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ORIGINAL PAPER

Assessing the invasion risk of the cnidaria *Blackfordia virginica* Mayer, 1910: a threat to the Baltic Sea ecosystem?

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Abstract The ecological role, bloom extent and long-term dynamics of jellyfishes are mostly overlooked due to sampling limitations, leading to the lack of continuous long-term datasets. A rise in frequency and magnitude of jellyfish invasion around the world is shedding new light on these organisms. In this study, we estimate the current and future distribution of the introduced jellyfish *Blackfordia virginica* in the Baltic Sea. We determine the combination of favorable levels of temperature and salinity for this species by analyzing presence/absence data from areas outside the Baltic Sea and project the distribution of suitable habitat in the Baltic Sea across different scenarios with variable climate forcing and eutrophication levels. Our results show that suitability increases with rising temperature and optimal salinity range from 13 to 20 for this species. In addition, a relatively large area of the Baltic Sea represents favorable abiotic conditions for *B. virginica*, enhancing the concerns on its potential range expansion. Spatial analysis illustrates that the coastal areas of the southern Baltic Sea are particularly at risk for the invasion of the species. The observation of the projection of habitat suitability across time highlights that future Baltic Sea environmental conditions increase suitability levels for *B. virginica* and suggest a potential expansion of its distribution in the future.

Keywords Invasive species · Jellyfish · Climate change · Spatial Distribution Modeling · Baltic Sea

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Introduction

In recent years, the ecological role of jellyfish has captured significant attention, mainly due to their potential impact on aquatic food webs and socio-economic factors (Bosch-Belmar et al. 2021). The presence of gelatinous plankton can disrupt recreational activities and the fishing industry by altering the abundance of economically important species and impacting their recruitment through predation (Stoltenberg et al 2024) and competition with the early life stage of fishes (Purcell and Arai 2001). Numerous factors have been recognized as contributors to jellyfish blooms, encompassing rising water temperatures, hypoxia, eutrophication, overfishing or coastal modifications (Brodeur et al. 2002; Richardson et al. 2009). The concern comes from the potential shift from a fish-dominated ecosystem to a jellyfish-dominated one (Daskalov 2002). Such a shift alters the structure and processes of the food web leading to cascading effects on biogeochemical cycles and ecosystem stability (Daskalov 2002). While some scientists question this claim (Purcell et al. 2007; Brotz et al. 2012; Gibbons and Richardson 2013), others argue that jellyfish blooms have shown a noticeable increase in both frequency and magnitude (Fernández-Alias et al. 2024). Although a potential increase of gelatinous plankton remains yet to be quantified, the rate of successful invasions of non-indigenous jellyfish species is rising (Bayha and Graham 2014; Stoltenberg et al. 2021). Specifically, a growth in the magnitude and distribution of jellyfishes has been suggested in response to increased habitat suitability caused by climate change. However, whether this rise will actually happen remains unknown because the ecological niches of most of the jellyfish species are not identified and the role of environmental factors in determining interannual variability remain unexplained.

The clarification of the suggested jellyfish biomass and distribution increase is key to our comprehensive understanding of future ecosystems as recent studies reassessed and highlighted the role of gelatinous organisms in nutrients cycles (Huang et al. 2021). The ecological role of jellyfish has been globally and historically underestimated and overlooked, possibly due to limitations in sampling and preservation methods efficiency, inducing the lack of long-term time series (Ruzicka et al. 2007). Yet, recent studies have indicated that cnidarian and ctenophore species may play a more substantial role channeling energy through the food web, challenging the dead-end point of view that has been attributed in some biogeochemical models (e.g., Stoltenberg et al. 2021). Most of the jellyfish blooms are known to seasonally alter marine food webs through competition and/or predation of fish (Richardson et al. 2009) and zooplankton species (Hansson et al. 2005), whereas the identification of jellyfish predators remains limited in most of the regions.

The Baltic Sea, a marginal sea of the Atlantic Ocean, exhibits notable salinity and temperature gradients spanning from the south-west to north-east (Fig. 1). It is considered as the world's largest brackish-water ecosystems. The Baltic Sea has experienced one of the most notable rises in water temperature due to climate change among marine systems (Belkin 2009; Reusch et al. 2018) and has transitioned in some areas from an oligotrophic state to a eutrophic state due to its enclosed nature, high coastal population density, and extensive drainage basin (Elmgren et al. 2015). This region is significantly influenced by various human-driven impacts, including eutrophication, climate change, and intense marine traffic, which contributes to an augmented concentration of jellyfish by changing environmental conditions or being a vector of introduction (Reusch et al. 2018). Due to its extensive ship traffic and infrastructures, like the Kiel Canal, which links the North Sea to the Baltic Sea, the Baltic Sea serves as a key hub for the transfer of non-indigenous species (Leppäkoski et al. 2002). Indeed, the Baltic Sea is home to around 100 non-indigenous species, many of which have been introduced through shipping activities (Leppäkoski et al. 2002). Frequent jellyfish blooms with substantial biomass have been observed in the Baltic Sea (Olesen et al. 1994; Goldstein and Riisgård 2016). Nevertheless, a conclusive overall increase in jellyfish density across the region has yet to be established.

The introduced hydrozoan species *Blackfordia virginica* Mayer, 1910 was first sporadically observed in 2014 and 2015 in the Kiel Canal (Jaspers et al. 2018). This species is now considered as established and presents an active recruitment in Kiel Canal (Jaspers et al. 2018). Moreover, recent reports have identified a spread of the distribution of the species in the south-west area of the Baltic Sea (Jaspers et al. 2021), which suggests that this species could fall under the

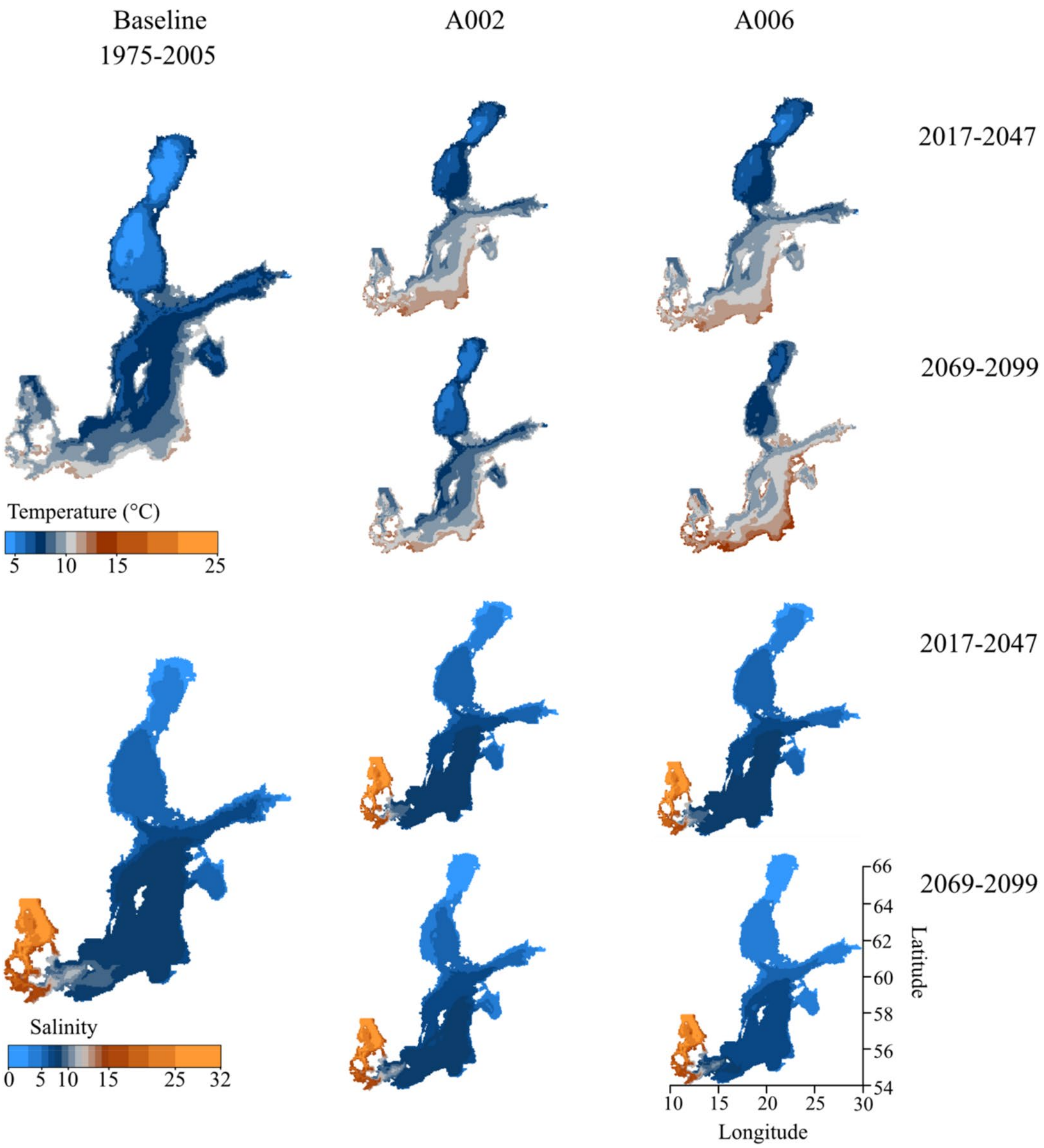


Fig. 1 Environmental conditions of temperature (°C, top panels) and salinity (bottom panels) across the different future climate scenarios and time periods from RCO-SCOBI model (Saraiva et al. 2019a,b)

definition of an invasive alien species according to Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2023). The hydromedusa exhibits a metagenic life cycle characterized by an asexually reproducing benthic polyp phase and a sexually reproducing medusa one. Despite its recognition, the scientific literature on this species remains limited. *Blackfordia virginica* is already regarded as an invasive species due to its successful establishment in various brackish regions of the Atlantic, Pacific, and Indian oceans (Mills and Sommer 1995; Mills and Rees 2000; Bardi and Marques 2009). Given its euryhaline characteristics (Bardi and Marques 2009), *B. virginica* exhibits a high potential for colonization in the Baltic Sea. During peak periods, the density of *B. virginica* can be exceptionally high, reaching up to 1700 individuals/m^3 (Marques et al. 2015; Jaspers et al. 2018). The observed diet of *B. virginica* includes a broad range of zooplankton species, fish eggs and larvae (Wintzer et al. 2013; Morais et al. 2015) as well as particulate organic matter (Morais et al. 2017). Therefore, the presence and development of *B. virginica* in the Baltic Sea could have significant ecological impacts by exerting grazing pressure on zooplankton and fish larvae (Marques et al. 2017).

The objective of this study is to explore the potential of *B. virginica* to spread and increase its distribution due to climate and nutrient changes in the Baltic Sea. To achieve this aim, we project the distribution of the suitable habitat on a past projection (1975–2005), thereafter called baseline, as well as two future scenarios (2017–2047 and 2069–2099) with variable climate forcings and eutrophication levels. We hypothesize that current temperature and salinity conditions are favorable for its establishment and that climate forcing will enhance, both in magnitude and surface, the suitability of the Baltic Sea environment for this species.

Material and methods

Occurrence data

We conducted a comprehensive investigation of the distribution of *B. virginica* by systematically reviewing published literature, personal communications and internet databases. Each record was accompanied by the corresponding salinity and temperature measurements of the surrounding water at collection time. Occurrence records that lacked water parameter information or were deemed uncertain were excluded from the analysis. Our data collection was not restricted by geographical boundaries, resulting in a total of 278 data points distributed among 119 occurrence records and 159 absence points spread across five distinct regions: the Gironde estuary in France, the Guadiana estuary in Portugal, the Xiamen Province in China, the San Francisco estuary in the US and the south-western part of the Baltic Sea (Kiel Canal) (Table 1). Both the presence and absence samples represent collection points occurring during the same sampling programs; we considered present when at least one individual was present and absent otherwise.

Model design and evaluation

To model the suitable conditions for *B. virginica*, ensemble modelling was employed based on the presence and absence of the species. This involved combining presence data with a set of six different model algorithms available in the BIOMOD2 package (Thuiller et al. 2009). The six models used were the Generalized Linear Model (GLM), Artificial Neural Network (ANN), Multiple Adaptive Regression Splines (MARS), Generalized Boosting Model (GBM), Flexible Discriminant Analysis (FDA), and Random Forest (RF). The models were parametrised to reduce class imbalance by ensuring that the summed weight of presences of the models was equal to the summed weight of the absences.

We assessed the individual performance of the models by applying a spatial block cross-validation procedure (Roberts et al. 2017). We performed this spatial block cross-validation on the basis of the distribution of the five areas of our dataset (US, Portugal, France, China and Baltic Sea), using, for each step, data from one source for the evaluation of the models whereas the four other sources were used for the calibration. We evaluated model performance by using both the Jaccard index and comparing the models' response curves with our knowledge of the ecology of the species (Leroy et al. 2018). The Jaccard index (Jaccard 1908) quantifies the degree of similarity between model predictions and observations on

Table 1 Number of presences and absences across the different sampling locations. CCMAR stands for Centre of Marine Sciences, Universidade do Algarve

Location	Presence	Absence	Source
US	2	1	Mills and Sommer 1995
France	30	47	Nowaczyk et al. 2016
Portugal	33	38	Cruz, J/CCMAR unpublished data
Baltic sea	40	63	https://doi.org/10.1594/PANGAEA.959714 and https://doi.pangaea.de/10.1594/PANGAEA.891209
China	14	10	Huang et al. 2021

the evaluation datasets. The models with a Jaccard index lower than 0.6 were discarded (Figure S1). Finally, we combined the outputs from all models that passed our quality assessment using the Jaccard index and response curves into a final prediction based on the average suitability across models (Thuiller et al. 2009).

Projections

The projected thermal and salinity conditions were determined using the RCO-SCOBI model, which is a high-resolution 3D physical-biogeochemical model of the Baltic Sea (Meier et al. 2003; Eilola et al. 2009; Saraiva et al. 2019a and b). The model, with a spatial grid of 2 nautical miles and a horizontal resolution of 3 m has been proven to be one of the models effectively capturing the physical and biogeochemical variability in the Baltic Sea from 1975 to 2005 (Eilola et al. 2009). For projections, the thermal and salinity requirements were considered for the top 50 m of the water column in the Baltic Sea under various scenarios. The first scenario, A002, involved a reduction in nutrient load input aligned with the goals of the HELCOM Baltic Sea Action Plan (Backer et al. 2010), combined with the RCP4.5 scenario from the Intergovernmental Panel on Climate Change (IPCC, 2014) and, therefore, a moderate increase of water temperature. The second scenario, called A006, combined the IPCC's RCP8.5 scenario with a consistent level of nutrient sources and thus, an increase in phosphorus and nitrogen concentrations. However, since we focused on salinity and temperature to evaluate the distribution of the species, we expect climate to be the main driver of our results, through changes in temperature and salinity. To estimate the distribution of suitable conditions for *B. virginica*, a 30-year timeframe was selected to capture the climate dynamics in the Baltic Sea, as suggested by previous studies (Meier et al. 2011; Gogina et al. 2020). Therefore, we explored the overall evolution of the habitat suitability identified by our ensemble model (Fig. 3) on three projections, the baseline, that is represented by a mean of the values comprised between 1975 and 2005 and two future periods, one from 2017 to 2047 and one from 2069 to 2099, for both A002 and A006 scenarios. For each of these projections, we first performed an analysis of the seasonality of the habitat suitability (Fig. 4). Then, we used only the summer months (July and August) to observe the spatial distribution and the evolution of the suitable conditions for *B. virginica* across the three scenarios, namely, baseline, A002 and A006 (Fig. 5). We chose to project the summer period for readability and computational reasons, which also corresponds to the highest density of the pelagic phase of *B. virginica*.

Results

Estimated niche

The number of presences and absences ranged, depending on location from 3 to 103 (Table 1). Occurrences from China, France, US and most of the Portugal samples were collected in relatively similar combinations of temperature and salinity (Fig. 2). Occurrences in the Baltic Sea appear to have lower temperatures in comparison to the others locations (Fig. 2). The responses of our ensemble models (Fig. 3), shows an overall positive correlation between suitability level and temperature. The suitability exhibits low levels until temperature reach 10 °C, thereafter increases until an optimal value of 25 °C is attained, beyond which higher temperatures lead to a diminution in suitability. Concerning the salinity, the suitability is low for values below 2, while salinities between 10 and 23 are highly suitable.

The analysis of the seasonal suitability of the Baltic Sea conditions revealed that conditions appear to be more favourable during the period from June to September (Fig. 4). In addition, our models suggest an increase in the suitability for this species in the Baltic Sea across scenarios (Fig. 4). The two future scenarios show higher proportion of pixels with high suitability levels compared to the baseline. The A006 scenario is the one with the highest proportion of pixels with suitability values greater than 0.7 (Fig. 4).

The projections on the two 30-year periods illustrate an increase in the suitability of the habitat in future scenarios in comparison to the baseline. This rise of habitat suitability is slightly more pronounced in the A006 scenario in comparison to the A002 scenario (Fig. 4). We observe that, based on summer months, 21.0% of the pixels have a suitability level over 0.2 in the baseline scenario whereas 28.0% and 29.2% have a suitability higher than 0.2 for A002 and A006, respectively, and for the 2017–2047 projection.

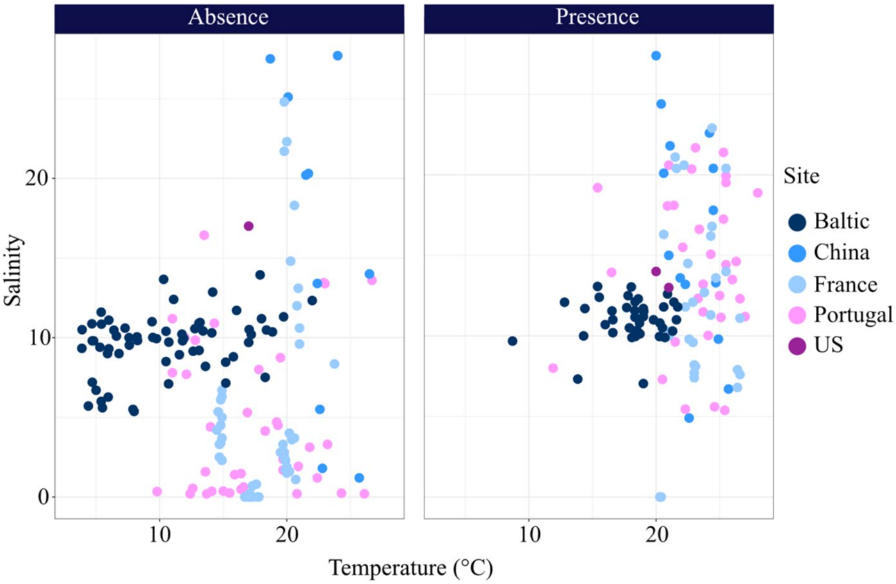


Fig. 2 Repartition of the absence (left panel) and presence (right panel) sampling points on environmental dimensions of temperature and salinity by sampling site

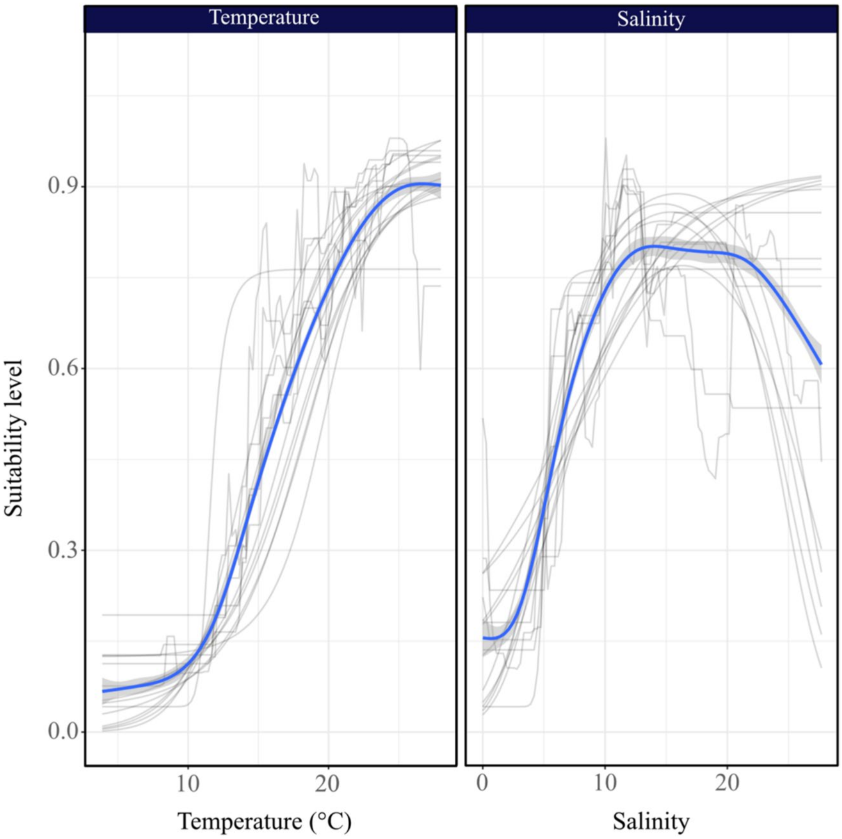


Fig. 3 The modeled suitability of *Blackfordia virginica* across temperature (left panel) and salinity (right panel) parameters. Each grey line represents one of the models and the blue line is the ensemble model. The y axes represent suitability level with 0 referring to low and 1 to high suitability, respectively, and the x axes the environmental parameters

In the 2069–2099 projection, a similar trend is observed with 27.4% for A002 and 30.1% for the A006 scenario. Overall, temporal projections show a seasonal pattern with an increase of habitat suitability during the summer period. Moreover, the spatial analysis of the habitat suitability revealed strong

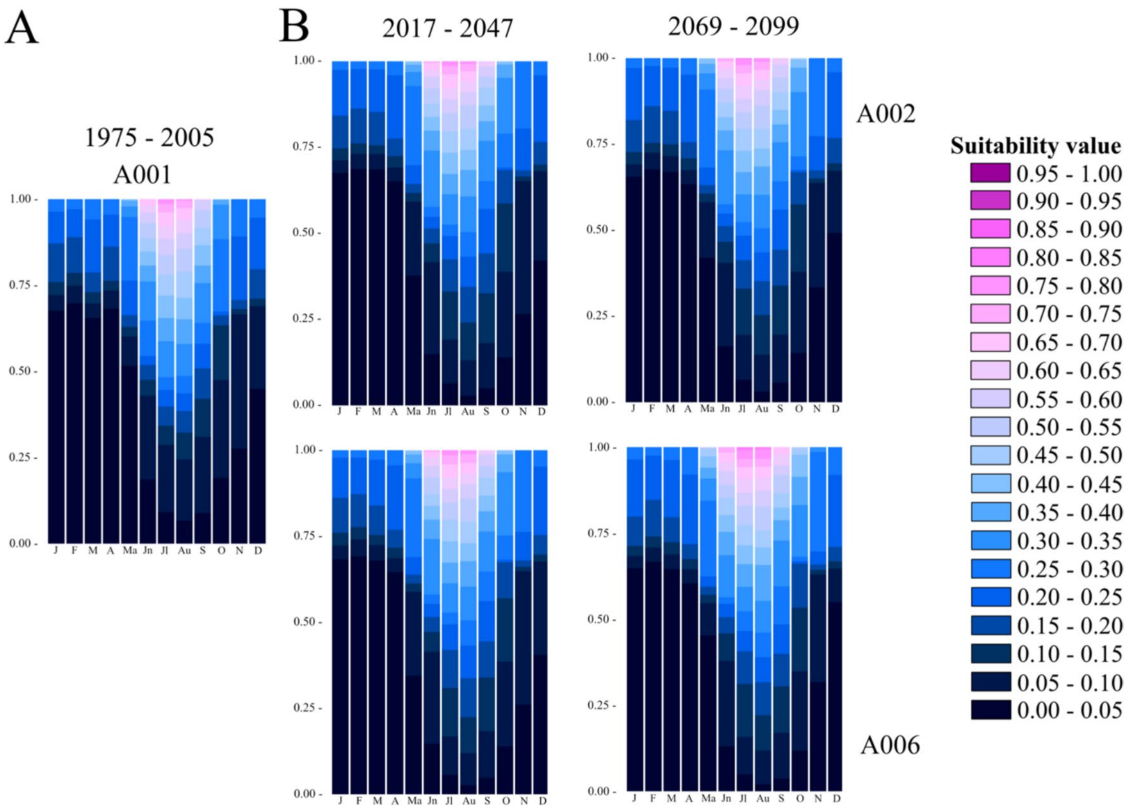


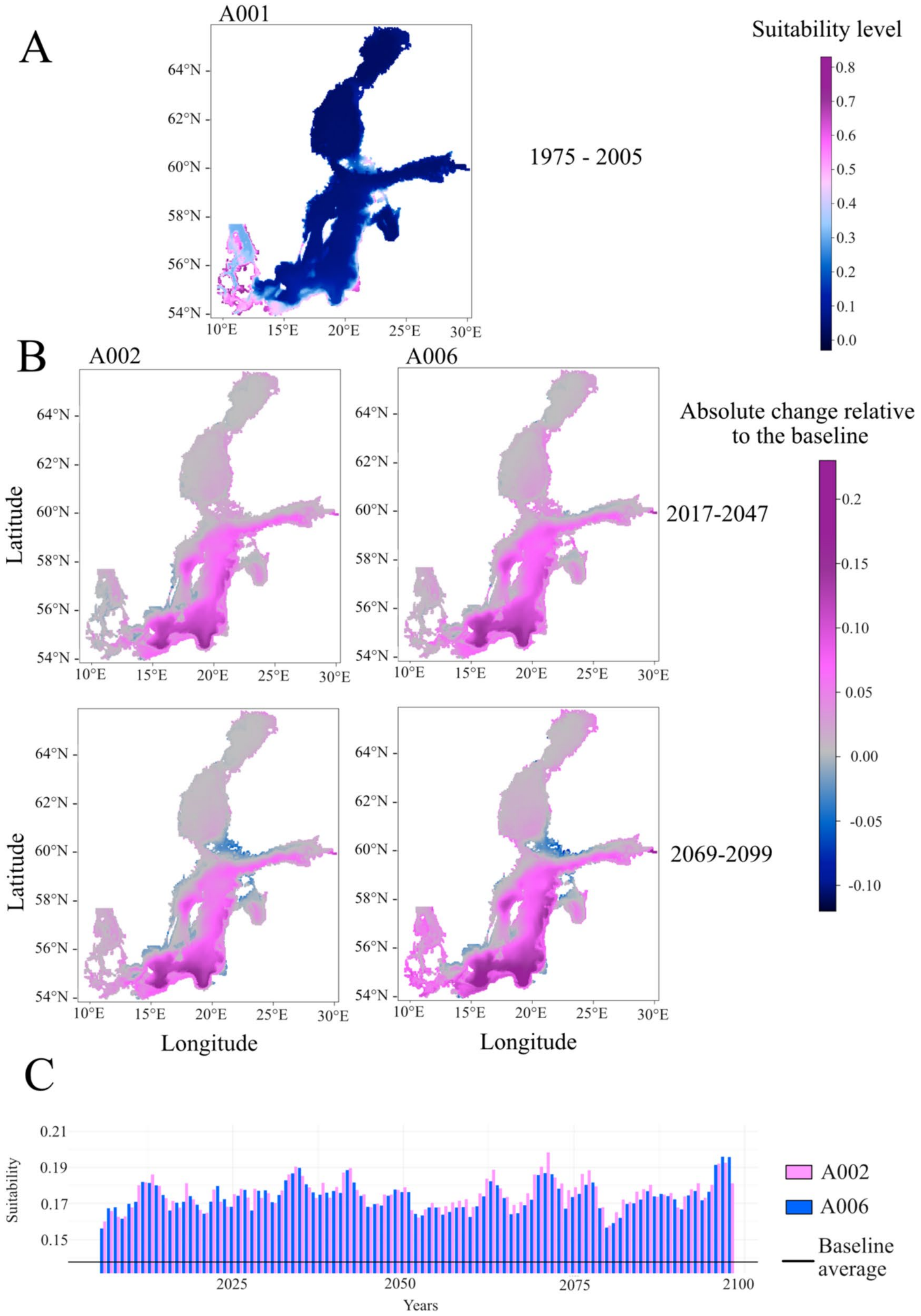
Fig. 4 Distribution of the pixels for *B. virginica* across suitability levels in the Baltic Sea for different scenarios. The left panel **A** represents the baseline scenario; the right **B** panels represent the different projection for A002 (top panels) and A006 (lower panels) for the periods 2007–2047 and 2069–2099, respectively

patterns across the Baltic Sea (Fig. 5A). Indeed, the projections of the summer distribution of *B. virginica* habitat illustrates various suitability levels across sub-basins. Our predictions identified, both for the baseline scenario and the future projections, a low habitat suitability in the eastern part and the open water areas of the Baltic Sea (Fig. 5A). In contrast, we observed high habitat suitability in the south-western part of the Baltic Sea as well as along the coasts of Estonia, Lithuania and Latvia when using the baseline scenario, with particularly high levels in the area connecting with the North Sea. Overall, we observed a spread of suitable conditions in the Baltic Sea (Fig. 5B), most of the Baltic Sea shows an increase in habitat suitability with future scenarios. However, the south of the Baltic Sea is a region that shows the highest suitability increase, both in the connection with the North Sea and the south-eastern part of the Baltic Sea (Fig. 5B).

Discussion

Niche analysis of the pelagic stage of *B. virginica*

The niche estimated in this study overall fits the global observations of the species with a spatial distribution more frequent in intermediate to high salinity levels and observation peaks occurring during the summer months. Our models identified a large salinity tolerance, which aligns with observation of this species occurring in salinity ranging from 2 to 36 (Moore 1987; Freire et al. 2014; Jaspers et al. 2021). In addition, the preference for brackish waters was identified in our model and confirms previous observations (Baumsteiger et al. 2018) and justifies the presence of the species in estuaries. An overall positive correlation with temperature was identified with an optimal temperature around 25 °C, which correlates with high summer


A
A001
1975 - 2005
Suitability level
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
B
A002
A006
Absolute change relative to the baseline
0.2
0.15
0.10
0.05
0.00
-0.05
-0.10
2017-2047
2069-2099
Latitude
Longitude
64°N
62°N
60°N
58°N
56°N
54°N
10°E
15°E
20°E
25°E
30°E
C
Suitability
0.21
0.19
0.17
0.15
Years
2025
2050
2075
2100
A002
A006
Baseline average

◂**Fig. 5** Spatial distribution of the habitat suitability levels of *Blackfordia virginica* in the Baltic Sea in summer for the baseline scenario (**A**). The panels in **B** represent the changes in habitat suitability for the different future scenarios, The panel **C** shows the evolution of habitat suitability across years. The values are given in absolute difference for the panels B and C

abundances in pelagic ecosystems (Jaspers et al. 2018; Nowaczyk et al. 2016).

High baseline suitability

Our baseline projection revealed that a significant proportion of the Baltic Sea area provides favourable salinity and temperature levels for *B. virginica*. According to these parameters, the water conditions along the southern and south-eastern coasts of the Baltic Sea are presently suitable. However, the current observed distribution of the species is limited to the Kiel Canal and surroundings (Jaspers et al. 2018). This restricted distribution is likely attributed to two main reasons. Sightings of *B. virginica* in the Kiel Canal were sporadic in 2014 and 2015 before a resident population was confirmed in 2016, occurring from June to October (Jaspers et al. 2018). This recent settlement could explain the current restricted distribution compared to our models as the species may not have had time to spread further. Secondly, it is important to consider that our study only utilised temperature and salinity as parameters. While these parameters have been shown to be crucial in explaining the distribution and dynamic of marine species (Ojaveer et al. 1998), additional abiotic and biotic factors may play a role in limiting the species' expansion. For example, the winter temperature conditions of the Baltic Sea could be a limiting factor in the expansion of the species as it has been observed for other gelatinous species (Thibault et al. 2014). Moreover, the life cycle of the hydrozoan *B. virginica* includes a polyp phase, which is likely to have different requirements than the pelagic phase, such as the availability of hard substrate, a commodity lacking in the open areas of the Baltic. It has been observed that the polyp of *B. virginica* is relatively small and competition with other species can result in its displacement (Boero 1984). At least seven hydromedusae species occurring only in its brackish environment (Stoltenberg et al. 2021), and in addition ctenophores, including *Mnemiopsis leidyi*, are present in the Baltic Sea. Among these species, the ones with benthic phase could outcompete the polyps of *B. virginica* for space. However, studies on the ecological needs of *B. virginica*, especially those focusing on the polyp phase, are limited. Additional parameters could impact the dynamic of the species, for instance Wintzer et al. (2011) demonstrated that water transparency levels positively affect the recruitment of *B. virginica* in an estuary. The Baltic Sea can be turbid during summer due to intense primary production, which may explain the observed restriction of the species so far. Overall, the determination of competition outcomes is a complex task as the multidimensionality of the niche could favour the coexistence of these species by reducing the niche overlap. The ecological niche complexity could interfere with the impact of biological invasions on the ecosystems (Borza et al. 2021).

The area of highest habitat suitability for *B. virginica* in the Baltic Sea is its connection with the North Sea. This region, already under considerable pressure from biological invasions, is hosting 120 non-indigenous species in 2020, excluding macro-zooplankton (Jensen et al. 2023). While most of these introductions have had minor ecological impacts, some, such as the ctenophore *Mnemiopsis leidyi*, have caused significant ecosystem disruptions through predation and competition (Shiganova et al. 2024). If the impact of *B. virginica* on the Baltic Sea food web remains undetermined, the combination of a high suitability, high biomasses during bloom period and a central position in the trophic network could lead to major impacts on this fine-tuned system.

Future projections

The applied future projections show an increase in habitat suitability in the Baltic Sea for *B. virginica*, both in terms of area extent and suitability level. Nevertheless, while an increase in habitat suitability was observed for A002 and A006 compared to the baseline, no significant change is evident at the Baltic Sea scale between 2006 and 2099 (Fig. 5C). However, notable spatial variability in habitat suitability was detected, which accounts for the lack of a clear trend at the Baltic Sea scale. Specifically, a more pronounced increase in habitat suitability was identified in the southern part of the Baltic Sea for A006 compared to A002, highlighting the localized nature of these changes. The species' preference for salinities higher than 10 identified in our model, associated with the salinity decrease in the projections of environmental parameters used in this study could limit the expansion. The positive relation between temperature and habitat suitability observed in our models correlates with the high summer abundances (Nowaczyk et al. 2016). However, a significant interannual variability in the magnitude of jellyfish abundance is observed (Fig. 5C; Parsons and Lalli 2002), and the underlying mechanisms driving this variability remain unexplained. Therefore, while an expansion of the distribution of *B. virginica* in the Baltic Sea could be predicted in the coming years and would likely lead to an overall increase in the abundance of the species, variations in the magnitude of the bloom across years can be expected.

The coastal areas of the Baltic Sea were identified as vulnerable regions for the potential development of *B. virginica* (Jaspers et al. 2021), which is in agreement with the results of our study. The dependence of hard substrate due to the polyp phase is expected to favour the development of the species in coastal areas. However, in our study, only temperature and salinity levels were used to determine the distribution of suitable habitats. We argue that the high coastal habitat suitability is related to the higher temperature in these environments in comparison to the open water. We believe that the thermal conditions are also the main factor inducing a suitability difference between the Swedish east coast and the west coast of the Baltic States, as the temperature at the same latitude is higher on the eastern part of the Baltic Sea, while the salinity levels are relatively similar (Fig. 1). The settlement and possible spread of *B. virginica* has been identified as a potential threat as a food competitor and direct predator of local fish population when reaching high densities. Jellyfish can have significant impacts on various trophic levels, including primary producers (Huang et al. 2021), primary consumers (Mills and Sommer 1995; Huang et al. 2021), and fish, both as competitor and as predators (Wintzer et al. 2013; Ayala et al. 2018). Our results highlighted that the most suitable habitats are matching with key spawning and nursery areas of ecologically and economically important species in the Baltic, such as herring (Von Dorrien et al. 2013). Consequently, the projected habitat suitability increase could have a significant effect on the fish production in the Baltic Sea.

Uncertainties

Three primary factors likely contribute to uncertainty in our outcomes: environmental projections, potential biological adaptation, and the Spatial Distribution Model (SDM) process. The variability of the biogeochemical model predictions, specifically regarding salinity projections due to the complexity of forecasting the ratio between precipitations increase and saline water inflow, as discussed in Meier et al. (2022). Since salinity plays a significant role in the distribution of species in the Baltic Sea, this particular source of uncertainty has the potential to impact our findings. The scenarios used in this study both project an overall decrease in salinity. However, we believe that this salinity decrease could hamper the rise in habitat suitability of *B. virginica*. Therefore, a scenario with a stable or a rising salinity would lead to a greater increase in habitat suitability. Moreover, the shallow feature of the Baltic Sea induces a rapid impact of perturbations such as climate change and eutrophication. Consequently, this may result in novel environmental conditions for species. These conditions might be challenging to capture accurately in SDMs that rely solely on current observations (Blenckner et al. 2021).

Furthermore, we recognize that factors beyond salinity and temperature may influence the distribution of *B. virginica*. As a hydrozoan, the species exhibits a complex life cycle that includes both a pelagic phase and a polyp benthic phase, as well as potentially resting stages (Wintzer et al. 2013). The ecological niche of the species can vary depending on the life cycle stage. We acknowledge that our study did not consider the polyp phase, which could be a limiting factor in the distribution of the species. For *B. virginica* to establish as an invasive species across a substantial portion of the Baltic Sea, its polyp stage must demonstrate the ability to endure unfavourable periods for the medusa stage and potentially withstand conditions that are too cold for polyp survival. Nevertheless, other factors could be positive to the development of *B. virginica*. For instance, it was observed that human-made structures can provide favourable environments for polyps, and an increase in such surfaces could potentially contribute to an expansion of the jellyfish population (Marques et al. 2017). Additionally, biological interactions have not been taken into account in this study but could strongly influence the distribution of the species. For example, it has been reported that some nudibranch species can predate on the polyp stage of jellyfish' species (Hernroth and Gröndahl 1985; Tang et al. 2021).

A limited number of occurrences have been used in this study due to the scarcity of data available. This data insufficiency could enhance the variability across models. However, based on our findings, we posit that the identified niche represents genuinely favourable conditions for *B. virginica*. Nonetheless, it is important to acknowledge that the ecological niche of the species may potentially be broader than the niche identified in our study. It is possible that we have underestimated the species environmental tolerances, which could result in a higher suitability of conditions in the Baltic Sea. In addition, it is important to note that environmental parameters are from different sources and sampling campaigns. The potential bias among the different sources could not be quantified. However, the exploration of the data show that occurrences from the different locations are forming a similar cloud (Fig. 2), indicating consistency in the environmental conditions. Moreover, previous research demonstrated the inclusion of imprecise environmental presence points in species modeling can yield better outcomes compared to excluding them (Smith et al. 2023).

Conclusion

This study identifies the suitable habitats of temperature and salinity for *B. virginica* in the Baltic Sea and suggests a potential expansion of its distribution in the future, as well as an increase in suitability levels. Because biological knowledge of this jellyfish species is scarce, the ecological impact of an invasion could not be quantified. However, the ability of the species to reach high densities, together with its predatory trait, raises concerns about the potential impacts on upper and lower trophic levels.

Additionally, this study underscores the importance of incorporating gelatinous plankton into monitoring programs in order to track the spatiotemporal dynamics of jellyfish distribution and biomass. Moreover, a substantial knowledge gap, regarding the ecological role and impact of the diverse species of jellyfish on ecosystem functioning should be implemented to increase the resolution of our comprehension of energy transfers in aquatic environments and thus, the quality of biogeochemical model outputs.

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Author contributions Baptiste Serandour: Idea and design, Data collection, Analysis, Writing, Reviewing. Boris Leroy: Idea and design, Reviewing. Thorsten Blenckner: Idea and design, Reviewing. Felix Mittermayer: Data collection, Reviewing. Catriona Clemmesen: Data collection, Reviewing. Joana Cruz: Data collection, Reviewing. Antoine Nowaczyk: Data collection, Reviewing. Monika Winder: Idea and design, Reviewing.

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Data availability The data that support the findings of this study are available on request from the corresponding author.

Declarations

Conflict of interest Authors declare they have no financial interests.

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