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Climate-induced habitat shifts of farmed mussel species

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ABSTRACT

Marine mussels are one of the most important sources of cultivated shellfish worldwide, particularly among middle- and low-income countries where they are a key food source for coastal communities. Climate Change is bound to have a large impact on the distribution of suitable habitats for the mussel species cultivated throughout the world. To examine these impacts on mussel aquaculture and global food security, we evaluated the distribution of suitable current and future habitats for the six more widely cultivated mussel species under a Representative Concentration Pathway 8.5 emission scenario using ecological niche modelling. Occurrence records were obtained from online databases and the literature. The models had a good performance in predicting the current distribution of the six study species. In future scenarios, suitable mussel habitats were projected to shift poleward, with gains at higher latitudes and losses at lower latitudes. By 2050, significant impacts were projected along the Mediterranean coast for *Mytilus galloprovincialis*, an important mariculture species in Europe, and in Southeast Asia for the tropical green mussel *Perna viridis*. Overall, our predictions suggested that range shifts could create opportunities to expand mussel farming to higher latitudes, yet loss of suitable habitat in historically productive growing areas could disrupt current mussel aquaculture regions, highlighting the need for immediate action. Therefore, achieving a more nuanced understanding of the spatial changes in the geographic distribution of suitable habitats should be the first step in increasing the adaptive capacity of the mussel aquaculture sector, and ensuring the future supply of this key source of aquafood.

1. Introduction

Following the trend in global population growth, the demand for high-quality food has brought aquaculture to the forefront as an alternative to globally depleted capture fisheries (Hoegh-Guldberg and Bruno, 2010). Furthermore, the cultivation of aquatic species is an essential source of nutrition and income in middle- and low-income countries (Tacon, 2020; Food and Agriculture Organization of the United Nations (FAO), 2022). In response to demand, global aquaculture production has tripled in only two decades (Naylor et al., 2021), making it the fastest-growing food production sector and a key source of food for many coastal communities (Tacon, 2020). This upward trend is bound to continue in the coming decades (Lovatelli and Holthus, 2008; FAO, 2022; Fong et al., 2024). Compared to terrestrial livestock, aquaculture stock exhibits high fecundity and high feed conversion rates, together with lower environmental impacts across multiple metrics, including energy use, and nutrient pollution (Hilborn et al., 2018; MacLeod et al., 2020). The difference in production efficiency is stark in terms of greenhouse gas (GHG) emissions: traditional land-based food systems (e.g. agriculture and livestock) are currently responsible for approximately 30 % of global GHG emissions (Crippa et al., 2021), whereas aquaculture represents <1 % (MacLeod et al., 2020). Hence, the sustainable expansion of shellfish aquaculture can achieve the sometimes conflicting goals of feeding the growing global population and reducing GHG emissions (Broitman et al., 2017; Hilborn et al., 2018; Naylor et al., 2021).

Shellfish aquaculture is the second largest source of protein from aquaculture after fishes (Froehlich et al., 2018; FAO, 2022). Importantly, shellfish aquaculture provides a low-cost source of high-quality

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protein for human consumption (Zippay and Helmuth, 2012; Azra et al., 2021). Mussels, like other shellfish, are usually grown suspended in the water column via wooden poles, ropes, and cages (Lovatelli and Holthus, 2008; Naylor et al., 2021). These bivalves feed by filtering organic matter and phytoplankton from the water column (Froehlich et al., 2018; Hilborn et al., 2018). Mussels attach to hard bottoms, and aquaculture uses this natural behaviour by suspending them on ropes or wooden poles to maximize growth and production. Unlike land-based food production systems, shellfish aquaculture is limited by environmental factors (e.g., seawater temperature, current velocity, and food availability), which fluctuate in time and space. Among the most limiting factors for mussel growth, seawater temperature is notable for its influence on numerous life history traits, particularly growth rate and reproduction (e.g. Arrieche et al., 2020; Tan et al., 2021; Ericson et al., 2023; Fong et al., 2024). In this way, the broadly predicted changes in seawater temperature patterns could be detrimental to mussel populations and, in turn, endanger the future of mussel aquaculture (Zippay and Helmuth, 2012; Froehlich et al., 2018; Maulu et al., 2021).

Ecological niche models (ENMs) are statistical approximations of a species' ecological niche, a volume with n-dimensions in the environmental space where the species can survive and persist over time (Sillero, 2011). Thus, modelling the species niche allows us to estimate how it uses the environmental space and project that niche into the geographical space to obtain its spatial representation (Fernandez et al., 2017; Sillero, 2011). If we assume the species' niche will remain the same over time and space (i.e. niche conservatism, (Wiens and Graham, 2005)), we can project the models to other areas and periods (Sillero et al., 2021), which is important to address future climatic scenarios (Melo-Merino et al., 2020). ENMs have been used to assess the impacts of Climate Change (CC) in the global distribution of many groups of marine species (Melo-Merino et al., 2020; Boavida-Portugal et al., 2018; Gonzalez-Aragon et al., 2024). However, very few studies have attempted to assess how CC may impact the suitability of aquaculture sites in the future at global scales (Froehlich et al., 2018; Zhou et al., 2023).

The locations used for the cultivation of any marine species in open systems represent a subset of suitable habitats for that species. Coastal regions are particularly exposed to changes in environmental conditions as they are highly exposed to multiple anthropogenic stressors (Oyinlola et al., 2018; Trégarot et al., 2024). Therefore, vast regions that are currently suitable or already in use for shellfish aquaculture will become unsuitable in the future.

This study uses ENMs to assess how future changes in climate may alter the distribution of habitats for six key mussel species worldwide. By integrating environmental variables under the Representative Concentration Pathway 8.5 (RCP 8.5) emission scenario, this study reveals regional responses among multiple mussel species. Our aim was to evaluate the potential changes that CC may drive in the distribution of 'suitable habitats' for the main cultivated marine mussel species and the implications that these changes may have on global aquaculture and food security. We hypothesized that the potential impact of CC on the marine environments currently used for shellfish farming can lead to changes in the suitability of such coastal habitats for aquaculture. We further hypothesized that spatial changes in the distribution of shellfish-suitable habitats would result from the interactive effects of multiple drivers such as temperature, salinity, and seawater depth. Our results provide a forecast of future changes in the biophysical space occupied by mussel aquaculture around the global coastal ocean, highlighting the need to plan for major changes in some parts of the world.

2. Methodology

We calculated the distribution of suitable habitats for mussel species (i.e. potential niche) using MaxEnt version 3.4.4 (Phillips et al., 2006; Phillips et al., 2017), which implements the Maximum Entropy (MaxEnt) algorithm, a machine learning method designed to make predictions from incomplete data (Baldwin, 2009), using presence and background records, together with a set of environmental predictors (Elith et al., 2011; Merow et al., 2013). MaxEnt estimates the habitat suitability index by finding the probability distribution of maximum entropy (most spread out) subject to the constraints imposed by the environmental variables and presence data. This results in a model that predicts habitat suitability in the study area (Osorio-Olvera et al., 2019).

2.1. *Species selection and occurrence records*

We identified the most important species for marine mussel aquaculture through FishStat, a global aquafood production database (FAO, 2023). We selected six mussel species that account for 99 % of global mussel aquaculture production in terms of landings and value. Mussel production is currently centred on: 'sea mussel nei' (51.7 %), *M. chilensis* (11.9 %), *M. edulis* (10.5 %), *M. galloprovincialis* (6.1 %), *M. unguiculatus* (2.8 %), *Perna viridis* (10.8 %), and *P. canaliculus* (2.8 %) (see Appendix 2 - Fig. S1). The acronym 'NEI' (i.e. Nowhere Else Included) is widely used in fisheries statistics in FAO reports and databases. FishStat reports the mussel production of some countries, notably China and Spain, under the 'sea mussel nei' category, grouping together landings that may include *M. edulis, M. unguiculatus, M. galloprovincialis*, and *P. viridis*. The precise identity of the 'nei' category is not relevant to the selection process of the present study, as all NEI species have already been selected for subsequent analyses.

Georeferenced records of the selected species were obtained from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org), and all records without explicit coordinates were filtered out. The records of some species were patchy in space and did not cover all the known geographic distribution, so GBIF data were complemented with records from the literature. We excluded isolated records of *M. galloprovincialis* around the world: many of them remain unconfirmed using molecular tools and their inclusion could confound the results. We only included the most recent records for all mussel species (2000–2023). The reason for doing this is twofold: (1) to avoid including unreliable records, as *M. edulis* used to be considered a cosmopolitan species in the northern hemisphere (Seed, 1969), and older records could correspond to misidentification, and (2) to match the record data with the present environmental data. Furthermore, unreliable records were manually deleted with QGIS software (QGIS Development Team, 2023), such as records with zeros for coordinates or records far from the shore (both inland or offshore). Duplicate records were deleted to only retain unique records. The records per species used for the analyses are presented in Table 1 (Appendix 1.). We applied the 'thinning' process to reduce the number of clusters of records to avoid geographic bias (Sillero et al., 2021). We performed thinning in the open source R software 4.4.0 (Team, 2021) using a custom script that sets a radius of 0.83° to match the size of the raster cell.

2.2. *Environmental predictors*

We retrieved the explanatory variables from the Bio-ORACLE 2.0 and MARSPEC repositories (Assis et al., 2018; Sbrocco and Barber, 2013), with a spatial resolution of 5 arcmin (9.2 Km^2 at the equator). These

Table 1
Record data for selected species before and after filtering (unique records).

Species	Common Name	Initial Records	Filtered Records
Mytilus chilensis	Chilean Mussel	869	72
Mytilus edulis	Blue Mussel	124,802	2841
Mytilus galloprovincialis	Mediterranean Mussel	11,136	717
Mytilus unguiculatus	Korean Mussel	453	145
Perna canaliculus	Green-lipped Mussel	1490	208
Perna viridis	Green Mussel	562	184

included the annual minimum, maximum, and mean sea surface temperature (SST), salinity, current velocity (speed), and ocean bathymetry. The selection of variables was restricted by the availability of data, as the projection of the model requires the same collection of variables used to train the model in the present. The models for each selected species were projected to the nearest future available (2040–2050), under the Representative Concentration Pathway 8.5 (RCP 8.5). We selected this period because we aimed our research to be useful to stakeholders and decision-makers, to be able to foresee a collapse of the industry, and so, the period 2090–2100 might be far beyond the scope of interest of the people currently working in the mussel industry. We focus on the RCP 8.5 scenario, which, although the most aggressive one, is also the most consistent with current trends (Schwalm et al., 2020). Predictions of current and future models were visually compared in QGIS 3.24 (QGIS Development Team, 2023). Ocean bathymetry data were available only for the present and were also used for future projections. While sea levels are expected to rise from 0.57 m to 5.49 m in 2100–2500 (Jevrejeva et al., 2012), the coarse spatial scale of our study means depth changes by 2050 will still fall within the same bathymetry pixels. Thus, using the current bathymetric layer for future scenarios is reasonable due to minimal depth differences over this shorter timeframe.

2.3. Model fitting and evaluation

We restricted our analysis to the specific marine biogeographic region native of each species. This allows us to approach the accessible areas for the species, which optimizes the model performance metrics (Barve et al., 2011; Sillero et al., 2021). The boundaries were set following (Spalding et al., 2007). We used their higher level of 'Realm' since these species can inhabit broad extensions, occupying several 'Ecoregions'. By focusing only on the accessible area, models are better equipped to discriminate between suitable and unsuitable habitats within the known range of the species, improving their discrimination capacity (Barve et al., 2011). We calculated the distribution of suitable habitats for each species with MaxEnt 3.4.4 (Phillips et al., 2006; Phillips et al., 2017). We chose Maxent as it uses presence and background data and is more robust to sampling biases and less prone to over-fitting (Elith et al., 2011; Merow et al., 2013). Presence/absence algorithms such as Generalized Linear Models (GLM) or Generalized Additive Models (GAM) might model the sampling effort instead of the species distribution when modelling aquatic species (Fernandez et al., 2022). We used MaxEnt using the records of the selected species, together with the aforementioned environmental predictors.

We ran 10 replicates using bootstrap. In each iteration, 70 % of the occurrences were randomly selected for model training, and 30 % were reserved to test the model. We assessed model performance using the area under the curve (AUC) of the receiver operating characteristic (ROC), a commonly used discrimination metric that measures the model's ability to distinguish presences from background points (Phillips et al., 2006; Baldwin, 2009). The AUC depends on prevalence and its focus on discrimination rather than calibration when not using presences and absences (A. Jiménez-Valverde et al., 2013; Yates et al., 2018). Specifically, in presence-background models like MaxEnt, the maximum achievable AUC is constrained by the prevalence (i.e., AUC max = 1 - prevalence/2), meaning that only when prevalence is equal to 1 can AUC reach a value of 1 (Allouche et al., 2006; Sillero et al., 2021). To address these limitations, we generated null models for each species, creating random occurrence sets matching the same sample size as the empirical models, and then compared the empirical AUC values against these null models. By doing so, we demonstrated that our model predictions consistently outperformed random predictions, thus confirming their robustness. Additionally, we assessed the statistical significance of differences in AUC between empirical and null models. We checked the normality of AUC values with the Shapiro-Wilk test, applied Welch's *t*-test to compare means, and used the Wilcoxon rank-sum test to compare medians, following the methodology outlined by Raes & ter Steege (2007).

The outputs of each model were visualized as habitat suitability maps (HSM; sensu Sillero, 2011) assembled in QGIS 3.34. Then, to facilitate the interpretation of results, we applied a habitat suitability threshold to both the present and future raster outputs, creating binary maps of suitable and unsuitable areas with a custom R script. To determine the presence-absence thresholds for each species, we employed the Equal Test Sensitivity and Specificity (ETSS) criterion, which balances omission and commission errors, ensuring an equitable trade-off between overestimation and underestimation (Liu et al., 2005; Alberto Jiménez-Valverde and Lobo, 2007). This approach is particularly suitable for scenarios with varying environmental conditions and species-specific ecological requirements. The resulting thresholds were species-specific used are shown in Table S2.

Using these binary maps, we then categorized areas based on changes in suitability between the two scenarios (present and future): Unsuitable areas were those below the threshold in both scenarios; Stable areas were those above the threshold in both scenarios; Lost areas were above the threshold in the present but below in the future; and Gained areas were below the threshold in the present but above in the future. This sequential process highlights regions where habitat suitability is maintained, lost, or newly gained under projected environmental changes.

2.4. Estimation of suitable habitat area

To quantify changes in habitat suitability, we measured the area of the stable, gained and lost areas under projected environmental changes. Given the extensive latitudinal range of the species' distribution, calculating areas directly from geographic coordinate systems (e.g., WGS 84) would introduce significant inaccuracies due to distortions in distances and areas. To ensure accurate area calculations and avoid possible bias, we reprojected the data to the equal-area Mollweide projection (Budic et al., 2016). The reprojection was performed using the st_transform function from the sf package in R. The resulting areas were converted to square kilometres for reporting. Summarized results were then grouped by category to obtain the total area for each category. This approach ensures precise and reproducible calculations of habitat area across different scenarios and species distributions.

3. Results

While the distribution of suitable habitats predicted for the present models fits well with the observed distribution of the six species, their distributions are predicted to change in the future. Distributional changes will occur primarily at the upper and lower distribution limits of each species (Fig. 2–7). In addition to the maps in the main text that highlight projected differences, Figs. S2 to S7 (Appendix 2) present pairs of maps showing the Ecological Niche Model predictions separately for the present and future. The average AUC was a high, 0.958 (standard deviation, SD ± 0.007). Importantly, AUC from empirical models were significantly higher than the AUC values from the null models (AUC = 0.576 ± 0.040). The complete list of AUC statistics is shown in Table S1 (Appendix 2).

The jackknife analysis of variable importance revealed consistent patterns across species, with depth as a key variable for all mussel species. However, the relative influence of other environmental variables varied, with temperature, salinity, and current velocity playing more prominent roles depending on the species (Fig. 1). Depth was the most influential variable for all these coastal species, with the highest gain when used in isolation and the largest loss when omitted. The following description focuses on the relative importance of the other environmental factors, which varied between species (Fig. 1). For *M. chilensis*, mean and maximum salinity were the most relevant variables, while *M. edulis* and *M. galloprovincialis* were primarily influenced by mean

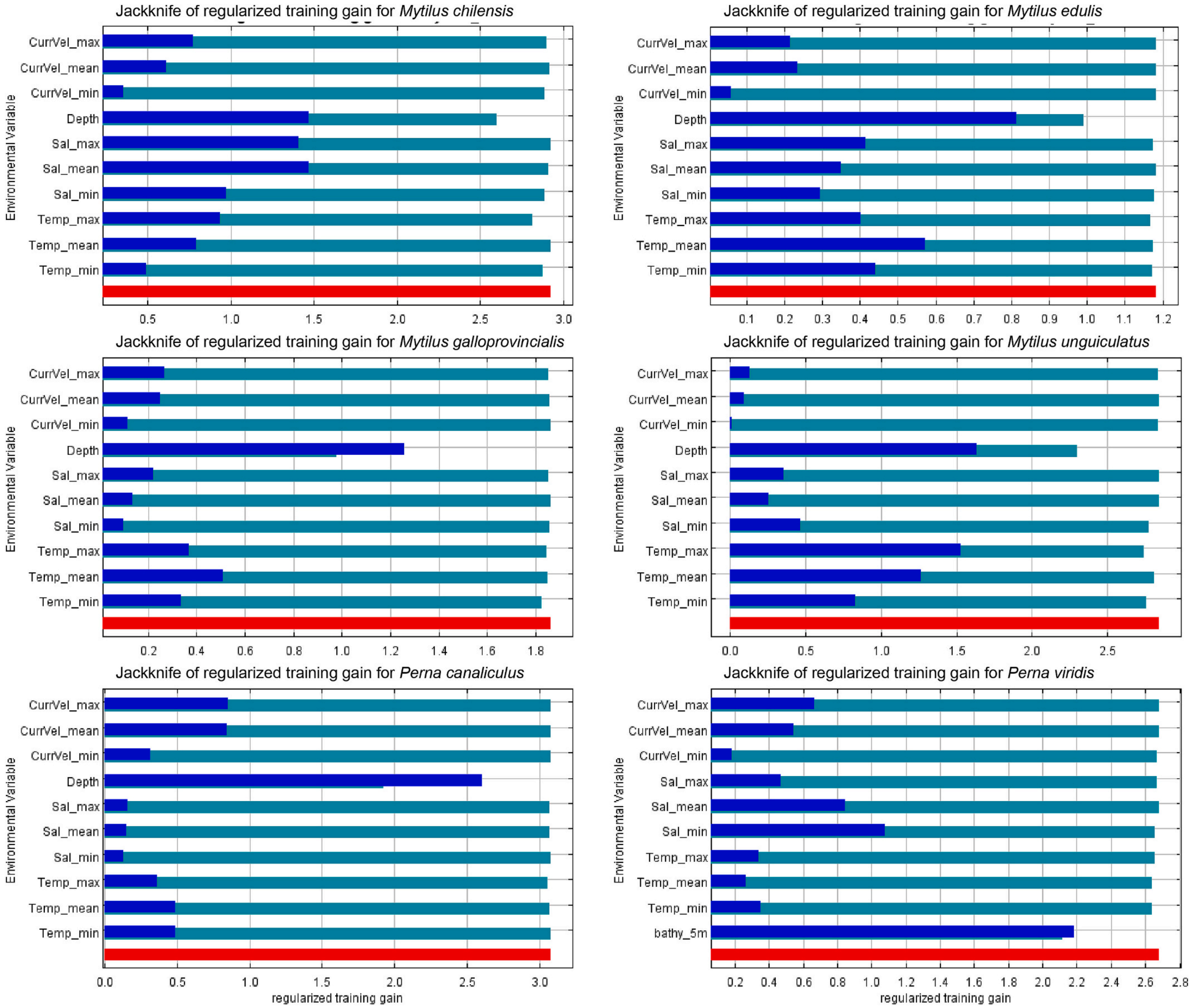

Fig. 1. Results of the jackknife test of variable importance for all six mussel species, showing the contribution of each environmental variable to the MaxEnt model predictions. Blue bars represent the gain achieved using only the given variable, indicating its unique contribution to the model. Cyan bars represent the gain when the given variable is excluded, showing the loss of unique information. The red bar represents the gain achieved using all variables together, reflecting the combined predictive power of the model. Variables considered: current velocity (CurrVel), bathymetry (depth), water salinity (sal), and water temperature (temp). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperature. *Mytilus unguiculatus*, however, was more affected by maximum and minimum temperature rather than mean temperature. For *P. canaliculus*, maximum and mean current velocity, along with the mean temperature, played a significant role, whereas for *P. viridis*, maximum and mean current velocity were also key factors, but with a stronger influence of the mean and minimum salinity.

3.1. Mytilus chilensis predictions

Predictions for the Chilean Mussel (*M. chilensis*) were restricted to temperate South America. For this species, the model predicted suitable habitats from 35.1°S down to the southern extreme of the continent at 56.6°S (Fig. 2a). A loss of habitats was predicted around 36°S in the northern edge. The extensive areas around 41–43°S, where its aquaculture takes place, are predicted to remain stable, with no major changes. Gains and loss of habitats are predicted, but mostly offshore. In the area assessments *M. chilensis* retained 227,561 km^2 of stable habitat, while 15,496 km^2 were lost and 18,013 km^2 gained, indicating a relatively balanced pattern of habitat change.

3.2. Mytilus edulis predictions

Blue Mussel *M. edulis* is broadly distributed in the northern hemisphere, spanning over two oceans and two marine realms: Temperate Northern Pacific and Temperate Northern Atlantic. Suitable habitats were found in the North Pacific and Atlantic, on both American and European shores for the latter (Fig. 3a). Our results showed suitable habitats on the Pacific coast of North America, from Baja California (36°N) along the United States poleward to the Gulf of Alaska (61°N) (Fig. 3b). On the Pacific coast, suitable habitats were found from Monterey Bay northwards (36.8°N), which were predicted to be lost in the future, though habitats in the San Francisco Bay area would remain stable (37.8°N). In the west of the Gulf of Alaska, habitat gains were predicted. Along the western Atlantic coast, habitats were found

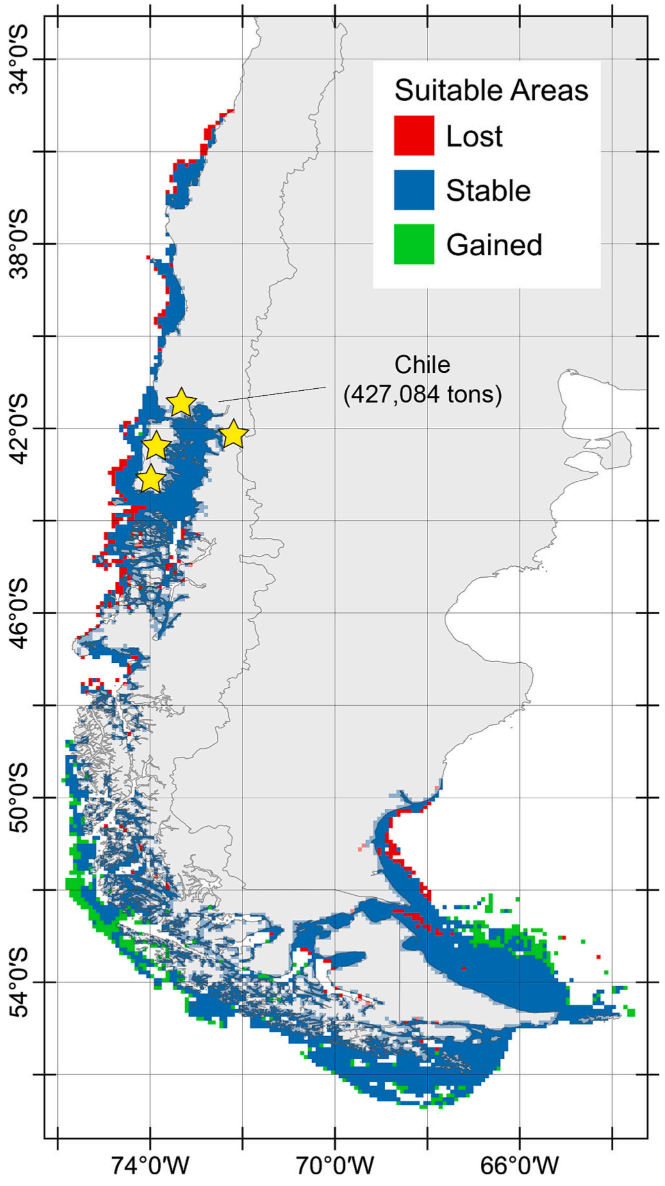

Fig. 2. Projected geographical distribution of suitable habitats for *Mytilus chilensis* under the Climate Change scenario Representative Concentration Pathway 8.5 (RCP 8.5) for the future period (2040–2050). Red areas represent habitats predicted to be lost, blue areas indicate stable habitats and green areas represent habitats predicted to be gained. Stars represent the main mussel aquaculture areas, while labels indicate every producing country for this species along with their reported production in tons for 2022 (FAO, 2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

38–48°N (Fig. 3c). In the future is predicted a loss of 500 linear Km of habitats along the southern edge of its distribution in the Delaware Bay and New York/New Jersey Bight. The model predicted loss of habitats along the Northumberland Strait (45.9°N), while the coast of Maine, New Brunswick and Nova Scotia would remain stable in this scenario, and with future northwards gains of suitable habitats around 50°N in the Gulf of St. Lawrence (Fig. 3c). Along the eastern Atlantic coast, suitable habitats were predicted from Portugal to Russia (37.8–67.9°N) (Fig. 3d). Loss of habitat is predicted in Portugal, northern Spain and southwestern France, with gains of habitat offshore and in the Faroe Islands (62°N). The predicted habitats for *M. edulis* maintained a large portion of its habitat, with 920,603 km^2 categorized as stable. However, the species also experienced a net loss, with 87,384 km^2 lost and 186,462 km^2 gained.

3.3. *Mytilus galloprovincialis* predictions

The Mediterranean Mussel (*M. galloprovincialis*) covers more marine realms than any other species, as it has been introduced in several countries for aquaculture. It is found in the Temperate Northern Atlantic (from where it is native), temperate northern Pacific, temperate southern Africa, and temperate Australasia. Currently, suitable habitats occur in the south from the Mauritania coast (21°N), in Africa, to northern Scotland, in the United Kingdom (Fig. 4). Also throughout the Mediterranean, up to the Black Sea. Currently, Greece, France, and Spain are the main producers of *M. galloprovincialis*. The prediction included an important loss of suitable habitats throughout the Mediterranean and the Black Sea. Some of this loss of habitat is predicted offshore or where this species is not cultivated (i.e. southern Mediterranean coast), although the model predicted loss of habitat in southern Italy and Greece, the two main producers of the Mediterranean Mussel. However, some pockets of suitable habitats remained along the north of the Aegean Sea. In the north, habitats would remain stable up to the United Kingdom and the Netherlands. The model predicted a northward expansion of suitable habitats in Scotland and Denmark (Fig. 4). Our results also predicted suitable habitats where this mussel has already been introduced and even became invasive, and in sites where this species could establish and spread in the future (Fig. S4). The area estimations for *M. galloprovincialis* exhibited a significant loss of habitat, with 293,369 km^2 classified as lost, compared to 170,477 km^2 gained. However, a considerable portion of its habitat, totalling 562,153 km^2, remained stable between the present and future scenarios.

3.4. *Mytilus unguiculatus* predictions

The Korean Mussel (*M. unguiculatus*) occurs in the temperate Northern Pacific, in the Yellow Sea and the Sea of Japan (Fig. 5). The species had suitable habitats beyond its observed distribution, including suitable habitats in Japan and on the Korean Peninsula. Future models predicted a loss of habitat mostly offshore in the Yellow Sea and a gain of suitable habitats toward higher latitudes, along western Russia (Fig. 5). Habitat in southern South Korea would remain stable in future models. The assessments for *M. unguiculatus* showed a predominance of lost habitat, with 459,502 km^2 lost compared to only 32,647 km^2 gained. The stable habitat area for this species was moderate, totalling 319,294 km^2.

3.5. *Perna canaliculus* predictions

The Green-lipped Mussel (*P. canaliculus*) is distributed only in the temperate Australasia realm, mainly on the coast of New Zealand. For the present, our results predicted suitable habitats for this species in the northern and southern islands of New Zealand from where this species is native and where it is cultivated (Fig. 6). The model also found suitable habitats in south-western Australia, including Tasmania (Fig. S6). In the predicted future, the species lost suitable habitats on the northern shores of the North Island of New Zealand. The model predicted habitat gains throughout the Southern Island, mostly offshore. *Perna canaliculus* showed relatively smaller areas across all categories than the other species, with 68,918 km^2 of stable habitat, 9572 km^2 lost and 12,389 km^2 gained. This species exhibited minimal changes compared to others.

3.6. *Perna viridis* predictions

The Asian Green Mussel (*P. viridis*) is widely distributed in two marine realms, the Central and Western Indo-Pacific. Currently, the species has highly suitable habitats from India in the west, to China and Japan in the north, and Papua-New Guinea in the south (Fig. 7). The Philippines

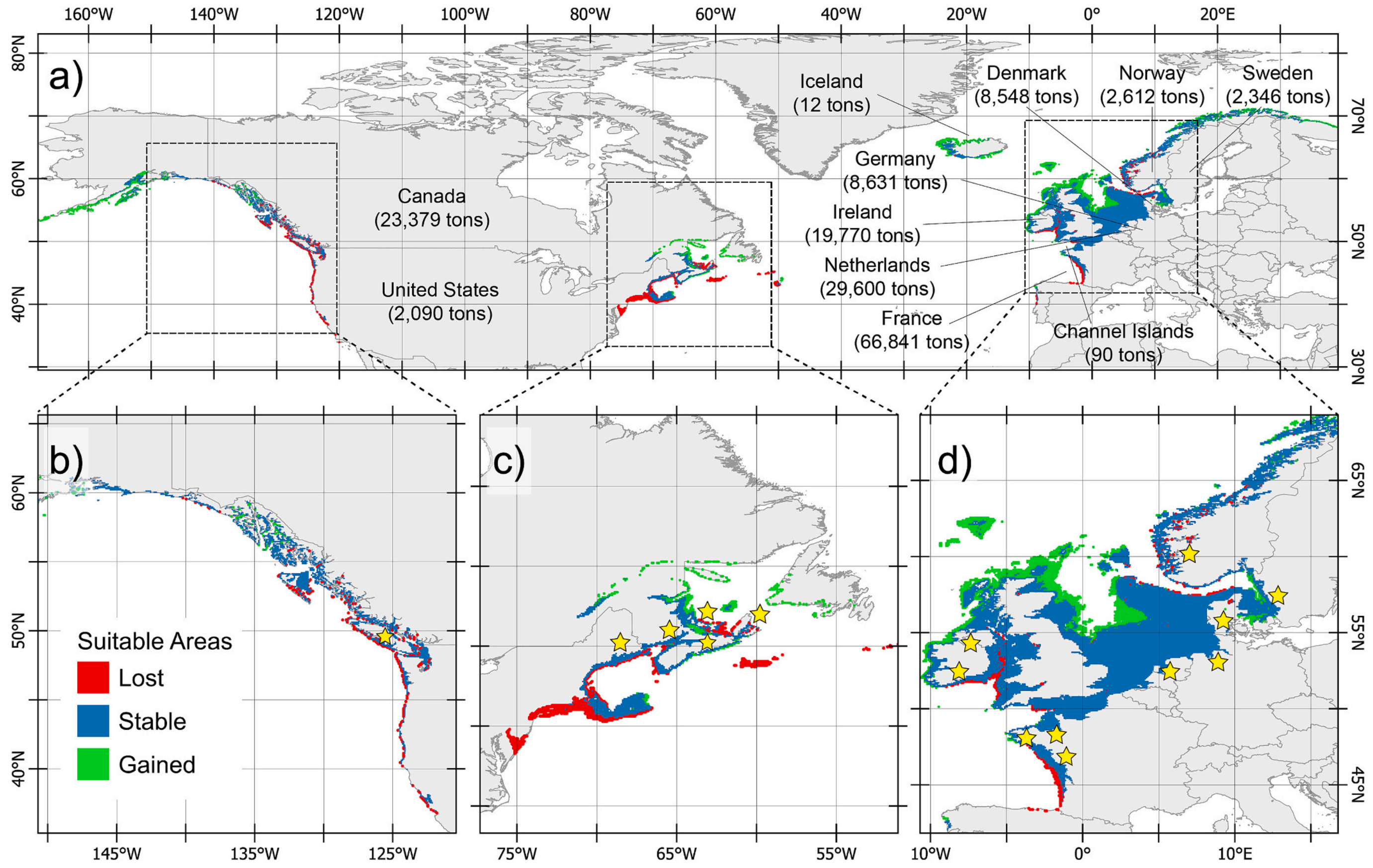

Fig. 3. Projected geographical distribution of suitable habitats for *Mytilus edulis* under the Climate Change scenario Representative Concentration Pathway 8.5 (RCP 8.5) for the future period (2040–2050). Red areas represent habitats predicted to be lost, blue areas indicate stable habitats and green areas represent habitats predicted to be gained. Stars represent the main mussel aquaculture areas, while labels indicate every producing country for this species along with their reported production in tons for 2022 (FAO, 2023). Not shown: Senegal (142 tons). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is currently its main producer, and the model suggests stable suitable habitats in the future. The model also predicts suitable stable habitats in India and southern Java. For the future, the model predicted an important loss of suitable habitats at the Equator, mostly through Thailand, Indonesia, and Malaysia. The present and future models indicated the presence of suitable habitats in Australia to the South. *Perna viridis* displayed the largest overall areas in all categories, including 1,838,293 km^2 of stable habitat. Despite this, it experienced substantial losses amounting to 1,271,975 km^2, while 535,210 km^2 of new suitable habitat was gained (Fig. 7, S8).

4. Discussion

Climate Change poses a threat to livelihoods and food security with wide-reaching implications for both ecological and human systems (Froehlich et al., 2018; Kaczan and Orgill-Meyer, 2020). Moreover, the climate-driven redistribution of biodiversity also contributes to the rearrangement of the goods and services provided by ecosystems (Poloczanska et al., 2016). As habitat engineers, marine mussels are an important ecological component of coastal ecosystems, providing biogenic substrate and refugia for other species (Buschbaum et al., 2009; Arribas et al., 2014; Norling and Kautsky, 2007). Our study predicted that suitable habitats for the most cultivated mussel species around the world will shift poleward by 2050 (RCP 8.5), with gains at higher latitudes and substantial losses at lower latitudes. The high AUC values obtained in our models demonstrate strong predictive power and robust capacity to delineate suitable habitats for the studied mussel species, providing valuable insights into potential future distribution patterns. The predicted spatial shifts arise from changes in the environmental conditions required for mussel culture, providing an early warning, and an opportunity to develop adaptation strategies (Froehlich et al., 2018; Fong et al., 2024).

The use of ENMs provides a robust approach to addressing concerns about future habitat loss. By leveraging extensive datasets of species records and environmental parameters, ENMs allow the examination of changes in distributional patterns over broad scales following predictions of future range shifts and trends (Boavida-Portugal et al., 2018). Significant portions of suitable habitats are predicted to be lost under future CC scenarios, particularly in regions depending on open aquaculture systems (Fig. 2–7). It is important to note that much of the projected habitat loss occurs offshore, away from existing aquaculture sites. This distinction highlights the need for careful interpretation, as not all habitat loss directly translates into reduced aquaculture potential. Conversely, gains in suitable habitats at higher latitudes, such as those predicted for *M. edulis* and *M. unguiculatus*, represent opportunities for relocating or intensifying production in the future. These shifts underscore the critical need for proactive spatial planning to minimize disruptions to aquaculture operations and coastal communities while ensuring resilience in the face of climate change.

4.1. Oceanographic changes and biological challenges

The projected habitat changes reveal notable differences among species, with *P. viridis* experiencing the largest net loss of suitable habitat, primarily at lower latitudes in the Indo-Pacific region, and *M. edulis* showing large habitat gains at higher latitudes in both the

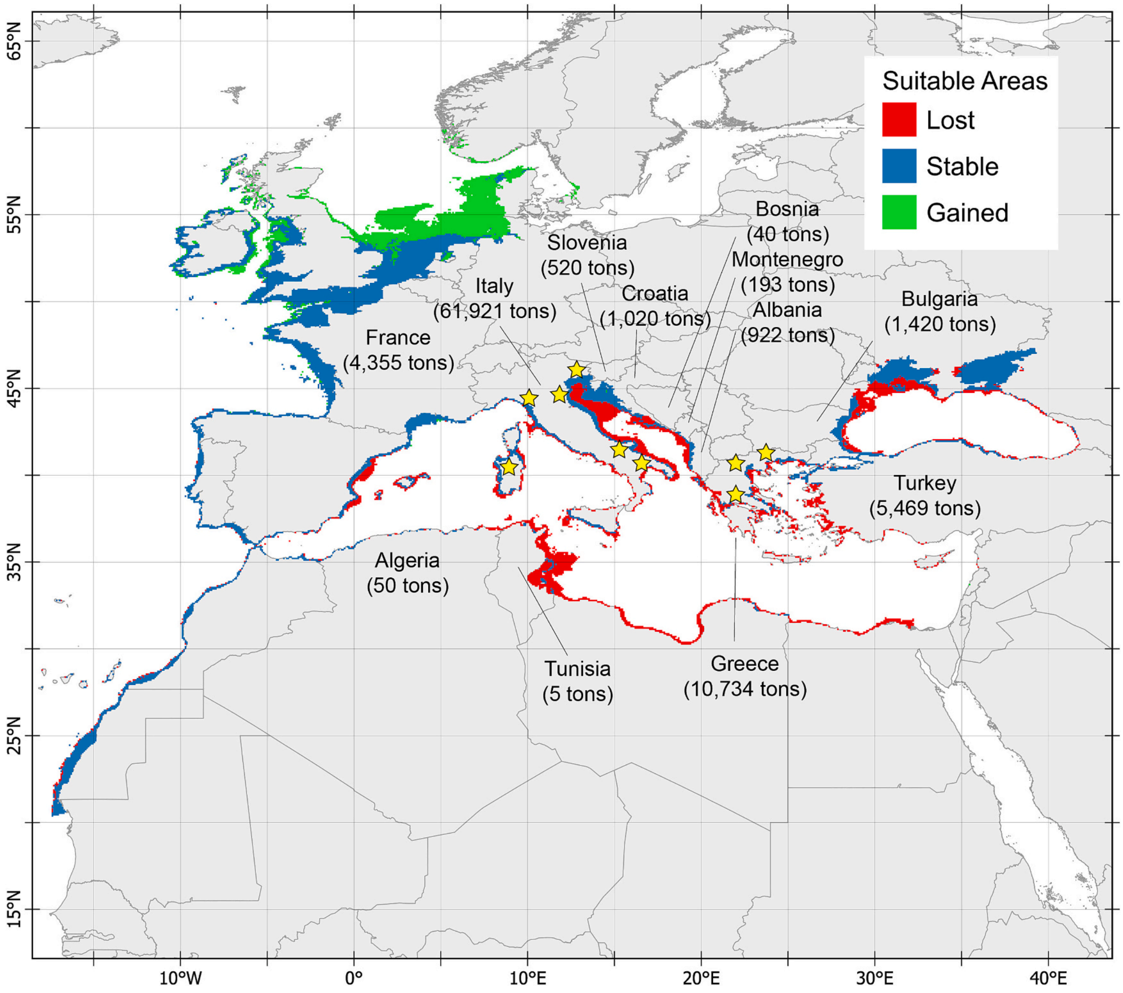

Fig. 4. Projected geographical distribution of suitable habitats for *Mytilus galloprovincialis* under the Climate Change scenario Representative Concentration Pathway 8.5 (RCP 8.5) for the future period (2040–2050). Red areas represent habitats predicted to be lost, blue areas indicate stable habitats and green areas represent habitats predicted to be gained. Stars represent the main mussel aquaculture areas, while labels indicate every producing country for this species along with their reported production in tons for 2022 (FAO, 2023). Not shown: South Africa (3261 tons). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Atlantic and Pacific Oceans. These shifts highlight contrasting opportunities and challenges for aquaculture. Regions currently relying on *P. viridis* for aquaculture may face significant production losses, requiring adaptive management strategies to mitigate impacts. Conversely, the expansion of suitable habitats for *M. edulis* presents opportunities for aquaculture growth in higher-latitude regions, particularly in areas such as the Gulf of St. Lawrence and northern Europe. These findings underscore the importance of incorporating habitat change predictions into spatial planning and developing region-specific strategies to enhance aquaculture resilience under future climate scenarios. In particular, for *M. chilensis* we anticipated small latitudinal shifts in habitat distribution, which may be attributed to the cooling trend in SST reported and predicted for central-southern Chile, one of the four main Eastern Boundary Upwelling Systems (Bakun et al., 2015; W. Schneider et al., 2017). The EBUS are highly productive regions where wind-driven upwelling transports deep, nutrient-rich, and cold waters to the surface, sustaining high levels of primary production (Bakun et al., 2015; Messie and Chavez, 2015). Coastal upwelling is expected to intensify in EBUS, bringing deep, acidic, nutrient-rich, cold, and salty waters to the surface layers of coastal zones (Bakun et al., 2015), which, in turn, can slow the impacts of global warming. Notably, salinity, rather than temperature, emerged as the environmental variable with the largest effect on *M. chilensis* habitat suitability, as shown in Fig. 1. This suggests that future habitat stability for *M. chilensis* in central-southern Chile may be more strongly linked to salinity patterns driven by upwelling intensification than to temperature changes alone. However, decreasing precipitation trends due to climate change may also elevate surface salinity in fjord systems, potentially reducing suitable habitats for *M. chilensis* while favouring competing species in the water column, with adverse implications for wild seed collection and aquaculture sustainability in Chile (Molinet et al. 2024).

Similarly, the weak upwelling intensification associated with the California and Canary current EBUS (Bakun et al., 2015; Sydeman et al., 2014), might also explain why suitable habitats for *M. edulis* are expected to experiment only small latitudinal changes (Fig. 3). The relative stability of these systems in terms of upwelling dynamics likely buffers the impacts of climate change in EBUS, providing thermal refuges for *M. edulis* populations. However, significant habitat loss is projected outside upwelling zones. This pattern highlights the importance of upwelling in moderating temperature increases and preserving suitable conditions for *M. edulis*, as regions without this oceanographic process are more susceptible to habitat loss driven by ocean warming. A similar trend is observed for *M. galloprovincialis*, with habitat loss concentrated in warmer regions such as the Mediterranean and the Black Sea. For both species, temperature is the most influential environmental variable after depth (Fig. 1), consistent with the observed habitat contraction in areas more affected by rising sea temperatures. These findings highlight the role of regional oceanographic conditions, such as upwelling, in

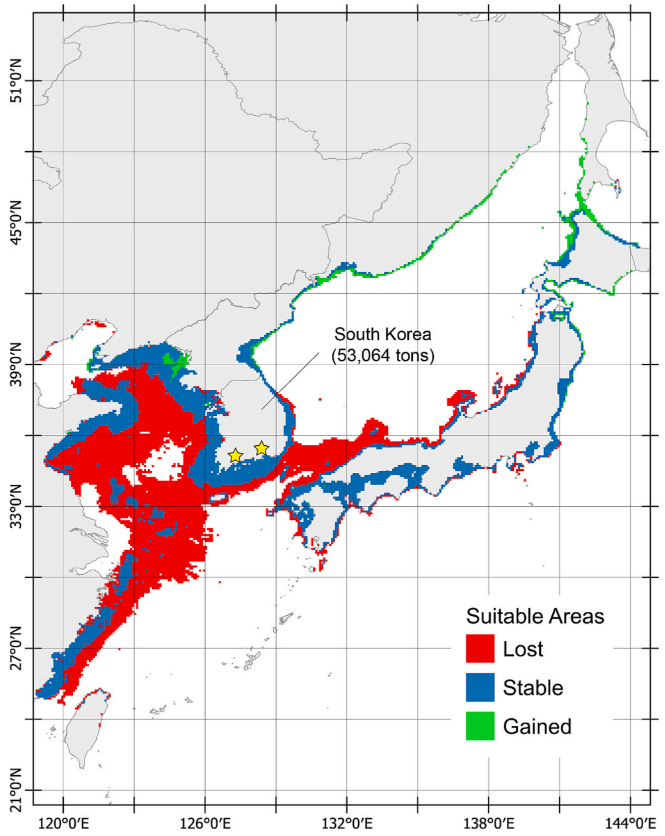

Fig. 5. Projected geographical distribution of suitable habitats for *Mytilus unguiculatus* under the Climate Change scenario Representative Concentration Pathway 8.5 (RCP 8.5) for the future period (2040–2050). Red areas represent habitats predicted to be lost, blue areas indicate stable habitats and green areas represent habitats predicted to be gained. Stars represent the main mussel aquaculture areas, while labels indicate every producing country for this species along with their reported production in tons for 2022 (FAO, 2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

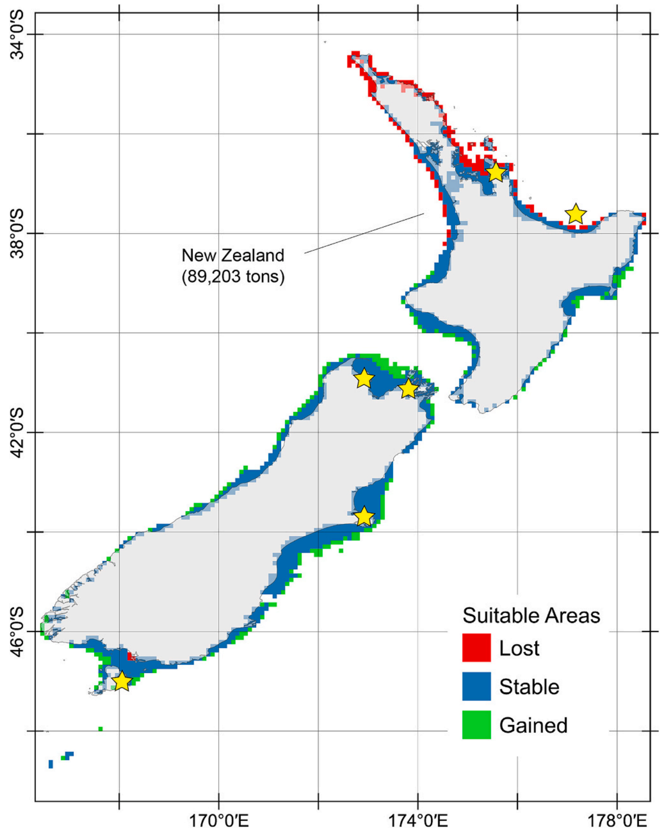

Fig. 6. Projected geographical distribution of suitable habitats for *Perna canaliculus* under the Climate Change scenario Representative Concentration Pathway 8.5 (RCP 8.5) for the future period (2040–2050). Red areas represent habitats predicted to be lost, blue areas indicate stable habitats and green areas represent habitats predicted to be gained. Stars represent the main mussel aquaculture areas, while labels indicate every producing country for this species along with their reported production in tons for 2022 (FAO, 2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

determining the future distribution of mussel habitats under climate change scenarios. The Mediterranean Sea is warming at different rates in space (Shaltout and Omstedt, 2014). The temperature in the Gulf of Lyon and the Adriatic Sea is expected to increase with average annual temperatures lower than the rest of the Mediterranean (Shaltout and Omstedt, 2014), a trend that aligns with the pockets of suitable habitats we project for *M. galloprovincialis* (Fig. 4).

The Korean Mussel is expected to lose suitable habitats at lower latitudes following documented distributional shifts (Pinsky et al., 2020; Rogers et al., 2019). For this species, the maximum temperature is the most influential variable in the habitat model after depth (Fig. 1), suggesting that rising sea temperatures at lower latitudes may exceed the species' physiological tolerance, driving habitat loss. For *P. canaliculus*, our results predicted habitat loss at the warm edge of the range. New Zealand's coastal waters are warming, with the strongest impacts in the east and the weakest in the north (Sutton and Bowen, 2019). However, predicted temperature changes do not match the spatial pattern of habitat change predicted by our analyses. This mismatch could be attributed to the relative importance of current speed as a key driver of habitat suitability for *P. canaliculus*, as suggested by the results of the Jackknife test (Fig. 1). Current speed appears to have a stronger influence than temperature in this species' habitat model, potentially explaining the discrepancy. This observation is consistent with previous findings that highlight the role of current speed as a critical factor in determining suitable habitats for mussels, including *P. canaliculus* (Benjamin et al., 2009), since it prefers moderately exposed environments with specific current flow conditions, further supporting this explanation (FAO, 2009). Lastly, for *P. viridis*, we projected a considerable loss of habitat that could be explained by ongoing environmental changes in the Indo-Pacific Ocean following the strengthening and expansion of the Indo-Pacific warm pool (Roxy et al., 2019).

Climate Change is already opening new habitats for mussels. During the austral summer of 2019 (Cárdenas et al., 2020) reported small individuals of *Mytilus* cf. *platensis* for the first time in the Antarctic Peninsula (Fildes Bay, 62°S). Later attempts to locate them were unsuccessful, suggesting that they did not survive the Antarctic conditions (Navarro et al., 2024). Recently, (Navarro et al., 2024) showed that Antarctic winter conditions could currently act as physiological barriers for *M. chilensis*, though future warming scenarios indicate a weakening of these barriers by the end of the century. Although we did not consider Antarctica in this study, the gain of high-latitude habitats is fully congruent with our findings. As such, our results from the ENMs predict that the suitability of the habitats occupied by most mussel species that are currently key for global aquaculture will change are consistent with the trends currently documented for many coastal marine species (Pinsky et al., 2020; Rogers et al., 2019).

4.2. *Climate change effects on mussel survival*

As ectotherms, mussels are highly sensitive to environmental conditions. Climate Change introduces multiple stressors that impact critical biological parameters in mussels, including growth, development,

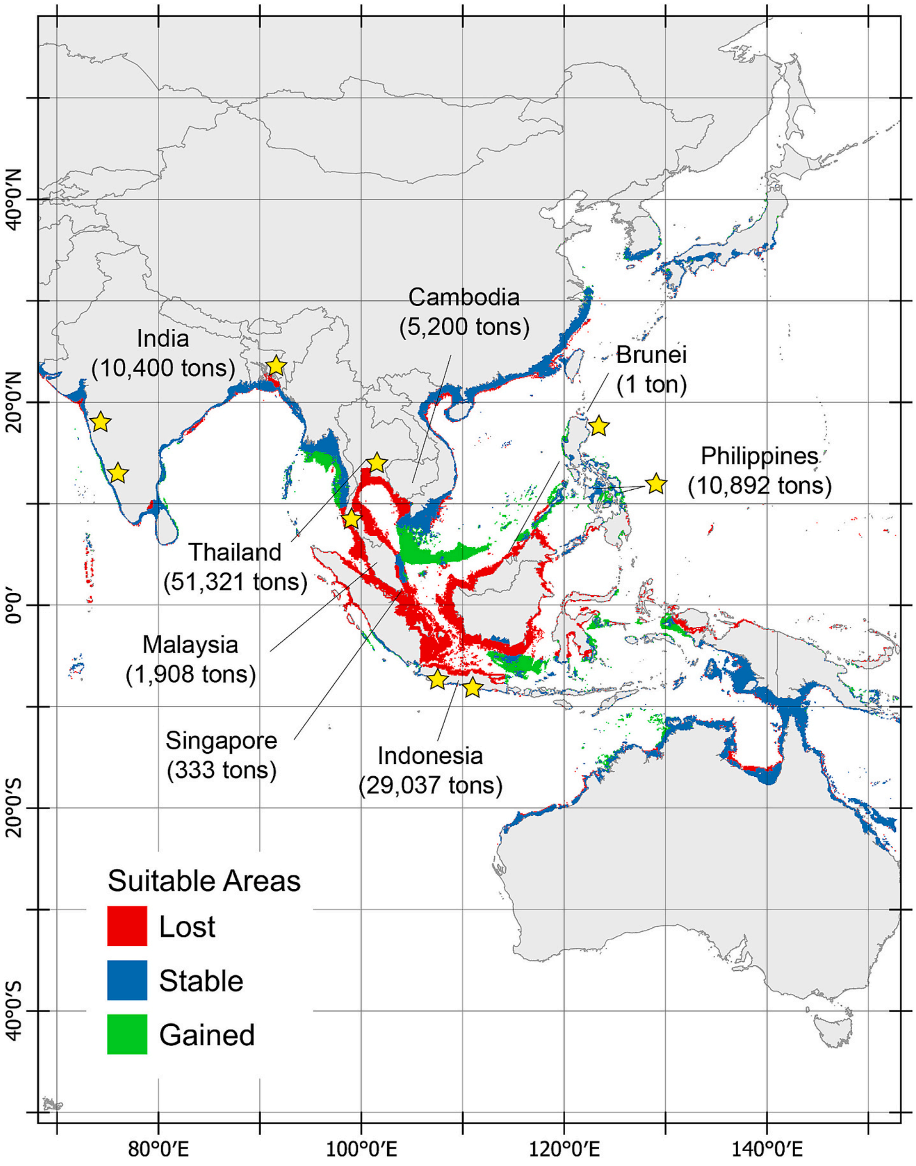

Fig. 7. Projected geographical distribution of suitable habitats for *Perna viridis* under the Climate Change scenario Representative Concentration Pathway 8.5 (RCP 8.5) for the future period (2040–2050). Red areas represent habitats predicted to be lost, blue areas indicate stable habitats and green areas represent habitats predicted to be gained. Stars represent the main mussel aquaculture areas, while labels indicate every producing country for this species along with their reported production in tons for 2022 (FAO, 2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and reproduction, which are fundamental for mussel production and food security (Maulu et al., 2021). Mussels display non-linear responses to these factors (Oliveira et al., 2021). Such interactions highlight the complexity of multiple stressors effects, which can have synergistic or antagonistic impacts (Stevens and Gobler, 2018; Manríquez et al., 2021).

While mussels have highly plastic responses to a wide range of temperatures, exceeding species-specific thresholds stops growth and becomes lethal (Zippay and Helmuth, 2012; Navarro et al., 2016; Arrieche et al., 2020; Ericson et al., 2023). On the other hand, salinity has significant impacts on mussel growth and physiological performance. Optimal salinity for marine mussels, such as *M. chilensis* and *Choromytilus chorus*, range between 18 and 24 PSU; lower salinities reduce clearance rates, filtration, oxygen uptake, and scope for growth (Navarro, 1988; Duarte et al., 2018). The impact of salinity on mussel physiology can even surpass that of elevated $p\mathrm{CO}_2$ levels, as demonstrated in studies on shell biomineralization under acidic conditions (Duarte et al., 2018; Grenier et al., 2020). Moreover, low salinity, when combined with other stressors such as parasite infections, exacerbates physiological strain and could trigger shifts in coastal ecosystems, particularly in freshening waters (Bommarito et al., 2022).

Although mussels have been shown to exhibit resilience to heat and salinity—such as heat-hardening and adaptability to moderate salinity changes (Georgoulis et al., 2023; Riisgård et al., 2012)—these mechanisms have limits. Rising temperatures, in combination with reduced food supply and lower salinity, could limit reproductive success and mussel distribution (K. R. Schneider et al., 2010; Tan et al., 2021). These impacts may propagate through ecosystems, degrading mussel body condition and leading to cascading effects on predators and associated assemblages (Melzner et al., 2020; Arribas et al., 2014).

4.3. Model limitations and future research

Our ENM models focused on temperature, salinity, current speed and depth, omitting other factors like food availability and pH, which are known to affect mussel distributions (K. R. Schneider et al., 2010; Tan et al., 2021). While these simplifications were necessary due to data limitations for future marine projections, they may overlook key ecological dynamics. Depth, as a static variable, is not directly influenced by climate change but plays a critical role in delineating the spatial extent of suitable habitats for mussel species confined to coastal areas. This highlights the importance of considering depth as a baseline factor while focusing on dynamic variables, such as temperature and salinity, to project habitat shifts under future climate scenarios. For instance, food availability, often linked to chlorophyll-a concentration, typically exhibits a 30-day accumulation period before influencing higher trophic levels, indicating that incorporating time-lagged environmental variables into the analysis could offer deeper insights into mussel habitat dynamics and ecology (Trujillo and Thurman, 2011; Wang et al., 2018). Biotic interactions, including predation and competition, are also important but remain underexplored in this study. Future studies should integrate these factors alongside high-resolution, time-lagged environmental data to better predict distributional shifts and aim toward sustainable aquaculture practices (Assis et al., 2024; Lara et al., 2016). Advances in remote sensing and bioenergetic models offer promising avenues for addressing these gaps and improving the accuracy of projections under climate change scenarios. It must be noted that there are other ENM frameworks. Mechanistic models integrate detailed physiological and ecological data to simulate species' responses to environmental variables, offering insights into fundamental niches and fitness across geographic space. In contrast, correlative models, like the MaxEnt approach used here, rely on statistical associations between species occurrences and environmental variables to predict realized niches, making them particularly suited for studies like this one, where presence-only data are available and large-scale patterns are the focus (Sillero et al., 2021; Melo-Merino et al., 2020). While correlative models provide robust predictions, future studies could benefit from hybrid approaches that incorporate mechanistic processes to better understand the drivers of geographic shifts and species responses to CC.

4.4. *Adaptive capacity and industry implications*

When faced with environmental change, a species can adapt to these changes or not. If a species adapts to the new environmental conditions, then its realized niche shifts and its geographic distribution remains stable (Sillero et al., 2022). In contrast, if a species cannot adapt–its realized niche remains the same– its distribution will change, tracking the habitat conditions included in its realized niche (Sillero et al., 2021; Sillero et al., 2022). This second scenario is called niche conservatism (Wiens and Graham, 2005) and is a necessary assumption of ENMs, which allows us to transfer the models to other areas and periods (Sillero et al., 2021). So, despite trends of habitat loss, it is important to consider that species have the evolutionary potential to adapt, this process lies beyond the time frame of our projections (2040–2050). Genetic diversity is frequently used as a proxy for adaptive potential since traits that modulate the ability to respond to environmental challenges reside within their genetic makeup (Grant et al., 2017; Castillo et al., 2024). The high genetic diversity of mussels has been linked to their ability to colonize new habitats (Han and Dong, 2020). The species *M. galloprovincialis*, for instance, has become an invasive species worldwide (Han and Dong, 2020). However, the highly dispersive reproductive strategy of some mussel species may bolster niche conservatism as an adaptive strategy (Segovia et al., 2024).

The transformation of global food systems is urgent (Naylor et al., 2021; Friel et al., 2020). Climate change is reshaping the environmental conditions underpinning aquaculture, with significant implications for sustainability and food security. Aquaculture is expected to become the main source of aquafood and a key supplier of animal protein in general (Azra et al., 2021; Costello et al., 2020). The expansion of shellfish aquaculture is a viable strategy for the future given its low GHG emissions, high fertility of the broodstock, and efficient feed conversion ratios (MacLeod et al., 2020; Costello et al., 2020; Hilborn et al., 2018). In fact, some authors have referred to shellfish as 'future food', highlighting their nutritional attributes, cost-effective production, and markedly smaller carbon footprint compared to other aquaculture stocks (e.g. fishes) (Azra et al., 2021). However, the very systems that support shellfish aquaculture are changing (Froehlich et al., 2018; Maulu et al., 2021). Rising temperatures, ocean acidification, and reductions in chlorophyll concentration are among the stressors that threaten mussel growth, reproduction, and survival (Froehlich et al., 2018; Reid et al., 2019). Adapting to these challenges will require substantial innovation. Technological advancements, selective breeding, and region-specific management strategies are essential to enhance the resilience of shellfish aquaculture (Mugwanya et al., 2022; Maulu et al., 2021). Recent projections, together with the results presented here, highlight the uneven impact of CC on marine aquaculture and identify regions where shifting environmental conditions could favour mariculture and emphasize the need for policy changes favouring adaptation and support for emerging opportunities (Fong et al., 2024; Froehlich et al., 2018). Our projections may provide valuable insights for the aquaculture industry by identifying regions where production could be relocated, maintained or intensified. Hence, our assessment of habitat suitability for these commercially important species can provide forward guidance for large-scale spatial planning strategies that minimize risks to food security over the next 25 years.

5. Conclusion

Climate Change poses major challenges to mussel aquaculture worldwide and threatens its contribution to food security and local economies. Our ecological niche modelling approach predicted differential shifts in the suitable habitat distribution of the six mussel species that comprise almost the entire world's mussel production. The results showed poleward range expansions and substantial losses of optimal growing areas at lower latitudes. Although the development of suitable subpolar regions could facilitate aquaculture expansion, the disappearance of prime historical growing zones for some species could be devastating for food supply, livelihoods, and industry persistence where current habitats will become unsuitable. Taking into account the complexities of the effects of CC on mussel physiology, future research should include a multifaceted approach considering additional environmental and social factors. Moving forward, global mussel aquaculture will require a holistic approach that cultivates the adaptive capacity of the system. The provision of robust ecological forecasts that can increase resilience should be a priority in addressing the risks of CC for this globally important activity.

CRediT authorship contribution statement

Felipe I. Torres: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carlos Lara:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Neftalí Sillero:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization. **Bernardo R. Broitman:** Writing – review & editing, Writing – original draft, Visualization, Investigation, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2025.742304.

Data availability

All data used in the present study is available in the supplementary material or in repositories online.

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