Estimation of the risk of introduction of non-indigenous species through ship ballast water in the Port of Douala (Cameroon).

Yannick Nkouefuth Nfongmo[1,2]*, Fils Mamert Onana[1], Estelle Masseret[2], Paul Alain Nana[1], Thomas Efole Ewoukem[1], Adel Kacimi[3]

[1]Laboratory of Ecosystems and Fisheries Resources, University of Douala, Cameroon
[2]MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France
[3]Marine and Coastal Ecosystems Laboratory (ECOSYSMarL), Department of Marine and Coastal Environment, National Higher School of Marine Sciences and Coastal Management (ENSSMAL), 16320 Algiers, Algeria

Corresponding author: Yannick Nkouefuth Nfongmo <yannickkou@gmail.com>

Highlights

- Ships' ballast water represents a major threat to marine biodiversity
- Biological invasion studied using the probabilistic Seebens model
- Port of Douala received ships from 41 ports and 20 ecoregions
- Treating ballast waters reduces biological invasion capacity
- Bioinvasion risk could be modified by climate change

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data underlying this study are available in the Supplementary Material.

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Keywords: ballast water, maritime traffic, modeling, biological invasion, risk assessment, Douala Cameroon

Author contributions

YNN, AK designed research; YNN and AK performed research; YNN, AK analyzed the data; YNN, AK, EM and FMO wrote the paper. TEE reviewed various drafts.

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Abstract

The transport of non-indigenous species in ships' ballast water represents a major threat to marine biodiversity. The Port Authority of Douala (PAD) in Cameroon's Gulf of Guinea is experiencing an increase in maritime traffic, hence the interest in identifying ports at high risk of invasion and the main source regions for bio-invasions. The PAD received ships from 41 ports and 20 ecoregions. Thus, the ports of Antwerp (North Sea), Durban (Natal), Dar es Salaam (East African Coral Coast), Pointe Noire (Gulf of Guinea South) and Dakar (Sahelian Upwelling) presented a major risk of invasion for the PAD (0.94, 0.66, 0.41, 0.37, 0.29 respectively). The 99% treatment efficiency of ballast water from these ports would reduce their bioinvasion capacity by -97.18, -98.43, -98.80, -98.77 and -98.84 respectively. Climate change would modify bioinvasion risks, particularly for ships from the North Sea ecoregion (Pij(Inv)2050 = 0.11) and the port of Antwerp (Pij(Inv)2050=0.08).

Keywords: ballast water, maritime traffic, probabilistic modeling, biological invasion, risk assessment, Douala, Cameroun

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1. Introduction

The role of human activities in transporting species beyond their original range has been widely described. The introduction of these non-indigenous species (NIS) is currently recognized as one of the main causes of global biodiversity loss (Simberloff et al., 2013; Lewis and Maslin, 2015; Bailey et al., 2020). Not only are they directly involved in the loss of native species (Gallardo et al., 2016), but NIS can also harm economic activities and human health (Pimentel et al., 2000; Vilà et al., 2017). To date, thousands of NIS have been observed in marine, brackish, and freshwater ecosystems worldwide (Seebens et al., 2017; Brondizio et al., 2019; Petr Pyšek et al., 2020). Even more can be expected in the future due to disruptions caused by climate change (Hellmann et al.,2008; Seebens et al., 2015). Progress in biosecurity research has guided policy-makers in their decisions to better manage NIS. For example, the Strategic Plan for Biodiversity calls for urgent action by signatory Parties of the Convention on Biological Diversity (CBD) to identify and prioritize alien species pathways for the implementation of management measures to prevent the introduction and establishment of NIS (CBD, 2014). Globally, international shipping, which contributes to 90% of global trade, is the primary pathway for the introduction and spread of NIS (IMO, 2017; Saebi et al., 2020; Tzeng et al., 2021), through biofouling and ballast water discharge (Kospartov et al., 2008; Hewitt et al., 2009).

In Cameroon, as in the entire Economic and Monetary Community of Central Africa (CEMAC), maritime transport contributes to 95% of merchandise trade (Bauchet, 1998; Tchimmogne, 2015). Heavy maritime transport activity therefore further increases in the risk of NIS introductions (Cardenas et al., 2020). This risk of NIS introduction via ballast water motivated Cameroon to ratify the International Convention for the Control and Management of Ships' Ballast Water and Sediments (known as the BWM Convention; IMO, 2004) on 23 April 2020. This convention provides a comprehensive approach to identifying species that are at high risk of becoming invasive in various geographic and climatic zones (Gordon et al., 2008). However, its effective and economically acceptable application (Saebi et al., 2020) requires the use of predictive models to understand invasion pathways in conjunction with the factors that influence propagule pressure (Verling et al., 2005). For example, the probabilistic model by Seebens et al. (2013) can be used to identify high-risk invasion pathways, biological invasion hotspots, and major source regions from which biological invasion is likely to occur. This type of model has been used to estimate the relative levels of the risk of NIS introduction via ballast water in Chinese ports, in the

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Mediterranean, and globally (Wan et al., 2021; Saebi et al., 2020; Wang et al., 2022a), but none have explored this risk of NIS invasion in Sub-Saharan African ports. Thus, this study on the Port of Douala (PoD) (run by the Port Authority of Douala, *Port Autonome de Douala*, known as the PAD) in Cameroon in the Gulf of Guinea, is the first to focus on the introduction of NIS transiting in ship ballast tanks. Our main objective is to provide the necessary information for the establishment of a ballast water management framework for ships calling at the PoD, in accordance with Regulation A-4 of the BWM Convention (IMO, 2004) to limit the risk of introduction of NIS via maritime transport. Thus, our objectives were (1) to establish the risk of invasion between PoD and each port where the ballast water originates between the recipient PoD ecoregion (Gulf of Guinea Central) and each donor ecoregion; (2) to test scenarios of ballast water management and treatment in ports and donor ecoregions with respect to the risk of NIS invasion at PoD; and (3) to predict the risk of invasion for 2050 based on the forecast variations in temperature and salinity values.

2. Methods

We used a large dataset to model the risk of NIS invasion ($P_{ij}(Inv)$) relative to each vessel movement to the Port of Douala (Fig. 1):

(a) Data on the location of ports of origin of vessels that called at PoD during the years 2018–2021 to estimate the probability that the species present in the port of origin i is alien to the port of call j (here, PoD) ($P_{ij}(Alien)$).

(b) An environmental dataset (temperature and salinity) of donor ports (of origin) to estimate the probability of establishment of species introduced via ballast water from ships calling at the PoD ($P_{ij}(Estab)$).

(c) Data on vessel traffic at the PoD and the coastal ecoregions the ports of origin to estimate the risk of introduction of NIS ($P_{ij}(Intro)$).

The combination of the three probabilities $P_{ij}(Alien)$, $P_{ij}(Intro)$ and $P_{ij}(Estab)$ allowed us to predict the risk of invasion ($P_{ij}(Inv)$) of NIS transported in the ballast water of ships that called at Douala from 2018 to 2021.

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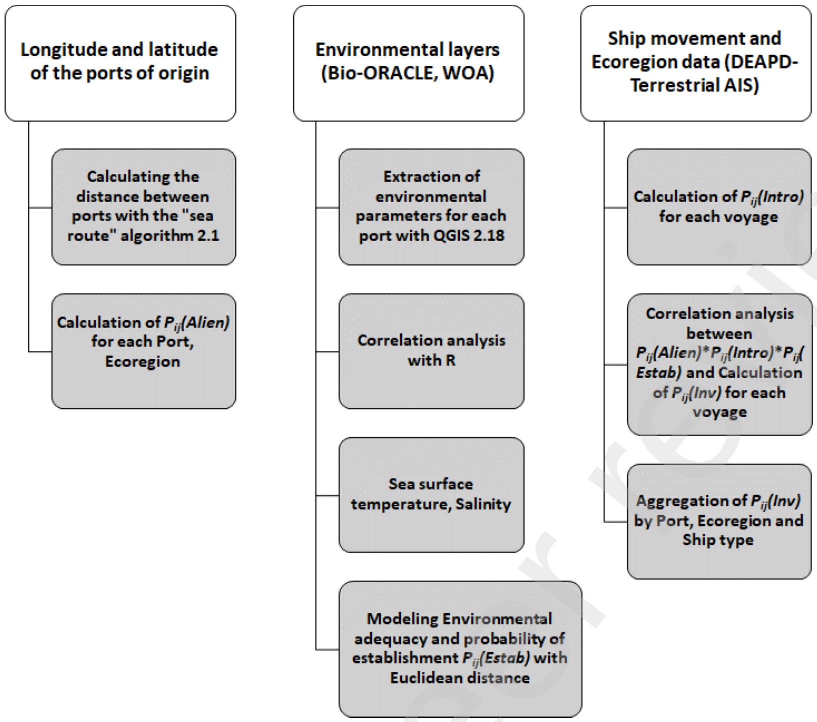

Fig. 1. Diagram showing the steps in the construction of the estimated risk of biological invasion for the Port of Douala.

2.1. Ballast water-mediated invasion risk assessment model

A probabilistic model of species spread mediated by ballast water was used to estimate invasion risk. This model was developed based on a model established by Seebens et al. (2013), which is composed of three parts: the probability of being an alien species for the port of call, the probability of NIS introduction, and the probability of NIS establishment (Eq. 1). Equation (1) presents the risk of species spread from a donor port *i* and a recipient port *j*.

$$P(Inv)_{ij}^{v} = P(Alien)_{ij} \times P(Intro)_{ij}^{v} \times P(Estab)_{ij} \qquad (1)$$

2.1.1 Probability of being a non-native species P_{ij} *(Alien)*

This model describes the probability that a species native to donor port *i* is non-native in recipient port *j* (Eq. 2). This probability is based on the biogeographic dissimilarity between the receiving and donor communities, and is assumed to increase sigmoidally with the geographic distance *dij* between sites *i* and *j* (Thieltges et al. 2009).

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$$P_{ij}(Alien) = \left(1 + \frac{\gamma}{d_{ij}}\right)^{-\beta} \tag{2}$$

Here, β is a shape parameter ($\beta > 0$) and γ is a characteristic geographic distance beyond which species composition begins to change (Spalding et al. 2007). We used the same parameter values as in Seebens et al. (2013): γ =1000 km and β=8.

This model assumes that a port j located near port i primarily contains species already present in port i (Seebens et al. 2013). However, this probability does not take into account the phenomenon of secondary spread, in which the risk of invasion between two nearby ports can be higher than between two distant ports.

2.1.2 Probability of introduction $P_{ij}(Intro)^v$

$P_{ij}(Intro)^v$ (Eq. 3) is the probability of introduction. The probability of introduction is determined by the ballast water discharge volume ${D_{ij}}^v$, the sailing time of the voyage (Δt_{ij}), and the ballast water management efficiency ($1 - \rho^v$). In Equation 3, λ represents the potential for species introduction and μ describes the mortality rate of the species during the voyage. We used the same parameter values as in Seebens et al. (2013): λ=0.002 m^{-3} and μ =0.02 day^{-1}. Ballast water discharge volumes were estimated using the theoretical ballast water discharge estimation model of David et al. (2012), based on vessel deadweight (DWT), the amount of cargo loaded and unloaded by each vessel at PoD.

$$P_{ij}(Intro)^v = \rho^v(1 - e^{-\lambda {D_{ij}}^v})e^{-\mu \Delta {t_{ij}}^v} \tag{3}$$

2.1.3 Probability of establishment $P_{ij}(Estab)$

The probability of species establishment $P_{ij}(Estab)$ is determined by the similarity of the environmental conditions between the two ports i and j (EQ. 4). This probability is modeled as a Gaussian function of the Euclidean distance between the temperatures and salinities of ports i and j, represented by ΔT_{ij} and ΔS_{ij}, respectively, and standardized by the standard deviations δT and δS, which represent the width of the ecological niches, with α=0.00015, δT=2 °C and δS=10 ppt (Seebens et al. 2013). In the case of ballast water, the Euclidean distance is well suited because it accounts for the gradual change in abiotic parameters that affect species in ballast tanks.

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$$\boldsymbol{P_{ij}(Estab)} = \alpha \boldsymbol{e}^{-\frac{1}{2}\left[\left(\frac{\Delta T_{ij}}{\delta T}\right)^2+\left(\frac{\Delta S_{ij}}{\delta S}\right)^2\right]} \qquad \textbf{(4)}$$

The risk of invasion between each port of origin *i* and the PoD, between each donor ecoregion and the Central Gulf of Guinea ecoregion, and according to vessel type was obtained by aggregating all the risks calculated for each vessel voyage *v* to the PoD (Eq. 5).

$$\boldsymbol{P_{ij}(Inv) = 1 - \Pi_{r,v}(1 - P_{ij}(Inv)^{v})} \qquad \textbf{(5)}$$

2.2. Data

2.2.1. Ship movement data

The maritime traffic database used in this study comes from the Port Authority of Douala (PAD) and its Operations Directorate. It is a digital database containing for each vessel calling at the PAD during the years 2018, 2019, 2020 and 2021, the type of vessel, its deadweight, the date of entry, the port of last call and the quantity of goods loaded/unloaded. This original database is confidential. A total of 182 vessels discharged ballast water at the PoD from 2018 to 2021 with 411 voyages from 41 ports (Supplementary material, Table S1a). This database was supplemented with data from the Vesseltracker network (AIS system: https://cockpit.vesseltracker.com/#/cockpit/live/vessels), providing precise information on the vessels: length of stay in each port of call, the distance traveled between two ports of call, the time and date of entry and exit from each port. This information was used to estimate the sailing time of each voyage to the PoD. The data was downloaded individually for each vessel (identified by its IMO number) in CSV format, and then incorporated into the database file containing all 182 vessels.

2.2.2. Environmental data

The layers representing the environmental data were provided from Bio-ORACLE: https://www.bio-oracle.org/downloads-to-email.php, as described in Tyberghein et al. (2012) and Assis et al. (2017). The package All.Present.Surface.BOv2_1.asc (70 N - 70 S Real Values), comprising 65 raster layers at a resolution of 5 arc.min was used for our analyses. Data extraction for each of the donor ports was performed with QGIS 2.18 software using the "Point Sampling

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Tool" extension. These data were extracted for all 41 ports and then analyzed using *R* software to remove variables causing collinearity. For the simulation of the change in environmental variables, we used the "All.2050AOGCM.RCP85.Surface.BOv2_1.asc" package containing the forecasts up until 2050, with the scenario "RCP85". This scenario predicts the increase in greenhouse gas emissions over this period, with very high levels of greenhouse gas concentration being reached by 2040–2050 (Assis et al. 2017; Tyberghein et al. 2012). These datasets were used for analysis of environmental suitability and species establishment probability. Two variables, mean sea surface temperature and mean salinity were selected to implement the $P_{ij}(Estab)$ model (EQ. 4). Environmental parameters for ports not included in the Bio-ORACLE layers were documented from the World Ocean Atlas (Zweng et al. 2019; Locarnini et al. 2018).

2.2.3. Biogeographic data

Marine ecoregions are geographic regions of the ocean that share sets of species with a common evolutionary history. We used the Marine Ecoregions of the World (MEOW) data (Spalding et al., 2007) to characterize the probability of invasion by donor ecoregion. The Flanders Marine Institute IHO-V3 World Seas layer was used as the base shapefile to create the risk maps.

2.3. Prospective evolution of NIS invasion dynamics according to ballast water treatment and environmental parameters forecast for 2050

2.3.1. Ballast water treatment

The PoD is not subject to any ballast water management or treatment regulations. We designed four scenarios of ballast water management policies on an increasing number of donor ports to examine whether the application of these measures could sufficiently reduce the biological invasion risks for the PoD. Scenario 1 (S1): regulations are applied to one key donor port; Scenario 2 (S2): regulations are applied to two key donor ports; Scenario 3 (S3): regulations are applied to four key donor ports; and Scenario 4 (S4): regulations are applied to all 41 donor ports. Two ballast water treatment practices were tested for each of the four scenarios: (a) the current ballast water treatment applied to the world's ports, and (b) the full application of the IMO BWM Convention (2004) D-2 standards. The efficiency of current ballast water treatment systems was estimated from the experimental results described by Wang et al. (2021). In contrast, when fully applying

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the BWM Convention D-2 standards, treatment efficiency was calculated from the concentration of organisms in untreated ballast water relative to the IMO numerical standards (Wang et al. 2021; Wang et al. 2022b). The efficiency of current treatment systems is about 76% and about 99% upon full compliance with the IMO BWM Convention (Wang et al., 2021). This simulation of ballast water treatment changes the parameter ρ^v in Equation. 3, i.e., 1-ρ^v =76% or 99%.

2.3.2. Changing environmental parameters

The simulation of changes in environmental parameters with respect to climate change was carried out using the temperature and salinity forecasts predicted for 2050 (Tyberghein et al. 2012;Assis et al. 2017). These data were used to estimate the probability $P_{ij}(Estab)_{2050}$ for all donor ports and as well as the PoD to estimate the new risk $P_{ij}(Inv)_{2050}$.

3. Results

3.1. Risk of invasion by ecoregion

Each ecoregion is associated with a unique shipping route that has a corresponding level of risk of biological invasion via shipping. These different levels of risk per ecoregion arise from a combination of several parameters, described in Seebens et al. (2013). Thus, the following parameters were taken into account: (i) the intensity of traffic; (ii) the environmental similarity between the ecoregions from which the ballast water originates and that of Douala; (iii) the duration of the crossing between the donor and recipient ecoregions; (iv) the volumes of ballast water exchanged between the donor and recipient ecoregions; and, finally, (v) the geographical distance between ecoregions (Seebens et al., 2013). The PoD is part of the Gulf of Guinea Central ecoregion (GGC-17), the Gulf of Guinea province and the Tropical Atlantic biogeographic realm (Fig. 2). In total, the PoD received ballast water discharges from 20 coastal ecoregions, of which 15 ecoregions pose low risk as an invasion source, 2 ecoregions pose moderate risk, 2 ecoregions pose high risk, and 1 ecoregion poses a very high risk of being a source of bioinvasion (Fig. 2). Three ecoregions appear to stand out in terms of their potential of being a source of bioinvasion via ballast water discharges in the PoD: (1) the NS-2 ecoregion which presents a very high risk ($P_{ij}(Inv)$ = 0.94); (2), the N-51 ecoregion ($P_{ij}(Inv)$ = 0.69); and (3) the EACC-20 ecoregion ($P_{ij}(Inv)$ = 0.53) (Table S2b; Fig. 2.). Statistical Analysis by ecoregion shows that, the amount of ballast

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water $\boldsymbol{D_{ij}}^{v}$ is weakly correlated with invasion risk (r= 0.086).Crossing time $\Delta \boldsymbol{t_{ij}}$ and geographical distance $\boldsymbol{d_{ij}}$ are inversely correlated with invasion risk/ecoregion (r= -0.17 and -0.082 respectively) (Table S2a).On the other hand, the probability of invasion (P(Inv)) per ecoregion was strongly correlated with the risk of introduction P_{ij}($Intro$), with r=0.50, establishment P_{ij}($Estab$), with r=0.62, and the probability of being a non-native species P_{ij}($Alien$), with r=0.67 (Table S2a).

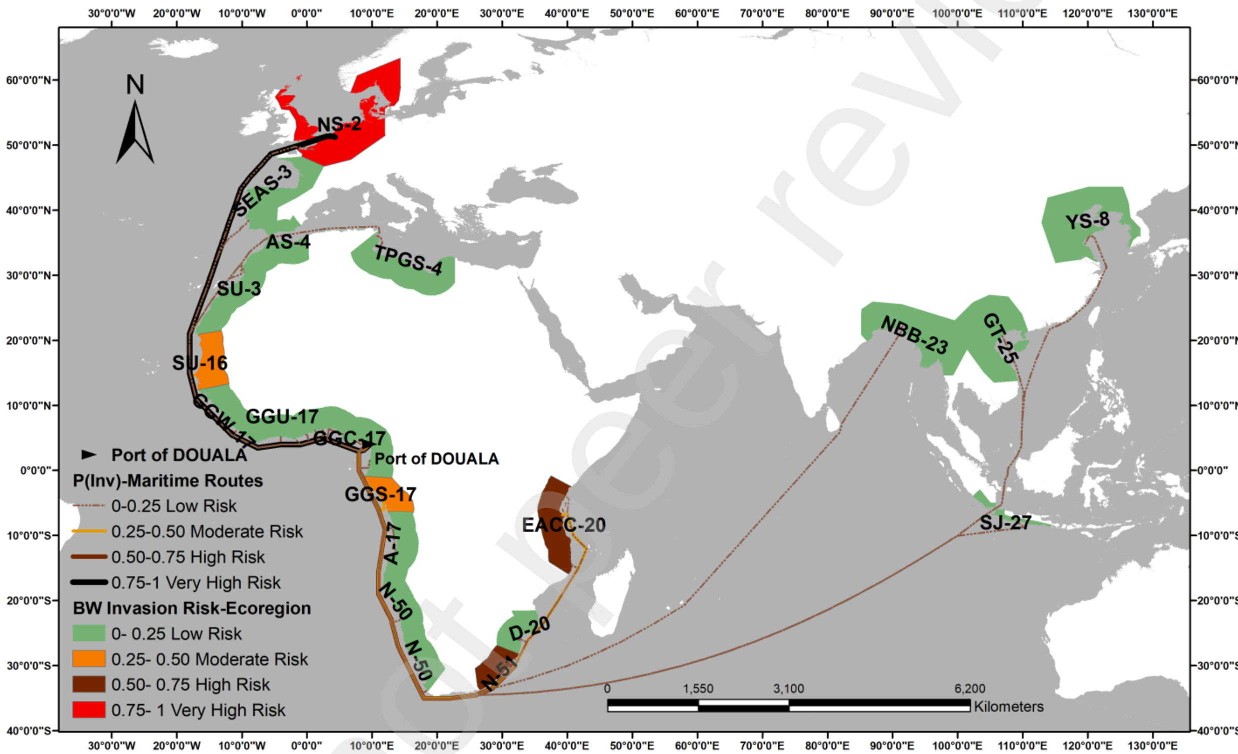

Fig. 2. Map showing the risk of ballast-water-mediated biological invasion at the Port of Douala from donor ecoregions during 2018–2021. Lines represent risk levels associated with ship trajectories from marine ecoregions (ArcMap 10.4). The background map was produced by Flanders Marine Institute, available online at: https://doi.org/10.14284/323. The shipping routes were generated with the searoute algorithm, available online at: https://github.com/eurostat/searoute. (Arc Map 10.4).

3.2. Risk of invasion by donor port

From 2018 to 2021, the PoD recorded 4647 ship movements from 152 ports belonging to 45 ecoregions on four continents: Africa, Asia, America and Europe (confidential data from PAD). In total, 411 vessels from 41 ports (20 ecoregions) discharged their ballast water in the PoD (confidential data from PAD). On the African continent, the donor ports are located in 14

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ecoregions: in the Atlantic Ocean (9 ecoregions, 26 ports), the Indian Ocean (3 ecoregions, 6 ports) and the Mediterranean (2 ecoregions, 2 ports) (Table 4). In Asia, two ports are located on the Indian Ocean in two ecoregions and two ports are located on the Pacific Ocean in two ecoregions. In Europe, three ports are in two ecoregions. The PoD received vessels from 36 ports with low invasion risk($0 \leq P_{ij}(Inv) < 0.25$), accounting for 77.37% of the ballast water discharged in the PoD or exactly 532,379.99 t. Among these ports, 16 ports are located in the Gulf of Guinea ecoregions GGC-17 (Lagos, Cotonou, Warri, Escravos, Lome, Port-Gentil, Bata, Zafiro, Onne, Calabar, Punta Europa, Owendo and Malabo) and GGU-17 (Tema, Accra, Takoradi). They discharged 48.73% of ballast water into the PoD (Table 3, 4 Suppl. data). The PoD ran moderate biological invasion risks($0.25 \leq P_{ij}(Inv) < 0.50$) when hosting vessels from the ports of Dakar (Senegal), Dar es Salaam (Tanzania) and Pointe-Noire (Republic of the Congo); high invasion risk ($0.50 \leq P_{ij}(Inv) < 0.75$) with respect to the donor port of Durban and very high invasion risks ($0.75 \leq P_{ij}(Inv) < 1$) with respect to the donor port of Antwerp (Fig. 3, Table S1a).

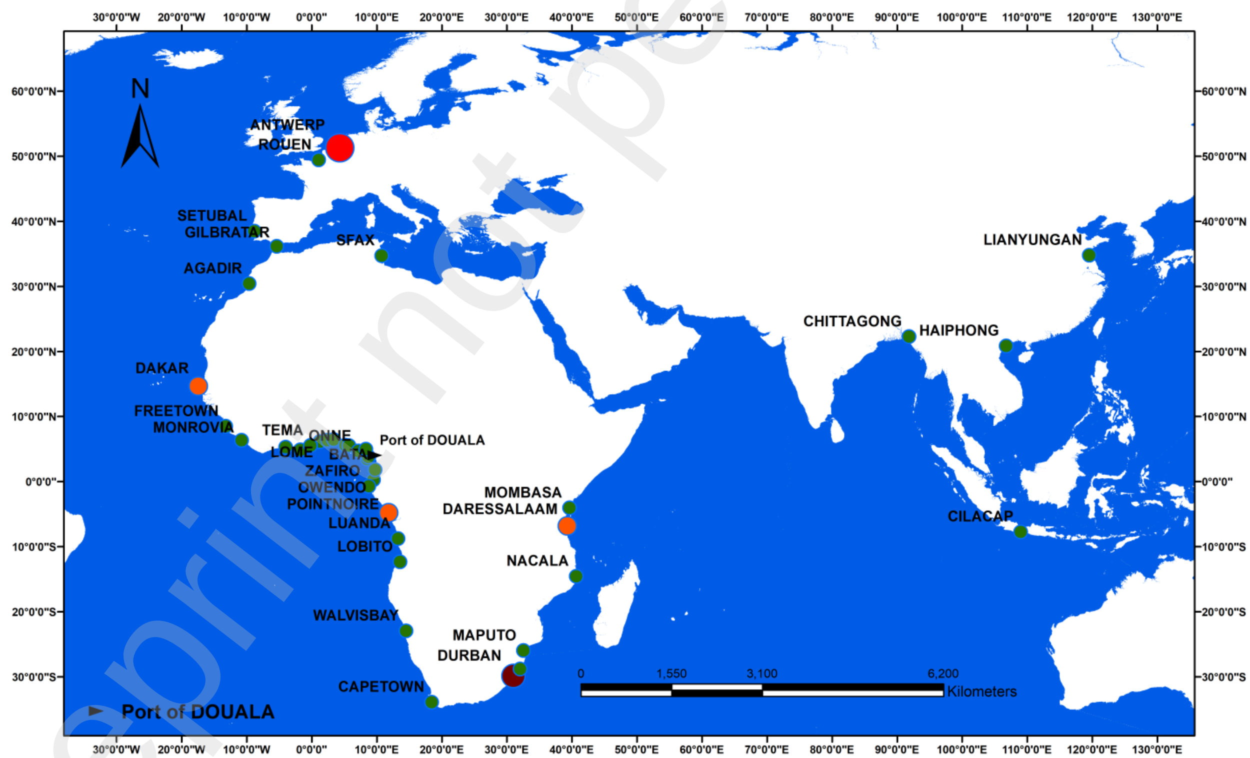

Fig. 3. Map showing the probability of biological invasion through ballast water for all donor ports during the years 2018–2021, expressed as the relative risk of each port to the Port of Douala(PoD). The size of each point indicates the relative contribution $\boldsymbol{P_{ij}} = P_{ij}(Inv)/$

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$\sum_i P_{ij}(Inv)$ of source port *i* to the total invasion risk of all ports. Green dot indicates low risk ($0 \leq P_{ij}(Inv) < 0.25$), orange dot moderate risk ($0.25 \leq P_{ij}(Inv) < 0.50$), brown dot high risk ($0.50 \leq P_{ij}(Inv) < 0.75$), red dot very high risk ($0.75 \leq P_{ij}(Inv) < 1$)(Arc Map 10.4).

The ports of Antwerp (Belgium, North Sea), Durban (South Africa, Indian Ocean), Dar es Salaam (Tanzania, Indian Ocean), Pointe Noire (Congo-Brazzaville, Atlantic Ocean) and Dakar (Senegal, Atlantic Ocean) (Table 1) are considered major sources of bioinvasion ($P_{ij}(Estab)$ ranging from 0.32 to 0.94) with a significant probability of being a source of NIS ($P_{ij}(Intro)$ = 0.98–1) (Table S1a). These results suggest that there ballast water is discharged at each call of a ship from these ports.

Table 1: Ranking of the 10 ports of origin of vessels whose ballast water poses the greatest risk of introducing non-indigenous species into the Port of Douala. Low risk ($P_{ij}(Inv)$<0.25), *Moderate risk ($P_{ij}(Inv)$<0.50), **High risk (⟦$P_{ij}(Inv)$<0.75), ***Very high risk ($P_{ij}(Inv)$<1).

Table 1
Ranking of the 10 ports of origin of vessels whose ballast water poses the greatest risk of introducing ENI into the PAD. low risk ($0 \leq P_{ij}(Inv) < 0.25$), *moderate risk ($0.25 \leq P_{ij}(Inv) < 0.50$), **high risk ($0.50 \leq P_{ij}(Inv) < 0.75$), ***very high risk ($0.75 \leq P_{ij}(Inv) < 1$).

Ecoregion	Country	Port	Rank	Invasion risk (P_{ij}(Inv))	Probability of species arrivals (P_{ij}(Intro))	Environmental similarity (P_{ij}(Estab))	Proportion of ship arrivals (%)	Proportion of Ballast Water Discharge (%)
North Sea	Belgium	Antwerp	1	0.94***	1	0.4	7.3	2.84
Natal	South Africa	Durban	2	0.66**	1	0.32	3.89	7.39
East African Coral Coast	Tanzania	Dar-Essalaam	3	0.41*	0.98	0.46	0.97	1.84
Gulf of Guinea South	Congo	Pointe-Noire	4	0.37*	1	0.94	8.76	8.99
Sahelian Upwelling	Senegal	Dakar	5	0.29*	0.99	0.35	2.43	1.55
Saharan Upwelling	Maroc	Agadir	6	0.23	0.96	0.4	0.97	0.31
East African Coral Coast	Kenya	Mombasa	7	0.18	0.97	0.21	0.73	1.77
Angolan	Angola	Luanda	8	0.16	1	0.44	3.89	5.24
Northern Bay of Bengal	Bangladesh	Chittagong	9	0.14	0.61	0.37	0.24	0.36
Natal	South Africa	Richards-Bay	10	0.11	0.82	0.32	0.97	1.98

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3.3. Invasion risk by ship type

Eleven vessel types discharged ballast water into the PAD between 2018 and 2021: container ships, pinarders, general cargo ships, bulk carriers, car carriers, refrigerated vessels, roll-on roll-off (ro-ro) ships, tankers, clinker in bulk ships, hybrid vessels, and coasters (Table S3a). The risk of invasion by vessel type was dominated by refrigerated vessels ($P_{ij}(Inv)$ = 0.96), which made 104 trips to the PoD and discharged 8.69% of the total accumulated ballast water from 2018 to 2021 (Fig. 4, Table S3a). General cargo ships occupied the second position in the risk of invasion ($P_{ij}(Inv)$ = 0.88) with 39.39% of the ballast water discharged and 102 arrivals. Bulk carriers came in third position, exerting a high risk of invasion on the PoD ($P_{ij}(Inv)$ = 0.55) with 25.30% of ballast water discharged in only 55 voyages. In addition, container ships presented a moderate bioinvasion risk ($P_{ij}(Inv)$=0,313) with 15.72% ballast water discharged in 73 arrivals. Ro-ro, clinker in bulk, tankers, hybrid vessels, car carriers, coasters and "pinarders" vessels generally showed a low risk of invasion ($P_{ij}(Inv)$ = 0.16, 0.05, 0.04, 0.04, 0.02, 0.015 and 2.68×10-5, respectively) (Fig. 4, Table S3a).

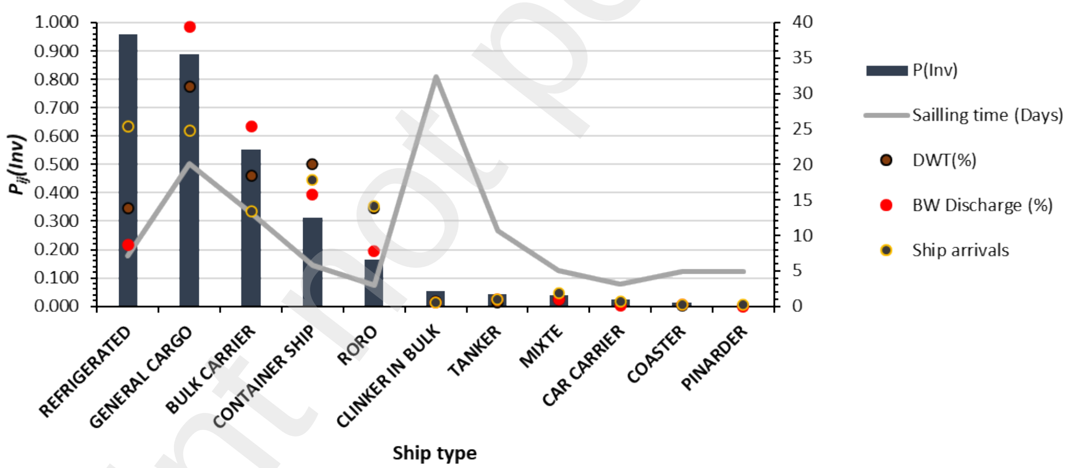

Fig. 4. Variation in invasion risk by vessel type and as a function of deadweight, ballast water discharge, number of arrivals and ship sailing time.

In the model, the probability of invasion by vessel type was significantly correlated with the deadweight tonnage of the vessels (r=0.81), the amount of ballast water discharged (r=0.77), the total number of vessels (r=0.92) (Table S3b). In addition, there were significant differences in the probability of invasion according to ship type (ANOVA, p-value= 4.08×10^{-7}) (Table S4).

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3.4. Simulation of the impact of two ballast water treatment practices on bioinvasion risk

a. Implementation of current ballast water treatment measures

Scenario 1: By applying current ballast water treatment methods only to the Port of Antwerp (NS-2), the reduction of the risk of biological invasion is -47.62% from this port and -46.77% from the NS-2 ecoregion as a whole (Figs. 5–6 and Table S5a). The application of Scenario 1 can help reduce the overall invasion risk in the PoD by 0.70% (Table S5b).

Scenario 2: By regulating the ports of Antwerp and Durban (N-51 ecoregion), our predictions show a reduction in the invasion risk by -47.62% and -65.08%, respectively, from these two ports, with a reduction in the risk of bioinvasion from the Natal ecoregion (N-51) of -55.12% (Figs. 5–6 and Table S5a). The overall risk in this Scenario 2 is reduced by 1.69% (Table S5b).

Scenario 3: By introducing specific management measures at the four leading high-risk ports in this study, i.e. Antwerp, Durban, Dar es Salaam (EACC-20) and Pointe-Noire (Gulf of Guinea South, GGS-17), the risk of invasion from Dar es Salaam and Pointe-Noire is reduced by 71.24% and 70.71% (Figs. 5–6, Table S5a). These results lead to an overall reduction in the risk for the PoD of 3.66% (Table S5b). Similarly, the risk from the EACC-20 and GGS-17 ecoregions are reduced by 44.08% and 70.71%, respectively (Figs. 5–6, Table S5a).

Scenario 4: By generalizing ballast water treatment with 76% efficacy across all donor ports over the last four years, the overall risk to the PoD would have been reduced by only 18.28% (Table S5b). This scenario would also reduce the risk of invasion from all donor ports and ecoregions (excluding the four major donor ports) at rates ranging from 72.10% to 75% (Figs. 5–6, Table S5a).

b. Application of ballast water treatment measures according to the BWM Convention D-2 standards

The risk of invasion is decreased by 97.18%, 98.43%, 98.80%, 98.77% for Antwerp (NS-2), Durban (N-51), Dar es Salaam (EACC-20), and Pointe-Noire (GGS-17) in the S1, S2, S3 scenarios, respectively (Figs. 5–6, Table S5c). At this stage, the risk of bioinvasion from high-risk ecoregions undergoes a strong decrease estimated at 98.65%, 98.67%, 98.36%, 97.17%, for the EACC-20, GGS-17, N-51 and NS-2 ecoregions, respectively) (Figs. 5–6, Table S5d). The overall bioinvasion risks at the PoD decrease by 1.42%, 4.30%, 11.54% and 93.49% respectively in scenarios 1 to 4 by regulating 1, 2, 4 and all 41 ports (Table S5d). Scenario 4 shows an increased

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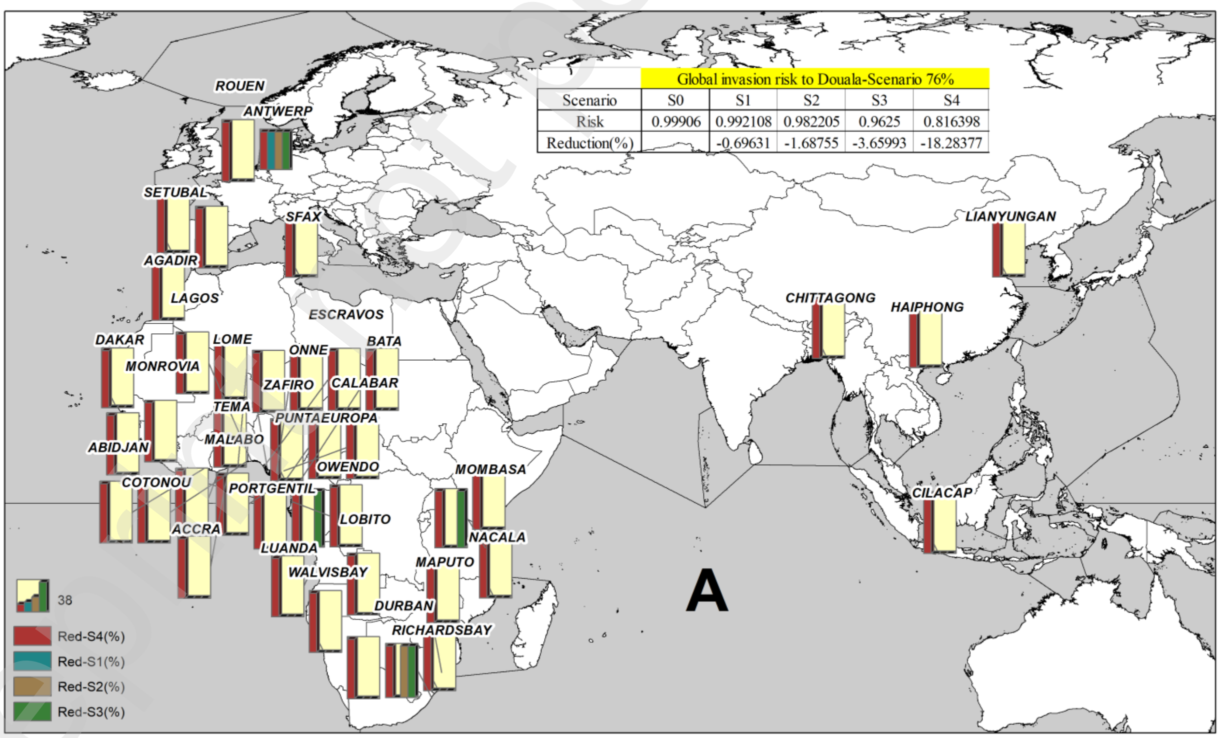
reduction in invasion risk for all of these same donor ports (from 98.84–99%) and ecoregions of origin (98.91–99%) (excluding the four donor ports and four donor regions) (Table S5c).

Furthermore, the application of a two-factor ANOVA with repetition on the change in risk according to the chosen scenarios and the effectiveness of the treatment (α=0.05) showed that the effectiveness of the treatment significantly impacts the reduction of risk at port (p-value=1.52×10^{-05}) and ecoregion (p-value=3.05×10^{-03}) levels (Table S10/S6ab). The same test shows that the generalization of the BWM Convention regulation to all donor ports would play a decisive role in reducing the risk of invasion of ports and ecoregions of origin (p-value=1.91×10^{-121} and p-value=5.03×10^{-44}, respectively) (Table S1, S6ab). In addition, the combination of the adapted management strategy (76% or 99%) and the number of ports to be regulated (Scenarios 1 to 4) proved to be a crucial element in reducing the invasion rate at the PoD (p-value=2.04×10^{-06} and p-value=0.03, respectively for donor ports and ecoregions) (Table S1, S6ab). Overall, the analysis showed that specific regulation of the ports with the greatest threat of marine bioinvasion to the PoD (S1–S3, Table S1), would not be sufficient to reduce the overall risk of invasion to the PoD.



	Global invasion risk to Douala-Scenario 76%				
Scenario	S0	S1	S2	S3	S4
Risk	0.99906	0.992108	0.982205	0.9625	0.816398
Reduction(%)		-0.69631	-1.68755	-3.65993	-18.28377

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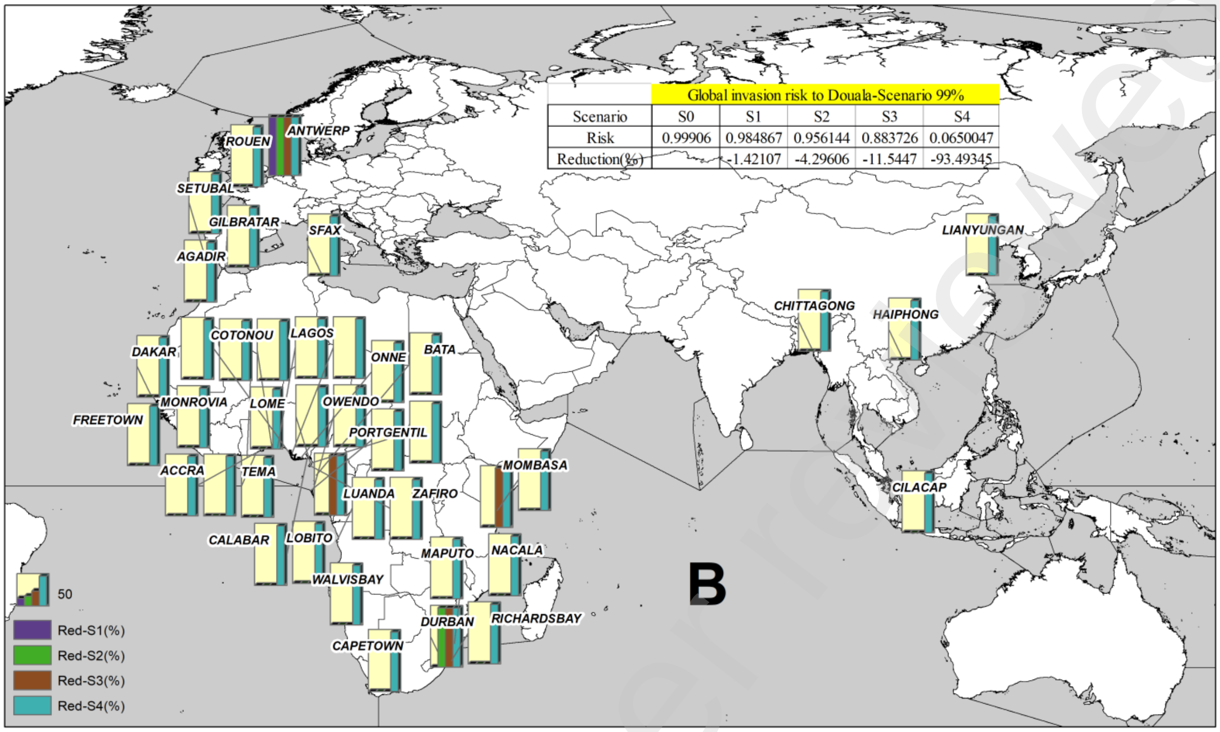

Fig. 5. Reduction of the risk of invasion by donor port according to ballast water treatment scenarios. A: treatment efficiency equal to 76% (current ballast water treatment system). B: treatment efficiency equal to 99% (OMI, 2004).

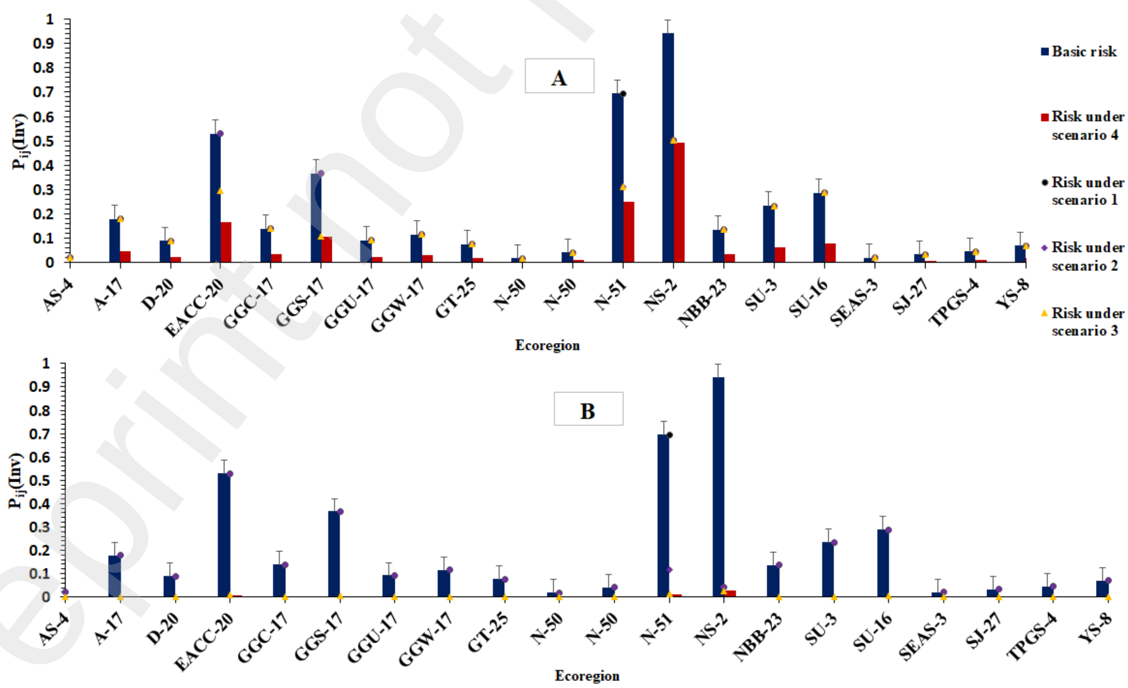

Fig. 6. Change in invasion risk from donor ecoregions at the Port of Douala under different ballast water treatment scenarios (2018–2021). A: 76% treatment efficiency. B: 99% treatment efficiency.

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3.5. Simulation of the projected change in environmental parameters on bioinvasion

Projected global warming would alter species establishment rates and ineluctably affect the transfer of NIS (Redding et al., 2019). Using projections to 2050, with a scenario of increasing emissions over time leading to high levels of greenhouse gas concentration by 2040–2050 (RCP85) generated alarming results (Fig. 7A, Table S7 Suppl. data). The settlement probabilities of most ballast-water-donor ports may be altered as demonstrated by the strong correlation between the current settlement probability and that of the 2050 forecast ($r = 0.88$) (Table S8). Global warming appears to have a direct impact on current invasion risk values. Referring to the five ports with moderate to very high bioinvasion risks (Table 1), the projection to 2050 shows that the ports of Durban, Dar es Salaam, Dakar and Pointe-Noire would show increases in bioinvasion risk of 33.84%, 40.05%, 60.20% and 3.38%, respectively (Fig. 7A, Table S7). At these values, the Port of Durban with a value of ($P_{ij}(Inv)_{2050} = 0.88$) would become a donor port with a very high bioinvasion risk for the PoD (Fig. 7A, Table S7).

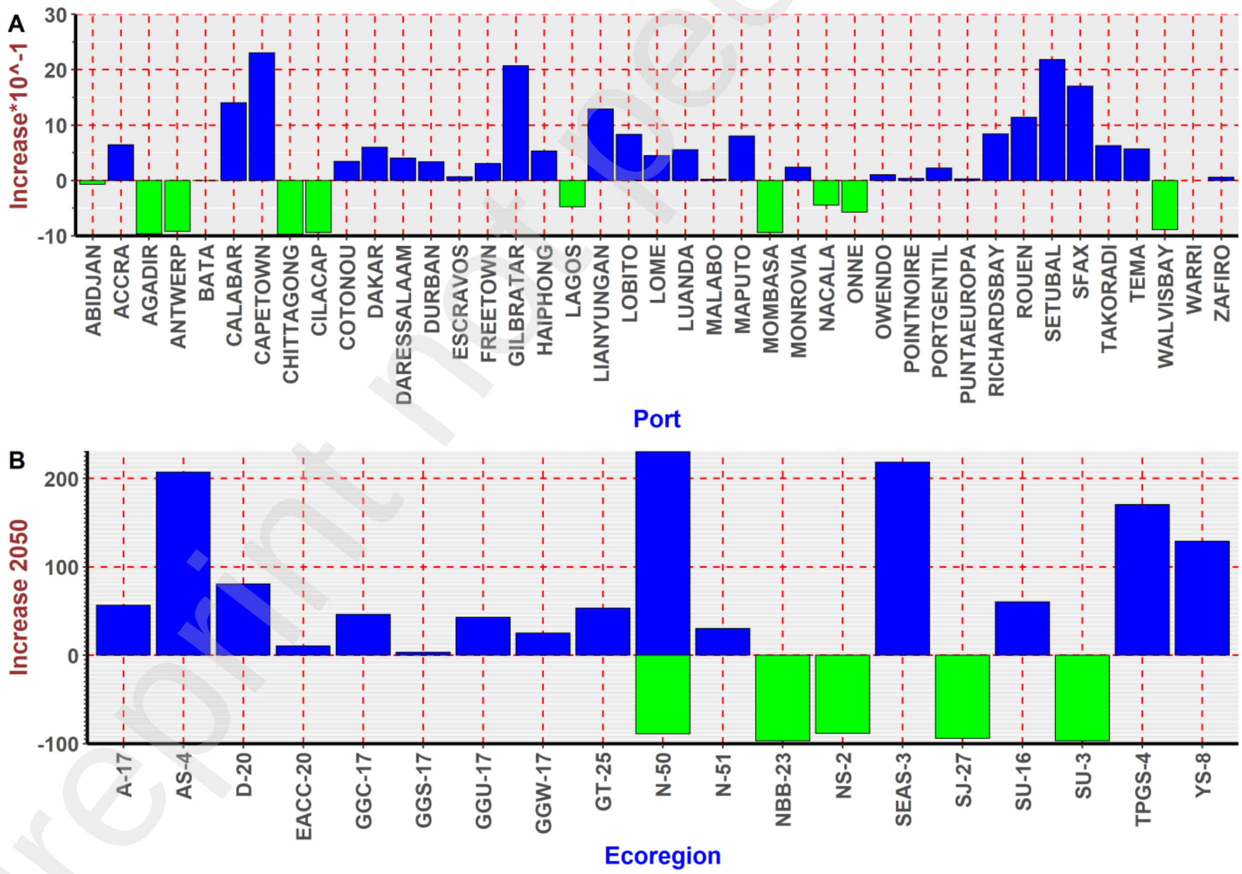

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Fig.7 Change in invasion risk caused by change in environmental parameters by 2050. A: Change in individual ports of origin. B: Change by donor ecoregion. (*R*.4.1.1).

On the other hand, the Port of Antwerp, which was considered in this study for the period 2018–2021 as a port with a very high risk of biological invasion with respect to the PoD, appears to present a low risk of invasion by 2050 ($P_{ij}(Inv)_{2050}$ = 0.08) with a reduction of 91.76% (Fig. 7A, Table S7). Similarly, the NS-2 ecoregion, to which Antwerp belongs, seems to show a low invasion risk ($P_{ij}(Inv)_{2050}$ =0.11) with a reduction of 88.25% (Fig. 7B, Table S9). In contrast, the N-51, EACC-20, Sahelian Upwelling (SU-16), Angolan (A-17), and GGS-17 ecoregions may see an increase in their bioinvasion risk for the PoD (Fig.7.B, Table 9 Suppl. data). Although the increase in bioinvasion risk for the Delagoa, Yellow Sea, Tunisian Plateau/Gulf of Sidra, Alboran Sea, South European Atlantic Shelf and Namaqua ecoregions range from 80% to 230%, the bioinvasion risk values forecast for 2050 remained lower than 0.25 (Table S9).

4. Discussion

4.1. Risk of invasion by ecoregion

The risk of invasion from one ecoregion to another results from the combination of several parameters: the volume of maritime traffic, the environmental similarity, the distance between the most connected ecoregions (Seebens et al., 2013; Sardain et al., 2019), and the presence of ports acting as hubs at the ecoregion level. Thus, the high invasion risk values ($P_{ij}(Inv)$ ranges from 0.53 to 0.94) from the North Sea, Natal (South Africa) and the East African Coral Coast ecoregions can be attributed to the three following reasons:

First, the high value of the probability of receiving NIS from these three ecoregions ($P_{ij}(Alien)$ = 0.99–1, Table S2b) due to the high heterogeneity between donor and recipient communities. This heterogeneity may be linked to the origin of ship ballast water from port hubs in the NS-2 and N-51 ecoregions, and to environmental similarities with the EACC-20 ecoregion in the Indian Ocean.

Second, the large volumes of ballast water discharged $\boldsymbol{D_{ij}}^{\boldsymbol{v}}$ (23,949.65 to 64,479.82 t of water per ecoregion) in the PoD according to Lockwood (2005), who linked the tonnage of water discharged to the risk of invasion, and the duration of ship crossings from NS-2, N-51 and EACC-20 Δt_{ij}=14.07 to 33.73 days. Indeed, these relatively short crossing times allow the survival of many NIS (Chu et al., 1997).

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Third, the probability of establishment in the GGC-17 ecoregion, calculated by integrating salinity and temperature from the NS-2, N-51, and EACC-20 ecoregions, is also high ($P_{ij}(Estab)$ = 0.96–1, Table S2b). Organisms present in ballast water from the NS-2, N-51, and EACC-20 ecoregions may thus have an increased probability of establishing in the GGC-17 ecoregion. Again, this can be explained by the fact that the ports of Antwerp and Durban are hubs receiving ships from all over the world (Peng et al., 2019; Port of Antwerp 2021; Gerhard and Gunsch 2019). Organisms capable of growing at summer seawater temperatures recorded in temperate environments (e.g. NS-2) can potentially adapt to tropical conditions (Seebens et al., 2013). In the case of Durban (N-51), the main ocean current near South Africa flows from the equator towards the poles. The ecophysiological characteristics of the biota present in the waters loaded along the route to Durban may then favor its acclimatization to the environmental conditions of the GGC-17 ecoregion and subsequent settlement in the PoD (Gerhard and Gunsch, 2019).

The biological invasion risk values for the donor ecoregions just to the north (SU-16) and south (GGS-17) of the GGC-17 ecoregion were moderate for the PoD ($P_{ij}(Inv)$ =0.29 and 0.37, respectively) (Fig. 2, Table S2b). These relatively low values can be attributed to the combined effect of three factors: (i) the high diversity of aquatic organism communities in these ecoregions compared with those in the GGC ecoregion ($P_{ij}(Alien)$ = 0.82 for SU-16); (ii) the high environmental similarity between these three ecoregions ($P_{ij}(Estab)$ = 0.98–1); and (iii) the high potential for introduction of NIS ($P_{ij}(Intro)$ = 0.99–1) (Table S2b). Our results are consistent with those described by Saebi et al. (2020) for the N-51 and EACC-20 ecoregions, which are at high risk of biological invasion from the PoD in the Tropical Atlantic realm. Regarding the risk of moderate invasion from the GGS-17 and SU-16 ecoregions located in the Tropical Atlantic biographical realm, Saebi et al. (2020) do not consider this risk to be completely zero. Moreover, the risk of bioinvasion at the ecoregion level can also occur between the close ecoregions (Wang *et al*., 2022b). The high risk of invasion between the NS-2 (Temperate Northern Atlantic realm) and the GGC-17 (Tropical Atlantic) observed in our study was not highlighted in the study by Saebi et al. (2020). This very high invasion risk thus appears to be mainly linked to the intensity of shipping between these two marine ecoregions (Fig. 2), climate change and the hub role of the Port of Antwerp, as demonstrated by the high probability of invasion observed between the East Asian and North European seas (Seebens et al., 2016).

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4.2. Risk of invasion by port

The geographical distribution of donor ports recorded during our study was vast. They are spread over five large marine realms: Central Indo-Pacific, Western Indo-Pacific, Temperate Southern Africa, Tropical Atlantic and Temperate Northern Atlantic. This exposes the PoD to potential risks of invasion by NIS. Thus, the PoD presented moderate biological invasion risks ($0.25 \leq P_{ij}(Inv) < 0.50$) by hosting ships from the ports of Dakar, Dar es Salaam and Pointe-Noire; high invasion risks ($0.50 \leq P_{ij}(Inv) < 0.75$) from the port of Durban; and very high invasion risks ($0.75 \leq P_{ij}(Inv) < 1$) from the port of Antwerp (Fig. 3, Table S4). Thus, the large volumes of ballast water exchanged between these ports and the PoD (*r*=0.39) combined with the relatively short voyage times (*r*=-0.75) are likely the main factors. In addition, the number of ships from these ports is strongly correlated with the quantities of ballast water discharged at the PoD (*r*=0.89). These discharges can lead to a potential transfer of NIS from these high-risk ports, as has been observed for the toxic dinoflagellate species *Karenia* sp. and *Alexandrium minutum* established on the Belgian and South African coasts, respectively (Gollasch et al., 2009; Pitcher et al., 2007). The very high invasion risk from the Port of Antwerp can also be linked to the intense maritime traffic between these two ports, represented by 30 ship arrivals out of the 411 recorded, i.e.7.3% of ships in total. These ports have even been described as "bioinvasion hotspots" solely on the basis of shipping intensity (Levine and Antonio, 2003; Drake and Lodge, 2004). Currently, the Port of Antwerp is one of the main ports for the exchange of goods with Sub-Saharan Africa, with respectively 8.7 Mt of goods unloaded and 17.7 Mt of goods loaded in 2021 (Antwerp, 2021). The low invasion risk observed between the PoD and the 16 ports located in the Gulf of Guinea, which nevertheless contribute to 48.73% of the ballast water discharged into the PoD, appears to be linked to the high biogeographical similarity between these ports and the PoD located within close biogeographical similarity distances (≤1000–1500 km) (Spalding et al., 2007; Wan et al., 2021). This result confirms that the distance between ports strongly influences the risk of NIS invasion (Verling et al., 2005; Minton et al., 2005), but also shows that large quantities of water from a port do not necessarily lead to successful invasion (Leung et al., 2004; Lo et al., 2011). On the other hand, the low invasion risk obtained at other ports located at distances greater than 1500 km (20 ports) and the PoD means that there may be little biogeographical similarity between those ports and the PAD. This apparent discrepancy may also be attributed to the fact that, over long distances, the crossing speed is reduced, crossing times are long, and the chances of survival of

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organisms during transport are low. In fact, the long residence times of these organisms in ballast tanks lead to prolonged unfavorable conditions, such as hypoxia and lack of light, which will cause the death of many organisms inside the ballast tanks (Seebeens et al., 2013). Deballasting operations during the trip must also be taken into account, which can further reduce the number of surviving species from donor ports (Wan et al., 2021).

4.3. Risk of invasion by ship type

The volume of ballast water discharged into the PoD depends on the size of the ships, the volume of their ballast tanks and the number of crossings. Consequently, bioinvasion dynamics can be associated with a specific ship type (Seebens et al. 2013; Tzeng et al., 2021). Establishing correlations between invasion probabilities by vessel type by considering the vessel's maximum cargo tonnage (DWT), the quantities of ballast water discharged and the number of crossings highlighted the change in invasion risk as a function of vessel type. These correlations showed that ship size, ballast water discharge and number of calls to PoD influenced the variation in invasion risk by vessel type. The highest risk of invasion by vessel type was recorded for refrigerated vessels, with $P_{ij}(Inv) = 0.96$. Indeed, the number of voyages made by this type of vessel at the PoD was among the highest, with 104 voyages (Table S3). This type of vessel is widely used to export fresh produce from the PoD, particularly bananas, to the European market. Bananas ranked sixth among the goods exported from the PoD in the first half of 2021, at 96,749 t (CNCC, 2021). This ranking of invasion risk by type of vessel differs according to region and type of commodity, which depends on trade (Saebi et al., 2020).

4.4. Simulation of ballast water treatment efforts impact on bioinvasion

Our analysis showed that the ports of Antwerp, Durban, Dar es Salaam and Pointe-Noire were high-risk bioinvasion ports during the study period (2018–2021). The ports of Antwerp, Durban and Dar es Salaam are considered to be hubs, connecting several other ports. It can be assumed that, due to this characteristic, these ports may act as springboards that facilitate the spread of NIS between different ecoregions. The Port of Antwerp is an important hub of world trade due to its central location and extensive connections to global markets (Peng et al., 2019). The Port of Durban serves as a transshipment hub for East Africa and the Indian Ocean islands. The Port of Pointe-Noire is at the crossroads of the major shipping routes of Europe, Asia, and America. The

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port is an ideal transshipment hub on the West African coast. Owing to these strategic characteristics, these key ports were chosen as the target for regulation in this study. The results of the simulation of ballast water treatment scenarios showed that the risk of hosting a new invasion at the PoD during the study period (2018–2021) would have been reduced using the BWM Convention treatment efficiency of 99%, if this level of efficiency was to be generalized to all ports of call. Similarly, Wang et al. (2021) argued that regulation of ports of call prior to arrival at the destination port studied, combined with regulation of the "hub" ports themselves, would be necessary to reduce the risk of invasion. Thus, global and regional regulations are necessary to reduce the risk of invasion by NIS. The full application of IMO standards on ballast water management remains the most effective means of limiting the spread of NIS.

4.5. Simulation of projected changes in environmental parameters on bioinvasion

The warming of water masses due to climate change predicted for 2050 is likely to alter the environmental conditions of many marine ecoregions, thus affecting the likelihood of invasion from one ecoregion to another (Seebeens et al., 2016). An increase in the bioinvasion risk sourced from the South African N-51, East African EACC-20, West African SU-16, Angolan A-17 and/or the Gulf of Guinea South (GGS-17 ecoregions could therefore be expected at the PoD due to potential changes in the population structure and taxonomic composition of organisms present in these ecoregions. As such, one study predicted an increase in dissimilarity in the community composition of these ecoregions (Molinos et al., 2016). On the other hand, the decrease in dissimilarity would be responsible for the reduced risk of the North Sea ecoregion.

5. Conclusion

This study of the estimated risk of introduction of NIS through ship ballast water at the PoD over the 2018–2021 period, showed that ballast water discharged at the PoD (≃ 688,053 m^3) came from 41 ports, belonging to 20 ecoregions. The ports of Antwerp, Durban, Dar es Salaam, Pointe-Noire, and Dakar, and their respective ecoregions, are important sources of potentially invasive NIS for the PoD. The Port of Antwerp and the North Sea ecoregion presented a very high risk of NIS introduction via ballast water, with a $P_{ij}(Inv)$ of 0.94. Furthermore, of the 11 ship types responsible for ballast water discharges, refrigerated ships presented the highest risk of invasion ($P_{ij}(Inv)$ = 0.96). Applying a ballast water treatment efficiency of roughly 99% in full compliance

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with the IMO BWM Convention (Scenario 4) can lead to a better reduction in the risk of invasion from all donor ports and ecoregions, with rates ranging from -99% to -98.84 and from -99% to -98.98%, respectively. An analysis of invasion risk forecasts for 2050, based on surface temperature and salinity, showed that the Port of Durban ($P_{ij}(Inv)_{2050} = 0.88$) can potentially become the donor port qualified as a source of "very high risk of biological invasion" for the recipient PoD. On the other hand, the donor Port of Antwerp, currently considered as a source of "very high risk of biological invasion" for the PoD, can potentially reverse its current trends and present a low risk of invasion ($P_{ij}(Inv)_{2050} = 0.07$) with a reduction of 91.76%. Similarly, the North Sea (NS-2) ecoregion, which would also as a whole present a low invasion risk ($P_{ij}(Inv)_{2050} = 0.11$) with a reduction of 88.25%. At a more global ecoregion level, forecasts indicate an increase in invasion probabilities for the Natal (N-51), East Africa Coral Coast (EACC-20), Sahelian Upwelling (SU-16) and Angolan (A-17) ecoregions.

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