebrate communities with literature-based synthesis, to evaluate our hypotheses of asymmetry of invasion between oceans.

### *Field-based comparisons*

We characterized species composition across 10 different sites near each entrance to the Panama Canal; Limon Bay in the Caribbean basin of the Atlantic Ocean in 2004 and Bay of Panama in the Pacific Ocean in 2008 (Fig. 1, Appendix S2: Table S1). Our approach provided standardized measures of community composition (non-native, native, and cryptogenic species richness) for high-salinity sites (averaging >25 psu salinity) between oceans. At each site, we deployed ten 14 × 14 cm PVC panels that served as substrate for colonization of sessile invertebrates over a 3-month period (Ruiz and Hewitt 2002, Chang et al. 2018). This allowed us to control for substrate type, history, age, depth, and orientation in our analysis. The panels were deployed from surface structures of docks, ports, marinas and piers in a stratified, random design at each site. Importantly, marine NNS are often associated with artificial hard substrate (Ruiz et al. 2009a), especially at these types of sites. Further, artificial substrates (such as these panels) can accumulate disproportionately more NNS than native species, including solitary tunicates (Blum et al. 2007, Freestone et al. 2013, Tyrell and Byers 2007), compared with natural substrates over time. Thus, use of these sites and methods provide an especially effective method to detect benthic NNS already established across multiple (natural and artificial) habitats in the area. Panels were suspended 1 m below the water surface at mean low water. Panels were sanded on one side to create a rough surface (target surface for recruitment), attached to a brick (to provide weight), and hung in a horizontal (downward) position, facing the benthos. Environmental conditions (salinity, temperature, dissolved oxygen, water clarity) were measured at each site at the beginning and end of the 3-month period, and temperature data loggers were deployed at each site for the duration of the survey. While interannual differences in ocean conditions (e.g., temperature) could influence our sampling, both deployments were initiated at the beginning of the rainy season (April–May for Atlantic and May–June for the Pacific) to control for seasonal variation.

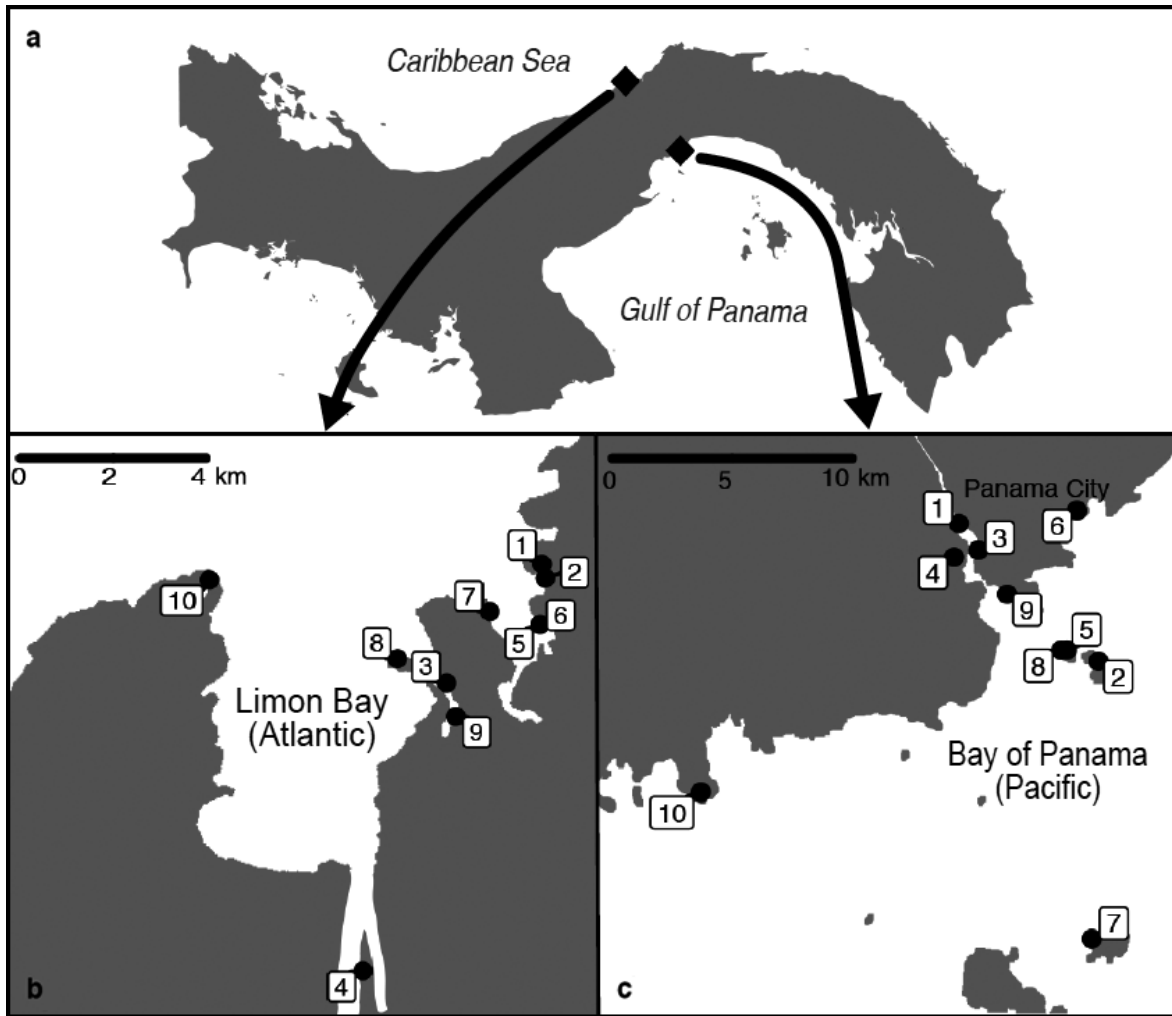


FIG. 1. Map of (a) Panama showing sampling sites on (b) Atlantic and (c) Pacific coasts (see Appendix S2: Table S1 for geographic coordinates and sampling dates).

Sampling in the Pacific coincided with a moderate ENSO cool-phase that preceded the wet season of 2008 (data available online).<sup>6</sup>

After 3 months of submersion we retrieved and photographed the surface of each panel. We identified species and measured species composition of sessile invertebrates for five randomly selected plates per site; additional plates were included to account for potential loss and to assure sufficient vouchers for identification. Specifically, we examined each panel under a dissecting microscope, noting each morphologically distinct sessile invertebrate. We collected and preserved five specimens as morphological vouchers of each morphotype (where available) per panel, for taxonomic identification. We identified vouchers to the lowest possible taxonomic group (species whenever possible), based on commonly

<sup>6</sup> <https://climatedataguide.ucar.edu/climate-data/nino-sst-indices-nino-12-3-34-4-oni-and-tni>

used external diagnostic characteristics, and classified each species as nonnative, native, or cryptogenic (of unknown origin; Carlton 1996) following established methods (Cohen and Carlton 1995, Ruiz et al. 2000). Due to taxonomic uncertainty and poor biogeographic knowledge of some invertebrate groups, we limited our analyses to a subset of taxa, including bivalves, bryozoans, tunicates, cirripeds, hydroids, and serpulid worms. These taxa are relatively well studied and represented the most common taxa on our panels.

Using the field survey data, we compared observed species richness in the Atlantic and Pacific and constructed species accumulation curves using all settlement panels from the 10 sites in both oceans. Species accumulation curves were calculated in R using the `specaccum` function in the `vegan` package (Oksanen et al. 2019). The resulting species accumulation table was then plotted using the `ggplot2` package (Wickham 2016). We used these curves to compare relative rates of accumulation

and estimated richness, for both NNS and all species, in the two oceans. To evaluate the distribution and test for normality in the occurrence of NNS introduced to both the Atlantic and Pacific coasts, we used a Shapiro-Wilks test on the frequency distribution of NNS across sites from each coast.

#### *Literature synthesis*

We searched the literature for records of marine NNS, which were previously reported to occur in Panama, to compare and combine with our field survey results. We developed a database for marine NNS in Panama, characterizing the known first record for each species to each coast of Panama, the native range (origin), additional historical and background information. We used these data for analyses, as outlined below, and provide access to occurrence records reported here through a publicly accessible website of the Smithsonian Institution (Fofonoff et al. 2017) and as an appendix (Appendix S2: Table S3).

We used these data to evaluate marine NNS detected per coast in the literature, field surveys, and both sources for sessile invertebrates. Then, we tested for asymmetry of invasions between coasts by comparing the total number of marine NNS detected per coast in addition to reciprocal exchange (invasion) of species native from one coast or ocean and introduced to the other. We evaluated the latter for (1) sessile invertebrates detected in our surveys, (2) all sessile invertebrates from both the literature and surveys, and (3) all marine invertebrate taxa (sessile and mobile) from both the literature and surveys.

#### *Predation experiment*

To test and compare effects of predation on community assembly between oceans, we used the same field approach as above except that we constructed a cage around the panels using Naltex™ plastic mesh netting (Schweitzer-Mauduit International, Inc., Alpharetta, Georgia, USA, mesh size 7 mm) to restrict macropredators such as fishes from interacting with the organisms on the plates. Three predation treatments were used: (1) predator exclusion (caged), (2) control (no cage), and (3) partial cage control. Partial cages were constructed with the same caging material but had four sides only (hung upside down) to control for shading and alteration of flow dynamics due to the caging material. Ten replicates of each of the three treatments (caged, partial cage and no cage) were deployed in August 2012 at three sites per ocean. These included Flamenco Marina (site 2), Port of Balboa (site 3), and Naos Island (site 5) on the Pacific and Colon Container Terminal (site 1), Embarcadero Davis (site 4), and Shelter Bay Marina (site 10) on the Atlantic (Fig. 1, Appendix S2: Table S1). In addition to measuring species richness on each panel, following the same protocol used in our standardized surveys, we estimated biomass by recording the wet mass of each panel upon retrieval (this included the standardized

14 × 14 cm PVC panel plus the organisms attached to it). We also estimated species abundances as percent cover using an overlay grid of 50 points uniformly distributed across the surface of the panel.

We first tested for an effect of predator exclusion on total community biomass (grams of wet mass), using a standard least squares mixed model. The model contained fixed factors of ocean, treatment, and their interaction. Random effects of site and site × treatment, both nested in the factor ocean, were included to accommodate the spatial nesting of the data. Data were natural-log transformed. The response of the predator exclusion was compared against the two control treatments (partial cage and no cage) in each ocean using planned contrasts, which were decomposed from the ocean × treatment interaction term in the model. The analysis was conducted in JMP Pro 12 (SAS Institute, Böblingen, Germany). We then explored the effect of predation on patterns of occurrence of NNS, including only those NNS that occurred (were shared) on panels on both Atlantic and Pacific coasts (nine species), to allow direct comparison that controlled for taxonomic differences (Supplemental Material). Effects of predation on occurrences (presence/absence) of NNS were analyzed with a permutational ANOVA (PERMANOVA; Anderson 2001) using the Jaccard distance measure. The model included fixed effects of ocean and treatment, a random effect of site nested in ocean, and all interactions. A planned contrast was again used to test for the effect of predator exclusion against the two control treatments. *P* values were generated using Monte Carlo tests. Similarity percentages (SIMPER) tests on Bray Curtis distance measures were used to explore species contributions (abundances based on point count data) to patterns of similarity/dissimilarity among treatment groups. The two control treatments did not differ in patterns of species occurrence ( $P > 0.1$ ); therefore, these data were pooled for comparison to predator exclusions in post-hoc pairwise PERMANOVA and SIMPER tests. Compositional analyses were completed in PRIMER 6 v. 6.1.13.

## RESULTS

### *Interocean comparison of NNS richness from field surveys*

For sessile marine invertebrates across all sites, NNS richness was higher on the Pacific coast than the Atlantic coast, whereas the opposite pattern existed for total species richness (Fig. 2). For the Pacific, 18 of the 60 species detected (30%) were considered NNS, compared to 11 of 85 (13%) on the Atlantic, for all 50 panels analyzed per ocean basin. Although species accumulation curves did not reach an asymptote for either ocean, especially for total richness (including all native, cryptogenic, and nonnative species), the results were consistent when comparing estimates of NNS and total richness among our observed values and commonly used species richness

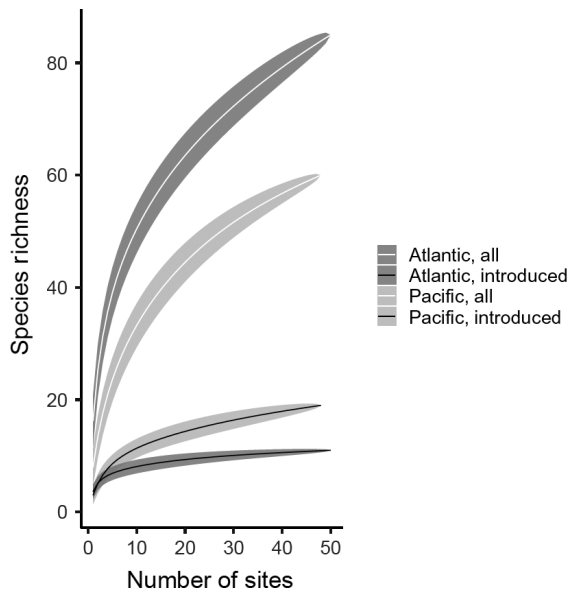


FIG. 2. Total invertebrate species richness of sessile invertebrates (bivalves, bryozoans, tunicates, cirripeds, hydroids, and serpulids) is higher on plates from the Atlantic coast of Panama (Atlantic, all and Pacific, all). Species richness of nonnative species is higher on the Pacific coast of Panama (Atlantic, introduced and Pacific, introduced). Shaded areas represent  $\pm 95\%$  confidence intervals. Each panel represents a site. Species accumulation curves were calculated in R using the `specaccum` function in the `vegan` package (Oksanen et al. 2019). The resulting species accumulation table was then plotted using the `ggplot2` package (Wickham 2016).

estimators (Canning-Clode et al. 2009; Appendix S2: Table S2).

Further, the percent NNS was consistent across spatial scales in the Pacific, but the proportion of NNS increased at smaller spatial scales in the Atlantic (Fig. 3). This difference between coasts was driven, at least in part, by the different accumulation rates for NNS vs. total species richness per coast. As shown in Fig. 2, total species richness increases more rapidly for the Atlantic, and NNS richness increases more rapidly for the Pacific, causing percent NNS to decline between panel and coast levels for the Atlantic relative to the Pacific. In addition, almost half (48%) of NNS on the Pacific occurred only at a single site, compared to 15% of the NNS on the Atlantic (Appendix S1: Fig. S1), thus, the distribution of NNS were over-dispersed (aggregated) in the Pacific (Shapiro-Wilks,  $W = 0.81$ ,  $P = 0.0018$ ) but not in the Atlantic (Shapiro-Wilks,  $W = 0.91$ ,  $P = 0.21$ ).

#### *Cumulative detected richness and asymmetrical exchange of NNS*

The difference in NNS richness between oceans observed in the survey is also reflected in the cumulative record of invasions, when including results from our

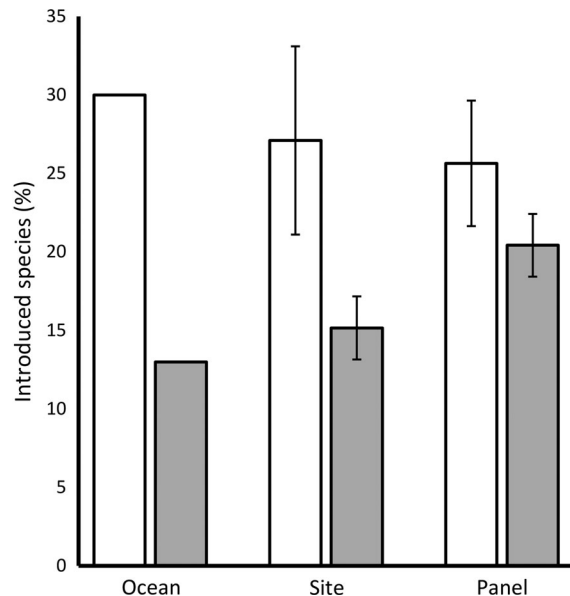


FIG. 3. Percentage of nonnative species out of the total number of species found in our surveys in the Atlantic (solid bars) vs. Pacific (open bars) coast of Panama, at ocean (across all 10 sites), site, and panel scale. Error bars are 95% confidence intervals.

literature synthesis (Fig. 4). To date, 37 NNS of sessile marine invertebrates are known to occur on the Pacific coast of Panama, including (1) 19 NNS unique to the literature, (2) 9 NNS new records from our surveys, and (3) 9 NNS that were detected in both literature and surveys. In contrast, 22 NNS of sessile marine invertebrates were detected on the Atlantic coast, including (1) 11 NNS unique to the literature, (2) 4 NNS in both literature and surveys, and (3) 7 NNS in our surveys that were previously unreported. The full list of NNS is publicly available online (Fofonoff et al. 2017) and in Appendix S2: Table S3.

We found exchange of species between oceans was asymmetrical, with more species invading the Pacific coast from the Atlantic compared to the opposite direction, using multiple data sets. For sessile invertebrates detected in our standardized field survey, eight of 18 NNS (44%) on the Pacific were native to the Atlantic, but only one of 11 NNS (9%) on the Atlantic were native to the Pacific (Fig. 5a). When considering total species for each ocean from our surveys, the ratio of Atlantic : Pacific species richness is 1.4:1 (85/60; Fig. 2). This ratio was also consistent across four species richness estimators (Appendix S2: Table S2). To account for differences in total species richness for each coast, which could influence the probability of invasion, we estimated the size of “exchange pools,” the total number of species in each ocean minus those species shared between oceans (*sensu* Fridley and Sax 2014), for an expected Atlantic : Pacific ratio of 1.6:1. We observed an exchange of 8:1 (Fig. 5a), suggesting a fourfold increase

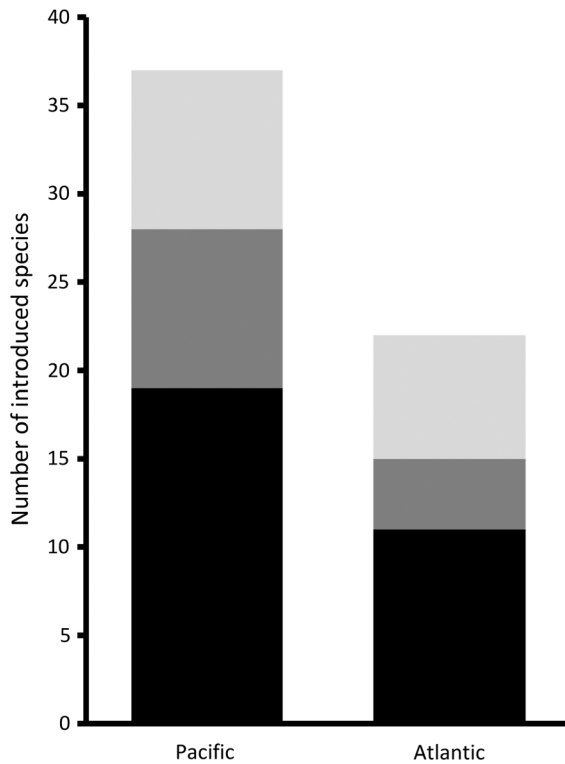


FIG. 4. Comparison of the number of nonnative species of sessile invertebrates reported in the literature (black), in literature and our surveys (dark gray), and new records from our surveys (light gray) of nonnative species for the Atlantic and Pacific coast of Panama.

from the predicted interchange based solely on the size of the respective species pools. This magnitude of exchange asymmetry of NNS was observed consistently, whether using settlement panels in our surveys, all sessile invertebrates detected in the surveys and literature synthesis, or all species reported (Fig. 5a–c), suggesting that this is a robust pattern.

#### Predation of shared NNS

Predation strongly reduced invertebrate biomass, including NNS occurrence, in the control treatments in comparison to the predator exclusion treatment on the Pacific coast ( $R_{\text{adj}}^2 = 0.90$ ,  $N = 89$ , ocean  $\times$  treatment  $F_{2,7.99} = 4.61$ ,  $P = 0.047$ ; cage-control contrast  $F_{1,7.99} = 9.25$ ,  $P = 0.016$ ; Appendix S1: Fig. S2), resulting in a mean biomass of control treatments that was over 3.7 times lower than in predator enclosures. There was no significant effect of predators on biomass on the Atlantic coast (cage-control contrast  $P > 0.1$ ; Fig. 6a).

Predation also shaped patterns of NNS occurrence, but again this effect was asymmetrical across the two oceans (PERMANOVA, ocean  $\times$  treatment pseudo- $F_{2,8.02} = 3.08$ ,  $P = 0.009$ ; ocean  $\times$  cage-control contrast pseudo- $F_{1,4} = 5.00$ ,  $P = 0.009$ ; site pseudo- $F_{4,71} = 14.0$ ,  $P = 0.0001$ ). Predation had a strong effect on patterns

of occurrence on the Pacific coast (PERMANOVA pairwise tests, Pacific, cage vs. controls  $t = 2.59$ ,  $P = 0.016$ ), while no effect was observed on the Atlantic coast (PERMANOVA pairwise tests, Atlantic, cage vs. controls  $P > 0.1$ ).

The effect on the Pacific coast was driven primarily by variation in abundance of the nonnative solitary ascidian, *Ascidia sydneiensis*, which contributed 85.9% to the similarity among caged treatments and 52.4% to the variation (dissimilarity) between treatment and control groups. On the Pacific coast, *A. sydneiensis* dominated primary space occupation in caged treatments, representing an average percent cover of 64.4% when predators were excluded, but was completely absent in control treatments (Fig. 6b, c). *Ascidia sydneiensis*, which was first reported on the Pacific coast of Panama in 2011 (Carman et al. 2011), was the most common species on our caged panels in the Pacific. Although *A. sydneiensis* is also introduced to the Atlantic coast, its percent cover did not differ between treatment and control groups. The second most abundant NNS that occurred on both coasts was the encrusting bryozoan, *Arbopercula bengalensis* (Fig. 6d). All other shared NNS contributed less than 2% cover. Overall, percent cover of *A. sydneiensis* was strongly correlated with total biomass on the settlement panels for both the Pacific and Atlantic combined (Appendix S1: Fig. S2;  $R^2 = 0.90$ ,  $P = 0.0001$ ;  $\text{Ascidia sydneiensis} = -269.4707 + 51.753163 \times \log[\text{g wet mass}]$ ).

#### DISCUSSION

Consistent with the evolutionary imbalance hypothesis (Fridley and Sax 2014) and some ecological expectations of the biotic resistance hypothesis, we found considerable asymmetry in invasion patterns and exchange between two tropical oceans, which differ in patterns of diversity and evolutionary history. While total species richness of sessile marine invertebrates was higher on the Atlantic coast of Panama compared to the Pacific coast, the proportion of NNS (regardless of origin) was over twice as high in the Pacific. Further, based on our standardized surveys as well as literature review, we detected an asymmetrical exchange of species across oceans, with the net direction of invasion export being from higher (Atlantic) to lower (Pacific) diversity. Over 44% of the NNS on the Pacific coast were from the Atlantic compared to only 9% in the opposite direction. The expected Atlantic : Pacific exchange ratio (sensu Fridley and Sax 2014), based on total number of species in each region minus those species shared between regions, was 1.6:1, but the exchange ratio observed here was five times higher (8:1). These results suggest that variation in other processes, such as colonization and interaction strength, has contributed to observed asymmetry beyond that predicted by species exchange pools alone.

These results are consistent with classic and contemporary predictions for faunal interchange and invasion dynamics. For example, Briggs (1968) hypothesized that

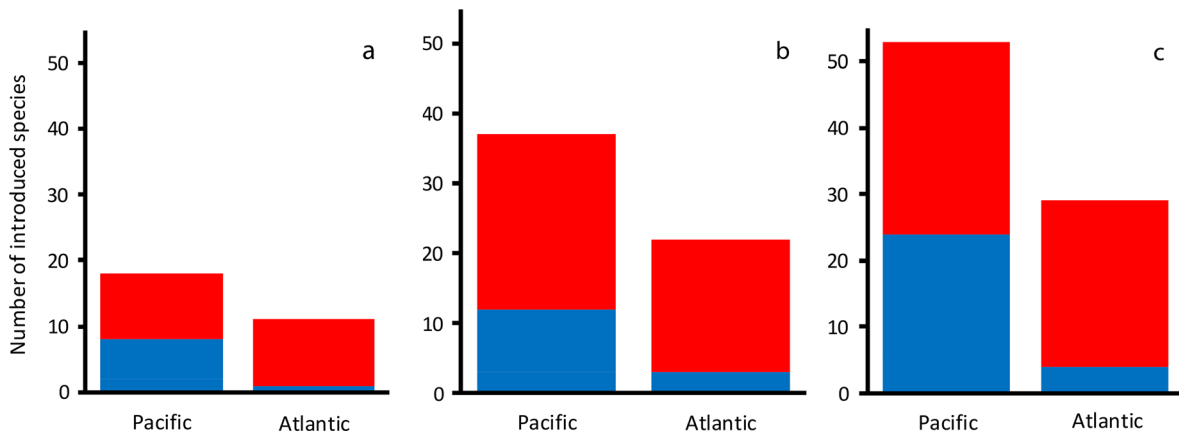


FIG. 5. Asymmetrical exchanges of species from the Atlantic to the Pacific in Panama with higher proportion of invasion from Atlantic to Pacific across (a) species observed in our surveys only, (b) sessile invertebrate species reported from literature and also observed in our surveys, and (c) all species reported in literature (mobile and sessile species) and sessile species observed in our surveys. Blue bars are nonnative species introduced from the opposite ocean. Red bars are nonnative species introduced from elsewhere (outside of the Panama bioregions).

a proposed sea-level canal through Panama would result in a predominantly southward (Atlantic to Pacific) invasion of Caribbean species into the Pacific, reasoning that the greater diversity in the Atlantic would resist invasion from the Pacific due to strong competition from the more diverse biota. Further, estimates of both recent and historical biotic interchange between biogeographic regions have provided support for asymmetrical exchange from high to low diversity (Vermeij 1991a, Bowen et al. 2013, Fridley and Sax 2014, Leigh et al. 2014). These previous studies have examined biotic interchange using the fossil record (Vermeij 1991a, b), phylogeographic inference (Bowen et al. 2013), and literature-based records of recent invasions (Fridley and Sax 2014). Unlike previous studies, we estimated invasion and biotic interchange using standardized quantitative measures and abundances in each region (ocean), to complement literature-based analyses, providing the most robust standardized analysis to date of recent invasions across two oceans.

While our panels provide a useful standardized method to compare sessile invertebrate communities and NNS richness by controlling for substrate type, history, age, depth, and orientation (Ruiz and Hewitt 2002, Chang et al. 2018), they are artificial substrates. While these artificial substrates are generally colonized by the same species as natural substrates, and provide a quantitative basis for direct comparisons, we also may expect community structure and composition to vary among specific benthic habitats (e.g., rock, coral or oyster reef, mangrove). We selected panels specifically as an efficient means to detect NNS already established in the surrounding area across different habitat types (Marruffini et al. 2017), but patterns across other habitat types remains to be tested.

Our results support predicted patterns of NNS between oceans, including asymmetrical exchange (EIH) and

higher overall NNS richness in the Pacific (BRH), but the outcome of the predation experiment reflects a potentially contrasting view. Much of the focus historically on biotic resistance has been on competition, but resistance due to consumers is another mechanism that can shape invasion patterns. In our experiments, removing large predators, mostly fishes, increased total biomass and almost doubled the total cover of shared NNS in the Pacific, but there was no effect of predator removal in the Atlantic. This is contrary to our predictions based on the BRH, which suggests that resistance due to predation should be stronger where species richness is greater.

In addition to a higher species richness for sessile invertebrates, the Caribbean harbors approximately 25% more marine fish species compared to the Tropical Eastern Pacific (Robertson and Cramer 2009, 2014), though recent modelling of richness of tropical reef fishes suggests that the accumulation of species across space is strongly associated with smaller body size and lower dispersal capabilities (Barneche et al. 2019). The association between body size and species richness may, in part, explain the strong consumer pressure reported across taxa in the comparatively less diverse Tropical Eastern Pacific (Vermeij 1976, Bertness et al. 1981, Hay and Gaines 1984, Lubchenco et al. 1984, Leigh et al. 2014), where higher metabolic demands of larger-bodied predators would likely require increased consumption (Brown et al. 2004). Similarly, differential abundances of fishes and other predators could influence the patterns we observed; however, there are currently insufficient comparable data to examine this.

Once NNS are established, local effects of biotic interactions may be important in determining the distribution and abundance of invaders (Levine 2000, Fridley et al. 2007). If these interactions are strong but variable in space or interact with abiotic conditions, it could influence the abundance of established NNS. This prediction is



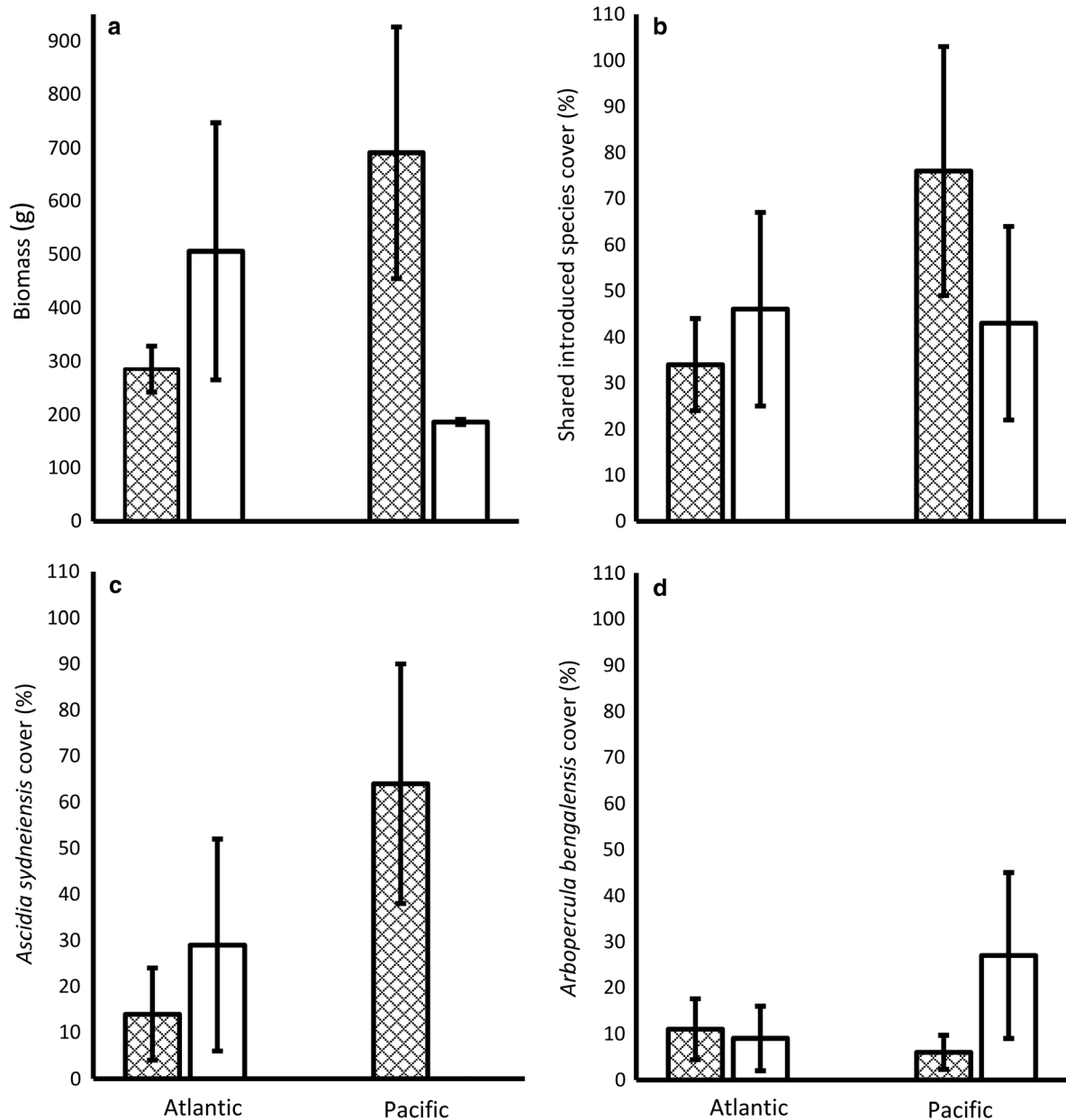


FIG. 6. Experimental results demonstrating the effect of predation on (a) biomass of sessile invertebrates, (b) percent cover of shared nonnative or introduced species, (c) *Ascidia sydneiensis* (NNS to both oceans), and (d) *Arbopercula bengalensis* (NNS to both oceans) across the Pacific and Atlantic Oceans in Panama. Shared nonnative species contributing a mean cover of less than two percent across treatments are not shown. Caged treatments (hatched bars) prevented macropredators from foraging on invertebrates whereas uncaged (open bars) treatments allowed predation. Error bars are 95% confidence intervals.

consistent with our results from the Pacific where almost half of NNS were found only at a single site (Appendix S1: Fig. S1), indicating substantial heterogeneity in abundance of introduced species. In comparison, NNS were more evenly distributed across sites in the Atlantic with about one-third of NNS occurring at over 90% of the sites. This contrast is most striking for the tunicate *Ascidia sydneiensis*, which was introduced to both oceans. In the Pacific, *A. sydneiensis* covered over one-half of the available

space on experimental (caged) panels and accounted for most of the biomass in the Pacific when large predators were excluded (Appendix S1: Figs. S2, S3), but was never detected in exposed (control) panels for this experiment (Fig. 6c and Appendix S1: Fig. S3).

Strong predation shaped the distribution and abundance of NNS on the Pacific coast, but given the high number of NNS compared to the Atlantic, predation was insufficient to limit invasions entirely. Indeed, biotic

interactions may be more effective in limiting the distribution and abundance of NNS than impeding invasion (establishment), especially across multiple habitats and potential refugia from predation. Such a reduction in abundances of some species, particularly for some otherwise dominant space occupying invaders, such as *A. sydneiensis*, may make occurrences spatially patchy and difficult to detect. This pattern could partly explain discrepancies between larger scale comparative studies and smaller scale experimental studies or mathematical models, which are often calibrated to examine effects common at smaller local scales. Perhaps a more nuanced consideration is not necessarily the presence or absence of NNS but rather variation in distribution and abundance in the invaded range. Consistent with this, early studies across the Isthmus of Panama suggest that variation in strength of consumers and competition can interact to differentially shape benthic marine communities (Birkeland 1977, Hay and Gaines 1984). Additional standardized comparisons and ecological experiments are needed to understand species distributions and test for differences in interaction strength between oceans.

While we focus on the potential for biotic interactions to shape invasion patterns, environmental variation also likely influences the distribution and abundances of species, and conditions are notably different on the Atlantic and Pacific coasts. After the closure of the Isthmus of Panama, the Atlantic experienced a reduction in productivity due to the cessation of upwelling, whereas productivity in the Pacific increased and the ocean is characterized by higher variability in temperature, turbidity, and larger tidal ranges (Leigh et al. 2014). This may also partly explain the high variability of the association between native and exotic species richness at small spatial scales in the Pacific. Indeed Davis et al. (2000) postulated that fluctuating resources might facilitate invasions and that environments that experience pulses in resource supply are more invasible. Further, fluctuation in resources may also interact with consumer pressure to influence invasion dynamics (Blumenthal 2006). Recent studies have shown that periodic upwelling and associated nutrient pulses along the Pacific coast of Panama alter top-down control by herbivores in the rocky intertidal (Sellers et al. 2021). While the latter work has focused on native species, similar processes could influence NNS and interactions between NNS and native species. Similarly, interannual differences in ocean conditions driven by ENSO events that alter both temperature and nutrients could influence variation in species abundances and consumer effects. While all sampling and experiments were conducted during the rainy season, sampling in the Pacific (2008) coincided with a moderate ENSO cool-phase. Nevertheless, the paucity of data across spatial scales, particularly for tropical regions, limits generalization across ocean conditions, habitats, and geographic regions (Fridley et al. 2007).

Similarly, while propagule supply can also strongly influence patterns of invasion and successful

establishment (Ruiz et al. 2009, Simberloff 2009), the relative number of vessels transiting to Pacific and Atlantic sides of the Panama Canal have been similar over time and may control for gross differences in propagule supply (Ruiz et al. 2009b). It is important to note that the Panama Canal is not a sea level canal and it operates using a series of locks, and Gatun Lake, the freshwater portion of the Panama Canal, has in the past served as an effective barrier for most marine species (Rubinoff 1968, Schlöder et al. 2013). While some species, mostly fishes, such as the Atlantic Tarpon, have transited the canal on their own (Rubinoff 1968, Rubinoff and Rubinoff 1968, Castellanos et al. 2020), shipping through the Canal is likely the main pathway by which marine organisms move across the Isthmus (Ruiz et al. 2009). Differences in shipping behavior (such as ballasting operations, time at port, etc.) can influence propagule supply across oceans, independent of number of vessel arrivals (Miller et al. 2011, NRC 2011), even though the relative proportion of ships transiting in either direction across the Canal is similar (Ruiz et al. 2009b). The actual propagule supply associated with these ships has not been quantified for either hull fouling or release of ballast water. To our knowledge, data on the amount of ballast water discharge are not yet available for Panama.

In general, there is a paucity of data on tropical invasions (Fridley et al. 2007), especially quantitative data, limiting robust geographic comparisons of invasion patterns. Our standardized sampling revealed nine new records for introduced sessile invertebrates on the Pacific coast of the Panama Canal and seven on the Atlantic coast. It is important to note that, while these are newly reported herein (Fofonoff et al. 2017), it does not mean they are new invasions. Rather, limited research on the frequency of invasions, particularly in the Tropical Eastern Pacific, could explain the pattern. Further, we encountered several cryptogenic species of unknown origin (Carlton 1996) that require further research to elucidate their origins. Importantly, there were also several reported NNS that we did not detect in our surveys, possibly due to the high spatial variation observed in abundance of NNS on the Pacific. While previous studies documented introduced species associated with the marine entrances of the Panama Canal (Rubinoff and Rubinoff 1968, McCosker and Dawson 1975, Cohen 2006, Carman et al. 2011), this is the first quantitative comparison of invasion patterns across the Isthmus of Panama, providing a novel test of biogeographic processes that drive invasions. Our findings suggest that marine invasions in the Atlantic and Pacific oceans of Panama are more frequent than reported, contributing further evidence that NNS are possibly common and largely underestimated in tropical marine communities (Ruiz et al. 2009, Carlton et al. 2019). Further, the asymmetrical invasions we document here, which resulted in differences in richness and abundance of NNS across two tropical ocean basins, suggest that global invasion dynamics are driven by both ecological and evolutionary

factors that shape susceptibility to and directionality of invasions across biogeographic scales.

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