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Using biophysical modelling and marine connectivity to assess the risk of natural dispersal of non-indigenous species to comply with the Ballast Water Management Convention

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Abstract The introduction of Marine Non-Indigenous Species (NIS) poses a significant threat to global marine biodiversity and ecosystems. To mitigate this risk, the Ballast Water Management Convention (BWMC) was adopted by the UN International Maritime Organisation (IMO), setting strict criteria for discharges of ballast water. However, the BWMC permits exemptions for shipping routes operating within a geographical area, known as a Same-Risk-Area (SRA). An SRA can be established in areas where a risk assessment (RA) can conclude that the spread of NIS via ballast water is low relative to the predicted natural dispersal. Despite the BWMC's requirement for RAs to be based on modelling of the natural dispersal of NIS, no standard procedures have been established. This paper presents a methodology utilizing biophysical modelling and marine connectivity analyses to conduct SRA RA and delineation. Focusing on the Kattegat and Øresund connecting the North Sea and Baltic Sea, we examine two SRA candidates spanning Danish and Swedish waters. We provide an example on how to conduct an RA including an RA summary, and addressing findings, challenges, and prospects. Our study aims to advance the development and adoption of consistent, transparent, and scientifically robust SRA assessments for effective ballast water management.

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Introduction

Marine Non-Indigenous Species (NIS) pose a significant global threat to biodiversity and ecosystem functioning and services (Vitousek et al. 1996; Bax et al. 2003; Alidoost Salimi et al. 2021), and Ballast Water (BW) is a key transporting vector of NIS between geographically separated regions (Carlton et al. 1995; Gollach 2006; Galil et al. 2014). The Ballast Water Management Convention (BWMC) was adopted in 2004 by the United Nations International

Maritime Organization (IMO) to address this issue. The BWMC, in force since 2017, mandates ships that operate internationally between 2 or more countries to manage ballast water discharges, de facto primarily through treatment using on-board Ballast Water Management Systems (BWMS), with full compliance required by the shipping industry by September 8, 2024 (Stuer-Lauridsen et al. 2018).

Regulation A-4 of the BWMC allows exemptions from compliance for ships and routes deemed low risk for NIS transport via BW, subject to a 5-year period and adherence to the G7 Guidelines (IMO 2017). The G7 Guideline outlines Risk Assessment (RA) principles and methods, including the Same-Risk-Area (SRA) concept, where ships within the SRA are not obligated to treat BW. The RA must show that NIS transfer within the SRA by BW presents a low, acceptable risk compared to natural dispersal. Further, the G7 Guideline requires modelling for natural NIS dispersal analysis but lacks details on analysis procedures and interpretation in the RA context. Currently no standardised procedure or protocol exists (Outinen et al. 2021).

SRA studies have been conducted in transboundary marine areas between Belgium and The Netherlands (Baetens et al. 2018), Denmark and Sweden (Hansen & Christensen 2018), and within Canada's national boundaries (Outinen et al. 2021). Øresund, between Denmark and Sweden, received an SRA designation in 2020 (Miljøstyrelsen 2020). Australia has implemented the SRA approach nationally, designating four SRAs (Commonwealth of Australia 2020).

Biophysical modelling in marine science predicts the dispersal of marine organisms during pelagic life stages, utilising ocean circulation models predicting ocean currents and Lagrangian particle tracking models (agent-based models), that consider biological processes (Cowen and Sponaugle 2009; Sebille et al. 2018; Swearer et al. 2019). The output of such modelling quantifies the exchange of pelagic life stages between geographically distinct habitats or populations, known as marine connectivity (Cowen et al. 2006; Selkoe & Toonen 2011; Swearer et al. 2019). Network analysis techniques, rooted in graph theory, can be applied to understand emergent network properties, providing insights into sub-population recovery, gene exchange, and other population dynamics (Treml et al. 2008; Ospina-Alvarez et al. 2020a, 2020b; Balbar & Metaxas 2019).

In the past two decades, studies have linked the outcome of biophysical models predicting marine population dispersal and connectivity with empirical indices (Mertens et al. 2018 and references herein). A meta-study suggests genetic differentiation in marine populations is explained by predicted dispersal of pelagic life stages (Jahnke and Jonsson 2022). A study on coral reef fish (Fontoura et al. 2022) established links between marine connectivity metrics and empirical data on biodiversity indices and species abundances. Despite recent progress, quantifying marine connectivity remains challenging (Cowen et al. 2006; Treml et al. 2012; Jacobi et al. 2012; Darnaude et al. 2022; Hansen et al. 2023). While biophysical models often consider species specific data like pelagic larval duration (PLD), spawning period and habitat preferences, they often overlook factors such as spawning biomass, reproductive output, and mortality. These factors are essential for comprehending how connectivity influences population dynamics in habitats, and for distinguishing between "potential connectivity" and "realized connectivity" (Watson et al. 2010). Within the framework of SRA RA and delineation, the assessment of marine connectivity for NIS is limited to potential connectivity. This limitation arises because many NIS are either not introduced, not widely spread, or their distributions are unknown. Consequently, biophysical modelling and connectivity analysis cannot establish definitive criteria for delineating a specific SRA. Nonetheless, these methods offer valuable insights into the potential and intricate dispersal pathways of NIS (in the following referred to as "dispersal pathways"), aiding in SRA RA.

This paper outlines a methodology utilizing biophysical modelling to analyse marine connectivity of NIS for SRA RA and delineation. We recognise that data quality and availability vary globally, as do environmental conditions such as climate, seasonality, hydrography, coastline, and seabed topography. Therefore, local adaptations may be necessary. The proposed approach serves as a step towards the development (and adoption) of consistent, transparent, and scientifically robust assessments of SRA for ballast water management.

Methodology

The overall approach of the presented methodology is based on an SRA case study from 2018 (Hansen and Christensen 2018). The methodology consists of 4 main steps: (1) Creating a shortlist of species; (2) Conducting biophysical modelling; (3) Analysing the connectivity between relevant ports and habitats; and (4) Translation of connectivity outputs into an RA context (Fig. 1). Each step is explained in the sections below.

Step 1. Species selection

The NIS species selection is based on the following criteria: (1) the species is known, or expected, to be taken up by BW, *and* (2) the species is registered in the study area or in its vicinity, *or* (3) the species is not registered but identified as a potential NIS in the region by experts.

The criteria for NIS not to be considered include: (4) the species is already fully established in the study area, (5) the species has a salinity tolerance range outside the salinity regime of the study area, (6) the species entire life cycle takes place in the water column, or (7) the species is a macroalgae.

Fully pelagic species such as planktonic organisms generally have high dispersal potential between very distant locations (e.g. the entire Atlantic Ocean) given enough time although environmental constraints such as temperature or salinity may impose limitations in connectivity (Manral et al. 2023). Zoogeographical evidence suggests that the dispersal of many pelagic species is more likely to be limited by their ability to maintain viable populations rather than hydrographic barriers (Noris 2000). For these reasons, we propose in criteria 6 to disregard fully pelagic species as part of an SRA RA.

Similarly, while gametes and propagules of many macroalgae have limited dispersal capabilities, shredded thallus from macro algae (e.g., *Fucus sp.*, *Macrocystis pyrifera* and *Durvillaea antarctica*) may drift for many months and over vast distances (greater than hundreds of kilometres) and are generally considered an important mechanism for connecting potentially isolated regions (Pereyra et al. 2013; Rothäusler et al. 2015; Batista et al. 2018). Due to this potential of long dispersal distances of thallus (also referred to as "rafting") we suggest in criteria 7 to disregard macroalgae as part of an SRA RA unless dispersal via thallus is not known for a given NIS. This implies that the ability of these NIS to disperse over long distances is not considered limiting for the size and extent of an SRA. Species trait data for each NIS (refer to Step 2) can be obtained from various data portals (e.g., AquaNIS 2015; HELCOM/OSPAR 2020) or through a literature review.
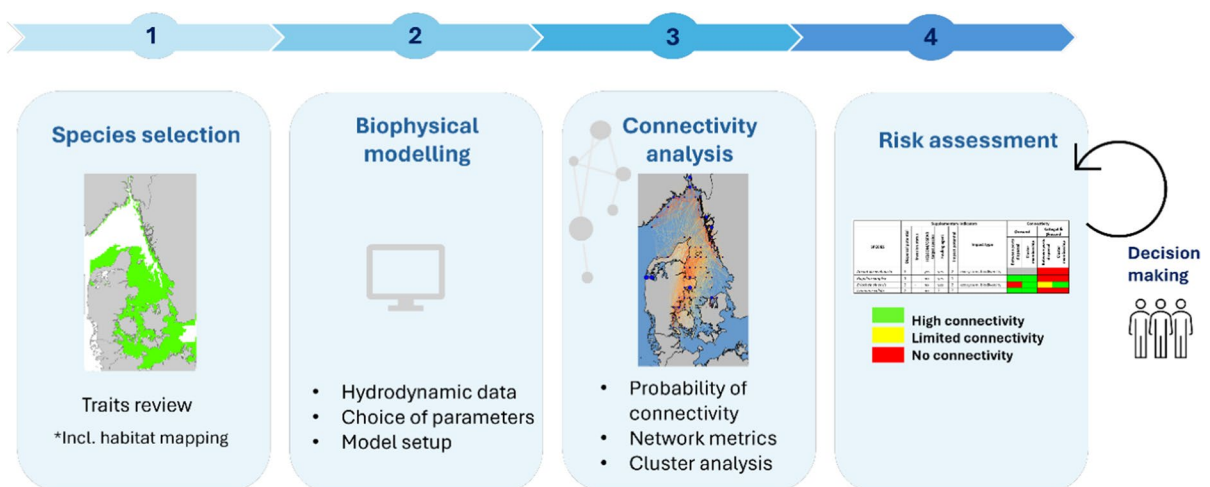

Fig. 1 Overview of the methodology proposed for applying biophysical modelling and connectivity analysis as a basis for an SRA RA

Step 2. Biophysical modelling

Hydrodynamic data

Biophysical models often use data on ocean currents from hydrodynamic models designed for various purposes such as current and water level forecasts, scouring processes, or coastal erosion predictions. The calibration of the original hydrodynamic model, depending on its intended use, can impact the predicted trajectories of pelagic life stages. Key factors affecting realistic trajectory predictions also include the spatial and temporal resolution of the computational grid, the number of vertical layers, and the time step for storing hydrodynamic data (e.g., hours vs. days), particularly in tidal systems (Williams & Esteves 2017; Vasile et al. 2018; Swearer et al. 2019; Sciascia et al. 2021; Saint-Amand et al. 2023; Ward et al. 2023). While these topics are not discussed here in detail we refer to above mentioned references.

Choice of parameters

In biophysical modelling for marine connectivity, key determinants, in addition to hydrodynamics, include PLD, spawning biomass, reproductive output, spawning biomass location, suitable habitat configuration, spawning season, drift depth, settling competence period, and mortality of pelagic, juvenile, and adult life stages (Corell et al. 2012; Treml et al. 2012, 2015; Robins et al. 2013; Dorenbosch et al. 2007; Grober-Dunsmore et al. 2009; McMahon et al. 2012; Assis et al. 2021; Swearer et al. 2019).

While some of these processes can be supported by data or literature values, others remain unknown. Thus, for the SRA RA and delineation, we recommend incorporating processes and parameters with available data or reasonable estimates. For those with unknown values, we suggest addressing them during the interpretation of results, ideally supported by sensitivity analysis to test the model's outcome space within the expected range or uncertainties of relevant parameters. Processes and parameters proposed for inclusion in the biophysical model are those that predicts potential connectivity (Watson et al. 2010). These are listed in Table 1 and discussed further in Supplement 1.

The excluded processes and parameters in the biophysical model are those scaling potential connectivity in space and time to represent realized connectivity (Watson et al. 2010). These include spatial distribution of spawning biomass (unknown for NIS, not yet surveyed), reproductive output, larval mortality (up to 20% per day), and post-settlement juvenile mortality exceeding 90% for many marine benthic invertebrates (Gosselin and Qian 1997; Swearer et al. 2019). These processes, crucial for NIS recruitment, establishment, and succession, are challenging to predict mechanistically. However, insights into NIS dispersal potential can be gathered from invasion histories and species-specific traits, considered separately in the SRA RA (see: "Step 4 – Risk assessment criteria").

Parameter values in the biophysical model can represent conservative or optimistic estimates, depending on the modelling effort and sensitivity analyses (Swearer et al. 2019). We recommend applying at least conservative yet realistic estimates to avoid overestimating dispersal. In cases where literature-derived parameter values may reflect different environmental conditions, adjustments should be made, considering available knowledge or assumptions about how environmental differences may impact the parameters.

Model setup

To ensure robust and reproducible results in a biophysical model, the number of released agents should be iteratively increased until modelling endpoints remain unchanged or only marginally changed (Quigley et al. 2022). For optimal spatial and temporal distribution, released agents are recommended to be evenly or randomly distributed across all habitats and within the expected spawning period (e.g., Hansen et al. 2023). If detailed knowledge on spawning behaviour is available, incorporating information such as lunar cycle-linked or temperature-induced spawning is advisable (Cowen et al. 2006; Bayne et al. 1976; Bernard et al. 2011).

Depending on the hydrodynamic dataset and study scope, multiple years can be included to address interannual variations, or representative years can be selected based on oceanographic oscillation indices (e.g. Hansen and Christensen 2018; Pastor et al. 2023). Examples of indices include the North Atlantic Oscillation (NAO) index, Oceanic Niño Index (ONI), and Southern Oscillation Index (SOI) (Hurrell et al. 2023; NOAA 2023; AGBM 2023).

Table 1 Processes and parameters relevant for SRA studies

Name	Definition	How to incorporate in the model (examples)	References
Pelagic larval duration (PLD)	Duration of the pelagic life stage from the time of spawning until time of settling	Constant (hours or days)	Bradbury et al. (2008), Hilário et al. (2015), O'Connor et al. (2007) and Kendall et al. (2016)
Settling	The transition between the pelagic and the sessile phase	Instantaneous at the end of the PLD, or when suitable habitat is reached (i.e., active settling behaviour). In case of active settling a competency, period may be included during which settling occur when suitable habitat is reached. Constant (day number)	Brooker et al. (2016) and Swearer et al. (2019)
Spawning/ Settlement habitat	Suitable seabed habitat for juvenile and adult life stages	A map based on species preferences, for example, seabed substrate, water depths, and tolerances to environmental variables such as salinity and temperature	Hansen and Christensen (2018) and Lindegren et al. (2022)
Spawning time	Time period where the pelagic life stages are spawned/released	Start and end dates	Bernard et al. (2011) and Zippay & Helmuth (2012)
Drift depth	Depth interval of the vertical position of the pelagic life stage	Upper and lower depth threshold (m)	Corell et al. (2012)
Vertical migration (VM)	Vertical movement behaviour upwards/downwards	Vertical movement speed and direction initiated/triggered by factors such as sunset, sunrise, and/or tidal cycles, constrained within a given depth interval or a maximum depth	Hill (1991); Baetens et al. (2018) and Jahnke and Jonsson (2022)
Larval environmental tolerance	Larval tolerance interval of individual environmental factors. (e.g., salinity and temperature conditions)	Experienced conditions evaluated at each time step relative to minimum and maximum thresholds. Threshold exceedance induces mortality	Torres et al. (2021), Lett et al. (2010), Hansen & Christensen (2018)
Horizontal dispersion	The horizontal transport of agents not resolved by the spatial resolution of the hydrodynamic model	Constant (m²/s)	Peliz et al. (2007), Rossi et al. (2014), Brennan et al. (2019), Hinata et al. (2020)
Vertical dispersion	The vertical transport of agents not resolved in the hydrodynamic model	Constant (m²/s)	Visser (1997)

Model boundary interactions

When simulated agents interact with model boundaries, it's crucial to prevent agent behaviour from introducing biases and errors. Four types of boundaries should be considered: (1) open water boundaries, (2) land–ocean boundary, (3) sea-floor boundaries, and (4) flooding-and-drying. Agents crossing the open boundary may introduce bias, but extending the model domain until the dispersal of most agent trajectories is confined within the model domain can avoid this issue. In addition, agents may get "stuck" at land–ocean boundaries, coarse seabed topography, or during sudden water level decreases in computational grid cells (e.g., during tidal cycles or wind-driven processes). Various computational strategies, such as passive response, re-bouncing of agents, or discarding agents causing unintended bias, can be applied. Sensitivity analyses can further investigate how a chosen strategy may affect the final endpoints.

Step 3. connectivity analysis

A connectivity analysis necessitates dividing the study area into discrete areal units. A common approach is applying a Cartesian grid of uniform size to ensure consistent and comparable analysis (Rossi et al. 2014; Van der Molen et al. 2018; Pastor et al. 2022). Connectivity matrices, here referred to as "raw connectivity matrices," are created by counting pairwise connections between all grid cells (Watson et al. 2010). These matrices are then translated into two types of connectivity probability matrices: 1) export of agents between grid cells relative to the number of released agents, and 2) import of agents between grid cells relative to the number of agents settled within the grid cell. The diagonal elements in these matrices represent the local retention (LR) and self-recruitment (SR) respectively (Lett et al. 2015; Treml et al. 2015). These matrices, referred to as export+LR and import+SR matrices (Hansen et al. 2023), describe connectivity from different perspectives. Probabilities of larval export+LR, are proportionally independent from the number of released agents, and identify potential NIS suppliers. In contrast, probabilities of larval import+SR depend on the number of released agents at different locations supplying larvae.

Marine connectivity can be analysed using graphical representation of connectivity matrices (Cowen et al. 2006; Gamoyo et al. 2019), cluster analysis to detect highly connected habitats and dispersal barriers (Nilsson Jacobi et al. 2012; Treml et al. 2015), and connectivity metrics derived from network or graph theory (Andrello et al. 2013; Cristiani et al 2021; Pastor 2022). A graph data structure represents habitats as vertices or nodes and connections as edges, with weights representing connectivity probabilities or agent counts. In the SRA RA context, we propose to analyse connectivity in two scenarios of a bioinvasion: (1) early stages following primary NIS introduction and (2) later stages of secondary introduction when NIS has spread within the SRA candidate. These scenarios represent the extremes of the succession from the point in time and space of the primary introduction until the NIS is successfully established within the SRA candidate via secondary introduction.

Visualization involves matrices or networks depicting dispersal potential and cluster analysis evaluating dispersal barriers. Various metrics support cluster analysis interpretation, including import/export of agents between clusters, local retention/self-recruitment in each cluster, and cluster strength (Csárdi and Nepusz 2006). Cluster analysis may be done for both the original matrix and its transposed matrix which may result in different but complementary cluster outlines (Moutsinas et al. 2021; Hansen et al. 2023). The clustering method chosen must account for the directionality of bi-directional connections in the connectivity matrices.

Step 4. Risk assessment criteria

The G7 guideline for risk assessment mentions "low acceptable risk" as a prerequisite for an exemption without providing a clear definition. Therefore, proposed criteria for an SRA RA are indicative, and in principle decision-makers must define what constitutes "low acceptable risk." To provide a basis for such decisions, three criteria (High, Limited, and No connectivity) are defined for evaluating the results of the connectivity analysis in two scenarios representing different bioinvasion stages (Table 2). Criteria should be evaluated for each NIS included in the SRA RA (step 1) based on the outcome from the connectivity analysis (step 3). If one or more NIS fail to comply with the "High" or "Limited" connectivity an SRA candidate may be discarded.

Table 2 Criteria and scenarios proposed for the interpretation of the connectivity analysis results into an SRA RA

	Between-ports connectivity	Cluster analysis
Criteria	*Scenario 1: Early stage of the bioinvasion*	*Scenario 2: Late stage of the bioinvasion*
High Connectivity	All ports connected via 1 generation bidirectionally	All ports belong to the same cluster
Limited Connectivity	Some ports are not connected via 1 generation, but these must be connected via 2 generations bidirectionally	Some ports do not belong to the same cluster, but these ports must belong to separate clusters connected bidirectionally
No Connectivity	If 2 or more ports are NOT connected bidirectionally via 1 or 2 generations	Some ports belong to separate clusters NOT connected bidirectionally

Between-ports connectivity

In scenario 1 ("Early stage of the bioinvasion"), we define "high connectivity" if the dispersal of pelagic life stages via 1 generation connects two ports bidirectionally. This assumption is supported by the argument that the number of agents representing pelagic life stage export from each port in a biophysical model is much less than the expected reproductive output from an established subpopulation in each port location (Dare et al. 2004; Treml et al. 2012; Magris et al. 2016; Romero-Torres et al. 2018). The choice of using conservative estimates of the species specific PLD values contributes to this confidence margin. We designate "limited connectivity" if some ports are not connected via 1 generation, but these are connected via 2 generations in both directions, providing insights into potential connections beyond direct ones. Notice that the dispersal via 2 generations is not simulated explicitly in the biophysical model, but retrieved from the connectivity matrices, i.e. where the export and import of the two ports respectively in both directions share the same node. "No connectivity" is assigned if two or more ports are not connected bidirectionally via 1 or 2 generations. While NIS introduced and established in a port may eventually spread through stepping-stone dispersal, predicting the succession rate beyond a few generations is challenging. Hence, we propose evaluating existing knowledge on NIS invasiveness as part of the SRA RA (see "Supplementary RA indicators" later in this section).

Cluster analysis

In scenario 2 ("Late stage of the bioinvasion"), we employ a cluster analysis interpretation and use the same three criteria (Table 2). "High connectivity" is assigned if all ports belong to the same cluster. Ports within a cluster are assumed to be interconnected either directly or indirectly via a network of connected habitats where NIS sub-populations may already be established. This assumption aligns with previous work on native species, showing that detected clusters of habitats from biophysical models coincide with both short-term demographic connectivity and long-term evolutionary connectivity (Jahnke and Jonsson 2022; Lett et al. 2023). In some cases, clusters of subareas may be more or less tightly intraconnected, and the graph metric "global transitivity" can be calculated for each cluster as one value describing the proportion of realized triangular networks within the cluster (Csárdi and Nepusz 2006). The higher the transitivity value the more dispersal pathways may exist between ports within the cluster. "Limited connectivity" is assigned if some ports do not belong to the same clusters. These ports must belong to neighbouring clusters bidirectionally connected. The boundary between clusters suggests a dispersal barrier supporting limited exchange, quantifiable by counting the number of agents exported/ imported. In some cases, a primary link between two clusters may be localized to a single node, representing a potential bottleneck, identified using "betweenness centrality" (Costa et al. 2017).

The detection of clusters and graph metrics may be sensitive to habitat configuration. This can be tested systematically through iterative procedures involving subsampling of habitat maps. This reveals the robustness or sensitivity of cluster analysis and graph metrics to changes in habitat configuration and NIS succession stage. The criterion indicating no or only unidirectional connectivity between clusters implies no potential dispersal pathways between some ports located in different clusters, independent of NIS succession state.

Exceptions may exist, such as unidirectional connectivity within a circular sequential chain of clusters.

Supplementary RA indicators

The proposed criteria primarily focus on potential connectivity, overlooking processes related to realized connectivity and the succession state of the NIS within the SRA candidate. To address this, we suggest incorporating supplementary RA indicators to enhance the assessment process. These indicators can include:

1. *Dispersion Potential Indicator*: Provides insight into the extent to which the NIS may utilize the identified potential connectivity.
2. *Impact Potential Indicator*: Evaluates the potential impact of the NIS.
3. *Invasion Status Indicator*: Indicates the presence, absence, or distribution of the NIS in the SRA candidate.
4. *Recognition by Authorities Indicator*: Notes whether the NIS is recognized by local/regional authorities as a target species.
5. *Anthropogenic Dispersal Indicator*: Considers whether the NIS may be subject to additional anthropogenic dispersal vectors, such as hull fouling, or via networks of aquaculture sites.

For further inspiration, expert judgments and ranking tools have been developed to assess NIS in specific regions (Vilizzi et al. 2021; Jensen et al. 2023). We acknowledge that anthropogenic vectors beyond BW are not covered by the BWMC and G7 guidelines. Nevertheless, in cases where other anthropogenic vectors are considered equally or more significant as vectors compared to BW for a particular NIS, treating BW may not prevent the dispersal of the NIS within an SRA candidate. Thus, if other vectors beyond BW can be considered to play decisive roles for dispersal a risk assessment must be based on research and guidance related to the vector(s) in question, e.g. aquaculture or biofouling.

Case study

Study area

The study area encompasses the transition zone between the North Sea and the Baltic, including the Skagerrak, Kattegat, the Inner Danish Straits (IDS), and the western parts of the Baltic Sea (Fig. 2). Two SRA candidates are examined: one covering Kattegat and Øresund as a larger candidate, and Øresund as a smaller sub-candidate. Both are transnational marine territories between Denmark and Sweden. As of 2020, six major ports in the area facilitated frequent ferry operations between the two countries: Frederikshavn, Grenå, Elsinore, Gothenburg, Varberg, and Helsingborg (Fig. 2). Copenhagen's port was also included to represent vessels like those involved in bridge or windfarm maintenance operating locally within Øresund. Average depth is approximately 24 m for Kattegat and 12 m for Øresund, with maximum depths of around 112 m and 42 m, respectively (GEBCO bathymetry dataset: IOC, IHO and BODC 2003). Salinity ranges from about 8 PSU in the western Baltic Sea to over 31 in the North Sea (Westman et al. 1999; Lehmann et al. 2002).

Species data

Hansen and Christensen (2018) initially considered 23 species in their study. However, for simplicity, the present study focuses on four species chosen to represent diverse biological traits, habitat preferences, and environmental tolerances: the mussel *Arcuatula senhousia*, the bryozoan *Bugulina simplex*, Chinese mitten crab *Eriocheir sinensis*, and the polychaete *Laonome calida* (Table 3).

A habitat map for each NIS was generated (Fig. 3) using compiled information on species-specific preferences for seabed substrate (EMODNET 2018), categorized into mud, sand, and hard substrates. The map also considered water depth (IOC, IHO, and BODC, 2003) and salinity thresholds for adult life stages, classifying habitat quality as "optimal" or "sub-optimal" based on consistent adherence to adult salinity tolerance. "Optimal" conditions indicate habitats where bottom salinity consistently aligns with NIS tolerance, while "sub-optimal" conditions involve periods where salinity exceeds tolerance thresholds.

Biophysical model

The hydrodynamic data used for the Kattegat and Øresund study, was based on the HBM model with a nested horizontal quadratic grid with 3 nm (~5.6 km) in the North Sea and Baltic Sea, and 0.5 nm

Fig. 2 The study area including Skagerrak, Kattegat, Øresund, the Inner Danish Straits, and the western parts of the Baltic Sea. Yellow and red hatched areas indicate the extent of the Kattegat and the Øresund regions respectively. White and black dotted lines indicate the outer boundaries of the biophysical model and the Danish Exclusive Economic Zone (EEZ) respectively. Colour legend indicates the depth intervals based on the GEBCO bathymetry dataset (IOC, IHO and BODC 2003). Ports in this study are indicated in red
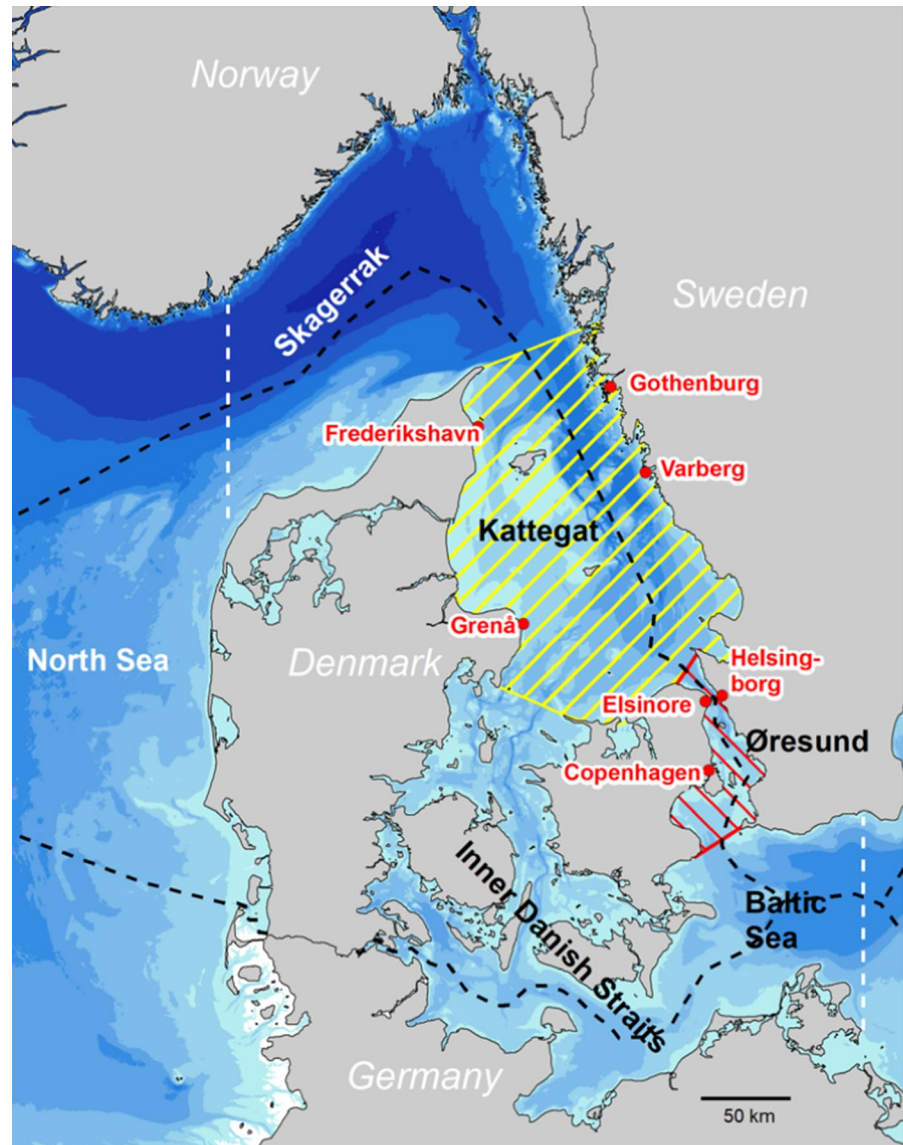
(~ 0.9 km) in the Kattegat and the IDS, including 52 z-type vertical layers and a data storage interval of 1 h (for more information, see: Berg & Poulsen 2012). For comparisons, of 87 studies combining population genetics and biophysical modelling, most used horizontal grid resolutions of 3–10 km, while complex coastlines will require resolutions of 1 km or less (Jahnke and Jonsson 2022; Saint-Amand et al. 2023). Data for 3 years, 2005, 2010 and 2012 were selected to represent a neutral, a negative and a positive NAO index, respectively.

The agent-based modelling library IBMlib (Christensen et al. 2018) was used for our biophysical

modelling framework. Each simulation, representing a combination of years and species, released 200,000 agents randomly within the species-specific habitat extent (Fig. 3) and during the spawning period (Table 3). We adopted the minimum PLD value for each NIS for a conservative estimate of dispersal duration and distance, ensuring reliable connectivity metrics. The dispersal depth for all NIS was limited to 0–40 m, following Corell et al. (2012) (Supplement 2). Vertical positioning of simulated agents was determined by a constant vertical dispersion factor of 0.001 m²/s (Visser 1997). To account for unresolved hydrodynamic processes within the computational

Table 3 Information on the selected NIS including life history traits, habitat preferences and environmental tolerances retrieved or estimated from exiting databases and the literature. For further details, see Hansen and Christensen (2018)

Species	Taxon	PLD (min) days	PLD (max) days	Generations per year no	Spawning start month	Spawning end month	Habitat Substrate type	Habitat Depth m	Temp. Min (Adult) C	Temp. Max (Adult) C	Salinity Min (Adult) PSU	Salinity Max (Adult) PSU	Temp. Min (Larvae) C	Temp. Max (Larvae) C	Salinity Min (Larvae) PSU	Salinity Max (Larvae) PSU
Arcuatula senhousia	Mollusca	14	55	1	7	8	All	20	0	33	17	35	22.5	30	17	30
Bugulina simplex	Bryozoan	1	1	1	7	9	Hard	20	0	25	18	40	0	25	18	40
Eriocheir sinensis	Crustacea	30	60	0.5	3	7	All	10	0	25	0	30	12	35	15	32
Laonome calida	Annelida	1	1.5	1	7	8	All	40	0	30	0.1	35	0	25	0.1	35

grid, a horizontal dispersion of 10 m²/s was applied. Agents reaching land boundaries rebounded in a direction mirroring the angle of incidence. Mortality was excluded from the model, except for agents deemed dead when exposed to salinity levels beyond tolerance thresholds (Table 3). The simulation timestep was 1800s. A sensitivity analysis, testing the impact of the number of agents and dispersal depth on connectivity analysis results, was conducted for each NIS (Hansen & Christensen 2018).

Connectivity analyses

Connectivity analyses were based on a subdivision of the model domain (8°–14° E and 54°–60° N) into a regular grid of 20×20 grid cells with a spatial resolution of 0.3 degrees in both the longitudinal and the latitudinal direction (≈ 18×33 km) (Supplement 2). Connectivity matrices were generated both in terms of "raw connectivity matrices" and matrices representing the connectivity probability of both import+SR and export+LR (Step 3 in the methodology section), and connectivity to and from each port were extracted to evaluate "between ports connectivity". Cluster analyses were conducted using the Infomap algorithm (Rosvall & Bergstrom 2008) and evaluated following the criteria described (Step 4 in the methodology section). All analyses and plots were carried out using R 4.1.0 (R Core Team 2021) and associated packages (Supplement 3).

Results

The results of the connectivity analysis and the supplementary RA indicators are presented below for each NIS. Notice that while the ports of Frederikshavn, Grenå, Gothenburg, Varberg and Copenhagen are located in separated grid cells, the two ports of Elsinore and Helsingborg are located in the same grid cell due to their proximity.

Arcuatula senhousia

The 14-day PLD leads to low local retention and robust dispersal pathways in the central and northern parts of Kattegat (Fig. 4A) primarily west-to-east. Southward dispersal is restricted due to larval intolerance to lower salinity conditions. Early-stage
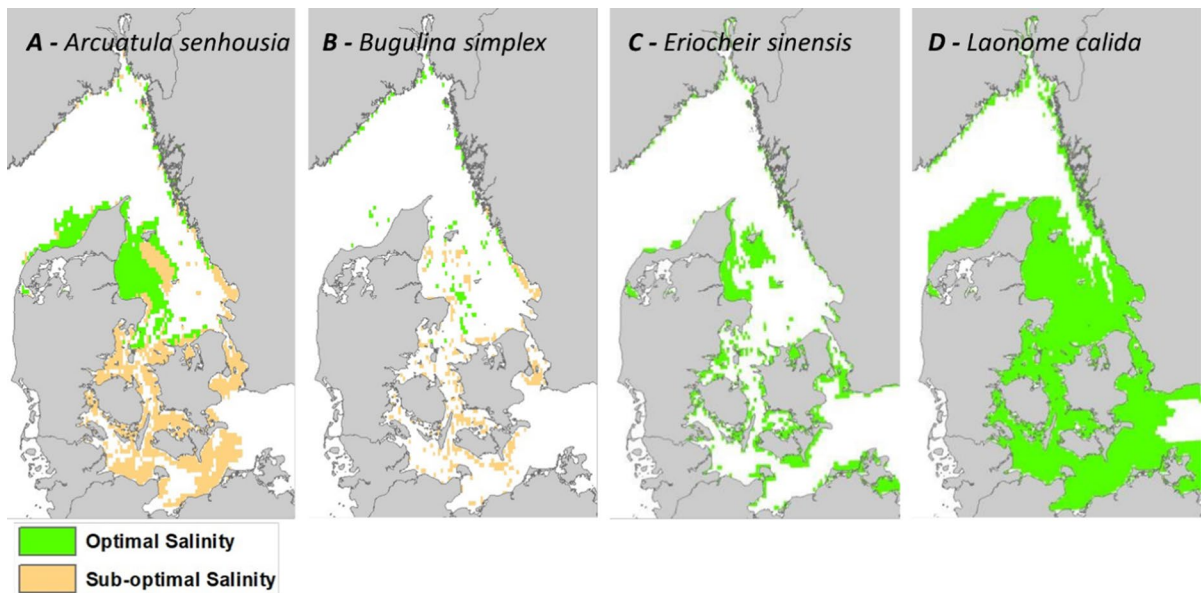
Fig. 3 Predicted habitat maps based on species specific seabed substrate preferences, preferred water depths, and salinity tolerances of adult life stages of the NIS: **A** *Arcuatula senhousia*. **B** *Bugulina simplex*, **C** *Eriocheir sinensis*, **D** *Laonome calida*. Colour legend discriminates between "optimal" (green) and "suboptimal" (orange) salinity conditions for adult life stages, where sub-optimal salinity conditions refer to conditions where salinity minimum or maximum tolerance thresholds are exceeded over varying time periods

invasion connectivity analysis reveals limited support for between-port connectivity between Danish and Swedish ports within 1 or 2 generations, except for a connection between Gothenburg and Frederikshavn over two generations (Figs. 4B–C, 6). In the later stages of bioinvasion, a unidirectional dispersal barrier emerges between western and central Kattegat (including the Danish port Frederikshavn) and the eastern parts along the Swedish coastline (including Varberg and Gothenburg) (Figs. 5A, 7). The port of Grenå, lacks direct connectivity with Swedish ports. Consequently, the connectivity analysis for *A. senhousia* does not meet the two RA criteria for the larger SRA candidate, Kattegat and Øresund. Additionally, the smaller SRA candidate, Øresund, falls outside the larval salinity tolerance range.

Considering supplementary indicators (Table 4), *A. senhousia* is already recognized as a target species in HELCOM/OSPAR, though it's not yet registered within the SRA candidates. *A. senhousia* exhibits a high dispersal potential and is considered a fouling agent, posing a risk of spreading between ports or within an SRA candidate following an introduction, despite ballast water treatment requirements.

Bugulina simplex

The 1-day PLD, coupled with small and fragmented habitats, result in limited dispersal pathways for *B. simplex*, occasionally leading to high LR (Fig. 4A). Uncertainties in habitat mapping, due to the exclusion of hard surfaces like mussel and oyster shell, scattered stones, and coastal structures, may underestimate the potential habitats for this species. Connectivity via 1 or 2 generations between Danish and Swedish ports during the early stages of invasion is absent in both directions except between Elsinore and Helsingborg (EH), where connectivity is reflected in LR (Figs. 4B–C, 6). The southern Øresund including the port of Copenhagen falls outside the larval salinity tolerance range. In the later stages of the bioinvasion, some clusters exhibit bidirectional interlinking via very weak connections (Figs. 5B, 7), and connections involving ports like Frederikshavn and Swedish ports of Varberg and Gothenburg traverse a sequence of three bidirectionally connected clusters. *B. simplex* fails to meet the two RA criteria for the larger SRA candidate, Kattegat and Øresund. Both criteria for the smaller SRA candidate, Øresund, are considered

Fig. 4 Connectivity networks for the NIS: (1) *Arcuatula senhousia*, (2) *Bugulina simplex*, (3) *Eriocheir sinensis,* and (4) *Laonome calida* divided into three panels (**A–C**). In panel A, blue nodes indicate the centre point of each grid cell and size represents LR relative to the maximum value in the dataset for each NIS. Only nodes with non-zero LR values are included. Edges represent export connectivity probabilities following a clockwise direction. In panels B and C, red nodes indicate a given port, and edges are the connections to adjacent grid cells. The connections represent export and import connectivity probabilities to each port respectively. Edges values in panels A and B are normalized (0–1) (yellow to red) relative to the maximum value of all connectivity probabilities in A and only edges with non-zero values are included. In C edges are normalized relative to the maximum value of connectivity probabilities in C. Ports are represented by abbreviations: Fr-Frederikshavn; Gr-Grenå; Co-Copenhagen; EH-Elsinore/Helsingborg; Got-Gothenburg Va-Varberg
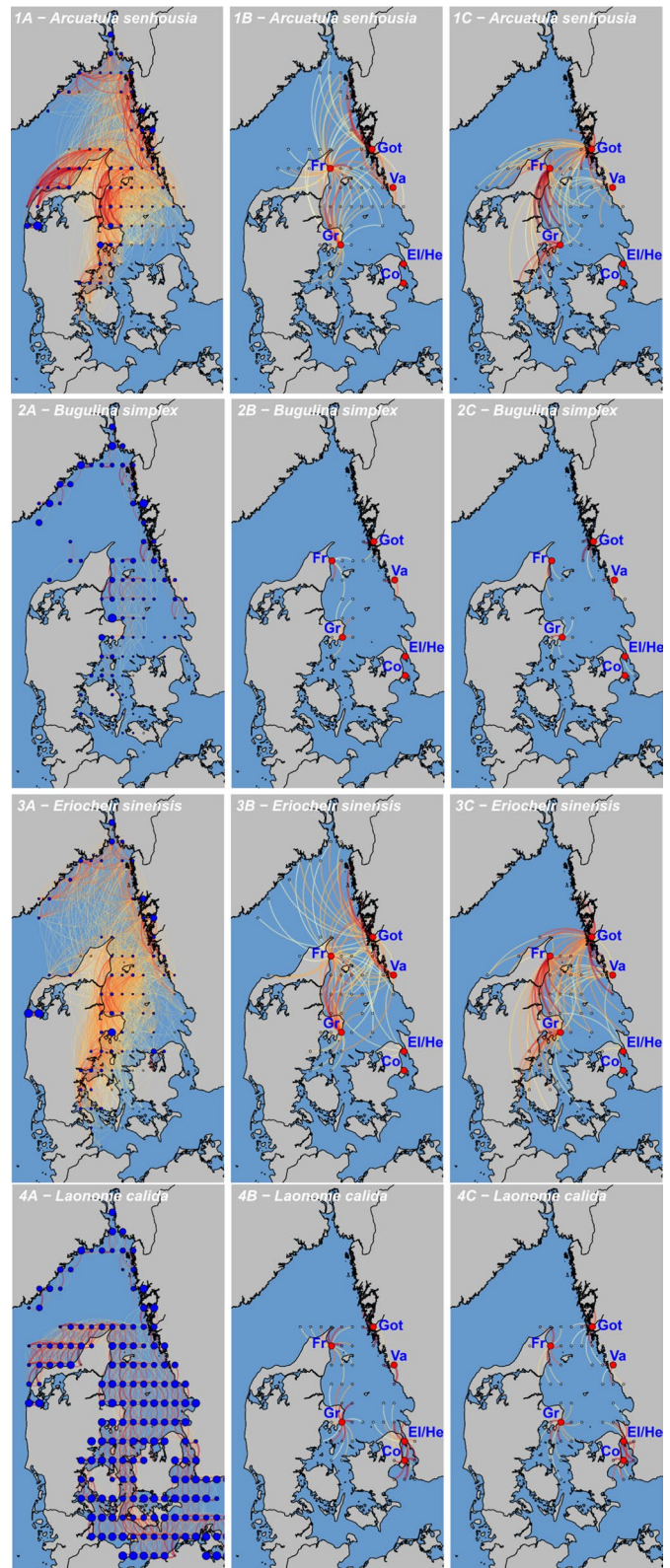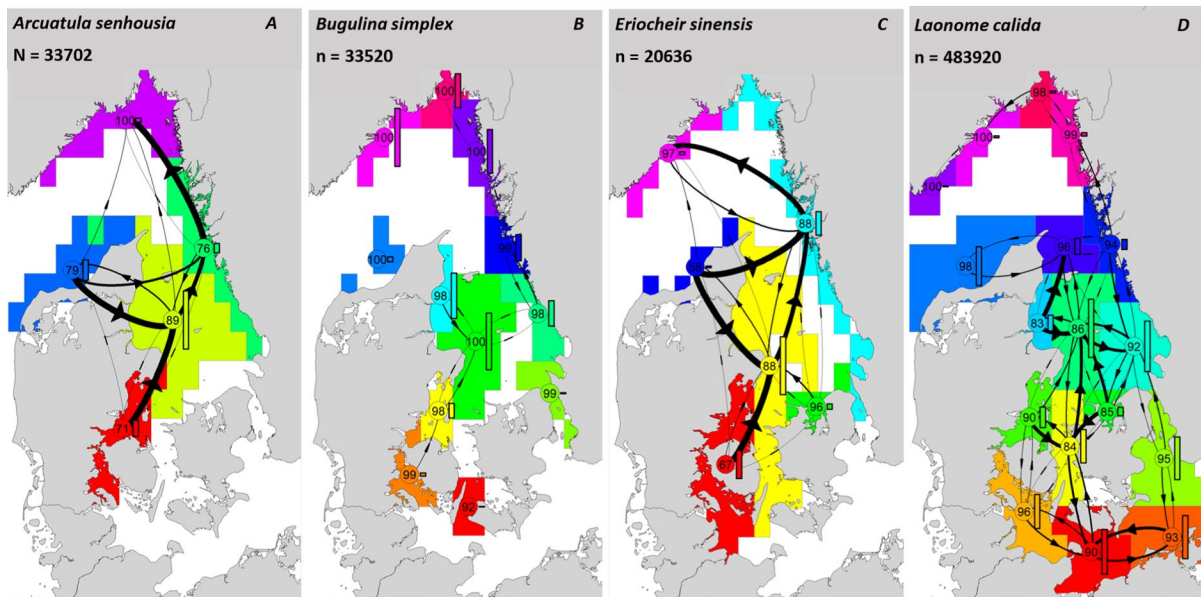
Fig. 5 Cluster analyses of the non-transposed (export + LR) connectivity matrices of (**A**) *Arcuatula senhousia*, (**B**) *Bugulina simplex*, (**C**) *Eriocheir sinensis* and (**D**) *Laonome calida*. Each cluster is represented by a polygon with a unique colour. Values in the cluster centroids (circles) indicate the local retention of each cluster (in % of total no. of released agents). The thicknesses of arrows represent the export of agent between clusters, relative to the total number of agents. Bars beside each cluster centroid indicate the relative number of larvae that defines each cluster normalized relative to the cluster based on the highest number of larvae. An upper threshold for arrow thickness was set to 10%. For cluster analyses of the transposed connectivity matrices see Supplement 4, figure S2

full-filled due to LR (criterion 1) of the port location of Elsinore/Helsingborg, which also belongs to the only cluster identified in the SRA candidate (criterion 2) with dispersal further south prohibited by salinity conditions.

Considering supplementary indicators (Table 4), *B. simplex* has a low dispersal potential, is not a target species in HELCOM/OSPAR, and has not yet been registered. These characteristics suggest that the NIS may have low potential for utilizing connection across parts of Kattegat during the initial bioinvasion stage, while local connectivity between ports like Elsinore and Helsingborg in Øresund may be relatively high.

Eriocheir sinensis

The 30-day PLD leads to low LR and long dispersal pathways across the SRA candidates and beyond, within the larval salinity tolerance range (Fig. 4A). While some connections between Danish and Swedish ports exist via 1 generation, all ports within the larval salinity tolerance are connected via 2

generations in both directions (Figs. 4B, 6). Elsinore and Helsingborg ports, located at the larval salinity tolerance boundary, show no LR due to very few successful agents in the simulation, indicating they are considered outside the NIS's salinity tolerance. In the later stage of the bioinvasion, the cluster analysis (Figs. 5C, 7) reveals that Danish and Swedish ports belong to two individual clusters bidirectionally connected, with limited east-to-west connectivity. *E. sinensis* meets the two RA criteria for the larger SRA candidate, Kattegat and Øresund, while the criteria may also be considered fulfilled for the smaller SRA candidate, Øresund, if the lack of calculated local retention in Elsinore/Helsingborg is ignored.

Considering the supplementary indicators (Table 4), *E. sinensis* is considered to have intermediate dispersal potential and is not a target species in HELCOM/OSPAR. While the species has been present in Denmark since 1927, it remains sparsely distributed, possibly due to suboptimal conditions of salinity or temperature limiting reproduction (Miljøstyrelsen 2017). These characteristics suggest that
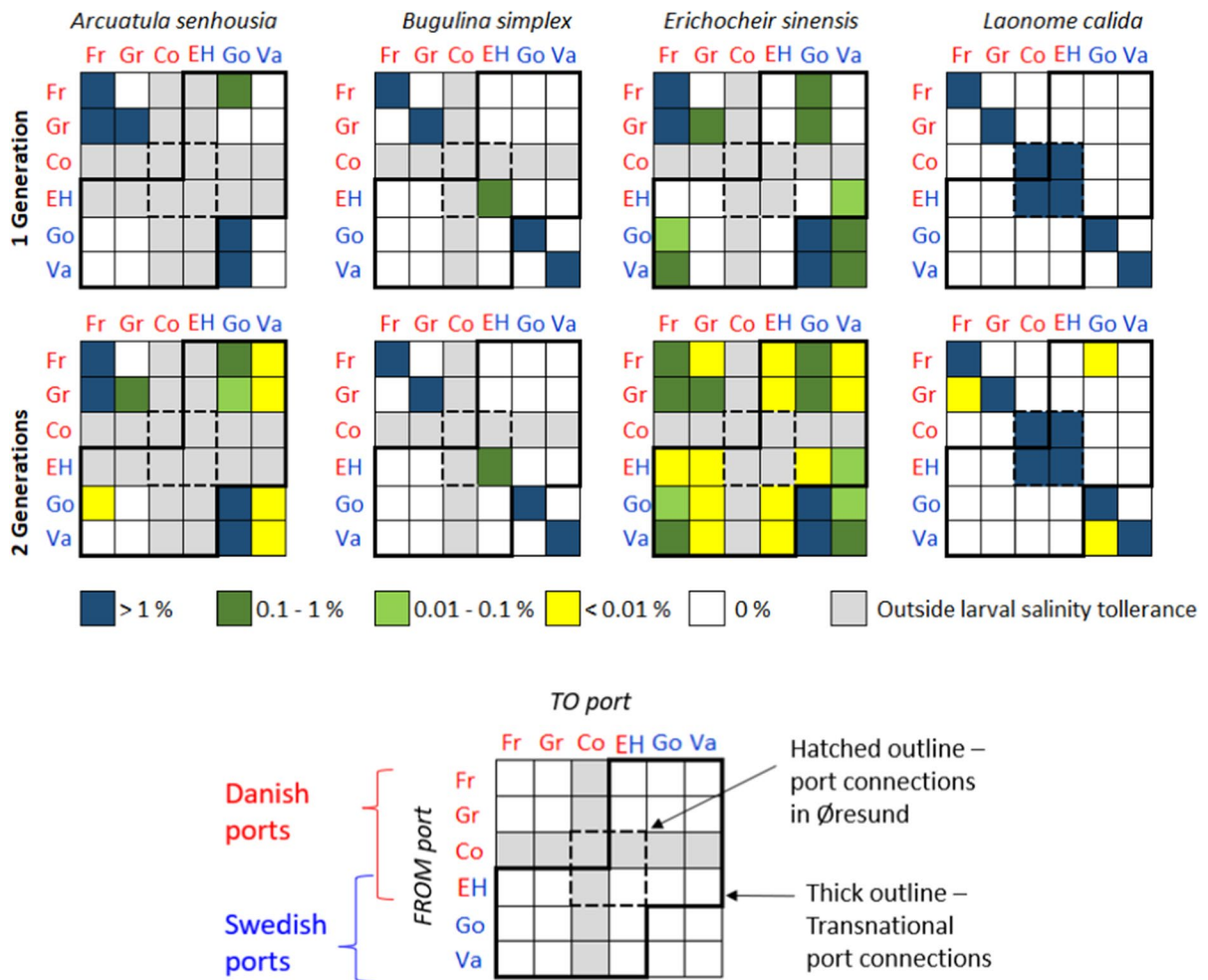
Fig. 6 Connectivity probability matrices between ports representing 1 generation dispersal (top row) and 2 generations dispersal (bottom row), for *Arcuatula senhousia*, *Bugulina simplex*, *Eriocheir sinensis* and *Laonome calida*. Ports are represented by abbreviations: Fr-Frederikshavn; Gr-Grenå; Co-Copenhagen; EH-Elsinore/Helsingborg; Go-Gothenburg; Va-Varberg. Port abbreviations are coloured representing Danish ports (red) and Swedish ports (Blue). Vertical and horizontal entries represent sources (=From) and sinks (=To) respectively. Transboundary connections between Danish and Swedish ports in both Kattegat and Øresund are indicated by thick outline. Connections within Øresund only are indicated by hatched outline. Colours of cells in each matrix represent connectivity probabilities from low (yellow) to high (dark blue). White cells indicate no connectivity. Grey cells indicate connections outside larval salinity tolerance. Connectivity probability values for each matrix are available in Supplement 5

that *E. sinensis* is in a late stage of bioinvasion, and connectivity between ports in the larger SRA candidate can be considered high without resulting in a widespread invasion.

Laonome calida

The 1-day PLD results in high local retention and limited dispersal pathways to neighbouring habitats.

However, the expansive and contiguous habitat suggests a potentially well-connected system, facilitating stepping-stone dispersal (Fig. 4A). Connectivity via 1 or 2 generations between Danish and Swedish ports during the early invasion stages is limited in both directions (Figs. 4B–C, 6), except between Elsinore and Helsingborg (HH) with high LR, and between HH and Copenhagen within Øresund with high connectivity. In the later bioinvasion stage, numerous
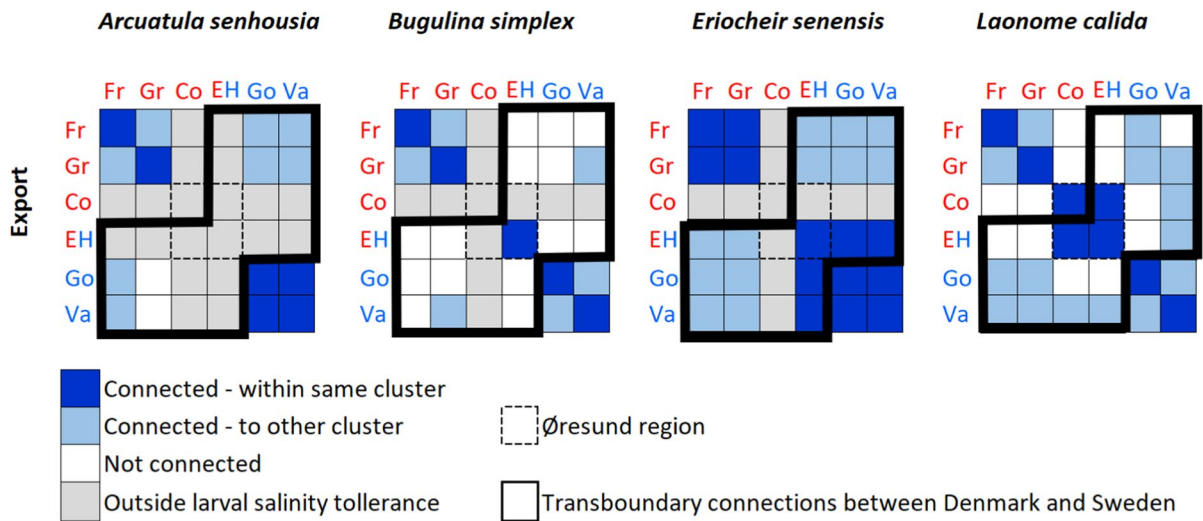
Fig. 7 Cluster analysis between ports for *Arcuatula senhousia, Bugulina simplex, Eriocheir sinensis,* and *Laonome calida*. Coloured cells indicate ports that belong to the same cluster (dark blue), and ports that belong to different clusters but where clusters are connected (light blue). White cells indicate no connectivity and grey cells indicate connections outside the larval salinity tolerance. Ports are represented by abbreviations: Fr-Frederikshavn; Gr-Grenå; Co-Copenhagen; EH-Elsinore/Helsingborg; Go-Gothenburg; Va-Varberg and coloured representing Danish ports (red) and Swedish ports (Blue). Vertical and horizontal entries represent sources (=From) and sinks (=To) respectively. Transboundary connections between Danish and Swedish ports are indicated with a thick outline

clusters are identified. Some interlinked bidirectionally (Figs. 5D, 7). However, ports like Frederikshavn and Varberg, or Grenå and Helsingborg, are connected through a sequence of three bidirectionally connected clusters not meeting the RA criteria. Thus, *L. calida* fulfils the two RA criteria for Øresund but not for the larger SRA candidate, Kattegat and Øresund.

Considering supplementary indicators (Table 4), *L. calida* is considered to have an intermediate dispersal potential. However, it is not a target species in HELCOM/OSPAR, and the NIS has not yet been registered. These characteristics suggest that the NIS may have a limited potential for dispersal across Kattegat in the initial bioinvasion stage, while locally, the dispersal and connectivity between ports in Øresund can be considered high.

Risk assessment summary

The interpretations of the "between-ports connectivity" and the "cluster analysis" concerning the RA criteria above, are summarized in Table 4. From a connectivity perspective and based on the suggested RA criteria for the four NIS, an SRA covering both

Kattegat and Øresund is not recommended, and an SRA covering Øresund may be considered (Notice that between-ports connectivity for *E. sinensis* is disregarded due to the location of Øresund outside or on the edge of the larval salinity tolerance, Figs. 4A–C, 6). However, considering supplementary indicators reveals that the 4 NIS may be at different succession stages, posing varying invasive potentials, and potentially utilizing hull fouling as an additional anthropogenic dispersal vector. Effective fouling species could disrupt BW treatment efforts, leading to a failure in preventing NIS introduction. These and other potential indicators may be considered in the final SRA RA for the inclusion or exclusion of NIS in the assessment.

Discussion

Findings

This paper introduces a methodology for utilizing biophysical modelling and connectivity analysis in the context of SRA RA. While suggesting RA criteria, we emphasize the importance of supplementing them

Table 4 SRA RA matrix combining species-specific invasion potential data, and connectivity analysis results for the "Øresund" and "Kattegat and Øresund" SRA candidates. Sup-plementary RA indicators, such as "Dispersal potential" and "Impact potential" are ranked as low (1), medium (2) or high (3)

| SPECIES | Supplementary indicators | | | | | | Connectivity | | | |
| | | | | | | | Øresund | | Kattegat & Øresund | |
	Dispersal potential	Invasion status	HELCOM/OSPAR target species	Fouling agent	Impact potential	Impact type	Between ports dispersal	Cluster membership	Between ports dispersal	Cluster membership
Arcuatula senhousia	3	-	yes	yes	2	ecosystem, biodiversity	🟫	🟫	🟥	🟥
Bugulina simplex	1	-	no	yes	1		🟩	🟩	🟥	
Eriocheir sinensis	2	+	no	yes	2	ecosystem, biodiversity	🟥	🟩	🟨	🟩
Laonome calida	2	-	no	?	?		🟩	🟩	🟥	🟥

Invasion and impact potential:	Between Ports connectivity Criteria:	
1 = Low	🟩 = High connectivity	All ports connected via 1 generation
2 = Medium	🟨 = Limited connectivity	All ports connected via 1 or 2 generations
3 = High	🟥 = No connectivity	1 or more ports not connected

Invasion status:	Cluster membership Criteria:	
- = Not registered	🟩 = High connectivity	All ports belong to the same cluster
+ = Registered	🟨 = Limited connectivity	Ports belong to separate clusters bi-directionally connected
++ = Widely distributed	🟥 = No connectivity	Ports belong to separate clusters NOT bi-directionally connected

The invasion status in the SRA candidates is categorized as "Not registered" (−), "Registered" (+), or "Widely distributed" (++). Information on whether the NIS is on the HELCOM/OSPAR target species list and if it is known to be a fouling agent is included. Connectivity analyses are color-coded as "high" (green), "limited" (yellow), or "no" (red) connectivity

with additional indicators and species-specific knowledge. Currently, the application of any RA threshold on connectivity should be qualitatively evaluated by experts, considering the available biological knowledge. Acknowledging its limitations, our systematic and transparent approach allows testing proposed criteria, evaluating their fulfilment or violation through sensitivity analysis, and understanding their sensitivity to uncertainties and variabilities in model parameters and assumptions.

Previous SRA studies have applied various biophysical modelling approaches to inform an SRA RA. Baetens et al. (2018) assessed the ecological implications of an SRA between Belgium and the Netherlands using dispersal duration time between ports of passive drifters as a measure for ports connectivity. A cut-off values of 40 days of minimum dispersal time was used as a criterion for identifying potentially connected ports. Outinen et al.

(2022) evaluated the use of the SRA based exemptions in the Gulf of St. Lawrence within the national boundaries of Canada. This study relied on a trait-based approach including combinations of PLD, release period, and vertical swimming behaviour. In both studies, agents were released in individual ports and connectivity between ports were evaluated considering direct dispersal. In both studies no habitat preferences and environmental tolerances specific to species were included. While these studies contribute with valuable and general information about dispersal potentials between ports following the primary introduction, they overlook both multiple generational stepping stone dispersal and the fact that many NIS already introduced in one port may be more widely distributed beyond the port location itself due to secondary introduction. To address these deficiencies, a species-specific approach is necessary. This is primarily because

habitat configuration is species specific and the unique combinations of habitat preferences and traits such as PLD, spawning period and environmental tolerances etc., are essential to understand the potential marine connectivity of individual species (Dorenbosch et al. 2007; Weeks 2017; Cristiani et al. 2021). Thus, the study presented here differs from previous studies by using a species-specific approach, considering dispersal beyond a single generation, and addressing dispersal and connectivity of NIS within the entire SRA candidate.

Challenges

Thresholds for marine connectivity

Determining marine connectivity thresholds poses a significant challenge, requiring discrimination between weak and strong connectivity (Cowen et al. 2006; Treml et al. 2012; Swearer et al. 2019). The migration rate threshold has been utilized to discern successful settlers and evolutionarily relevant connectivity from demographic connectivity (Cowen and Sponaugle 2009; Treml et al. 2012; Magris et al. 2015; Romero-Torres et al. 2018). For NIS, not yet introduced or widely spread within an SRA candidate, estimating these thresholds relies on limited empirical evidence. Cassey et al. (2018) studied propagule pressures related to ballast water-mediated NIS introduction, calculating the probability of establishment based on propagule size and number. Propagule establishment approached 1 when propagule size and propagule number exceeded around 100 and 10, respectively. Applying consistent assumptions for NIS pelagic life stages through natural dispersal, migration rate threshold estimation could guide between-ports connectivity criteria in early bioinvasion stages. This involves scaling the number of agents reaching a port to individual NIS reproductive output, assumptions about the donor port's established sub-population size, and daily mortality rates during the pelagic stage. Migration rate threshold can be incorporated into later bioinvasion stage criteria by (1) scaling raw connectivity matrices for hypothetical population densities and reproductive outputs; (2) excluding connections below a given migration rate threshold; and (3) reassessing cluster analysis and other graph theory metrics proposed in this study.

Connectivity and spatial scales

When considering the migration rate thresholds, the size of areal units (grid cells) in connectivity analysis may have an impact on the outcome of the analyses. Additionally, connectivity between ports may vary based on whether connections are strictly defined by the geographical outline of ports or if they include larger areas around each port. The latter is common in studies evaluating connectivity between discrete habitats, like coral reefs (Cowen et al. 2006; Fontoura et al. 2022), where larval settlement success relies on explicit thresholds, such as 9 and 8 km from a reef. In continuous habitats, settlement success depends on the resolution of the connectivity grid, e.g., 10×10 km (Robins et al. 2013), 7.5×7.5 km (Moksness et al. 2015), 15×15 km (Van der Molen et al. 2018).

In the SRA RA context, available hydrographic data often overlooks conditions within port basins, preventing accurate consideration of hydrodynamic processes. Ballast water released within a port's basin might encounter localized hydrographic conditions, limiting water exchange with the external environment. This constraint can prevent or delay NIS dispersal to other ports or areas within the SRA candidate. Although introduced NIS in a port could establish subpopulations in favourable conditions, the extent of this phenomenon remains unexplored. Thus, the assumption in this paper's methodology, treating port locations as individual ports and their surroundings, might, in some cases, overestimate potential connectivity between ports, especially in early bioinvasion stages.

Connectivity and temporal scales

Distinguishing between connectivity across temporal scales is important to consider, as populations can be genetically interconnected while demographically isolated (Leis 2002; Swearer et al. 2002; Treml et al. 2012). Demographic connectivity, requiring a sufficient number of successful settlers and recruits per generation, significantly influences population growth rate or maintenance on an interannual scale. In contrast, genetic differentiation may occur with far fewer successful recruits per generation (Slatkin 1993; Treml et al. 2012). In the SRA RA context, time is explicitly considered for

a 5-year exemption period (Stuer-Lauridsen et al. 2018). Thus, assessing connectivity between ports or within an SRA candidate should align with this timeframe. However, if a RA determines that natural dispersal is unlikely within 5 years but remains possible at longer intervals (e.g., 10 or 20 years), preventing NIS spread might still fail despite BW treatment efforts. Currently, there is no resolution on handling temporal scales within the context of SRA RA.

Future perspectives

The applications of biophysical modelling and marine connectivity analysis for SRA RA and other marine ecosystem management scenarios are constrained by the high costs in terms of expert manhours. Developing models, running scenarios, and conducting connectivity analysis demands specialized expertise. To make marine connectivity more accessible to decision-makers, a shift is needed from project-specific endeavours to a more generic approach. An effective solution will be to create databases containing connectivity matrices that can be organized and queried to generate the desired connectivity endpoints. Although the 23 species in Hansen and Christensen (2018) exhibit diverse traits, habitat preferences and environmental tolerances, the data analysis presented here could have been done rapidly and automatically with such a database. Building such a database requires access to hydrodynamic datasets and computational efforts to calculate numerous biophysical modelling simulations, enabling the connectivity matrices with high temporal and spatial resolution. This approach offers a promising path forward.

Declarations

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