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Title	Predicting the future distribution of a commercially important clam (Ruditapes philippinarum) in a changing climate
Authors	Johnson, Alexandra S.;Bridges, Amelia E.H.;Knights, Antony M.
Publication date	2025
Original Citation	Johnson, A. S., Bridges, A. E. and Knights, A. M. (2025) 'Predicting the future distribution of a commercially important clam (Ruditapes philippinarum) in a changing climate', Estuarine, Coastal and Shelf Science, 320, p.109307. DOI: 10.1016/j.ecss.2025.109307
Type of publication	Article (peer reviewed)
Link to publisher's version	10.1016/j.ecss.2025.109307
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Download date	2026-10-30 18:16:52
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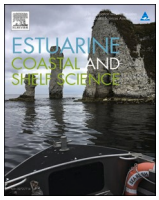
Estuarine, Coastal and Shelf Science 320 (2025) 109307



Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



Predicting the future distribution of a commercially important clam (*Ruditapes philippinarum*) in a changing climate

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ARTICLE INFO

Keywords:
Sustainability
Aquaculture
Climate resilience
Biogeography

ABSTRACT

The Manila clam, *Ruditapes philippinarum*, is a valuable commercial species for aquaculture, which in 2020, accounted for 24 % of global mollusc aquaculture. Given its economic importance, there is concern over whether this species may be vulnerable to the effects of climate change including changes in its distribution and sustainability. To test its vulnerability to climate change, we used Maximum Entropy (MaxEnt) modelling to predict both its current distribution and its future distribution under climate scenarios for end-of-century with focus on temperature and salinity changes. Future scenarios identified widespread local and regional changes in suitability. Across northern Europe and Alaska, a combination of continued or increased suitability for *R. philippinarum* was predicted. However, in the Mediterranean, and especially around Italy who are a major aquaculture producer of Manila clams, habitat suitability is predicted to decrease by more than 50 %. In Asia, especially below 20° N and above 40°N latitudes, habitat suitability is predicted to markedly increase but decrease dramatically between these latitudes. This is particularly the case along the coastline of China; the current global leaders in Manila clam production. Our results suggest the long-term sustainability of this species in countries like China and Italy may be threatened by climate change and action may be needed to conserve this species and support industry. Elsewhere, in countries like Norway, Alaska and Indonesia where increases in suitability are predicted in the future, expansion and/or investment in clam aquaculture production may represent an opportunity for economic growth and sustainable food production.

1. Introduction

Anthropogenically driven climate change is affecting the global ocean, manifesting as an increase in average water temperature and decrease in average salinity, especially in inshore water masses (Halpern et al., 2008). While the rate of warming is accelerating globally (Storto and Yang, 2024), ocean warming is not occurring uniformly, with prominent 'hotspots' developing in the North Atlantic and Southern Ocean (Bilbao et al., 2019). Concomitantly, ocean salinity is also changing locally as the balance between precipitation and evaporation varies with latitude. In polar regions, salinity is decreasing due to ice melt or an increase in frequency and severity of heavy precipitation events (Hoegh-Guldberg et al., 2018) but also increasing in areas of higher sea surface temperatures (SST) that drive increased evaporation. These changes in ocean physico-chemistry are expected to impact the distribution of species, including those of commercial importance with potentially negative consequences for food production including shellfish aquaculture (IPCC et al., 2023). There are, however, regional and/or national differences aquaculture production (Cisneros-Montemayor et al., 2016), such that understanding how environmental suitability might change the sustainability of cultured species in the future is key to food security, both nationally and internationally (Froehlich et al., 2018).

Aquaculture plays a crucial role in supporting the growing global population providing 56 % of aquatic food for human consumption in 2020 (FAO, 2022). In Asia, especially, aquaculture production has dramatically increased since the 1990s (Jennings et al., 2016) with China generating 57 % of the world's aquaculture production in 2020 (FAO, 2022). Marine shellfish make up over half of the 73 important global aquaculture species listed by the FAO and play an important role in future food security (Azra et al., 2021). However, many major production regions are predicted to be vulnerable to the effects of climate

This article is part of a special issue entitled: The Manila Clam published in Estuarine, Coastal and Shelf Science.

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https://doi.org/10.1016/j.ecss.2025.109307
Received 29 November 2024; Received in revised form 8 April 2025; Accepted 10 April 2025
Available online 10 April 2025
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change, particularly key production areas including China and Western Europe (Stewart-Sinclair et al., 2020).

One species of particular commercial value is the Manila clam, *Ruditapes philippinarum*. In 2020, *Ruditapes philippinarum* accounted for 24 % of global mollusc aquaculture production with a harvest of over 4 million tonnes (FAO, 2022). Over 2 million tonnes per year are produced through Chinese aquaculture (Fang and Lin, 2016), and in 2021, 92 % of European farmed *R. philippinarum* were produced in Italy (Eurostat, 2023). *R. philippinarum* inhabits the shallow waters of estuaries and bays and is native to eastern Asia but was introduced to North America in the 1930s. During the 1970s and 80s, aquaculturists introduced the species to Europe; these original populations spread, resulting in the establishment of wild populations in the Mediterranean Sea and northeast Atlantic around the UK (Gosling, 2015). As an invasive species, *R. philippinarum* has outcompeted the native species and now dominates over the European *Ruditapes decussatus* (Linnaeus, 1758; Pranovi et al., 2006).

Several studies have shown that *R. philippinarum* stocks may be threatened by increasing SST (Ponti et al., 2017). While Manila clams are tolerant to environmental fluctuations within the dynamic coastal environment, research suggests they cannot withstand extreme temperatures over extended time periods without recovery (Bertolini and Pastres, 2021), which has led to recent declines in production. This decline is thought to be related to a combination of stressors associated with climate change including increases in frequency and severity of marine heatwaves and salinity changes (Oliver et al., 2019). While stress resulting from temporarily-reduced salinity has sub-lethal effects including reduced burrowing behaviour, which can lead to increased predation (Domínguez et al., 2020), extended periods (>9 days) of moderate of salinity (<15) can also lead to mortality (Parada et al., 2012). Mortality-causing conditions driven by extreme precipitation are thought to be worse during neap tides due to reduced saltwater dilution (Des et al., 2021) suggesting regions with smaller tidal ranges may be more stressful for *R. philippinarum*.

While there have been several studies into life cycle (Turolla et al., 2020) and behavioural changes (Jiang et al., 2023) of *R. philippinarum* in response to climate change, there is little research into how the distribution of this valuable and important commercial species might change. Species distribution modelling (SDM), also known as habitat suitability modelling, mathematically characterises the relationship between species presence/absence and environmental conditions, and is a commonly used method to predictively map the distribution of a species and/or habitat (e.g., Howell et al., 2022). Where predicted future environmental data exist, SDMs can be temporally transferred, enabling the prediction of future distributions of species (e.g., Morato et al., 2020). Here, using Maximum Entropy (MaxEnt; Phillips et al., 2006) modelling, we predict the global distribution of *R. philippinarum* under a future climate scenario to test to what extent the spatial distribution of this key aquaculture species might be affected and identify the potential risks and opportunities for commercial development.

2. Methods

2.1. Environmental data

The physiological and ecological sensitives of *R. philippinarum* were reviewed. Mean sea surface temperature (SST) and mean sea surface salinity were identified as drivers of distribution at a global scale. Datasets for these variables were download from the Bio-ORACLE repository for the period 2000–2014 (Tyberghein et al., 2011; Assis et al., 2024). For the temporal transfer, predicted mean SST and mean sea surface salinity data for the year 2100 (also from Bio-ORACLE) based on the IPCC climate projection model Representative Concentration Pathway 8.5 (RCP 8.5) were also downloaded. All data were downloaded as raster data with a resolution of 1/12th × 1/12th degree; equivalent to a grid cell size of approximately 9.25 km^2 at the equator.

2.2. Species observation data

Presence data for *Ruditapes philippinarum* were downloaded from the Global Biodiversity Information Facility (GBIF Occurrence Download, ; for full details see supplementary material). In total, 7699 presence records are reported. Given the grid cell size of the environmental data, records where the coordinate uncertainty was >9 km were removed to ensure the correct environmental conditions were attributed to each presence location and to reduce spatial error (Graham et al., 2007). To avoid over-/underweighting of certain environmental conditions that would result in model overfitting, presence data were reduced to one point per cell (i.e., a single point per ~9 × 9 km), which reduced observations to a total of 4457 presence locations (Fig. 1). In lieu of absence data, we randomly generated 10,000 background points to represent the environmental conditions across the study area and serve as a reference for comparing against the environmental conditions at presence locations (see Elith et al., 2006). For both presence and absence point coordinates, values for each environmental variable were extracted and points that did not have a corresponding value for all environmental variables were removed. The final presence-background data set comprised 8998 observations, of which 163 (1.8 %) were presences and 8835 were absences.

2.3. Modelling

Maximum entropy (MaxEnt; Phillips et al., 2006) modelling has been shown to be successful, especially where the datasets are characterised by low prevalence (a low number of presence records; Elith et al., 2006) and was therefore employed to build the habitat suitability maps for this study. All analyses were performed in R 4.3.2 (R Core Team, 2023). The full model dataset was randomly split into training (70 %) and testing (30 %) partitions to enable internal cross validation of predictions. Although MaxEnt can tolerate covariance in predictor variables (Feng et al., 2019), some studies have found pre-selection of variables can lead to better model performance (e.g., Ross and Howell, 2012). We therefore chose to assess covariance in our data a Pearson's correlation analysis. No strong correlation was found between the temperature and salinity datasets, and thus both were used in the final model. After preliminary trials, a regularisation parameter of 1 was selected for the final model to avoid over-/underfitting. Informed by the known ecological tolerances of *R. philippinarum* to SST and sea surface salinity, linear, quadratic and product were the only feature classes offered to the model. Hinge and threshold features were removed due to lack of ecological applicability in these types of responses (as per Howell et al. (2022)).

Once the performance of the present-day SDM was assessed using the threshold-independent metric known as the AUC value (area under the ROC- receiver operating curve; Peterson et al., 2008), the model was exposed to the climate-projected data layers to calculate the future predicted distribution. Both present-day and future distribution maps were created, as well as anomaly plots to identify areas of change using the raster package (Hijmans, 2024). In the absence of globally available high-resolution depth for many inshore areas to constrain predictions to inshore environments, a buffer was used to limit potential habitat to within 10 km of the coastline. Spatial analysis was focused on three *R. philippinarum* habitat regions: East Asia, Western North America and Europe.

3. Results

3.1. Model evaluation

Internal model validation produced an AUC score 0.88 indicating good model performance, with SST identified as the strongest driver of *R. philippinarum* distribution followed by sea surface salinity (Fig. S1, supplementary material). For SST, the highest probability of occurrence occurs at 15 °C, dropping to <50 % likelihood below ~8 °C and above

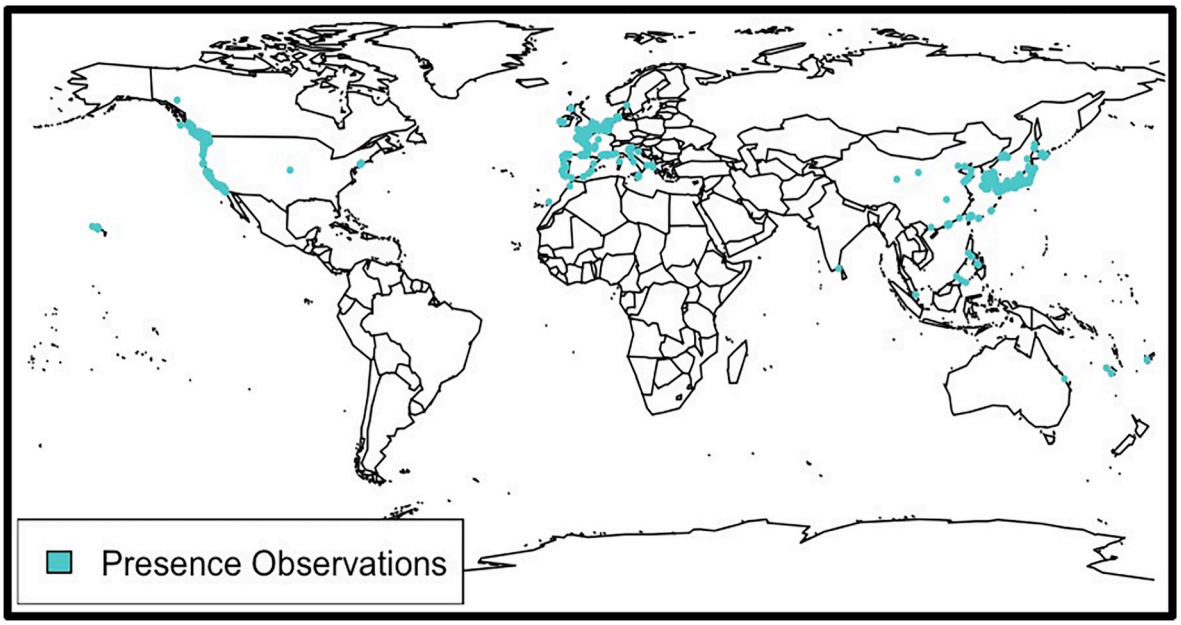


Fig. 1. Locations of cleaned occurrence data downloaded from GBIF. Blue points represent presence data for R. philippinarum, highlighting populations in east Asia, Europe and the west coast of North America. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

~22 °C. Highest probabilities of occurrence occur in salinities of between 20 and 25, peaking at ~22.5. Under increasingly fresh (salinity <11) and hypersaline conditions (>35), probability of occurrence is below 50 % (Fig. S2, supplementary material).

3.2. Present day spatial distribution

Contemporary model predictions of the distribution of *R. philippinarum* (column 1, Fig. 2) aligned with the original downloaded observations used (Fig. 1). Probability of occurrence plots indicated a high probability of presence around Korea and Japan as well as along China's east coast, but a low probability of presence (<30 %) to the south around the Philippines and western Indonesia driven by temperature and salinity conditions. In North America, a high probability of occurrence (>80 %) is predicted along the Canadian west coast and very low probability (<20 %) along the south Alaskan coast. The model shows low probability of 'natural' occurrence due to the environmental conditions, however, there were many observations around the Spanish and UK coastlines, likely due to the presence of aquaculture. Around the Italian and Greek coasts, current environmental conditions support a moderate probability of occurrence (>60 %), and southern Scandinavia and the Netherlands appearing especially suitable (>80 %).

3.3. Future spatial distribution

Predicted future temperature and salinity conditions led to a marked change in habitat suitability for *R. philippinarum* (column 2, Fig. 2). Under RCP 8.5, *R. philippinarum* suitable habitat shows a northward shift in North America and Europe with higher probabilities of occurrence (>80 %) along both the Alaskan and Norwegian coasts. In the Mediterranean, probability of occurrence is predicted to decrease, particularly around Italy and along the east coast of Greece, to below 20 %. In Asia, the habitat range is predicted to expand with higher probabilities of occurrence (>60 %) around Indonesia, Malaysia and up along the Thai and Myanmar coasts. Suitable habitat is also predicted further north with high probabilities of occurrence (>80 %) around Hokkaido, Japan's northernmost main island, and the coast of Russia.

3.4. Change in distribution

Anomaly plots revealed areas of positive and negative probability of occurrence under future climate conditions that were regionally context-dependent (column 3, Fig. 2). Across Asia, the coast of central China exhibited a decrease of ~50 % in probability of occurrence under RCP 8.5, whilst along the coasts of south-east Asia, probability increased by >50 %. Suitability along the coastlines of Korea and central Japan is predicted to not change. Probability of occurrence along the coastline of north America is predicted to typically increase everywhere, notably so in Alaska where probability of occurrence goes from entirely unsuitable today (i.e. a probability of 0) to 100 % likelihood of occurrence by the end of century. Across Europe and like Asia, change in suitability varied with region with a major decrease in probability of occurrence along Italy's Mediterranean coastline (>50 %), while in the north Atlantic region, a 100 % increase in probability at 70°N and ~50 % around the north coasts of the UK was predicted. No change in suitability is predicted around the Dutch and Danish coastlines, which were highly suitable under both contemporary and future scenarios, whereas the Baltic Sea remains entirely unsuitable under both scenarios.

4. Discussion

MaxEnt has been used extensively to predict the potential distribution of commercially important fish species (Silva et al., 2018; Zhang et al., 2019; Petatán-Ramírez et al., 2019), and here, for the first time, we use this approach to assess the impacts of future climate change on the commercially important clam, *Ruditapes philippinarum*. Predictions for 2100 under IPCC climate scenario RCP 8.5 suggest a northerly poleward expansion in many regions, although in south-east Asia, their distribution was predicted to shift toward the equator. The coastlines of China and Italy were predicted to be most negatively affected, where current aquaculture investment in this species is particularly high, while the entire coastline of north America is predicted to become more suitable. This poleward shift is a phenomenon being observed in a wide range of marine species (Sorte et al., 2010; Hastings et al., 2020). This change in distribution was predicted to be strongly driven by change in SST; a variable previously shown to be an important driver of distribution in other bivalve species including the razor clam (Saeedi et al.,

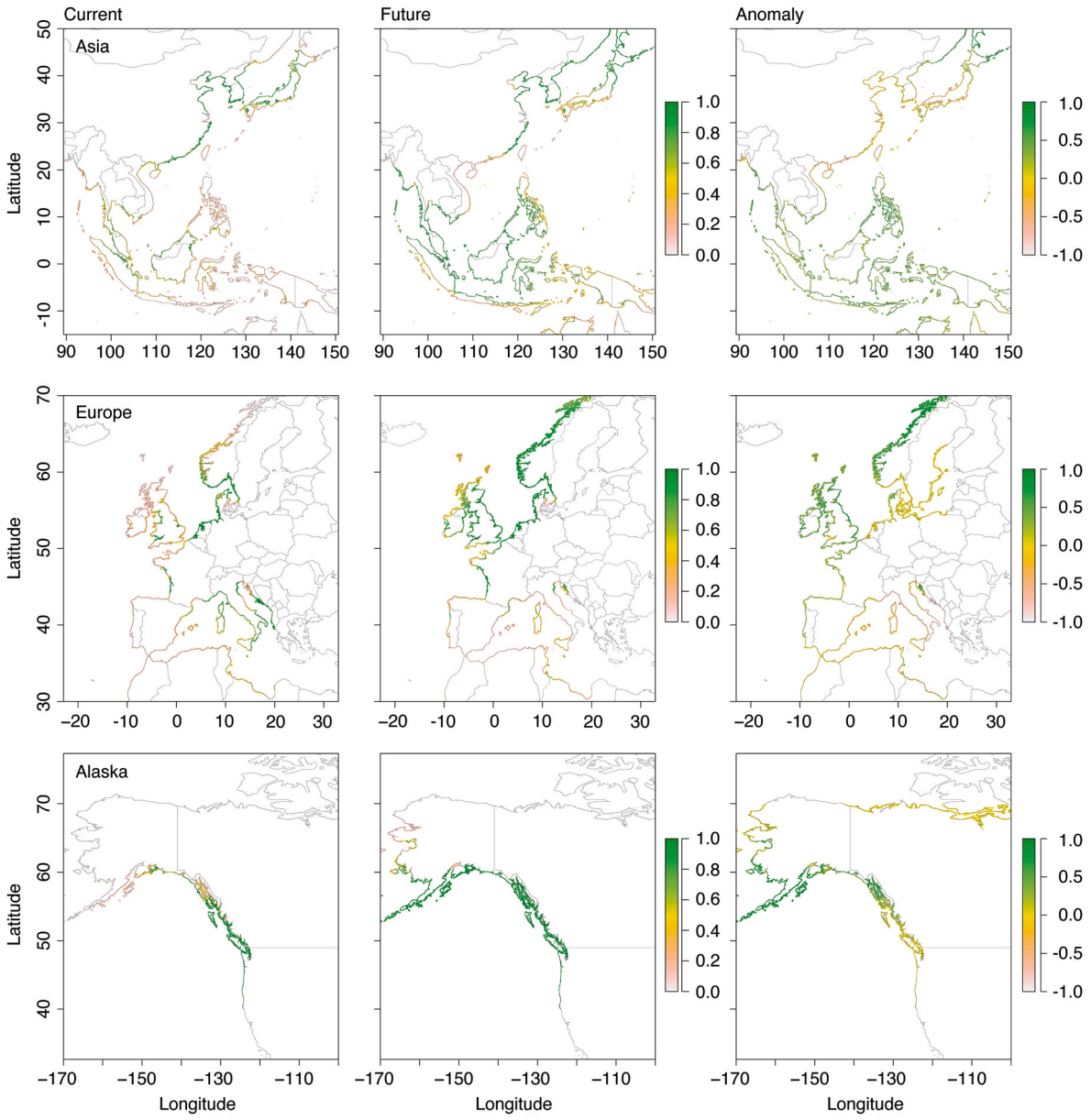


Fig. 2. First and second columns show current and future distribution of *R. philippinarum* respectively in three major regions: top) East Asia, middle) Western North America and bottom) Europe. Colourbar scales to the right of future plots represent the probability of species occurrence where dark green is 100 % and red-white is 0 %. Anomaly plots (last column) showing change in distribution. Colour bar scales to the right represent the change in probability of presence where dark green is +100 % and red is −100 %. Yellow (0) indicates no change in probability of presence between contemporary and future scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2016; Raybaud et al., 2015).

Cross validation of the model, trained on present day data, indicated good performance, thus allowing for its temporal transfer and prediction of future distribution under a climate change scenario. Increased sea surface temperatures (SST) were identified as the main driver of reduced probability of occurrence for *R. philippinarum*, especially when temperatures exceed 20 °C. Previous studies have shown *R. philippinarum* can induce mechanisms to mitigate the impacts of increasing temperatures above 21 °C (Velez et al., 2017), however, prolonged exposure (>15 days) to temperatures >24 °C result in reduced valve closure and increased mortality (Bae et al., 2021). Although it has been suggested that an initial increase in temperature might benefit settlement, the strong warming expected under RCP 8.5 is expected to lead to higher pre-settlement mortality (Ghezzo et al., 2018). The optimum salinity range for *R. philippinarum* in aquaculture has been previously reported as 20–30 (Coughlan et al., 2009). Here, our model supports this finding, predicting highest probability of occurrence in salinities between 20 and 25. Multiple studies have also shown that low salinities (<14) induce oxidative stress (Velez et al., 2016) from which the clams cannot recover (Kim et al., 2001). While other variables may also be important drivers of distribution (e.g. dissolved oxygen and pH related to coastal hypoxia and acidification), at time of writing, global layers were unavailable but may in the future be beneficial to include. However, given our model performance was good based on temperature and salinity only (AUC = 0.88), additional variables may only add incremental improvements to predictions.

While MaxEnt is a popular choice of SDM for ecologists given its relative ease of use, we must be careful to consider the limitations (Elith et al., 2010; Merow et al., 2013). The model presented here is designed to serve a preliminary assessment on which further investigation and

testing can be based. Specifically, we ran a single iteration of the model and assessed performance using standard cross-validation approaches. Whilst this is entirely valid, future works should see multiple iterations and/or ensemble approaches used to ensure predicted patterns in distribution are truly representative of natural environments. These models should then be independently validated, an approach whereby the model is confronted by a truly 'new' datasets (i.e., in no way connected to data on which the model was trained) – a process considered the gold standard of model validation. Only a small number of studies have independently validated their models; some results suggests that AUC scores can decrease compared to cross-validated models, but remain acceptable (Rooper et al., 2016, 2017). However, it has been postulated that models built on low resolution spatial resolution data may see larger drops in performance when independently validated (Anderson et al., 2016; Bowden et al., 2021). Given global climate models typically have, at best, 1/12th x 1/12th degree resolution, we were limited to using relatively coarse environmental data. In the future, as climate projections are available at higher spatial resolutions, SDMs should seek to use higher resolution data to ensure accuracy of predictions.

Change in SST is not occurring uniformly across space (Bilbao et al., 2019). Our predictions highlight this variability as spatial variation in habitat suitability, making them as a species of choice for aquaculture, both high and low risk depending on location. Areas predicted to see an increase in suitable habitat include Norway, Canada and Alaska, suggesting these countries could further benefit from an aquaculture stand-point although proactive planning will be required to ensure limited negative effects on the already vulnerable polar regions (Froehlich et al., 2018). Similarly, in south-east Asia, benefits could also be realised. Elsewhere, in countries including Italy and China, where 2022 production exceeded 23,000 tonnes (USD$223m) and 4.3m tonnes (USD$6.96b), respectively, predictions suggest habitats will become increasingly unsuitable in the future and mitigation against changing SST and salinity through conservation and management strategies will likely be required (Froehlich et al., 2017). Failure to implement strategies to mitigate this risk could result in significant financial losses for the industry in those countries. For instance, García-Souto et al. (2024) showed that habitat type played an important role in mitigating against heat stress with seagrass beds acting as a thermal refuge for clams during heatwaves. Reduced stocking density may also promote short-term resilience (Liu et al., 2023), although whether these mitigation strategies are viable and/or financially sustainable may be in question. Adaptive management may therefore play an important role for the sustainability of this stock into the future (Oyinlola et al., 2020).

Aquaculture is an industry expected to be key to food security in the future. Indeed, current production of *R. philippinarum* is already significant, with worldwide production in 2022 exceeding 4.4 million tonnes and valued at >€7.4b (FAO, 2022) and continues to increase year-on-year. It may also be important at a local scale for climate regulation, acting as a carbon sink (Turolla et al., 2020, Tamburini et al., 2022). In the case of Manila clam, their uptake of nitrogen and phosphorus can reduce the effects of eutrophication and provide ecosystem services including improving environmental quality (Turolla et al., 2020). Clams have been shown to play a positive role in the stability of macrobenthos community structure (Hou et al., 2023); a function that could be reduced or lost in areas of lowered suitability Therefore, the predicted reduction in probability of occurrence, especially around China – the world leader in Manila clam aquaculture which accounts for ~96 % of global production - could have a major impact on food production, food security and wider ecosystem effects. In areas where probability of occurrence is predicted to decrease, countries will likely need to consider what, if any, mitigation strategies might be employed to ensure longer term sustainability of the industry. Where probability of occurrence is predicted to increase, opportunities may arise to support increased aquaculture, sustainable food security and economic benefits.

CRediT authorship contribution statement

Alexandra S. Johnson: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Amelia E.H. Bridges:** Writing – review & editing, Visualization, Supervision, Methodology, Data curation. **Antony M. Knights:** Writing – review & editing, Visualization, Supervision, Methodology, Conceptualization.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109307.

Data availability

Data will be made available on request.

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