Using the Panama Canal to Test Predictions about Tropical Marine Invasions

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ABSTRACT. As humans alter the landscape of the Earth and economic globalization expands, biological invasions increasingly homogenize the world's biota. In temperate marine systems, invasions are occurring at a rapid pace, driven by the transfer of organisms by vessels and live trade (including aquaculture and fisheries activities). In contrast, little is known about patterns and processes of tropical marine invasions, although the same species transfer mechanisms are in operation. This disparity may be the result of limited studies of invasions in the tropics relative to temperate regions. Alternatively, the tropics may be less susceptible to invasion than temperate regions for reasons of environmental unsuitability and biotic interactions. This paper provides a brief summary of the current but limited information of marine invasions across latitudes, focusing particular attention on the eastern Pacific north of the Equator. Within this latitudinal framework, the Panama Canal provides an especially important model system for testing predictions about marine invasions in the tropics for reasons of (a) the high level of shipping traffic since the Canal opened in 1914; (b) the permeability of the Canal as a conduit for marine invaders, despite the apparent freshwater barrier; and (c) the current expansion of the Canal that is expected to increase the size and number of ships visiting the region.

INTRODUCTION

Biological invasions are common in coastal marine ecosystems around the world (Cohen and Carlton, 1995; Orensanz et al., 2002; Fofonoff et al., 2008). In fact, reports of new invasions are increasing exponentially in many well-studied regions (Cohen and Carlton, 1998; Ruiz et al., 2000; Hewitt et al., 2004). Although invasions can result from natural dispersal, most contemporary invasions derive from human-mediated transfer associated with a variety of activities. As economic globalization continues to expand, creating a high degree of connectivity through the movement of commodities and people, opportunities for new invasions also increase. Bays and estuaries have been the most invaded marine systems, probably because they are hubs for shipping, aquaculture, and other human endeavors known to transfer organisms (Ruiz et al., 1997; Wasson et al., 2005).

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To date, most human-mediated invasions (hereafter introduced species) in marine habitats have been reported in temperate latitudes (Ruiz and Hewitt, 2008, and references therein). Relatively few introduced species have been reported from tropical or polar regions. This difference across latitudes may result partly from historical research effort and taxonomic knowledge, which are greatest in the temperate zone. However, a small but growing literature for high latitudes suggests that marine invasions may be limited in polar regions by a combination of current low temperatures and low propagule supply (Barnes et al., 2006; Aronson et al., 2007; Ruiz and Hewitt, 2008).

It is evident that marine invasions can occur in tropical marine systems (Agard et al., 1992; Guerrero and Franco, 2008), but the extent to which they occur remains largely unexplored. Few studies have evaluated marine invasions in the tropics. The exceptions are extensive analyses of introduced species on the Hawaiian Islands and Guam (Eldredge and Carlton, 2002; Paulay et al., 2002). It is uncertain whether these island ecosystems are broadly representative of the tropics, including especially mainland sites that may differ from islands in susceptibility to invasion (Elton, 1958; MacArthur and Wilson, 1967; Sax, 2001).

In a preliminary analysis of marine invasion patterns for mainland Australia, Hewitt (2002) reported an increase in introduced species richness with increasing latitude. The study included four tropical and four temperate sites, spanning 13°–38°S latitude. Despite a significant relationship with latitude, there is uncertainty about the taxonomic identification and biogeographic origin of many tropical species, resulting from limited information and relative lack of study for low latitude biotas. For this reason, Hewitt urges some caution and underscores the need for further analyses to interpret the observed pattern. It is nonetheless intriguing that this preliminary analysis provides results similar to those reported for tropical terrestrial systems, where relatively few exotic species of birds, mammals, and plants are established (Sax, 2001).

We have begun to explore latitudinal patterns of marine invasions for the mainland (continental) habitats within the Americas. To date, most of our analyses have focused on bays and estuaries within the United States, particularly on the Pacific Coast. We are currently initiating a research program to compare the number of introduced species, scale of vector operations (propagule supply), and ecology of invasions across temperate and tropical latitudes. Here, we briefly review the current state of knowledge about invasions and invasion processes along the Pacific Coast of the Central and North America and discuss the potential significance of Panama as a model system to evaluate regional and latitudinal patterns of marine invasion.

LATITUDINAL PATTERN OF INVASIONS ALONG THE NORTHEASTERN PACIFIC

Outside of the tropics, there is a clear increase in the number of nonnative species reported with decreasing latitude, from Alaska to California, 61°–32°N (Ruiz et al., 2006a). An extensive review and synthesis of the literature indicate that more than 250 nonnative species of invertebrates and algae are established in coastal waters of California (NEMESIS, 2008). Most of these invasions are attributed to commercial shipping and live shipments of organisms, especially oysters and their associated biota (Cohen and Carlton, 1995; Miller, 2000; Ruiz et al., unpublished data). Some of the California invasions have spread northward through natural dispersal, and other species have been introduced independently to the north. However, compared to California, far fewer nonnative species are known from Oregon, Washington, and Alaska (Cohen et al., 1998; Wonham and Carlton, 2005; Ruiz et al., 2006a).

Although this latitudinal pattern of invasion could result from reporting biases in the literature, particularly in the level of research (search effort) among regions, recent surveys suggest that the pattern is robust for sessile invertebrates in hard substrate fouling communities. Using standardized surveys to sample sessile invertebrates, deRivera et al. (2005) and Ruiz et al. (2006a) found that the number of introduced species increased with decreasing latitude from Alaska to southern California. It appears that the northern spread of many nonnative species from California may have been limited by dispersal as a result of the relatively low level of human activities (and, thus, species transfer opportunities) that have been present historically (Ruiz and Hewitt, 2008).

Similar analyses are not yet available to extend this comparison to lower latitudes along the eastern Pacific. Although there have been some studies reporting introduced marine species in Central America (Rubinoff and Rubinoff, 1969; Lambert and Lambert, 2003; Wysor, 2004, Roche and Torchin, 2007; Roche et al., 2009; Bastida-Zavala, 2008), standardized, quantitative community-level comparisons are lacking. In particular, synthetic studies focused within bays and estuaries of Central America targeting those taxonomic groups for which invasions are often most prevalent do not exist. Even where syntheses from the literature have been attempted, the paucity of available data limits conclusions about the scope of invasions. For example, Cohen (2006) provides a useful summary of available information on invasions surrounding the Panama Canal, which has received considerable attention for a tropical system. Despite the historical interest on biotic exchange in Panama, Cohen characterizes the current state of knowledge as follows: "The Panama Canal lies in a region of the world where the marine biota is both diverse and relatively poorly known, and there has been remarkably little investigation of the effect that the Canal has had on the distribution of that biota."

With a broad goal to evaluate patterns and processes in marine invasions using a latitudinal framework, we have initiated a research program in Central America (a) to compile available data from the literature on nonnative marine species, as part of our database (NEMESIS, 2008), and (b) to conduct standardized surveys at multiple sites. Our approach will allow direct comparisons with more than two dozen sites surveyed on the Pacific and Atlantic coasts of the USA. Our initial effort is focused primarily on sessile invertebrates (including ascidians, barnacles, bryozoans, hydroids, mussels, and sponges), which comprise a large proportion of marine introductions, are relatively well studied, and are conducive to standardized, quantitative field surveys.

A preliminary review of the literature for barnacles suggests the number of introduced species increases from Alaska to Panama (Figure 1A), consistent with an increase in the magnitude of shipping (see next section). At least four nonnative species of barnacles are reported to occur on the Pacific coast of Panama, including *Amphibalanus amphitrite*, *A. reticulatus*, *Balanus trigonus*, and *Fistulobalanus pallidus* (Matsui et al., 1964; Jones and Dawson, 1973; McCosker and Dawson, 1975; Laguna, 1985). Three introduced barnacles are known from California: *Amphibalanus amphitrite*, *A. eburneus*, and *A. improvisus* (Carlton, 1979; Carlton and Zullo, 1969; Cohen and Carlton, 1995; Cohen et al., 2002). *Amphibalanus reticulatus* has also been detected in recent surveys in southern California, but it is not yet known to be established (Ruiz, unpublished data). Only one introduced barnacle, *A. improvisus*, is reported in Oregon and Washington (Carlton, 1979; Wonham and Carlton, 2005), and there are no introduced barnacles known from Alaska (Ruiz et al., 2006a). It is noteworthy that the reported number of nonnative barnacle species in Panama exceeds that along the western USA, considering the latter is relatively well surveyed. Thus, we expect that strength of this inverse relationship with latitude may increase with additional information.

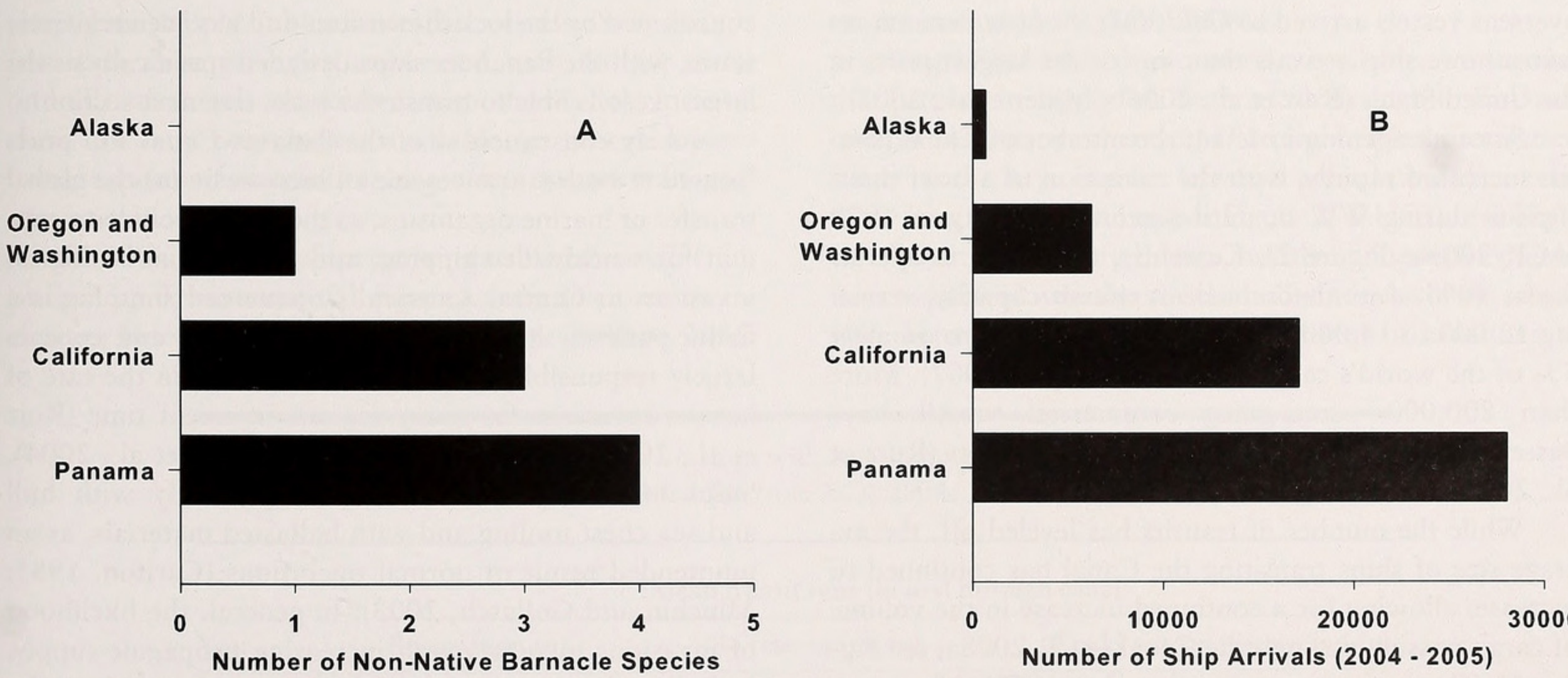

FIGURE 1. A. Number of nonnative barnacle species established by geographic region. Shown are the numbers of nonnative barnacle species reported to be established from Alaska to Panama (see text). B. Number of vessel arrivals by geographic region. Shown are the numbers of commercial vessel arrivals from overseas to different geographic regions, from Alaska to Panama, over a two-year period (2004–2005). Coastwise domestic traffic is excluded from arrivals to U.S. locations. (Data from Miller et al., 2007; ACP, 2008b.)

At the present time, the relationship between introduced species richness and latitude is poorly resolved for the northeastern Pacific and other global regions. The pattern presented in Figure 1A should be considered as preliminary, and it may change with further research. We also caution that these data are restricted to barnacles, a very small subset of species present in the fouling community.

PANAMA: A TEST CASE FOR TROPICAL MARINE INVASIONS

Panama is a potential hotspot for tropical marine invasions, because of the country's historic significance as a hub of world trade since the fifteenth century, expanding greatly since construction of the Panama Canal. The Canal created a new shipping route between the Atlantic and Pacific basins, resulting in a large influx of commercial ships, which have been an important source of introduced species in North America (Cohen and Carlton, 1995; Cohen et al., 1998, 2002; Ruiz et al., 2000; Wonham and Carlton, 2005; see discussion below). Figure 1B compares the magnitude of commercial shipping to several major port systems, indicating that ship arrivals to Panama exceed those to major port systems in the western United States by a large margin. Over the two-year period 2004–2005, nearly twice as many vessels arrived to Panama as overseas vessels arrived to California. In fact, Panama receives more ship arrivals than any of the largest ports in the United States (Ruiz et al., 2006b; Miller et al., 2007).

Since its opening in 1914, the number of Canal transits increased rapidly, with the exception of a brief interruption during WW II, until reaching capacity in 1970 (ACP, 2008a; Figure 2). Currently, the Canal is operating at 90% of its theoretical maximum capacity, servicing 12,000 to 14,000 vessels and carrying approximately 5% of the world's cargo annually (Reagan, 2007). More than 800,000 ocean-going commercial vessels have passed through the Canal since its completion (Ruiz et al., 2006b).

While the number of transits has leveled off, the average size of ships transiting the Canal has continued to increase, allowing for a continued increase in the volume of cargo passing through the Canal (ACP, 2008a; see Figure 2). The average tonnage (based on CPSUAB, a universal system of tonnage for the Panama Canal, or Canal ton, which is equivalent to approximately 100 cubic feet of cargo) per transit has increased from 4,832 in 1955 to 21,963 in 2005 (ACP, 2008a). This change in cargo capacity reflects an increase in the size of vessels over time;

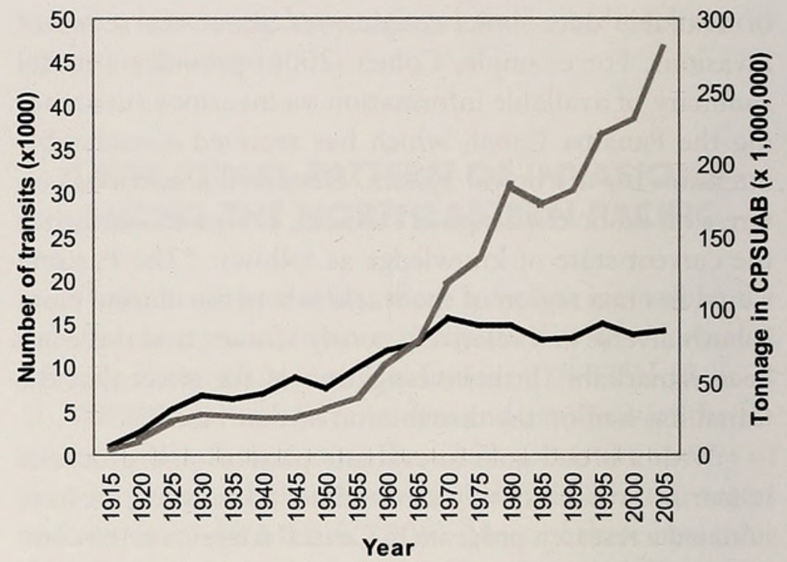

FIGURE 2. Number of commercial vessel transits (black line) through the Panama Canal and associated cargo tonnage (gray line); CPSUAB is a universal system of tonnage for the Panama Canal, or Canal ton, which is equivalent to approximately 100 cubic feet of cargo. (Figure modified from ACP, 2008a.)

these changes are the topic of a future analysis that will characterize changes both in vessel size and in underwater surface area available for colonization by organisms. In recent years, however, the size of vessels has been constrained by the lock dimensions and has been relatively static, with the Panamax ships designed specifically as the largest vessels able to transit the locks (see next section).

Likely consequences of the Panama Canal and ports located at both entrances are an increase in (a) the global transfer of marine organisms, as the canal provides a conduit for worldwide shipping, and (b) regional biological invasions in Central America. Commercial shipping is a major pathway for the movement of species and appears largely responsible for a dramatic increase in the rate of known invasions for many regions in recent time (Ruiz et al., 2000; Fofonoff et al., 2003; Hewitt et al., 2004). Ships move organisms associated primarily with hull and sea chest fouling and with ballasted materials, as an unintended result of normal operations (Carlton, 1985; Minchin and Gollasch, 2003). In general, the likelihood of invasions increases with increasing propagule supply, including the magnitude and frequency of organisms delivered (Ruiz and Carlton, 2003; Lockwood et al., 2005). Thus, the chance of colonization by introduced species in Panama is likely to have increased over time with the high frequency of vessels arriving to Panama from around the globe.

Given the high number of vessel arrivals, we might also expect the relative magnitude of propagule supply and invasions to be high in Panama. However, this remains to be tested, and there are several reasons why this may not be the case. First, different ship types and operational behaviors vary in their potential to transfer marine organisms (Verling et al., 2005; Miller et al., 2007; NBIC, 2008). Second, independent of propagule supply, some sites are less susceptible to invasion for reasons of either environmental conditions or biological interactions (Lonsdale, 1999; Ruiz et al., 2000; Roche et al., 2009).

Past studies have certainly highlighted the potential significance of vessels as a source of invasions to the Panama Canal and surrounding waters (see Cohen, 2006, and references therein for recent review). For example, Chesher (1968) discusses the potential importance of ballast water. Menzies (1968) considers the capacity of vessels to transfer fouling organisms. Hay and Gaines (1984) suggest that small pleasure boats may be especially important in the transfer or organisms across the Isthmus of Panama. A few studies also test the capacity of marine organisms to survive freshwater exposure for the duration of a transit through the Canal (Chesher, 1968; Hay and Gaines, 1984). Despite the long interest and recognition in ship-mediated transfer, the estimates given above are limited to few (if any) data on species composition or direct quantitative estimates of propagule supply (abundance) on vessels. Surprisingly few data exist on biota associated with ballast water or hulls of vessels associated with the Canal. Instead, there are only coarse data available on general operational aspects of vessels that may affect species transport opportunities.

Most commercial ships arriving to Panama will transit the Canal, but some will have considerable time at anchorage before entering the Canal. From 2000 to 2005, the average service time (from arrival to complete transit) of ships passing through the Canal was 16 hours when holding reservations. However, many ships have not had reservations, and average service times for these ships can reach 57 hours (Table 1). Although the proportion of ships holding reservations has increased in recent years, half of all ships still experienced some delay. Such increased residence time is likely to also increase the opportunity for reproduction and colonization of organisms associated with ships' hulls (Minchin and Gollasch, 2003; Davidson et al., 2008), relative to shorter residence times. It is evident that some organisms arrive to Panama on the hulls of vessels (Figure 3). However, a lack of quantitative information on the biota associated with outer surfaces of vessels transiting the Panama Canal and surrounding ports limits any detailed analyses.

For ballast water, we are not aware of any reliable estimates of the historical patterns of ballast water management and discharge of vessels arriving to Panama, including those ships delivering cargo to the terminals and those simply transiting the Canal. Even a coarse estimate of volume is challenging, given large differences in operations among vessels (Verling et al., 2005; but see Chesher, 1968). Presumably, ballast water discharge today is rather limited because many vessels conduct ballast operations to compensate for loading or off-loading cargo. In addition, Panama prohibits ballasting operations in the Canal under most circumstances (ACP, 2008b).

Despite the limited information available, we surmise that propagule supply has been relatively high in Panama, compared to many other temperate and tropical sites. Based solely on the large number of vessel arrivals and their relatively long residence times (see Figure 2, Table 1), it is likely that Panama has received large inocula of nonnative organisms associated with the vessels' hulls and sea chests, which have been historically important sources of invasions in

TABLE 1. Comparison of service time for ships with and without reservations transiting the Panama Canal; n = number of ships. (Source: Modified from ACP, 2008a.)

Year	Mean transit time (hours) through canal					
	Reservation (n)		No reservation (n)		Could not get reservation (n)	
2000	16.7	(1,944)	35.7	(6,864)	42.1	(121)
2001	15.7	(5,008)	26.3	(6,590)	43.7	(306)
2002	16.1	(5,692)	29.0	(5,134)	57.1	(1,062)
2003	16.2	(5,527)	24.9	(4,596)	45.1	(1,361)
2004	16.4	(6,419)	30.5	(3,568)	49.8	(2,531)
2005	16.5	(6,972)	27.3	(3,406)	45.8	(2,270)

FIGURE 3. Photograph of a vessel hull upon arrival to Panama showing associated biofouling organisms. Inset: Close up of bow with barnacles.

other regions (Coutts, 1999; Coutts et al., 2003; Coutts and Taylor, 2004; Hewitt et al., 2004).

As a result of its shipping history, Panama provides a unique opportunity to test hypotheses about patterns and processes of invasions to tropical marine systems. If propagule supply drives invasion patterns, we predict that Panama may be a hotspot for invasions. If tropical systems are inherently less susceptible to invasions (Elton, 1958; Sax, 2001), we would expect to see low introduced species richness despite high historical propagule supply. Our current research seeks to estimate nonnative species richness and advance our understanding of historical propagule supply in Panama, in the context of a broader latitudinal comparison as discussed above.

EVALUATING FUTURE CHANGES IN PANAMA

In October 2006, the Republic of Panama passed a referendum to expand the capacity of the existing Canal. The modernization will include (a) two new sets of locks, one at the Pacific entrance and one at the Atlantic; (b) two new navigational channels to connect the locks to existing channels; and (c) deeper and wider shipping lanes (Reagan, 2007). The expansion project is now under way and is scheduled to be completed by 2015 (Reagan, 2007).

When the expansion is completed, the Panama Canal Authority estimates that Canal transits will most likely increase from 12,700 per year in 2005 to approximately 19,600 in 2025, with an optimistic forecast as high as 22,100 transits per year (Figure 4). Further, the largest vessels currently capable of transiting the Canal are Panamax ships reaching 320 m in length that can carry 65,000 tons of cargo. After the completion of the new locks, the Canal will accommodate vessels up to 425 m long, carrying about twice the amount of cargo of today's ships (Gawrylewski, 2007; Reagan, 2007).

While efforts have been made to evaluate potential environmental effects of the Panama Canal expansion (ACP, 2008a), the possible effects of this expansion on invasion dynamics have not received much attention to date. One might expect an increase in propagule supply associated with the increased number and size of vessels transiting the

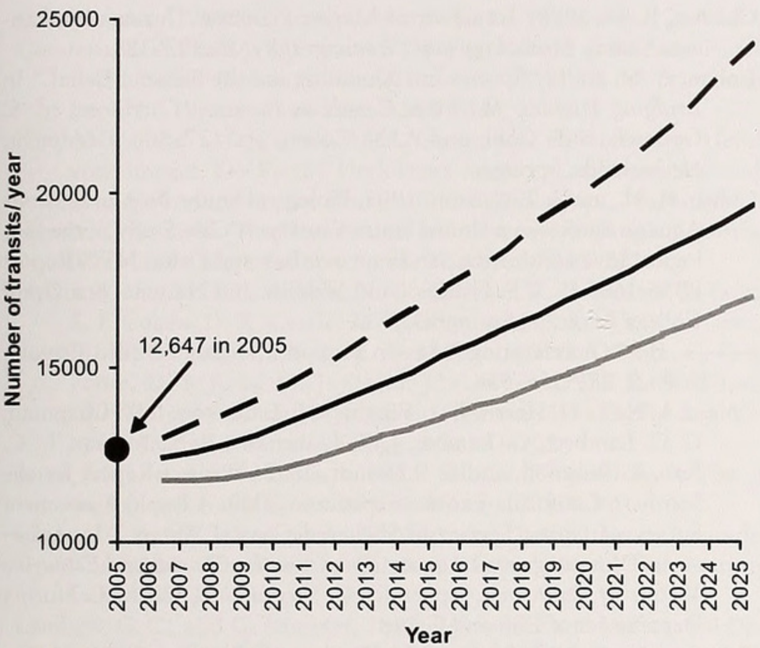

FIGURE 4. Forecast of demand for Canal transits. Solid black line = probable demand, dashed line = high (optimistic) demand, and shaded gray line = low (pessimistic) forecast demand. In 2005, there were 12,647 recorded Canal transits (solid circle). (Figure modified from ACP, 2008a.)

Canal. There may also be shifts in trade routes that could expand the species pool associated with ships' arrivals, resulting from either new markets or previous constraints on the size of vessels that could previously use this corridor. Alternatively, the service time of vessels may decrease as the capacity to accommodate more transits increases. This decrease could reduce the establishment probability of organisms attached to the hulls of arriving vessels, as residence time and likelihood of invasion are thought to be positively correlated (Davidson et al., 2008).

Potential changes in environmental conditions associated with both the ships and the Canal entrances could also influence future invasions. With the international ban on tributyl tin as an antifouling coating now coming into force, some have suggested that biofouling of ships' hulls, and hence ship-mediated propagule supply, may increase (Nehring, 2001). Additionally, changes in the salinity regimes will probably occur at both Pacific and Atlantic entrances to the Canal, as well as in areas within the Canal near the lockages, as a result of increased freshwater discharges into the oceans and potential seawater intrusion into the Canal. Such changes in salinities could alter the susceptibility to invasion for arriving organisms. However, any predictions about directional changes in propagule supply and susceptibility are currently speculative at best, as sufficient information presently is not available.

There is also a regional context for the Panama Canal that deserves consideration. Although the Canal provides a critical corridor across the Isthmus of Panama for global trade, Panama's ports are becoming increasingly important hubs for the regional distribution of commodities. More specifically, cargo that is delivered to Panama's ports is often transferred secondarily by other vessels to surrounding countries in the region. As Panama is a distribution center, any increase in introduced species increases the chances for ship-mediated dispersal to surrounding ports. Conversely, increased commerce with the other countries in the region also enhances the opportunity for delivery of organisms to Panama. The potential significance of such regional dispersal through this hub-and-spoke system of shipping has not been evaluated for the past, present, or future.

We are currently working with the Panama Canal Authority and the University of Panama to evaluate the role of the Panama Canal in regional and global marine invasions. Although the major focus of our efforts is to evaluate past and current levels of invasion, as well as to obtain some coarse estimates of propagule supply to the region, we hope to provide the baseline needed to forecast and evaluate potential impacts of future changes on invasion risks.

CONCLUSIONS

Panama provides exceptional opportunities to test hypotheses about invasions in tropical marine systems. The presence of the Canal and the magnitude of shipping to the region have undoubtedly increased the supply of nonnative species delivered to the shores of Panama. While there is limited information on actual propagule delivery, the Panama Canal Authority has maintained historical records on the number and characteristics of transiting vessels. This information provides a unique view of the magnitude of shipping and changes through time and could be used as an initial coarse proxy for propagule supply. We predict that invasions are common in Panama relative to surrounding regions as a result of the intensity of shipping in the area. If propagule supply is positively correlated to introduced species richness, as the literature suggests, we predict a relatively high number of invasions have occurred. However, if relatively few introduced species are detected in Panama, this suggests that some combination of environmental conditions and biotic resistance may limit invasions in this tropical region.

We have focused attention on Panama as a model system to understand marine invasion dynamics, but a robust analysis must also include comparisons to other locations that differ in the intensity of shipping and other transfer mechanisms. Ideally, such comparisons should be replicated across latitudes. Such a comparative approach is key to untangling patterns of marine invasions in tropical and temperate regions and, ultimately, in determining the processes that drive these patterns.

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