Evaluation of wetted surface area of commercial ships as biofouling habitat flux to the United States

Running title: Flux of underwater ship surface habitats

A. Whitman Miller[1]*, Ian C. Davidson[1], Mark S. Minton[1], Brian Steves[1], Cameron S. Moser[2], Lisa A. Drake[3], Gregory M. Ruiz[1]

1. Smithsonian Environmental Research Center, Edgewater MD 21037
2. Excet Inc., Springfield, VA 22151
3. Chemistry Division, Naval Research Laboratory, Code 6136, Key West, FL 33041

*Corresponding author; 443-482-2439 (telephone), 443-482-2380 (Fax), millerw@si.edu (e-mail)

ABSTRACT

Commercial ships inadvertently transfer vast numbers of living organisms beyond their evolutionary ranges, sometimes resulting in invasions of distant marine habitats. Biofouling on ship hulls translocate organisms that cling to the undersides and interstices of ships that function as hard substrate habitat for biota. Because biofouling accumulates over space and time continually, it poses risk to all ports visited. To better understand the potential magnitude of the biofouling vector in the United States, we compiled information on ship-specific dimensions as well as actual arrival histories of the fleets of ships calling at U.S. ports (2011-2014) in an effort to calculate wetted surface area (WSA) flux to the U.S. The annual mean flux of WSA from overseas bioregions to the U.S. is 333 $km^2 \cdot y^{-1}$. An additional 177 $km^2 \cdot y^{-1}$ of WSA moves among the eight distinct biogeographic regions of the lower 48 United States. We confirm that over 90% of all global marine bioregions (120 of 132 identified by IUCN) are visited by commercial ships within five port calls of arriving to the U.S. Our analysis is the first ever to quantify the extent of WSA flux among global marine bioregions and underscores the urgent need for management approaches and technologies that will reduce associated invasion risks.

Key words: aquatic nuisance species, biofouling, hull fouling, marine invasive species, non-indigenous species, vector

INTRODUCTION

Biofouling of commercial ship hulls has long been of concern to industry due to the adverse effects fouled hulls have on drag and fuel use (e.g., Callow & Callow 2002, Schultz et al. 2009, 2011). Further, the transfer of living organisms that cling to the hull or occupy niche spaces of ships outside the hydrodynamic slipstream and shear forces (e.g., sea chests, thruster tunnels, etc.) is widespread and recognized as a dominant vector for the transfer and introduction of marine species beyond their natural, evolutionary ranges (Ruiz et al. 2000, Carlton 2001, Fofonoff et al. 2003, Minchin 2006). Despite its operation over millennia, ship biofouling is a potent contemporary source of biological invasions throughout the world, with diverse management and policy approaches underway to minimize associated ecological and economic impacts (e.g., IMO 2011, Davidson et al. 2016).

Historically, wooden hulled vessels moved slowly and spent more time in port than modern-day ships (Carlton 1985, Hewitt et al. 2009). These ships were especially prone to biofouling and even structural damage. Damages from boring animals such as the molluscan shipworm (*Teredo navalis)* were dangerous and costly to the maritime industry due to the destruction of hulls and wooden pilings and support structures in harbors and marinas (Atwood & Johnson 1924, Carlton 1985). Biofouling and the widespread transport of marine biota associated with ship hulls remains active today and may actually be increasing in recent time for multiple reasons. First, some effective biocides have had unintended and adverse environmental consequences and are being discontinued, including the global ban on tributyl and organotins (Nehring 2001, Hewitt et al. 2009, IMO 2001). Second, the magnitude of shipping has been increasing over time, with vessels becoming more numerous and larger, increasing opportunities for biofouling colonization and transfers.

Ships' underwater surfaces, like other submerged artificial and natural hard substrates, serve as habitat for an enormous array of benthic marine species that settle, grow, and reproduce. Indeed, ships can be likened to mobile islands that shift habitat and associated species from place to place (Godwin

2003). The extent or proportion of a ship's hull that is fouled is related to a range of factors, including voyage routes and biological source regions, vessel operational profiles, maintenance schedules, and the amount of colonizing organisms that can remain attached to in-service ships. However, to date, few papers describe the extent and diversity of biota on submerged surfaces of contemporary commercial ships (Gollasch 2002, Davidson et al. 2009, Inglis et al. 2010, Sylvester et al. 2011), especially in the context of global shipping. As a result, accurate predictions of species assemblages and their flux around the world are lacking (Ashton et al. 2016).

Understanding the magnitude of biofouling on ships as a mechanism for species transfer is important but complex because of the overlapping influence of factors related to biological colonization of ships' surfaces (and subsequent introduction in ports of call) and shipping behavior (Inglis et al. 2010). Furthermore, the effect of oceanic passage or shifts in parameters such as temperature and salinity when transiting inter-ocean corridors, such as the Suez and Panama Canals, on hull biota is not yet fully understood. Similarly, biological responses to changing environmental conditions associated with emerging shipping routes such as Arctic passages (Miller and Ruiz 2014) are not yet known. Thus, despite the significant investment of ship owners in maintaining clean hulls ($5 billion per year and growing) of tens of thousands of ships plying the world's oceans, there are still many fundamental gaps in knowledge about biofouling communities associated with the wide diversity of vessel types and routes involved in global trade.

The magnitude of biofouling species transfers is related to both biological content of vessels and number of vessels arriving for a particular time period and geographic location. For the latter component, wetted surface area (WSA) is a common standardized measure of the maximum submerged surface area of a ship, and it represents the area of that ship that can potentially be colonized by marine organisms (Davidson et al. 2016; Moser et al. 2016). Despite not being a direct biological measurement, WSA provides a useful proxy for understanding the potential for ships to transfer biofouling organisms and how this is partitioned by vessel type, source or recipient regions, and time. The extent of biofouling that occupies WSA is highly variable and somewhat idiosyncratic, and is influenced by time since dry-docking, operational history, maintenance and a range of other factors (Inglis et al. 2010). This study estimated annual flux of total WSA to marine bioregions of the U.S. from both vessels arriving from overseas (OS) bioregions as well as vessels engaged in coastwise (CW) traffic that transit U.S. bioregion boundaries. In addition, we compared the relative contribution of different vessel types and different geographic source regions to the total annual flux. Finally, we estimated the WSA for niche areas by vessel type, for OS and CW vessel traffic. Our analysis illustrates clearly that OS WSA exposure to U.S. bioregions is uneven, suggesting important geographic components to vessel biofouling invasion opportunity.

MATERIALS AND METHODS

Using formalized naval architecture formulas, we calculated the WSA for a variety of prevalent ship types and modeled the relationship of WSA to an independent parameter (Net Register Tonnage) to determine WSA for individual ships. Combining data of ship arrivals (2011-2014) to the United States with WSA values for multiple ship types, calculated using the relationship between WSA and NRT, we were able to estimate the annual flux of WSA to ports in the U.S. Using a commercially available database of ship identity and statistics for the world fleet, IHS Fairplay World Register of Ships (http://www.ihs.com/products/maritime-information/ships/world-register.aspx), we collated dimensional measurements for six ship types (Bulkers, Tankers, Passenger, Container, Roll-on Roll-Off [RORO], and General Cargo). We then calculated WSA for several thousand individual ships of each category using the naval architecture formula of Van Maanen & Van Oossanen (1988). An independent dimension available for all ships, net register tonnage (NRT), was used to regress NRT to each vessel's corresponding WSA, yielding regression models that predict WSA from NRT for each ship type; this step was necessary, because the WSA of all ships arriving to the U.S. could not be calculated directly, as all ships' dimensional measurements were not available. This model was then applied to the population of ships arriving to U.S. ports according to geographic arrival region, last port region, and ship type in 2011-2014, as identified by the U.S. Department of Homeland Security's National Vessel Movement Center (NVMC). We confined our regression models to vessels of 100 NRT or greater to reflect arrivals by ships of this size and greater. The dataset of 373,833 arrivals included, in some cases, multiple arrivals to U.S. ports by a single vessel.

To evaluate WSA flux among global bioregions, and specifically to understand flux to U.S. regions, we estimated WSA of individual ships and paired these with actual voyage histories and arrivals. Importantly, ships connect geographically and biologically separated segments of the globe (i.e., ships move among marine bioregions that have evolved in various degrees of isolation) and move some organisms well beyond their native ranges. For this reason, we chose to bin individual arrivals according to the marine bioregion to which each ship arrived. We used the International Union for Conservation of Nature (IUCN) marine biogeographic regions (Kelleher et al. 1995), which includes eight regions in the contiguous U.S. (i.e., lower 48 states, see Figs 1 & 2). By definition, all OS arrivals to the U.S. cross between separate marine bioregions, so all were considered in this analysis as potential vectors for species transfers. In contrast, only CW traffic that moved between separate bioregions were considered potential invasion vectors for the purpose of this analysis, although we recognize invasions can occur within bioregions (especially as newly established invaders spread). For each of the 373,833 OS and CW arrivals considered here, the last ports of call and arrival ports were assigned to IUCN marine biogeographic regions. This approach enabled us to differentiate vessel transits that crossed *between* bioregions from those that remained *within* a single bioregion, and in this manner, each transit's potential for transferring invasive species among unique biogeographic regions containing distinct assemblages of marine species was assessed.

WSA calculation and regressions

WSA was calculated for a subset of ships in each ship-type category as follows (Van Maanen & Van Oossanen 1988):

$$WSA = L(2T + B){C_M}^{0.5}\left(0.4530 + 0.4425C_B - 0.2862C_M - 0.003467\frac{B}{T} + 0.3696C_{WP}\right) + 2.38\frac{A_{BT}}{C_B}$$

Where:

L = length overall

T = average molded draft

B = breadth

C_M = midship coefficient

C_B = blocking coefficient

C_{WP} = waterplane coefficient

A_{BT} = cross-sectional area of bulbous bow (calculated as a percentage of the immersed area of midship)

The coefficients and bulb area percentages for different vessel types are published in Van Maanen & Van Oossanen (1988). Although length should technically be the waterline length of the hull, such data are not available for the commercial fleet, and so length overall was used. For each ship type, the WSA per ship was regressed on an independent univariate measure of ship size (NRT), and the models with the best fit were selected.

WSA Flux

The four years of ship arrivals data was used to estimate the annual flux of WSA to the U.S., expressed as $km^2 \cdot y^{-1} \pm 1$ SD). Additionally, we evaluated the global source regions and associated magnitudes of WSA flux to each U.S. biogeographic region using four-year totals. Our analyses focused on commercial ocean-going ship types that are capable of making long haul passages across oceans or

CW transits (i.e., Bulker, Container, Passenger, RORO, Tanker, and General Cargo). Some ships, for which information was not widely available (e.g., Military, Tug/Barge), were excluded from this analysis. This approach provides the first ever estimate of WSA flux to the United States (or elsewhere) and across distinct bioregions. Two-way ANOVAs were used to test for differences in WSA by ship type and receiving coastal region for both OS and CW flux. WSA was log-transformed prior to analysis to conform to ANOVA assumptions.

Niche Area Flux

Mean annual niche area flux was estimated for each ship type investigated, both for OS and CW arrivals. Niche areas consist, broadly, of rudders, propellers, propeller shafts, thrusters, sea-chest grates, bilge keels, and dock-block surfaces for each ship type. Niche area was calculated by multiplying mean annual WSA flux by a ship-type-specific multiplier developed by Moser et al. (in review) in an analysis that quantified niche area by ship type, based on the global commercial shipping fleet. Moser et al. (in review) concluded that an area equal to 10.2% of the WSA of the global fleet could be attributed niche areas. Of this percentage, about half or ≈5% of total WSA is included in the WSA calculations (e.g., dry dock strips) and ≈5% is additional submerged surface area not included in WSA calculations. Applying the niche area multipliers to ship type WSA gives a conservative estimate of niche area flux, since on average, it discounts niche area by approximately 5%. Nevertheless, applying these across the fleet of vessel types that call at U.S. ports highlights the relative extent of niche WSA, that is, the areas with the highest probability of biofouling occurrence (i.e., hot spots for fouling, Coutts & Dodgshun 2007, Davidson et al. 2016). Based on Moser et al. (in review), the following multipliers were used to estimate the fraction of total WSA attributable to niche areas that are likely hotspots for biofouling organisms: Bulker (7%), Container (9%), General Cargo (9%), Passenger (27%), RORO (15%), and Tanker (8%).

Geographic/Biogeographic Analyses

Using a combination of database and GIS analyses, we determined both the quantity and origin (based on last ports of call, LPOC) of ships' WSA and niche areas arriving to U.S. locations. These data highlighted the strength of the connections among global regions and U.S. biogeographic recipient regions. Ship arrivals were evaluated in two ways, by calculating the total number of source bioregions accumulated by the ships arriving to the U.S. (i.e., source bioregion richness, based on previous 1 & 5 LPOC) and visualized by mapping the source locations visited by ships prior to arrival to the U.S.

RESULTS AND DISCUSSION

WSA by Ship Type and Arrival Record. Regression analyses relating WSA to NT for each of six major commercial design classes that visit U.S. ports yielded high r^2 values, ranging from 0.901 to 0.982 (Table 1). Nearly comprehensive WSA calculations were possible for these dominant design classes, because NRT and ship type information was available for 99.6 - 100% of qualifying arrivals.

Total WSA Flux. Between 2011 and 2014, the total WSA flux to US bioregions was 2.04 billion m^2. The mean total WSA flux was 510 million m^2 per year (510 km^2; approximately the area of New Orleans, LA), of which 65% of total was from OS (333 km^2, Fig. 1) and 34% (177 km^2) was CW (Fig 2).

It should be noted that these values are "total WSA" and therefore estimate the *potential colonizable* surface for marine species, including microbial biofilms, microalgae, as well as macrofouling organisms. Because the extent or species composition of biofouling organisms on these surfaces has not been measured, the WSA represents the area available for possible colonization. Nevertheless, understanding total WSA flux across biogeographical regions can be viewed as a proxy that allows investigators to refine estimates of realized ship biofouling flux and, therefore, the introduction and invasion risk by the ship biofouling vector. Such introduction opportunities are no doubt influenced by ship type, arrival frequency, operational profiles, and the extent of hull husbandry.

Overseas Flux. In the United States, the Gulf of Mexico coast (CAR-I) received by far the greatest annual OS WSA flux of any biogeographic region, 152 km^2, approximately 46% of total OS WSA, more than double that of the next busiest bioregion (the Mid-Atlantic region, NA-ET3), and more than 27 times the WSA flux observed in the Northeastern states (NA-ET2; Fig. 1). The Gulf of Mexico, Mid-Atlantic, and Southeastern U.S. (CAR-VII) receive a combined 246 km^2 (74% of total annual OS flux). Southern California (NEP-VI) had the highest flux of OS WSA of the Pacific Coast bioregions, raising the OS WSA flux of the top four bioregions to 292 km^2 per year (88% of total annual OS flux). The contribution of each ship type to annual WSA arrival varied greatly among U.S. bioregions (Fig. 1).

Coastwise Flux. By comparison, the mean annual WSA flux across bioregions of the U.S. (i.e., CW traffic) was 177 km^2, an area similar in size to Washington, D.C. (Fig. 2). CW flux is dominated by four bioregions (CAR-VII, NEP-V, NA-ET3, CAR-I) whose combined WSA exposure is 139 km^2, 79% of the mean annual CW WSA flux (Fig. 2). The Gulf of Mexico, Southeastern U.S., and Mid-Atlantic regions account for 58% of total CW WSA flux. In most cases, OS WSA flux exceeded CW flux in each bioregion, with the exceptions of Central California (NEP-V) and the Southeastern U.S. (CAR-VII) which receives 330% and 119% more CW than OS WSA, respectively.

If compared at the coastal scale, the Gulf of Mexico coast (CAR-I) receives 46% of all OS WSA flux but only 14% of CW WSA. The East and West coasts are more balanced in WSA flux: East coast receives 30% OS and 46% CW flux; West coast receives 24% OS and 30% of CW WSA flux (Figs 1 & 2).

Flux by Ship type. In most recipient bioregions there were marked shifts in the ship types that dominate OS and CW traffic patterns (Figs 1 and 2). For example, in Southern California (NEP-VI) there was a strong shift from 70% (OS) to 33% (CW) arrivals by Container ships accompanied by a parallel increase in Tanker arrivals from 15% (OS) to 48% (CW). The inverse relationships exist for Containers and Tankers arriving to Central California ports (NEP-V). When compared at the national scale, the relationship of OS and CW fluxes also varied by ship type. WSA flux from Containers and Roll-on Roll-off vessels were evenly balanced between OS and CW WSA flux, compared with all other ship types for which OS flux far outstrips CW flux (Fig 3.).

There were 13,820 unique vessels engaged in trade with U.S. ports during the timeframe studied (Table 2). Less than 2% of vessels were engaged in exclusive trade among U.S. ports, whereas 48% arrived exclusively from OS, and 50% operate in both OS and CW modes. A large majority of Containers (79%) and ROROs (86%) operate both OS and CW, but the ratio of 'Both':'OS' for these ship types was 4.1 and 8.0, respectively, while all other ship type had ratios of <2.0 (Table 2). Bulkers are only ship type dominated by exclusive OS trade (67% of unique vessels).

Two-way ANOVAs indicated that there were highly significant differences in mean annual overseas WSA among vessel types, but that these differences were not equal among the regions ($F_{34,139}$ = 73.03, $p < 0.001$). A similar statistical pattern was confirmed for CW WSA flux, ($F_{35,143}$ = 71.55, $p < 0.001$). These results reinforce the fact that strong differences in WSA flux exist among U.S. bioregions and that different assemblages of ship types serve them.

Niche Area Flux. Figure 3 also describes the estimated quantity of WSA corresponding to niche areas, surfaces that are widely recognized as more prone to biofouling than submerged portions of the hull (Coutts & Taylor 2004, Davidson et al. 2016). Overseas arrivals by Passenger vessels, although representing just 13% of overall WSA flux, comprised 33% of the total niche area arriving to U.S. ports from OS. By comparison, the OS flux of WSA by Containers and Tankers was more than two times greater than that of Passenger vessels, but the flux of niche area attributable to these ship types was roughly two-thirds that of Passenger vessels. This disparity was directly related to the prevalence of hull thruster tunnels and other niche areas on Passenger vessels, estimated as 27% of total WSA (Moser et al., in review). Based on differences in design, namely the extent of niche area, some ship types may be more readily fouled and thus potent vectors of invasive biofouling species. However, owing to differences in operations and trade patterns, ship types with similar OS WSA and niche area flux (e.g., Containers and Tankers) may pose very different threats to CW transport of ship biofouling species (Fig. 3).

Geographic Source Richness and Global Connectedness. As ships move from place to place, their hulls are exposed to ever-increasing varieties of biota. Thus, knowing the voyage history of ships provides insight into the diversity of bioregions visited prior to calling at a recipient port of interest. By compiling the geographic history of arrivals to U.S. bioregions, we were able to compare the cumulative source bioregion richness for each recipient region. Figure 4 plots total bioregion richness accumulated over four yrs for each U.S. receiving bioregion by both one and five LPOCs. There is substantial variability in richness among U.S. receiving bioregions with one LPOC (62.8 ± 6.38 bioregions). The Gulf Coast (CAR-I) is directly connected to more than twice as many source bioregions as Puget Sound (NEP-III). There was strong convergence among recipient regions when connecting to five LPOC (101.5 ± 2.25 per receiving bioregion; mean and SE). The combined total LPOC-5 richness for the contiguous US was 120 bioregions and the world is comprised of 132 bioregions under the IUCN scheme. As a whole, the US is sampling 91% of the world's coastal bioregions.

Mapping source bioregions accumulated by ships prior to arrival in U.S. bioregions across four yrs enabled us to visualize how each region of the U.S. is connected to the rest of the globe. Strong regional differences are especially apparent when evaluating the most recent last port (LPOC-1; Figure S.1., Supporting Information).

When the arrival history of ships was traced back beyond the immediate last port of call (e.g., from one to five last ports) the domain of global source/donor regions expands for all U.S. recipient bioregions (Fig. S.2, Supplemental Information). For example, connections to Southeast Asia, Australasia, and the Indian Ocean accumulate for all 8 U.S. recipient bioregions, but the North Atlantic remains a relatively minor source of WSA for West coast ports and bioregions. As voyage route history is more fully accounted for, last ports of call accumulate, a much greater range of biotic source regions are ‘sampled’ by ships, and greater numbers of inter-ocean transits result in accumulated exposures with potential physiologically stressful conditions (e.g., Panama Canal (warm water, low salinity exposure), the Suez Canal (warm water, marine-hypersaline exposure).

Our investigation sought to characterize and quantify both the extent and geographic nature of WSA flux across distinct marine biogeographic regions. Unlike ballast water (BW)—the most widely recognized transport vector associated with commercial ships, which has a growing variety of technologies and procedures by which invasion risk can be minimized (e.g., Minton et al. 2005, Miller et al. 2011, Davidson & Simkanin 2012)—there are no adopted technologies or procedures that are both highly effective and broadly used to prevent ship biofouling mediated invasions. In fact, explicit management of ship biofouling to prevent marine invasions is only emerging at present despite the long history of hull coating use (e.g., anti-fouling and foul-release) by shippers to promote vessel performance and fuel efficiency (Dafforn et al. 2011, Davidson et al. 2016). Hull coatings represent the focal point of the shipping industry’s biofouling management approach, which has had inadvertent benefits for invasion prevention, but modern ship biofouling remains a potent vector of marine invasive species (e.g., Inglis et al. 2010, Ruiz et al. 2011) and biofouling management for explicit biosecurity purposes is being promoted more broadly around the world (IMO 2011, Wells & Booth 2012, New Zealand Government 2014).

A ship that arrives to a U.S. port, or any port of the world for that matter, may pose near-zero risk of species introduction from ballast water (e.g., if no ballast water is discharged into a port, there is no risk of associated BW introduction); however, as ships move from place to place, there is continual opportunity for colonization of the submerged surfaces and a concomitant opportunity for biofouling species to disembark to the surrounding environment. Biota may be dislodged through accidental contact with a wharf or from the forces exerted on thruster tunnel inhabitants when thrusters are activated. Alternatively, and more commonly, animals and seaweeds may reproduce at any port during the ‘opportunity window’ that aligns with their reproductive life cycle. Moreover, stress-induced spawning may be an important mechanism of release from ships when organisms are exposed to highly variable and sometimes barely tolerable conditions that trigger spawning events in ports (Minchin & Gollasch 2003). In the absence of perfect anti-fouling solutions, ships experience the continual development and replacement (due to competition and death) of species assemblages that essentially integrate across the places they visit. In this sense, ship biofouling is a concatenation vector (C. Hewitt pers. comm.), perhaps more so than ballast water even though individual ballast tanks can contain water from different ports. Conversely, ships may leave a trail of biota in their wake, reflective of their particular voyage history, as has been postulated for certain voyage routes as explanations of both marine and terrestrial species distributions (Darling et al. 2012, Gotzek et al. 2015).

It was clear from our study that the total OS WSA flux was nearly double that of CW WSA flux (333 km^2 vs. 177 km^2). Interestingly, this value is similar in magnitude to the estimated total WSA of the entire global fleet of active commercials ships (≈120,000 commercial ships in the world fleet with estimated 325 km^2 WSA, Moser et al. 2016). Nevertheless, some marine bioregions receive far more OS flux than CW flux (e.g., Gulf of Mexico, Southern California, and the Mid-Atlantic) while others were dominated by CW flux (e.g., the Central/Northern California coast). These patterns no doubt directly reflect underlying commerce patterns to and from these regions, related to hub-and-spoke, point-to-point, short-sea, and pendulum models of trade and transport geography (Rodrigue et al. 2013). Such patterns imply that the conditions experienced by ship biofouling organisms will be quite different, depending on voyage history characteristics like route, voyage length, potential exposure to divergent environmental conditions, and overall differences in biota being mixed. Furthermore, overlaid on all of these parameters is climate change, which will further complicate these relationships.

By definition, all ship arrivals to the U.S. from OS artificially connect unique marine biogeographic regions and thus pose some risk of transferring invasive biofouling species (and populations) to coastal habitats of the United States. Likewise, ship voyages emanating from U.S. bioregions threaten to export North American biota to other parts of the world. However, it is critical to recognize that CW ship transits can transfer species among distinct bioregions, either by mixing U.S. natives across U.S. biogeographic boundaries or by secondary movement of an introduced invasive from one bioregion to another. It is also important to note that the same individual ship can engage in an OS arrival and subsequently conduct one or more inter-bioregion CW arrivals, as is the model voyage pattern for certain Containers (e.g., a pendulum voyage route). In this case, OS biofouling from a trans- or inter-oceanic source can be transferred to the original port of entry *and* adjacent bioregional ports, while the OS and domestic bioregional biotas can coexist on the same vessel.

A recent study by Moser et al. (in review) based on >120,000 commercial vessels that were part of the active global fleet (1999-2013) concluded that the equivalent of 10% of the total available WSA was comprised of niche areas. These are locations where biota accumulate most often on ships' submerged surfaces, typically areas outside the laminar hydrodynamic slipstream, and they are locations that can be more difficult to maintain than hull surfaces (Coutts & Taylor 2004) and where biofouling does not impose an immediate cost or performance penalty to ship operators (Davidson et al. 2016). Although some areas, such as dry dock strips and bilge keels are included in WSA calculations, other niche areas (e.g., propellers, rudders, sea chests, thrusters and thruster tunnels, etc.) are in excess of typical WSA estimates, providing an additional ≈5% of area that can be colonized by biofouling. Further, the extent and make-up of niche area is highly dependent on ship type, ranging from niche areas that are 7% of total WSA for Bulkers to 27% for Passenger ships. Because these niche areas tend to foul more readily, they are an elevated concern from an invasion risk and biosecurity perspective. Although we did not formally parse the fleet of vessels visiting U.S. ports into its proportional hull and niche area representation, applying niche area percentages of overall WSA for mean annual fluxes by ship type provides a conservative estimate of biofouling hot spots associated with vessel flux in the U.S.

WSA acts as the potential surface area available for colonizers, but the actual or realized percent cover of colonized space is likely highly variable and often linked to niche area hotspots for macro-organisms (Coutts & Taylor 2004, Davidson et al. 2009). Although larger studies (n > 30 ships) of biofouling on modern shipping have occurred in recent years (Inglis et al. 2010, Thomason 2010, Sylvester et al 2011), the amount of ship sampling that has occurred is not commensurate with the scale of the phenomenon and the range and complexity of factors that influence biofouling on ships. As such, the degree to which WSA acts as a proxy measure for biofouling is not known. WSA is probably a more accurate proxy measure for the extent of microbial organism transfers that are traversing the globe in biofilms, however. Despite anti-fouling technology, biofilms develop quickly on ships' surfaces and sterile surfaces are not possible, so biofilms develop to varying degrees across their surfaces. Fundamental questions regarding microbial biogeography remain unanswered (Hughes Martiny et al. 2006), however, and an even greater dearth of micro-organism investigations from ships' submerged surfaces (compared to macro-organism studies) hinders our understanding of biofilm composition, diversity, extent, and transfer on ships (Hunsucker et al. 2014. Leary et al. 2014).

How biofouling organisms from coastal environments withstand prolonged exposure to pelagic conditions during ocean crossings is not well documented. Likewise, the potential detrimental or lethal effects of temperature and salinity on exposed biofouling organisms that pass through the Panama or Suez Canals is not yet established. The expansion of these canals will amplify flux of ships (and WSA) between oceanic bodies, but is also expected to strongly affect the strength of connections among ports (Muirhead et al. 2015, Galil et al. 2015). Both conditions increase the opportunity for species transfer; however, passage through physiologically stressful environments may actually serve to filter or kill some fraction of the taxa on the undersides of vessels. If such a mechanism actually operates, then the frequency with which any given vessel traverses the Panama or Suez Canals may affect its degree of biofouling and by extension, its risk for moving invaders. Riverine and atypical salinity ports can exert similar disturbances on ship biofouling, and analyses of port network structure and environmental match among ports provide a useful basis for spatial comparisons of invasion risk (Kaluza et al. 2010, Keller et al. 2011).

As ships begin opting for Arctic routes, such as the Northern Seaway and Northwest Passage as a shortcut between oceans (Miller 2014), biofouling species will be increasingly exposed to cold water without drastic changes in salinity. It is altogether possible that mortality and moribundity to biofouling organisms will differ among inter-ocean corridors. Indeed, the spread of marine organisms between the North Pacific and North Atlantic via the Arctic Ocean has already been documented (Reid et al. 2007). If Arctic routes prove less destructive to ship biofouling than historically active inter-oceanic passages, the prospect for accelerated exchange of species across oceans and invasions of the Arctic seems likely (Miller and Ruiz 2014). Floerl (2014) has suggested that Arctic nations consider adopting a biosecurity approach based on that developed by New Zealand to reduce ship-mediated marine invasions.

WSA and BW Vector Contrast. Both WSA and BW represent vectors that transfer entire species assemblages (acting as 'habitat vectors'), and therefore interesting to compare and contrast. When mean annual OS WSA is plotted against mean annual discharge of OS ballast water to the U.S. (BW; NBIC 2016), there is a strong positive linear correlation between the two: mean annual BW Discharge ($10^6 \cdot m^3$) = 0.3668·mean annual WSA (km^2), $r^2 = 0.9182$). The characteristics of ship biofouling and ballast water vectors offer a contrast in biotic uptake by an external and internal vector of ships; ship biofouling accumulates throughout the inter-dry-docking period of each ship, which may result in a higher level of bioregion sampling *per ship* via biofouling than ballast water (the sediment accumulating in ballast tanks and microbial biofilms on ballast tank walls notwithstanding). These patterns underscore that invasion opportunity related to commercial shipping is strikingly uneven across the coastal United States. Indeed, the volume of unmanaged BW (either via open ocean BW exchange or onboard BW treatment) discharged to the Gulf of Mexico is more than three-fold greater than unmanaged BW discharge to the rest of the nation (NBIC Annual Report 2014). Federal regulations have required BW management from ships discharging water from OS since 2004 (33 Code of Federal Regulations 151.2005), but uneven compliance with such regulations have left large regions of the coastal U.S. under-protected from BW-borne invaders.

Management Implications. The limitations to effective BW management in the United States and globally (Miller et al. 2011) are minor compared to those associated with biofouling of commercial ships. Although there are IMO Guidelines concerning best practices for ship biofouling and invasive species (IMO 2011), and an emerging number of regional and state programs (McClay et al. 2015), U.S. federal regulations are incomplete with respect to biofouling management for biosecurity purposes such that their influence on the behavior of ship operators is unclear and their impact on invasion risk reduction is likely minimal. Currently New Zealand is the only nation state to have proposed an explicit policy for biofouling management and (soon-to-be) mandatory biofouling standards for invasion risk reduction (New Zealand Government 2014). Other countries have also proposed IMO-style guidelines, while some regions and states, particularly those with sensitive or highly-valued marine environments, impose mandatory rules governing levels of biofouling on arriving vessels (McClay et al. 2015). In the U.S., and most of the world, dry-docking frequency typically occurs on three to five-year intervals, as suggested in the International Convention for Safety of Life at Sea and for ship classification purposes (Takata et al. 2011). Dry-docking is aimed primarily at inspection, maintenance, and repair of a ship's submerged surfaces, equipment, and processes for structural and insurance reasons, and is nearly always accompanied by hull cleaning and re-application of coatings (typically anti-fouling or foul-release coatings). While periodic cleaning will reduce the risk of invasions and often resets this vector's biota to zero (until a biofilm is formed), efficacy of biofouling management strategies will depend on frequency of dry-dock visits, appropriate matching of coatings to operational profiles, and the quality of cleaning and coating application. For all coating types, but especially for foul-release coatings, the application process is quite prescribed and must be precise to ensure proper efficacy over time.

In-water cleaning (IWC) of underwater hull surfaces by divers or robotic cleaning technologies are management approaches designed to scour commercial ship hulls of their developing biological communities between dry-dock visits. Oftentimes, reduced vessel performance triggers IWC, like a downturn in propulsion efficiency and increased fuel costs. Such reactive cleaning can result in depositing non-native species into recipient environments. More frequent pro-active IWC may impede the development of extensive and biodiverse fouling communities, thereby reducing the risk of ship biofouling introductions. However, until hurdles regarding the incidental release of both viable biota and toxicants into local waters (McClay et al. 2016) are overcome, IWC may remain a response rather than a preemption of biofouling problems. Both pose serious environmental concerns that mandate improvements to the technology and practice before IWC can be truly effective for a broad range of vessels.

Forward-looking management that reaches beyond issues of ship performance and addresses marine bioinvasions seems prudent (Davidson et al. 2016), especially for a marine invasion vector as enduring and globally potent as ship biofouling (Darwin 1854, Hewitt & Campbell 2010). Biofouling has lagged behind BW management but is emerging as an international policy issue. Whether international guidelines or a few nascent management and regulatory programs will generate sufficient awareness and environmental concern to gain widespread attention from policy-makers in the U.S. and elsewhere is unclear. Given the scale of unfettered WSA in motion across Earth's oceans, combined with rapidly expanding and new shipping routes, the strength of port-to-port connections and the structure of shipping networks is certain to change, bringing with it changes to invasion risk worldwide.

ASSOCIATED CONTENT

Supporting Information. Analysis and mapping of the biogeographic histories of ships that arrived to U.S. bioregions (2011 – 2014), based on their immediate and last five ports of call. Comparison of WSA and BW flux to recipient U.S. bioregions.

ACKNOWLEDGMENTS

This work was partially supported by funding from the Smithsonian Institution (AWM, ICD, MSM, BS). Funding from University of Maryland Center for Environmental Science/ Maritime Environmental Research Center (funding agreement 2012-38) and the U.S. Maritime Administration provided additional support (LAD, CSM). We thank Mario Tamburri (MERC/UMCES) and Carolyn Junemann (MARAD) for their guidance and programmatic support.

REFERENCES

1. Ashton GV, Davidson IC, Geller J, Ruiz GM (2016) Disentangling the biogeography of ship biofouling: barnacles in the Northeast Pacific. *Global Ecol Biogeogr* 25(6): 739-750; DOI: 10.1111/geb.12450

2. Atwood WG, Johnson AA (1924) *Marine structures, their deterioration and preservation. Report of the Committee on Marine Piling Investigations of the Division of Engineering and Industrial Research of the National Research Council*, National Research Council, Washington, DC

3. Callow ME, Callow JA (2002) Marine biofouling: a sticky problem. *Biologist* 48:1-5

4. Carlton JT (2001) Introduced species in the U.S. coastal waters: environmental impacts and management priorities. Pew Ocean Commission, Virginia U.S.A.

5. Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanogr Mar Biol* 23: 313–371

6. Cohen AN (2006) Species introductions and the Panama Canal. In Gollasch S, Galil BS, Cohen AN (eds) *Bridging divides: maritime canals as invasion corridors*; Springer, Netherlands, pp 127-206

7. Coutts ADM, Dodgshun TJ (2007) The nature and extent of organisms in vessel sea-chests: A protected mechanism for marine bioinvasions. *Mar Pollut Bull* 54:875-886

8. Coutts ADM, Taylor MD (2004) A preliminary investigation of biosecurity risks associated with biofouling on merchant vessels in New Zealand. *New Zeal J Mar Fresh* 38:215-229

9. Dafforn KA, Lewis JA, Johnston EL (2011) Antifouling strategies: history and regulation, ecological impacts and mitigation. *Mar Pollut Bull* 62:453-465

10. Darling JA, Herborg L-M, Davidson IC (2012) Intracoastal shipping drives patterns of regional population expansion by an invasive marine invertebrate. *Ecology and Evolution* 2:2552-2561

11. Darwin C (1854) A monograph of the sub-class Cirripedia: The Balanidae; *London: Ray Society*

12. Davidson IC, Brown CW, Sytsma MD, Ruiz GM (2009) The role of containerships as transfer mechanisms of marine biofouling species. *Biofouling 25*(7): 645–655

13. Davidson I, Scianni C, Hewitt C, Everett R, Holm E Tamburri M, Ruiz G (2016) Mini-review: Assessing the drivers of ship biofouling management – aligning industry and biosecurity goals. *Biofouling* 32:411-428

14. Davidson IC, Simkanin C (2012) The biology of ballast water 25 years later. *Biol Invasions* 14:9-13

15. Floerl O (2014) Management challenges and opportunities for marine biosecurity in the Arctic. In Fernandez L, Kaiser BA, Vestergaard N (eds) *Marine invasive species in the Arctic*, TemaNord 2014:547, Nordic Council of Ministers, Copenhagen, pp 57-67

16. Fofonoff PW, Ruiz, GM, Steves B, Carlton JT (2003) In ships or on ships? Mechanisms of transfer and invasion for nonnative species to the coasts of North America. In Ruiz GM, Carlton JT (eds) *Invasive species: vectors and management strategies,* Island Press, Washington, DC, pp. 152–182

17. Galil BS, Boero F, Campbell ML, Carlton JT, Cook E, Fraschetti S, Gollasch S, Hewitt CL, Jelmert A, Macpherson E, Marchini A (2015) Double trouble': the expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. *Biol. Invasions* 17(4):973-6

18. Godwin LS (2003) Hull fouling of maritime vessels as a pathway for marine species invasions to the Hawaiian Islands. *Biofouling* 19:123–131

19. Gotzek D, Axen HJ, Suarez AV, Cahan SH, Shoemaker D (2015) Global invasion history of the tropical fire ant: a stowaway on the first global trade routes. *Molecular Ecology* 24:374-388

20. Gollasch S (2002) The importance of ship hull fouling as a vector of species introductions into the North Sea. *Biofouling* 18:105–121

21. Hewitt CL, Campbell M (2010) The relative contribution of vectors to the introduction and translocation of marine invasive species. Commissioned by The Department of Agriculture, Fisheries and Forestry, Canberra

22. Hewitt CL, Gollasch S, Minchin D (2009) The vessel as a vector – biofouling, ballast water and sediments. In Rilov G, Crooks JA (eds) *Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives*, Springer-Verlag, Berlin Heidelberg, pp 117-131

23. Hughes Martiny JB, Bohannan BLM, Brown JH, Colwell RK, Fuhrman JA, Green JL, Horner-Devine MC, Kane M, Adams Krumins J, Kuske CR, Morin PR, Naeem S, Øvreås L, Reyensenbach AL, Smith VH, Staley JT (2006) Microbial biogeography: putting microorganisms on the map. *Nat Rev Microbiol* 4: 102-11

24. Hunsucker ZK, Koka A, Lund G, Swain G (2014) Diatom community structure on in-service cruise ship hulls. *Biofouling* 30:1133–1140IHS Maritime World Shipping Encyclopedia https://www.ihs.com/products/maritime-world-shipping-encyclopedia.html

25. IMO (2001) International convention on the control of harmful antifouling systems on ships. International Maritime Organization, London

26. IMO (2011) International Maritime Organization: Guidelines for the control and management of ships' biofouling to minimize the transfer of invasive aquatic species. Marine Environment Protection Committee, Annex 26, Resolution MEPC.207 (62). London, International Maritime Organization

27. Inglis GJ, Floerl O, Ahyong S, Cox S, Unwin M, Ponder-Sutton A, Seaward K, Kospartov M, Read G, Gordon D, et al. (2010) The biosecurity risks associated with biofouling on international vessels arriving in New Zealand: summary of the patterns and predictors of fouling. Report to the Ministry of Agriculture and Forestry, Biosecurity New Zealand, Wellington

28. Kaluza P, Kölzsch A, Gastner MT, Blasius B (2010) The complex network of global cargo ship movements. *J R Soc Interface* doi:10.1098/rsif.2009.0495

29. Kelleher G, Bleakley C, Wells S (1995) A Global Representative System of Marine Protected Areas, vols. 2–4. Washington (DC): Great Barrier Reef Marine Park Authority, World Bank, IUCN (World Conservation Union), USA

30. Keller RP, Drake JM, Drew MB, Lodge DM (2011) Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. *Divers Distrib* 17: 93-102

31. Leary DH, Li RW, Hamdan LJ, Hervey WJ IV, Lebedev N, Wang Z, Deschamps JR, Kusterbeck AW, Vora GJ (2014) Integrated metagenomic and metaproteomic analyses of marine biofilm communities. *Biofouling* 30:1211-1223

32. McClay T, Zabin C, Davidson I, Young R, Elam D (2015) Vessel biofouling prevention and management options report. Report to the US Coast Guard Research & Development Center. New London, Connecticut

33. Miller AW (2014) Melting Sea Ice, Accelerated Shipping, and Arctic Invasions. In Fernandez L, Kaiser BA, Vestergaard N (eds) *Marine invasive species in the Arctic*, TemaNord 2014:547, Nordic Council of Ministers, Copenhagen, pp 35-55

34. Miller AW, Minton MS, Ruiz GM (2011) Geographic limitations and regional differences in ships' ballast water management to reduce marine invasions in the contiguous U.S. *Bioscience* 61:880-887

35. Miller AW, Ruiz GM (2014) Arctic shipping and marine invaders. *Nature Clim Change* 4:413-416

36. Minchin D (2006) The transport and the spread of living aquatic species. In *The ecology of transportation, managing mobility for the environment*; Davenport, J., Davenport, J.L. Eds.; Springer: Berlin Heidelberg New York, pp. 77–97

37. Minchin D, Gollasch S (2003) Fouling and ships hulls: how changing circumstances and spawning events may result in the spread of exotic species. *Biofouling* 19:111–122

38. Minton MS, Verling E, Miller AW, Ruiz GM (2005) Reducing propagule supply and coastal invasion via ships: effects of emerging strategies. *Front Ecol Environ* 3: 304-308

39. Moser CS, Wier T, Grant JF, First MR, Tamburri MN, Ruiz GM, Miller AW, Drake LA (2016) Quantifying the total wetted surface area of the world fleet: a first step in determining the potential extent of ships' biofouling. *Biol Invasions* 18:265-277

40. Moser CS, Wier TP, First MR, Grant JF, Riley SC, Robbins-Wamsley SH, Tamburri MN, Ruiz GM, Miller AW, Drake LA (2017) Quantifying the extent of niche areas in the global fleet of commercial ships: the potential for "super-hot spots" of biofouling. *Biol Invasions* 19:1745-1759.

41. Muirhead JR, Minton MS, Miller AW, Ruiz GM (2015) Projected effects of the Panama Canal expansion on shipping traffic and biological invasions. *Divers Distrib* 21(1): 75-

87, doi:10.1111/ddi.12260

42. National Ballast Information Clearinghouse (2015) *NBIC Online Database.* Electronic publication, Smithsonian Environmental Research Center & United States Coast Guard. Available from http://dx.doi.org/10.5479/data.serc.nbic. Accessed 09-Sep-2015.

43. Nehring S (2001) After the TBT era: alternative anti-fouling paints and their ecological risks. *Senck Marit 31*(2): pp. 341–351

44. New Zealand Government (2014) Craft risk management standards: biofouling on vessels arriving to New Zealand. Wellington, New Zealand Ministry of Primary Industries

45. Reid PC, Johns DG, Edwards M, Starr M, Poulin M, Snoeijs P (2007) A biological consequence of reducing Arctic ice cover: arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time in 800,000 years. *Global Change Biol* 13: 1910-1921.

46. Rodrigue JP, Comtois C, Slack B *The Geography of Transport Systems, Hofstra University, Department of Global Studies & Geography Website*; http://people.hofstra.edu/geotrans. Accessed 15 June 2016

47. Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* 2000:481–531

48. Ruiz GM, Fofonoff PW, Steves B, Foss SF, Shiba SN (2011) Marine invasion history and vector analysis of California: a hotspot for western North America. *Divers Distrib* 17:362-373

49. Schultz MP Bendick JA, Holm ER, Hertel WM (2011) Economic impact of biofouling on a naval surface ship. *Biofouling* 27:87-98

50. Schultz MP, Swain GW (2009) The influence of biofilms on skin friction drag. *Biofouling* 15(1-3):129-139

51. Sylvester F, Kalaci O, Leung B, Lacoursiere-Roussel A, Clarke-Murray C, Choi FM, Bravo MA, Therriault TW, MacIsaac HJ (2011) Hull fouling as an invasion vector: can simple models explain a complex problem? *J. Appl Ecol* 48:415-423

52. Takata L, Dobroski N, Scianni C, Falkner M (2011) Biennial report on the California marine invasive species program. Report to the California State Legislature. Sacramento, California

53. Thomason JC (2010) Fouling and shipping: data-mining the world's largest antifouling archive. In Durr S, Thomason JC (eds) *Biofouling* Oxford, Blackwell

54. U.S. Department of Homeland Security, Coast Guard (2004) 33 CFR (Ch. 1) Part 151 – Vessels carrying oil, noxious liquid substances, garbage, municipal or commercial waste, and ballast water. Fed. Register 258-306

55. Van Maanen JD, Van Oossanen P (1988) Resistance. In Lewis EV (ed) *Principles of Naval Architecture, Volume II;* The Society of Naval Architects and Engineers: Jersey City, New Jersey, pp 1-93

56. Wells F, Booth G (2012) Setting a new benchmark in managing biofouling on vessels in a sensitive marine environment. SPE/APPEA international conference on health, safety, and environment in oil and gas exploration and production. SPE conference paper – 2012, 156749-MS. Society of Petroleum Engineers

Table 1. Relationships between net registered tonnage (NRT) and wetted surface area (WSA) for six commercial ship types. Regressions are based on first order polynomial relationships with sample sizes (N) of 1709 to 8005. Mean WSA ± 1 SEM by ship types are included.

Table 2. Number of unique vessels calling at U.S. ports (13,820 during 2011-2014) by ship type, according to the type of trade each is involved in (Coastwise [CW], Overseas [OS], and Both).

Figure 1.
Arrivals of ships' WSA from overseas sources. Average (± 1 SEM) annual WSA entering each U.S. bioregion from overseas ports is shown for the nation (central panel; average 336.45 km^2 to the U.S. per year). The mean annual (± 1 SEM) contribution of each of six ship types to each bioregion's total is shown in the eight perimeter panels. B- Bulkers; C- Container ships; P- Passenger ships; R- Roll-on Roll-off (Auto) Carriers; T- Tankers; G- General Cargo ship types.

Figure 2.
Arrivals of ships' WSA from coastwise voyages. Average annual WSA entering each U.S. bioregion from bioregion crossing coastwise traffic is shown for the nation (central panel). The average coastwise flux among U.S. bioregions was 178.42 km^2. The mean annual (± 1 SEM) contribution of each of six ship types to each bioregion's WSA total is shown in the eight perimeter panels. Ship type codes are the same as Fig. 1 y-axes differ from Fig. 1.

Figure 3.
Mean annual WSA and niche area flux to U.S. ports from overseas and domestic bioregions. Ship type codes are the same as Fig. 1

Figure 4. Total number of source bioregions accumulated across 4 yrs by the collective ports in each U.S. receiving bioregion from the immediate single last port of call (LOPC, grey) and 5 LOPC (gray + white). The mean bioregion richness from 5 LPOC (± 1 SEM) = 101.5 ± 2.25 source bioregions.