COMMENTARY

Tracking marine alien species by ship movements

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Under human influence, plants, animals, and microbes are spreading beyond their native ranges faster and farther than ever before. Rates of invasion are increasing worldwide, especially in large aquatic systems (1). Many of these alien species appear to be innocuous, whereas others cause substantive impacts on biodiversity, ecosystem services, and human and animal health (2, 3). Effective management requires an ability to anticipate and prioritize significant invasion threats from among the enormous numbers and diversity of organisms being introduced by transportation mechanisms that facilitate human travel and trade, such as shipping. Global ship traffic has increased by fourfold since the early 1990s (4). Shipping is the dominant vector of unintentional species introduction in estuarine and coastal marine systems worldwide (2, 3, 5), and connects distant regions using ports as stepping stones (6). In PNAS, Seebens et al. (7) predict the probability of invasion by marine alien species, using a modeling approach that considers global ship movements, habitat suitability, and patterns of species occurrence.

Ships as Global Dispersers of Aquatic Organisms

Cargo ships carry large volumes of ballast water, which they take up and release at various times to regulate stability. This water typically contains an abundant and diverse assemblage of phytoplankton, zooplankton, bottom-dwelling invertebrates, and fish that were taken up at multiple ports of call along the shipping route (8). At any given moment, several thousands of species are being moved in the ballast tanks across distances they could not achieve by drifting on their own (5). Thus, modern shipping has created what invasion biologist James T. Carlton has described as "a conveyor belt of marine organisms wrapping around the world" (9). However, invasion success is highly probabilistic; it is essentially a game of ecological roulette, whose outcome depends on the successful uptake, transport, release, establishment, proliferation, and spread of a species. Amid this set of varying probabilities, many species will fail to complete a journey along a shipping route. The outcome is further influenced by myriad dynamic factors, including international trade patterns and climate change, which is not only altering habitat conditions at ports worldwide (10) but has opened up new shipping pathways (11).

Faced with such contingencies, predicting marine invasions is a challenging task. Invasion risks associated with shipping have been examined recently for specific recipient systems (6, 12) and for a small group of species (13). Studies have identified high-risk invasion routes and invasion hotspots (14, 15), but no previous study has tested a modeling approach that predicts both the identity and likelihood of establishment of alien species on a global scale. Moreover, insufficient validation of models casts doubt on the accuracy and certainty of their predictions. Seebens et al. (7) were able to predict the presence/absence of ship-vectored alien species in any given ecoregion with an accuracy of 77%, using a simple, but rigorous, statistical model. This model is a remarkably good fit, given that it ignores other presumably important factors, such as species traits, interactions with resident biota, and historical shipping patterns. The results appear to be robust to variation in the species pool, shipping intensity, and model parameterization.

After validating their approach, Seebens et al. (7) compiled a dataset of 97 species of marine algae with known native and invaded ranges so as to explore their invasion probabilities. Marine algae are appropriate model organisms because they are commonly spread by ships, have been reported in hundreds of invasions involving every continent but Antarctica, and include species known to cause strong ecological and socioeconomic impacts (16). Seebens et al. (7) identify global hotspots vulnerable to marine algal invasion, highlighting a high probability of biotic exchange between northern Europe and East Asia, for example. Among the top 10 species considered to be of high risk to the North Sea, two were confirmed to have recently colonized the region, thereby reflecting the predictive power of the model. The approach was also applied to examining the invasion probabilities of six selected species of toxic algae that cause fish and shellfish poisoning in humans, and revealed the vulnerability of swathes of coastline worldwide to invasion by these harmful species.

Another important finding by Seebens et al. (7) is that, early in the invasion history of a species, suitable

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habitats are colonized regardless of the distance from the donor region, followed by subsequent spread to suitable neighboring regions. Long-distance (~10,000 km) jumps are very common. Previous work by Seebens et al. (15) indicated that invasion risk was highest for intermediate geographic distances between donor and recipient ports. These patterns contrast with classical models of wavelike directional spread (17) in which the probability of invasion of any given target region is an inverse function of its distance from the nearest donor region. Ship-mediated invasions align better with modern vector-based invasion models that emphasize the importance of colonization opportunity and involve pathways that may be idiosyncratic (18). In such models, the probability of invasion is virtually independent of distance between donor and target regions. They more realistically reflect the current state of biological globalization in which a toxic bloom-forming alga can suddenly appear in a region thousands of kilometers distant from the nearest source population.

Invasion Risk Varies over Time and Space

On regional and global scales, shipping activity over time varies under the influence of, for example, economic trade patterns, altered shipping pathways, ship design, and enhancement of major canal systems (11, 19, 20). Environmental conditions in the donor and recipient ports, especially the degree to which they match, also shift through time. Climate change affects both of these major factors, and is thus expected to be a dominant driver of invasion risk (10). Using mean ocean surface temperatures projected for 2040–2060, Seebens et al. (7) predict a reduced future invasion risk for tropical regions and increased invasion probabilities for temperate regions, especially in the Northeast Pacific and the Baltic Sea. The researchers note that the largest donor region to the Northeast Pacific is the Northwest Pacific, and that elevated temperatures in the former will create a better environmental match for Asian species from the latter region. Another driver of temporal variation is revealed by the finding that total invasion probability varies with the number of ecoregions occupied such that propagule pressure (spreading opportunity) to unoccupied regions increases as neighboring regions become invaded (7). Therefore, the rate of spread of an emerging species through the shipping network is expected to increase over time until the number of available suitable ecoregions begins to saturate.

Models can predict which invaders will arrive, but predicting when they will arrive is another matter entirely. Forecasting the timing of invasions may prove to be an insoluble challenge, but risk assessment will nevertheless be enhanced by progress toward identifying emerging invasion threats. Seebens et al. (7) point the way forward by demonstrating the value of simple modeling approaches that combine knowledge of global vector activity, known species distributions, and environmental conditions. Further progress could be achieved through greater integration of network theory in invasion biology (19).

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