Marine species introduction via reproduction and its response to ship transit routes

Sarah C Donelan*, A Whitman Miller, Jim R Muirhead, and Gregory M Ruiz

The introduction of nonindigenous species (NIS) threatens global ecosystems and results primarily from human transportation and trade activities. Although some NIS can disperse immediately upon arrival (for example, mobile species), actual inoculation for other (sessile) species can require a reproductive event to produce propagules that disperse and establish. NIS reproductive potential, however, can vary with environmental conditions experienced during transit and upon arrival that differ substantially by route. We propose that variation in reproductive responses, both across species and transit routes, is a critical but overlooked driver of species invasions. We illustrate these concepts using vessel biofouling organisms, which are exposed to vastly different conditions during transport across the world's oceans. Current knowledge gaps prevent precise predictions of the potential for species to be introduced via reproduction. Integrating reproductive potential into management strategies is key to limiting NIS spread, particularly as climate change and novel events continue to alter global transportation networks.

Front Ecol Environ 2022; doi:10.1002/fee.2551

Human-mediated transport of nonindigenous species (NIS) is reshaping global biodiversity and species' abundance (Seebens *et al*. 2013) and generates widescale ecological and economic impacts in recipient communities (Diagne *et al*. 2021). Invasion dynamics and impacts are expected to respond to a variety of forces such as environmental conditions and trade patterns that are also changing through space and time. For example, climate change is affecting the range of suitable NIS habitats (Goldsmit *et al*. 2018) and available trading routes (Miller and Ruiz 2014), and pulse events, such as the COVID-19 pandemic, economic downturns, or geopolitical shifts, can disrupt trade and affect NIS movement (Floerl and Coutts 2009; Millefiori *et al*. 2021). Understanding the interactive effects of trade and changing environmental conditions is therefore a key area of focus for invasion ecology, management, and policy.

In a nutshell:

- Human transport is responsible for the introduction of nonindigenous species (NIS) to novel environments, but transport is often insufficient for introduction
- Reproduction upon arrival can be critical for the introduction of NIS, especially sessile species, but is rarely considered
- The ability of NIS to reproduce will be affected by environmental conditions experienced during transport, which vary widely but predictably along major shipping routes
- We examine the potential for reproduction to facilitate NIS introductions using biofouling marine invertebrates
- Incorporating reproductive responses into invasive species risk assessments can help managers better predict which species and routes are especially susceptible to invasion

Successful invasion requires NIS to pass through four stages of a well-described process: (1) survival of uptake and transit by a transport vector to a novel environment, (2) introduction to the novel environment through release from the vector, (3) establishment of a self-sustaining population in the novel environment, and (4) spread beyond the site of initial introduction (Blackburn *et al*. 2011). Certain traits and processes contribute to species' success at each stage. For example, reproduction is recognized as a critical component of NIS establishment and spread (stages 3 and 4) that ensures the formation of self-sustaining populations (Blackburn *et al*. 2011). Although less obvious, reproduction may also play a key role at early stages of the invasion process by affecting the number of propagules released into a non-native environment upon arrival.

Reproduction is likely critical in the initial inoculation of novel environments for many NIS and may in fact be necessary to reach the recipient environment. This is especially true for sessile species. Many NIS that are sessile and transported unintentionally cannot themselves exit a transport vector because they are immobile except for reproductive stages, such as gametes or larvae. This applies to a wide range of potential NIS, including marine and aquatic biofoulers attached to hulls of vessels, and terrestrial species associated with the cargo of ships and other transport vectors (Figure 1). If not physically removed, many sessile NIS will fail to establish in the new environment without reproduction if they lack other means of mobility. Reproduction may also be critical for the introduction of mobile NIS: while mobile NIS can and do disembark transport vectors (Gippet *et al*. 2019), the number of individuals may be too limited for a population to become established (eg Allee effects). Reproduction

Smithsonian Environmental Research Center, Edgewater, MD
(donelans@si.edu)

provides an additional means of introduction for both sessile and mobile species that can substantially amplify propagule pressure, an essential component of species invasion success (Lockwood *et al.* 2009). Moreover, introduction via reproduction enables repeated propagule delivery because reproductively mature adults – rather than dispersing into the environment themselves – may instead remain attached to vectors as those vectors move.

Notably, reproduction is often an implied aspect of propagule pressure if propagules are transported as larvae or immature life stages and delivered to non-native habitats upon vector arrival (eg via ballast water discharge by vessels). While previous research has suggested that reproduction may promote initial NIS introductions (Minchin and Gollasch 2003), and there are some reported cases where it has done so (Apte *et al.* 2000), the importance of reproduction in the initial delivery and release of non-native species is rarely considered explicitly (but see Davis *et al.* 2007; Schimanski *et al.* 2017), and the specific mechanisms that affect and promote reproduction for many NIS are poorly understood. We propose that, for many organisms, transit route may drive differences in NIS reproductive capacity and influence the readiness of NIS to reproduce upon arrival in novel, non-native habitats.

Our primary objectives here are to (1) highlight the critical role that reproduction can play in facilitating initial NIS introductions, (2) describe potential differences in NIS reproduction based on environmental conditions experienced during transit and after arrival, and (3) identify critical knowledge gaps that limit our current understanding of how reproduction affects NIS introductions. We illustrate these points using marine invertebrates that foul (attach to) ships' hulls; such biofoulers include a highly diverse group of taxa with an array of life history strategies whose reproductive phenology is strongly influenced by environmental exposure. Global shipping networks traverse predictable but environmentally disparate routes that expose organisms to vastly different conditions during transit. When these conditions overlap with those that trigger gametogenesis and spawning, reproduction may play a key role in NIS introductions and invasions, with certain routes and species especially susceptible. These concepts extend beyond marine biofoulers and may be crucial to integrate into invasion models more widely to better predict where NIS are likely to be introduced, particularly in response to global change and shifts in trade.

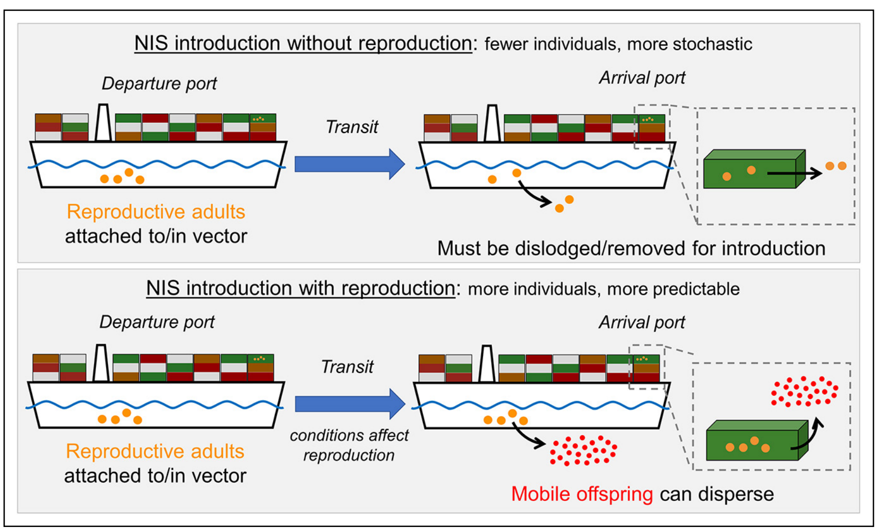

Figure 1. Reproduction can play a critical yet underappreciated role in facilitating nonindigenous species (NIS) introductions, particularly of sessile species. (top) Without reproduction, transported NIS must become physically dislodged (sessile species) or happen to depart (mobile species) from the vector while in port. Such non-reproductive dispersal events may be rare and limit NIS introductions. (bottom) In contrast, if introductions occur via reproduction, transported individuals not only release mobile larvae or gametes at numbers far greater than would be introduced without reproduction, but also remain on the vector to repeat this process in the next port. Because reproduction is frequently influenced by environmental conditions, introductions via reproduction are potentially predictable by transit route. These concepts apply to marine and aquatic NIS, but also to terrestrial NIS transported by vectors such as the shipping containers (dashed rectangle) shown here.

Environmental drivers of reproduction in marine biofoulers

Vessel biofouling is a potent vector and leading source of coastal NIS transfers and invasions across the world (Bailey *et al.* 2020). Marine biofouling organisms represent a diverse group of taxa across many phyla, including primarily sessile, filter-feeding invertebrates (eg mussels, barnacles, bryozoans, tunicates, hydroids, and tube-building polychaetes; Figure 2) and a rich array of mobile species associated with sessile invertebrates and niche areas of a ship (Minchin and Gollasch 2003). Fish, algae, and microorganisms (including pathogens and parasites) are also found on hulls (Minchin and Gollasch 2003), but here we focus on emblematic sessile invertebrates that can reproduce sexually and dominate hull biofouling communities (Drake and Lodge 2007), considering particularly taxa that likely require spawning to be introduced. However, the concepts presented here apply to species with varying life histories and reproductive modes, including species that can reproduce asexually (WebPanel 1).

Sessile marine biofouling invertebrates employ a diversity of life history and reproductive strategies. Some are permanently sessile (eg tunicates, barnacles) and will require reproduction to become established in a recipient port, whereas others are semi-sessile species that can detach themselves from the substrate (eg mussels) but may rely on spawning to introduce a critical number of propagules en masse. Biofouling species are often broadcast spawners whose larvae develop in the plankton for a period of hours to weeks, but some are characterized by internal fertilization and direct development when offspring are released as fully formed, crawl-away juveniles (Minchin and Gollasch 2003).

For many marine organisms, particularly ectotherms, gametogenesis and spawning are influenced by changes in external environmental conditions such as temperature, food quality/quantity, salinity, and light (Panel 1; Figure 3). Reproduction is energetically costly, and physiological constraints imposed by environmental conditions influence where and when gametogenesis can occur (Ricklefs and Wikelski 2002). Reproduction can only be a mechanism for NIS introduction if (1) gametogenesis has successfully occurred and (2) offspring release is then triggered to occur among transported individuals upon arrival in a non-native environment.

We conducted a literature review to identify potential commonalities in spawning triggers that may help predict how NIS reproductive potential varies with transit route (Panel 1). Although specific conditions and triggers vary across taxa, and knowledge gaps limit our current understanding (discussed below), our mini-review suggests that reproduction in many marine invertebrates is associated with (1) an abrupt or substantial change in conditions that signals an increase or decrease in environmental quality (eg thermal cycling consistently triggers spawning in the mussel *Perna canaliculus*, but the specific temperature can vary; Adams *et al.* 2009) or (2) a marked change in conditions that surpasses a critical environmental threshold at which reproduction is induced or enhanced (eg certain populations of *Amphibalanus improvisus* barnacles will only produce mature gonads at salinities above 6 practical salinity units [psu]; Wrange *et al.* 2014). All organisms, however, should be adapted to respond to environmental cues that maximize the chances of successful spawning and offspring survival in their native environment (Morgan 1995). For NIS, encountering similar conditions during transit or upon arrival in non-native habitats may also induce spawning and provide a means of NIS introduction. Because environmental conditions are highly variable across global transportation networks, transit route should be a key factor influencing NIS introductions.

Risk of reproduction will vary with transit route and vector behavior

Modern maritime transport moves goods across virtually all geographic regions of the oceans (Kaluza *et al.* 2010). In many cases, intra- and inter-oceanic commercial routes are well-established and therefore predictable, each exposing vessel biofouling organisms to vastly different environmental conditions known to affect reproduction, including different temperatures, salinities, food quantity/quality, and light availability (Panel 1; Figure 4; WebFigure 1). The Panama and Suez canals are used to move much of the world's intercontinental trade (Kaluza *et al.* 2010). Waters around the canals are tropical or subtropical, such that conditions are relatively warm and oligotrophic, and day length is relatively consistent throughout the year (Figure 4; WebFigure 1). Salinities differ markedly between the two canals: the Panama Canal passes through a series of inland, freshwater lakes, whereas the Suez Canal is hypersaline (Castellanos-Galindo *et al.* [2020]; but see below for recent changes in canal dynamics). Inter-ocean routes through Arctic corridors such as the Northern Sea Route are becoming increasingly reliable because of declines in summer sea ice (Miller and Ruiz 2014). The Northern Sea Route is relatively cold and eutrophic (Carvalho and Wang 2020), with historically stable salinities and near-constant daylight during the summer, when the route is primarily used. In general, ships sailing through the canals will expose organisms to warm, tropical conditions, in stark contrast to the extremely cold conditions experienced along routes that pass through the Arctic. Moreover, organisms spend different amounts of time in these conditions, as passage through Arctic routes can be substantially faster (~40% less travel time) than through the Suez Canal (Figure 4; Buixadé Farré *et al.* 2014).

In contrast to inter-ocean routes, intra-ocean voyages are generally shorter in duration but can also exhibit a range of environmental condition profiles. Trans-oceanic routes (eg Europe to the East Coast of the US) may lack the extreme environmental transitions of inter-ocean routes, particularly with regard to temperature, and therefore may not subject organisms to conditions necessary to trigger spawning except when

Figure 2. Marine biofouling organisms represent a diversity of taxa – including (a) soft-bodied tunicates and bryozoans (here, on a recreational vessel in Bermuda) (credit: K Holzer); (b) barnacles (here, attached to a bow thruster grate of a ferry in Alaska) (credit: G Ashton); and (c) mussels (here, on a day cruiser's hull in San Francisco, California) (credit: G Ashton) – whose reproductive capacity varies with the environmental conditions encountered during transit and in port.

entering ports. Port-hopping ships (ships that move frequently in and out of spatially proximate ports) can expose biofoulers to stark environmental transitions that may trigger spawning (Figure 4). Route conditions and duration may also serve as selective filters (eg Goldsmit *et al.* 2018) that affect which species survive and reach port to spawn.

Assuming they survive transit, conditions and residence time in port can also be critical for triggering NIS reproduction (Schimanski *et al.* 2017). Although port conditions vary across latitudes (ie ecoregions) and locations (ie coastal/estuarine sites), ports are generally relatively shallow, protected embayments and estuaries that are highly modified by human activity. As such, environmental conditions in port may be relatively warm as compared to deeper, adjacent waters (Paalvast and van der Velde 2011) and eutrophic due to high nutrient runoff from urbanization (Chen *et al.* 2016). Estuarine ports will also have lower salinities than ports on open coasts (Paalvast and van der Velde 2011). These conditions may contrast sharply with those experienced in the open ocean during transit, and thus create an abrupt or substantial change that triggers spawning in some biofouling NIS. Because many biofouling species are coastal, they may be especially likely to spawn upon arriving in non-native coastal ports because conditions may be similar to those in which they evolved (the "port renewal" hypothesis; Carlton 1999). Moreover, the amount of time vessels spend in port (ie port residence time) varies even during normal operations; in some cases (eg container ships) ships may spend fewer than 12 hours in port, whereas others (eg bulk carriers, barges) may remain for several days (Davidson *et al.* 2018). Unanticipated global events like the COVID-19 pandemic can dramatically increase port residence times, as vessels remain idle due to reduced trade activity (Millefiori *et al.* 2021), affecting opportunities for both vessel colonization and organism release. Specifically relevant to our focus here, longer port residence times may enhance rates of gametogenesis and spawning by ship-borne biofoulers by increasing time spent in warm, eutrophic waters (Panel 1). Relative differences between routes and ports will also vary with voyage timing, particularly in temperate regions with strong seasonality, but encountering favorable conditions may override any reproductive seasonality observed in a species' native region.

The sheer number of possible route/port combinations coupled with the diversity of hull fouling biota and a poor understanding of precise spawning triggers make it challenging to offer specific predictions of how reproduction will affect the introduction potential across biofouling taxa at this time. But case studies on relatively well-explored species can be illustrative of potential changes in reproduction driven by transit route. In WebPanel 2, we provide a case study using *Amphibalanus amphitrite*, a barnacle whose reproductive phenology is well-described relative to other hull fouling NIS. Although limited in scope, this case study highlights the staggering number of individuals (millions) that can be delivered by a single ship after a single reproductive event, as well as other important themes to consider and knowledge gaps to fill when evaluating the potential for reproduction to promote NIS introduction.

Conclusions

The global spread of sessile, non-native, biofouling species such as *A amphitrite* (WebPanel 2) suggests that reproduction does indeed facilitate NIS introductions, both as a primary means and an amplification of propagule supply. Current understanding of specific reproductive triggers and thresholds is poor for marine biofoulers (Panel 1) and other potential NIS. Focused experiments are needed to mechanistically quantify and understand NIS reproductive responses across a range of environmentally relevant conditions differing in both magnitude and duration. Ideally, such experiments would first manipulate single environmental factors (eg food quantity or quality) and then expand to integrate interactions among multiple factors that more closely align with natural conditions (eg covariation in temperature and food). While more challenging, such experiments should also evaluate responses among multiple and potentially distant populations to examine possible inter-population variability. Data obtained from these experiments could be combined with oceanographic data from major shipping routes and ports (similar to those used in Figure 4) to create models of where and when reproduction is most likely to occur for particular species or more generally.

Global change and stochastic events that affect global trade complicate efforts to predict how reproduction will affect NIS introductions. For marine NIS, new shipping routes and ports, especially in the Arctic, are increasingly being utilized as rising global temperatures reduce sea ice cover (Miller and Ruiz 2014), favor the survival of an entirely different suite of species (Goldsmit *et al.* 2018), and affect which species lose or build reproductive capacity en route. Conditions along existing routes and ports are also being modified by anthropogenic activities. For example, climate change and saltwater intrusion are making the Panama Canal warmer and more saline (Castellanos-Galindo *et al.* 2020), while salinities in the surface waters of the Bitter Lakes in the Suez Canal have fallen from 160 psu to 43–44 psu (Galil and Zenetos 2002). Estuaries that house many ports are also becoming warmer, less saline, and more eutrophic (Scanes *et al.* 2020), which may affect where and when potential NIS encounter spawning thresholds. Finally, unforeseen events can affect normal trade in diverse ways and alter vessel behavior and tempo, as highlighted by the grounding of the *Ever Given* in the Suez Canal in March 2021, which caused a remarkable traffic jam of hundreds of ships from around the world and extended vessel residence times in the adjacent coastal waters from hours to days (Ruiz *et al.* 2022). This event also occurred in springtime, when increased temperature and food availability trigger spawning in many temperate marine invertebrates (Panel 1).

While considerable management and policy action, including national and international regulations and agreements, has attempted to reduce invasions by commercial ships over the past 30 years, the primary focus of these efforts has been on ballast water, another major source of NIS coastal invasions (IMO 2004;

Panel 1. What triggers spawning in marine biofoulers? A mini-review

In an effort to identify environmental cues and conditions relevant for reproduction in biofouling marine invertebrates to generate predictions for spawning based on transit route, we conducted an informal but broad literature review of the reproductive biology of 60 marine invertebrates that are potential biofouling species across seven taxonomic groups: barnacles, bryozoans, hydrozoans, mussels, oysters, polychaetes, and tunicates (WebTable 1). Although not a formal meta-analysis, our survey identified common patterns that affect reproduction in emblematic sessile biofouling taxa from a range of life histories, but with mobile gametes/larvae. Among the species surveyed, four environmental cues emerged as primary putative causes of gametogenesis and spawning: temperature, food quantity/quality, photoperiod/light, and salinity (Figure 3; WebTable 1). The primacy of these cues varies among taxa, and in many cases organisms rely on multiple and potentially correlated cues. In several instances, relationships between environmental cues and reproduction were inferred from observational field data and remain experimentally untested. Species whose reproductive phenology has been explored more mechanistically in the lab often come from well-studied systems, such as model or commercially important (eg farmed) organisms that rely on established protocols known to consistently stimulate spawning (Helm *et al*. 2004). For example, 24–48 hr of darkness followed by exposure to bright light consistently triggers spawning in bryozoans (eg Schimanski *et al*. 2017), and therefore this protocol is widely used due to its predictable success. We found few experiments that were explicitly designed to test the relative efficacy of certain cues in inducing reproduction or to identify the specific physiological thresholds or performance continua (eg if it is the change in conditions or a crossing of a certain critical threshold) that support reproduction. In species for which spawning thresholds have been empirically determined (eg Starr *et al*. 1991), rarely have multiple experiments been conducted for the same species (but see WebPanel 2), and high inter-population variability in reproduction further obscures general relationships. Overall, we found a surprising paucity of manipulative, mechanistic data necessary to make precise predictions about how spawning in marine biofoulers will vary among transit routes, at least among the species we surveyed.

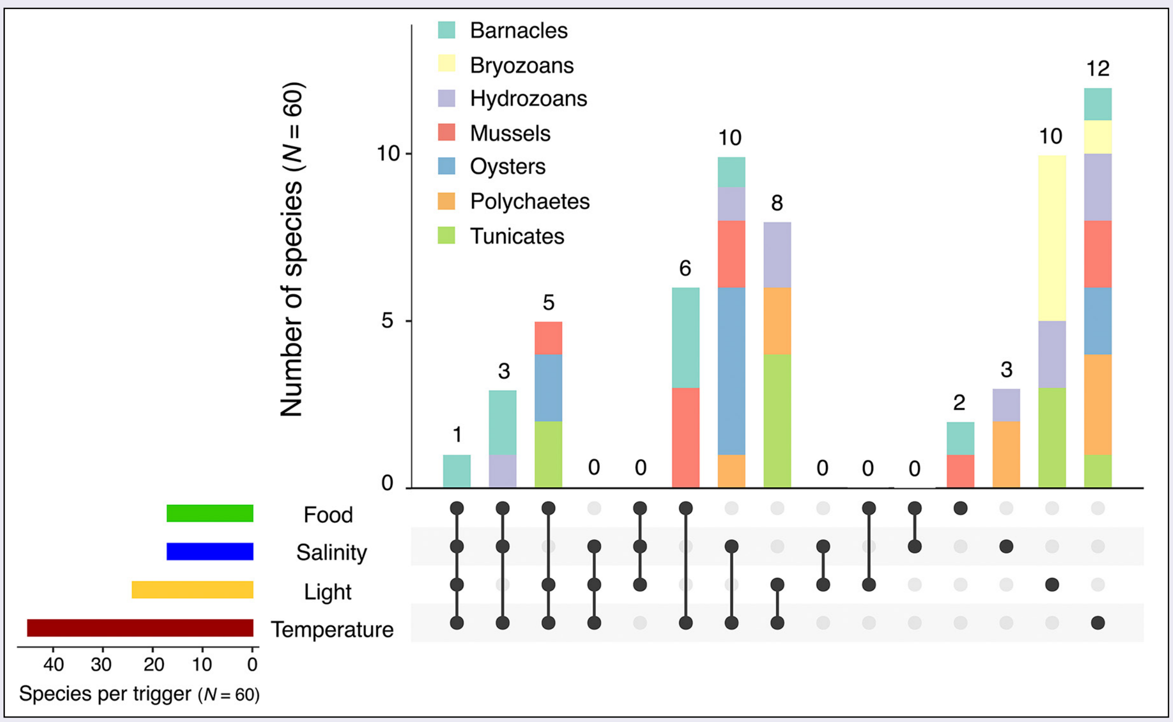

Figure 3. Species from seven marine vessel fouling taxa included in our literature review (*N* = 60 species) that are triggered to spawn by changes in food quantity/quality, salinity, light, temperature, or a combination of these triggers. On the x-axis of the larger bar graph, black circles indicate the presence of individual triggers and black circles connected by lines indicate the presence of trigger combinations. The smaller bar graph shows the number of species that are triggered to spawn by each of the four key environmental parameters.

NRC 2011). Management to reduce hull biofouling is relatively lacking, with a few exceptions (Davidson *et al*. 2018; Georgiades *et al*. 2020). Ships have operational and cost incentives to prevent biofouling (eg increased drag increases fuel consumption), but management thresholds still allow a substantial degree of biological fouling and transfer of NIS to occur (Davidson *et al*. 2016). Recent advances in policy and management are beginning to address NIS transfer via biofouling, including strategies to assess

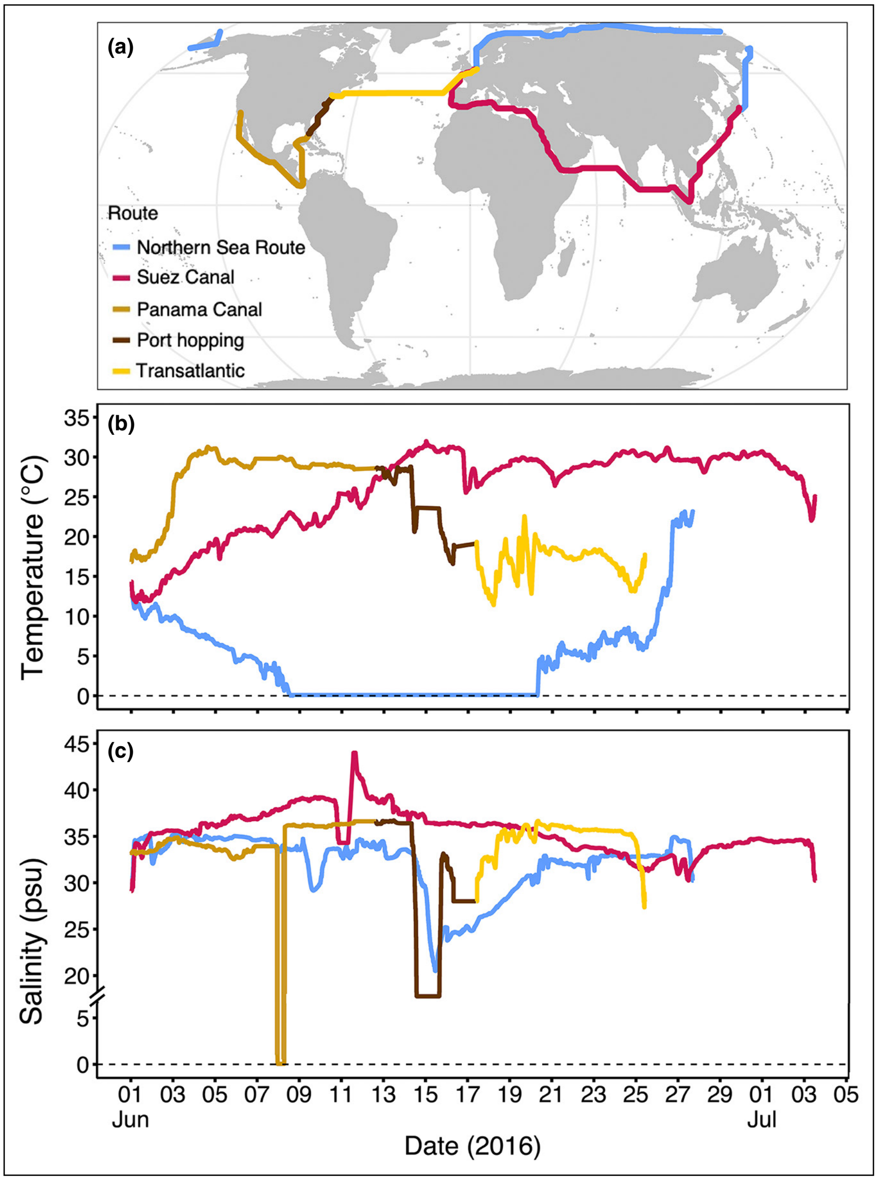

Figure 4. Commercial shipping is a major vector of marine nonindigenous species (NIS) invasions. (a) Inter-ocean shipping routes through the Suez and Panama canals, and increasingly the Northern Sea Route, move much of the world's intercontinental trade, along with shorter intra-oceanic (eg transatlantic) routes. Port hoppers make more frequent stops between spatially proximate ports (eg Miami, Florida, to Norfolk, Virginia, to New York/New Jersey; dark brown line). Environmental conditions, such as (b) temperature (°C) and (c) salinity (practical salinity units [psu]), that affect spawning in biofouling marine invertebrates can vary greatly along these five common shipping pathways, as shown here with data from June 2016, and affect the propensity of NIS to spawn upon arrival in a non-native port. Data were extracted from publicly available environmental databases/datasets based on ship position along specified trade routes (sea surface temperature data: Canada Meteorological Center Group for High Resolution Sea Surface Temperature; salinity data: EU Copernicus Global Reanalysis 001–030 Monthly); complete data citations and code are available on Figshare (doi.org/10.25573/serc.14333879).

invasion risk, conduct vessel inspections, and advance technology for in-water cleaning (Scianni and Georgiades 2019; Georgiades *et al*. 2020). Some of these strategies identify vessel residence time ("lay-ups") as a critical criterion to trigger elevated scrutiny (and potentially inspections and treatment) of vessel hulls. We suggest that voyage route may warrant similar scrutiny because of its capacity to influence NIS reproductive potential. Incorporating reproductive potential into vessel risk profiling models could allow resource managers to identify, prioritize, and inspect vessels that transited routes especially conducive to biofouling reproduction. This could be applied to particular target NIS of concern and combined with environmental niche models to focus management actions on specific regions where the species can establish and spread (eg Jiménez-Valverde *et al*. 2011). For example, if a certain NIS is known to inhabit a departure port and the vessel voyage route will traverse conditions known to trigger reproduction (eg high temperatures), the vessel could then be prioritized for inspection. Until broadscale adoption of standards and cleaning occurs for fouled vessels, identifying such vessels and routes that are likely to facilitate reproductive output provides an important opportunity to focus limited resources on targeted management and biosecurity actions. We urge further research to fully evaluate effects of route, including port profiles and residence times, on NIS reproduction from this perspective.

While we focused on reproduction in biofouling marine invertebrates, reproduction may also be an important means of introduction for other important biofoulers (eg macroalgae) and some terrestrial and aquatic NIS. For example, insects often enter reproductive diapause (arrest of gametogenesis and mating) at cool temperatures, but become reproductively active again once temperatures warm (Tatar and Yin 2001). Transit route and vector may expose stowaway insects to different temperatures that affect diapause initiation and reproductive capacity upon arrival in a non-native habitat (Figure 1). Overall, we expect interactions between species' reproductive triggers and vector transit routes to play a critical role in the introduction of NIS across the taxonomic spectrum, and greater effort should be expended to develop mechanistic models of reproduction in key NIS. Incorporating reproduction into invasive species risk assessments may improve their accuracy and efficacy, allowing managers to better predict which species and transit routes are especially prone to invasion.

Acknowledgements

We thank D Rittschof, JT Carlton, G Ziegler, and E Hancock for helpful discussions. Funding for this work was provided by the US Coast Guard.

Data Availability Statement

Data available on Figshare at doi.org/10.25573/serc.14333879.

References

Adams SL, Tervit HR, McGowan LT, *et al*. 2009. Towards cryopreservation of Greenshell™ mussel (*Perna canaliculus*) oocytes. *Cryobiology* **58**: 69–74.

Apte S, Holland BS, Godwin LS, *et al*. 2000. Jumping ship: a stepping stone event mediating transfer of a non-indigenous species via a potentially unsuitable environment. *Biol Invasions* **2**: 75–79.

Bailey SA, Brown L, Campbell ML, *et al*. 2020. Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: a 50-year perspective. *Divers Distrib* **26**: 1780–97.

Blackburn TM, Pyšek P, Bacher S, *et al*. 2011. A proposed unified framework for biological invasions. *Trends Ecol Evol* **26**: 333–39.

Buixadé Farré A, Stephenson SR, Chen L, *et al*. 2014. Commercial Arctic shipping through the Northeast Passage: routes, resources, governance, technology, and infrastructure. *Polar Geography* **37**: 298–324.

Carlton JT. 1999. Molluscan invasions in marine and estuarine communities. *Malacologia* **41**: 439–54.

Carvalho KS and Wang S. 2020. Sea surface temperature variability in the Arctic Ocean and its marginal seas in a changing climate: patterns and mechanisms. *Global Planet Change* **193**: 103265.

Castellanos-Galindo GA, Robertson DR, and Torchin ME. 2020. A new wave of marine fish invasions through the Panama and Suez canals. *Nature Ecol Evol* **4**: 1444–46.

Chen C-W, Ju Y-R, Chen C-F, *et al*. 2016. Evaluation of organic pollution and eutrophication status of Kaohsiung Harbor, Taiwan. *Int Biodeter Biodegr* **113**: 318–24.

Davidson IC, Scianni C, Hewitt C, *et al*. 2016. Mini-review: assessing the drivers of ship biofouling management – aligning industry and biosecurity goals. *Biofouling* **32**: 411–28.

Davidson IC, Scianni C, Minton MS, *et al*. 2018. A history of ship specialization and consequences for marine invasions, management and policy. *J Appl Ecol* **55**: 1799–811.

Davis MH, Lützen J, and Davis ME. 2007. The spread of *Styela clava* Herdman, 1882 (Tunicata, Ascidiacea) in European waters. *Aquat Invasions* **2**: 378–90.

Diagne C, Leroy B, Vaissière A-C, *et al*. 2021. High and rising economic costs of biological invasions worldwide. *Nature* **592**: 571–76.

Drake JM and Lodge DM. 2007. Hull fouling is a risk factor for intercontinental species exchange in aquatic ecosystems. *Aquat Invasions* **2**: 121–31.

Floerl O and Coutts A. 2009. Potential ramifications of the global economic crisis on human-mediated dispersal of marine non-indigenous species. *Mar Pollut Bull* **58**: 1595–98.

Galil BS and Zenetos A. 2002. A sea change – exotics in the eastern Mediterranean Sea. In: Leppäkoski E, Gollasch S, and Olenin S (Eds). Invasive aquatic species of Europe: distribution, impacts and management. Dordrecht, the Netherlands: Springer.

Georgiades E, Kluza D, Bates T, *et al*. 2020. Regulating vessel biofouling to support New Zealand's marine biosecurity system – a blue print for evidence-based decision making. *Front Mar Sci* **7**: 390.

Gippet JMW, Liebhold AM, Fenn-Moltu G, *et al*. 2019. Human-mediated dispersal in insects. *Curr Opin Insect Sci* **35**: 96–102.

Goldsmit J, Archambault P, Chust G, *et al*. 2018. Projecting present and future habitat suitability of ship-mediated aquatic invasive species in the Canadian Arctic. *Biol Invasions* **20**: 501–17.

Helm MM, Bourne N, and Lovatelli A (Eds). 2004. Hatchery culture of bivalves. A practical manual. FAO Fisheries Technical Paper No. 471. Rome, Italy: FAO.

IMO (International Maritime Organization). 2004. International convention for the control and management of ships' ballast water & sediments. London, UK: IMO.

Jiménez-Valverde A, Peterson AT, Soberón J, *et al*. 2011. Use of niche models in invasive species risk assessments. *Biol Invasions* **13**: 2785–97.

Kaluza P, Kölzsch A, Gastner MT, *et al*. 2010. The complex network of global cargo ship movements. *J Roy Soc Interface* **7**: 1093–103.

Lockwood JL, Cassey P, and Blackburn TM. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers Distrib* **15**: 904–10.

Millefiori LM, Braca P, Zissis D, *et al*. 2021. COVID-19 impact on global maritime mobility. *Sci Rep-UK* **11**: 18039.

Miller AW and Ruiz GM. 2014. Arctic shipping and marine invaders. *Nat Clim Change* **4**: 413–16.

Minchin D and Gollasch S. 2003. Fouling and ships' hulls: how changing circumstances and spawning events may result in the spread of exotic species. *Biofouling* **19**: 111–22.

Morgan SG. 1995. The timing of larval release. In: McEdward LR (Ed). Ecology of marine invertebrate larvae. Boca Raton, FL: CRC Press.

NRC (National Research Council). 2011. Assessing the relationship between propagule pressure and invasion risk in ballast water. Washington, DC: National Academies Press.

Paalvast P and van der Velde G. 2011. New threats of an old enemy: the distribution of the shipworm *Teredo navalis* L (Bivalvia: Teredinidae) related to climate change in the Port of Rotterdam area, the Netherlands. *Mar Pollut Bull* **62**: 1822–29.

Ricklefs RE and Wikelski M. 2002. The physiology/life-history nexus. *Trends Ecol Evol* **17**: 462–68.

Ruiz GM, Galil BS, Davidson IC, *et al*. 2022. Global marine biosecurity and ship lay-ups: intensifying effects of trade disruptions. *Biol Invasions* doi.org/10.1007/s10530-022-02870-y.

Scanes E, Scanes PR, and Ross PM. 2020. Climate change rapidly warms and acidifies Australian estuaries. *Nat Commun* **11**: 1803.

Schimanski KB, Goldstien SJ, Hopkins GA, *et al*. 2017. Life history stage and vessel voyage profile can influence shipping-mediated propagule pressure of non-indigenous biofouling species. *Biol Invasions* **19**: 2089–99.

Scianni C and Georgiades E. 2019. Vessel in-water cleaning or treatment: identification of environmental risks and science needs for evidence-based decision making. *Front Mar Sci* **6**: 467.

Seebens H, Gastner MT, and Blasius B. 2013. The risk of marine bioinvasion caused by global shipping. *Ecol Lett* **16**: 782–90.

Starr M, Himmelman JH, and Therriault J-C. 1991. Coupling of nauplii release in barnacles with phytoplankton blooms: a parallel strategy to that of spawning in urchins and mussels. *J Plankton Res* **13**: 561–71.

Tatar M and Yin CM. 2001. Slow aging during insect reproductive diapause: why butterflies, grasshoppers and flies are like worms. *Exp Gerontol* **36**: 723–38.

Wrange A-L, André C, Lundh T, *et al*. 2014. Importance of plasticity and local adaptation for coping with changing salinity in coastal areas: a test case with barnacles in the Baltic Sea. *BMC Evol Biol* **14**: 156.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2551/suppinfo