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Mapping Potential High-Yield Areas for Finfish Mariculture Using Physiological Models

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ABSTRACT

Mapping potential areas for finfish mariculture, particularly high-yield regions, is crucial for the proper utilization of marine space and global food security. Physiological models (growth performance models) that consider the spatiotemporal heterogeneity of the marine environment are a potentially effective approach to achieving this goal. In the present study, we developed an integrated model that combines the thermal performance curve and spatiotemporal heterogeneity of the marine environment to map the global high-yield potential mariculture areas for 27 commercial finfish species. Our results showed that the current sizes of the potentially suitable areas (achieving 50% of the maximum growth rate for at least six months annually) and high-yield areas (achieving 75% of the maximum growth rate throughout a year) are $(8.00 \pm 0.30) \times 10^6$ and $(5.96 \pm 0.13) \times 10^6$ km^2, respectively. Currently, the sizes of suitable and high-yield areas for warm-water mariculture fish are larger than those for other species. The growth potential of suitable mariculture areas is higher at mid and low latitudes than at high latitudes. Under the two shared socioeconomic pathway scenarios (SSP1-2.6 and SSP5-8.5), the sizes of both suitable and high-yield areas will increase by 2050. However, there is the potential for finfish mariculture to respond differently to climate change among species and regions, and cold-water fish may benefit from global warming. Overall, the global potential for suitable high-yield mariculture areas continues to increase, making finfish mariculture an important contributor to global food security.

1. Introduction

Mariculture provides a notable amount of seafood, serving as a crucial source of high-quality proteins and micronutrients for human consumption [1]. With rapid population growth, mariculture is important for ensuring food security [2–5]. From 2015 to 2050, the per capita fish consumption in most countries will gradually increase, with the total consumption in some countries more than doubling by the mid-century [4]. By 2050, 12%–25% of the incremental demand for meat will originate from the ocean, with mariculture expanding as the main component [3].

In relation to climate change, mariculture has experienced changes in temperature, pH, dissolved oxygen, sea level, and extreme events [2]. Adaptive reforms regarding climate change in marine capture fisheries and mariculture may help meet the increasing human demand for seafood [6]. However, despite significant human efforts to mitigate climate change, reforms in marine capture fisheries are unlikely to sustain the global per capita demand for seafood, necessitating further exploration of the immense potential of mariculture [6]. Climate change has increased the complexity and uncertainty of aquaculture systems [7–13].

Mapping potential global mariculture areas under current environmental and climate change conditions has garnered interest [7–13]. Gentry et al. [7] assessed the potential area for mariculture using the constraints of temperature, dissolved oxygen, depth, and other marine uses. The results showed that the suitable areas for finfish and bivalve mariculture were approximately 1.14×10^7 and 1.50×10^6 km^2, respectively. Froehlich et al. [9] used the same method to assess the potential for mariculture under climate change conditions without considering the limitations of other marine uses. The findings indicated an expansion in the potentially

suitable area for finfish mariculture, whereas the area suitable for shellfish mariculture decreased. Both studies used the growth performance index (GPI) to quantify the growth potential of different species [7,9]. GPI was calculated based on the asymptotic length and growth rate of the species [14]. The growth rates of the same mariculture species varied at different temperatures. Therefore, the use of the GPI across the entire range of thermal tolerance may overestimate the growth potential in many regions. Based on previous studies, models are urgently needed to accurately assess the growth performance of marine aquaculture fish.

The dynamic energy budget (DEB) model and simplified thermal performance curves (TPCs) are commonly used to assess the growth potential of mariculture species [8,12,13,15–19]. However, the DEB models often require numerous parameters. Collecting all the necessary data when conducting a meta-analysis is challenging. TPCs provide a more direct approach to describing the relationship between the growth rate of mariculture fish and environmental temperature. The TPCs increase with increasing temperature from the cold threshold, peak at the optimal temperature, and rapidly decline as the temperature increases [20–24]. More than 20 mathematical models are used to describe TPCs, including parabolic, Gaussian, and other complex mathematical models [25]. The shapes of TPCs vary among species, populations, individuals, and life history stages [26–31].

Although nonlinear models can describe the thermal growth performance curves of mariculture species more accurately, experimental physiological data reflecting growth processes at specific life history stages are relatively scarce and difficult to obtain for all mariculture species. Moreover, the construction of nonlinear models requires data from multiple experimental groups for parameter estimation. Therefore, previous studies assessing the potential of mariculture fish based on thermal growth performance have typically used a simplified piecewise function [8,12,15]. The simplified model only requires a low-temperature tolerance threshold, a high-temperature tolerance threshold, and an optimal growth temperature for each species, all of which are easily obtained from experiments or the literature. Klinger et al. [8] created a simplified model and estimated the global growth rates of *Salmo salar*, *Rachycentron canadum*, and *Sparus aurata* in the open ocean under current and future conditions. On a regional scale, this simplified model has been applied to assess potential mariculture regions in the Caribbean Sea [15] and China under current and future conditions [12].

Using simplified TPCs instead of nonlinear models affects the accuracy of the assessment because the simplified model cannot describe the growth rate of mariculture fish at continuous temperatures. To address this limitation, we developed thermal growth performance models for each species, integrated the thermal tolerance and growth experimental data at multiple temperatures, and used a mathematical model consisting of a Gaussian curve and parabola to describe the thermal growth performance of mariculture fish (Fig. 1(a); Section 2). This model has been used to estimate the global thermal growth performance of insects and extended to other ectotherms such as frogs, lizards, and turtles [21].
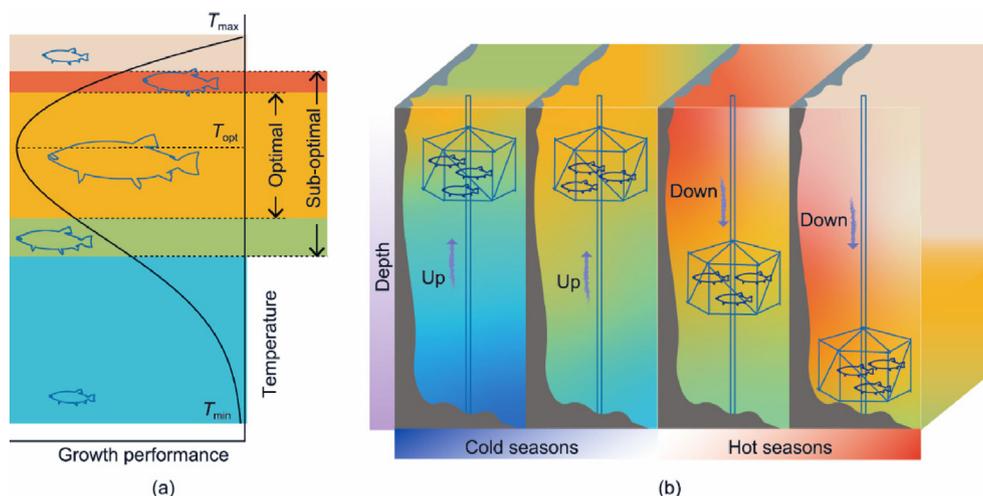
The high spatiotemporal heterogeneity of the marine environment can affect the survival of marine organisms [32]. Spatiotemporal heterogeneity of the marine environment refers to the variability and unevenness in ocean conditions, such as temperature and salinity, across spatial and temporal scales. For example, the temperature of the cold-water mass in the Yellow Sea during summer is much lower than the sea surface temperature, with a temperature difference of more than 15 °C. The Yellow Sea Cold Water Mass disappears in winter, and the temperature difference between the bottom and surface is minimal [11]. Oceanographic characteristics such as cold-water masses and upwelling currents

can create shelters that protect marine organisms from the impacts of high temperatures [33–35]. Fully utilizing environmental conditions can help identify potential mariculture areas [11,36]. An advantage of mariculture in offshore areas is the utilization of large depth spaces. For example, the sea surface temperatures in most of Democratic People's Republic of Korea exceed 20 °C in July and August, indicating the unsuitability of Atlantic salmon mariculture. However, the water temperatures at 25 m depth remain below 20 °C throughout the year, making Atlantic salmon mariculture feasible using submersible mariculture systems [36]. Studies on the potential of offshore mariculture for salmonids in the Yellow Sea have also emphasized the significance of utilizing the spatiotemporal heterogeneity of the Yellow Sea Cold Water Mass [11]. By adjusting the depth of mariculture cages throughout different seasons, China can utilize seasonal cold water masses, thereby obtaining the potential to cultivate cold water salmonids in temperate marine areas. Overall, effectively utilizing the spatiotemporal heterogeneity of the marine environment can assist in optimizing the use of marine spatial resources.

To accurately map the global potential mariculture areas and assess the growth rates of mariculture finfish, two key issues were considered in the present study: ① To assess the growth rates, we used a nonlinear model (Fig. 1(a)) that can describe the thermal growth performance curves of mariculture species more accurately than simplified TPCs. ② During the mapping of potential global mariculture areas, we integrated depth-adjustable mariculture methods into the assessment system. Mariculture cages can be adjusted to four depths, thereby allowing mariculture activities to effectively utilize the spatiotemporal heterogeneity of the marine environment (Fig. 1(b)). Previous studies lacked consistent standards for high-yield mariculture areas across different regions and species. Klinger et al. [8] used 50% of the maximum growth rate as the threshold for suitable growth. Therefore, to quantify the growth potential of mariculture in different regions, we established two criteria: potentially suitable and high-yield areas. The potentially suitable area for finfish mariculture refers to regions where the species can survive throughout the year, and the growth rates are not lower than 50% of their maximum growth rates for at least six months. Potential high-yield areas for finfish mariculture refer to regions where the growth rates of the species are not lower than 75% of their maximum annual growth rates throughout the year. In both areas, mariculture activities were conducted using a depth-adjustable farming approach.

2. Materials and methods

We developed an integrated model that combines nonlinear TPCs for the growth of mariculture finfish with the spatiotemporal heterogeneity of the marine environment. This model was used to project the growth potential of global mariculture under current conditions and future climate scenarios. The main steps were as follows: ① Building a physiological database of the thermal growth performance of mariculture fish: collecting global production and physiological data for 27 mariculture species. ② Developing thermal performance models for mariculture fish growth: using a mathematical model to describe the growth performance of different mariculture finfish at different temperatures. ③ Downloading and preprocessing environmental data: collecting current and future environmental data under different shared socioeconomic pathways (SSPs). ④ Incorporating spatiotemporal heterogeneity of marine environments to calculate the growth rate of mariculture fish: based on our models, the growth rates of each mariculture fish were computed across different water layers and months. Suitable depths for mariculture cages in different months were calculated by overlaying water layers. ⑤ Assessing potentially suitable and high-yield areas for global fish mariculture:

Fig. 1. Flowchart illustrating the assessment of potential suitable and highly productive areas for global finfish mariculture based on thermal growth performance. (a) The thermal performance curve for growth (75% and 50% of the maximum growth rates are defined as the optimal and suboptimal growth rates, respectively). T_{opt} is the optimal temperature for fish growth. T_{max} and T_{min} are the critical high and low temperatures, at zero growth rate, respectively. (b) The conceptual framework shows that suitable offshore mariculture environments can be achieved by adjusting the depths of cages. Cages can be adjusted in different water layers to obtain the optimal or suboptimal thermal environment.

mapping the potentially suitable and high-yield areas globally based on different thresholds.

2.1. Species list and physiological data

We surveyed common mariculture fish from literature and reports, including FishStatJ [37], *China Fisheries Statistical Yearbook 2023* [38], Gentry et al.'s species list of 120 fish [7], and Oyinlola et al.'s species list of 55 mariculture fish [10]. First, by searching the literature or reports, we only retained species that were proven capable of being cultured in sea cages. Simultaneously, to ensure the representativeness of these species, the species in the list were distributed from equatorial to subpolar regions. We then collected physiological experiments and mariculture data on these species and obtained a list of 27 mariculture fish species (Table S1 in Appendix A). The list included 17 warm-water fish (63%), seven temperate-water fish (26%), and three cold-water fish (11%), which was similar to the proportion in the previous list of 120 species [7], with a notable predominance of warm-water species. Fish species were identified primarily based on climate zone information from FishBase. The "tropical" and "subtropical" were defined as warm-water fish, "temperate" was defined as temperate-water fish, and "subpolar" was defined as cold-water fish. Simultaneously, we rechecked the types based on the temperature tolerance of the species and common knowledge. For example, we categorized *S. salar*, *Oncorhynchus mykiss*, and *Gadus morhua* as cold-water fishes. The types of fish used are listed in Table S1.

Using FishStatJ software [37], we evaluated the representativeness of our species list by analyzing the production of 27 mariculture finfish. We collected 27 mariculture and all mariculture fishes from 2017 to 2021. We then calculated the proportion of the 27 mariculture fish species by dividing their total annual production by the total production of all mariculture fish in that year. Notably, seabream and grouper are important components of mariculture fish in China, but no production data exist for each specific species of seabream and grouper in *China Fisheries Statistical Yearbook 2023* [38] and FishStatJ [37]. The pearl gentian grouper (*Epinephelus fuscoguttatus* ♀ × *E. lanceolatus* ♂), humpback grouper (*Cromileptes altivelis*), spotted coral grouper (*E. malabaricus*), orange-spotted grouper (*E. coioides*), and red seabream (*Pagrus major*) produce high yields in China. Therefore, the yields of seabream and grouper in China were used to represent the total production of these species.

The growth rate data of mariculture fish at different temperatures were collected from the literature [39–64]. To avoid the differences in TPCs at different life history stages and to align with the "land–sea relay" mariculture patterns, the growth performance data for large-sized juveniles and specific life history stages (such as the post-smolt of Atlantic salmon) was retained. In our study, the weights of most species exceeded 100 g, with only two species weighing less than 50 g (because of the limitations of physiological data for large-sized juveniles, we used physiological data for smaller-sized juveniles, *S. malabaricus* and *E. malabaricus*). The data for each species included different growth rates at no less than three different temperatures, and they were used to calculate the parameters of the nonlinear thermal performance models for growth. Experiments on fish growth rates at different temperatures can directly provide the required data. For continuous mariculture practices, the average temperature of each growth stage and the weight gain during the corresponding time were used to calculate the growth rate. The temperature and individual growth rate data units were converted to degrees Celsius and kilograms per month, respectively. Thermal tolerance data of mariculture fish were used to limit the growth rates at critically high or low temperatures and were collected from publicly available literature [46,58,65–95]. In addition, in the present study, thermal tolerance data were used to constrain the environmental layers that can survive mariculture fish during the process of mapping the potential globally suitable areas.

2.2. Thermal performance models for growth

The TPC in this study was based on a mathematical model developed by Deutsch et al. [21]. This model has been extensively validated in exothermic animals (insects, frogs, lizards, and turtles) and has been used in representative insect studies globally [21]. The TPC was a nonlinear piecewise function. A Gaussian function described the increase in the performance up to the optimal temperature, and the decline to zero was described by a quadratic function.

$$G(T) = \begin{cases} r_{max} e^{\left[-\left(\frac{T-T_{opt}}{2\sigma}\right)^2\right]} & T < T_{opt} \\ r_{max}\left[1 - \left(\frac{T-T_{opt}}{T_{opt}-T_{max}}\right)^2\right] & T \geq T_{opt} \end{cases} \tag{1}$$

where $G(T)$ represents the growth rates at different water temperatures, T is the water temperature, T_{opt} is the optimal temperature for fish growth, T_{max} is the critical high temperature at which the growth rate is zero, σ is the parameter for changing the shape of the Gaussian curve, and r_{max} is the maximum growth rate at the optimal temperature.

We estimated the parameters of the TPCs for growth using R packages rTPC [25] and nls.multstart [96] in R version 4.0.3 [97]. Notably, the growth rate provided by the Gaussian performance at cold temperatures never reaches zero [21]. Thus, we set a notably low growth rate (1.0×10^{-8} kg·month^{-1}) instead of zero at the critical low temperature. The growth rate at the critical high temperature was set to zero. The growth rates at different temperatures within the thermal range were obtained directly from the physiological database in the present study. The nls_multstart() function was used to calculate the parameters of the thermal performance models of the mariculture species. In the rTPC package, the mathematical model is rate~deutsch2008(). The number of iterations was set to 500.

We used the summary() to obtain the statistical values (p values and R^2) of the parameters. After calculating the parameters of each TPC for growth, we obtained the optimal growth temperatures and maximum growth rates of mariculture fish. The present study used 75% and 50% of the maximum growth rate as the thresholds for optimal and suboptimal growth rates, respectively.

2.3. Environmental variables and data

Many environmental variables, such as seawater temperature, dissolved oxygen, and current speed, can affect the physiological performance of mariculture fish. Temperature is the most important variable in the TPC of growth. The dissolved oxygen, current speed, and ocean depth were included in the model. These factors were also common variables in previous assessments of potential areas for global mariculture fish [7,8,10]. Salinity may also affect the growth of mariculture fish, particularly in nearshore and estuarine areas [98]. However, high-quality data for salinity in estuarine and nearshore areas are severely lacking locally and globally [98]. Additionally, pH may affect specific mariculture subsections, particularly bivalve mariculture [7,98–100]. Therefore, the salinity and pH were not considered in this study.

We used relatively fine-scale spatiotemporal marine environmental data to effectively utilize the spatiotemporal heterogeneity of marine environments. Monthly environmental data included multiple depths. The datasets of global sea-water temperature (thetao), current speed (vo and uo), and dissolved oxygen (o2) were downloaded from the Coupled Model Intercomparison Project Phase 6 with four Earth system models (ESMs) (Table S2 in Appendix A). To assess the changes in potential mariculture areas under different warming levels, we selected the SSP1-2.6 (low emissions) and SSP5-8.5 scenario (high emissions) for prediction. All environmental data were processed using the Climate Data Operator version 2.0.5 [101]. We obtained monthly environmental data at four depths (5, 25, 45, and 65 m) over six time periods (2010–2014, 2026–2030, 2031–2035, 2036–2040, 2041–2045, and 2046–2050). The results for the current and future (2030, 2035, 2040, 2045, and 2050) were the average results of these six time periods. The data were resampled to standard latitude and longitude resolutions of 0.1°. Ocean depth data with a spatial resolution of 15 arcs were downloaded from the General Bathymetric Chart of the Oceans [102] to limit the maximum mariculture depth. A maximum depth of 200 m was used to constrain the potential offshore mariculture areas because it is considered practical and economically feasible for mariculture operations [7].

2.4. Calculation of growth rate and constraints on potential mariculture areas

The growth rates of each mariculture species in different water layers and months were calculated based on the TPCs for growth. The marine environment was constrained by optimal (75% of the maximum growth rate) and suboptimal growth rates (50% of the maximum growth rate). The potential mariculture areas were further limited by dissolved oxygen and current speed. Based on a previous study [7], the threshold for dissolved oxygen in potential finfish mariculture areas was set at 4.41 mg·L^{-1}, which is the sublethal limit for fish [103]. The threshold for the current speed was set to 1 m·s^{-1} to avoid the impact of strong currents on mariculture activities [8]. Although low current speeds may lead to poor nutrient diffusion, hypoxia, and an increased risk of disease outbreaks [104,105], we did not limit the potential mariculture areas to the minimum current speed because technological advancements can help reduce these potential risks [106–109].

2.5. Mapping the global potential suitable areas and high-yield areas

To calculate the mariculture potential in each pixel, all constrained raster data were overlaid by month and depth. First, for the raster layers of the same month, the following criterion was used: If the growth rate in a pixel reached the optimal or suboptimal growth rate in at least one of the water layers (5, 25, 45, or 65 m), the pixel was considered to have the potential for mariculture in that month. The maximum value among the different water layers represents the maximum growth rate that the mariculture fish could achieve in the pixels during the month. Second, the raster layers for all 12 months of the year were overlaid. If the growth rate in a pixel reached the suboptimal growth rate for at least six months of the year and the environmental conditions met the survival requirements for mariculture finfish (temperature, dissolved oxygen, and current speed), the pixel was considered a potentially suitable area for mariculture. If the growth rate in a pixel reached optimal values throughout the year, the pixel was considered a potentially high-yield area for mariculture.
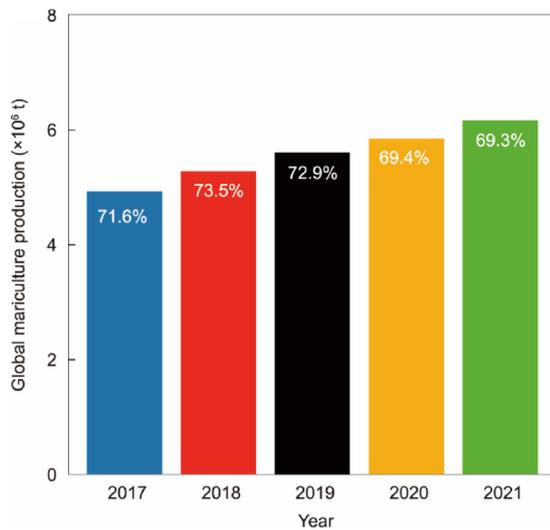
To compare the differences in the average mariculture potential of all species among different pixels, the growth rates of different species were standardized to the range [0, 1]. After standardization, the relative growth potential of the mariculture species in a pixel was averaged to obtain the regional average mariculture potential.

We calculated the sizes of potentially suitable and high-yield areas using the R package raster [110]. The results were averaged across the four ESMs. We then compared the changes in the relative growth rates between the current and future conditions. Finally, we calculated changes in the potential mariculture area for each species under different climate scenarios.

3. Results

3.1. Representativeness of species lists

The species list used in the present study included 27 of the world's major mariculture finfish species (Table S1). From 2017 to 2021, these 27 species accounted for approximately 70% of the total mariculture fish production (Fig. 2), including *S. salar*, the global highest-yield species, as well as other high-yield species such as *O. mykiss*, *R. canadum*, *Larimichthys crocea*, and *Chanos chanos*. The thermal tolerance ranges of the 27 mariculture species covered all latitudes from the equator to the subpolar regions. The species list included 17 warm-water, seven temperate-water, and three cold-water species. Consistent with Gentry's earlier compilation

Fig. 2. Historical production of representative mariculture fish. From 2017 to 2021, 27 species in our species list accounted for approximately 70% of the total mariculture fish production. The percentage represents the proportion of all representative species in the total annual mariculture fish production.

of 120 mariculture fish, warm-water species showed numerical predominance, whereas cold-water species were comparatively fewer [7]. The list of species used in this study provides a good overall representation.

3.2. Thermal growth performance models

The parameters and statistical analysis results of the thermal growth performance models for all species showed that the models accurately described their thermal growth performance. The p values of the thermal physiological parameters were all less than 0.05 (Table S1). For most species, the p values of the Gaussian curve shape parameter σ were also less than 0.05. Additionally, the coefficient of determination (R^2) of the mariculture species indicated that these models could accurately describe the growth performance of mariculture fish at different temperatures (Table S1).

Thermal growth performance models were constructed for each species (Fig. S1 in Appendix A). These TPCs showed the growth rates of different species at various temperatures. In addition, these curves provided critical high and low temperatures, optimal temperatures, and maximum growth rates for different species. The maximum growth rates of *G. morhua*, *Sciaenops ocellatus*, *R. canadum*, and *Seriola lalandi* were approximately 0.15 kg·month⁻¹, whereas the maximum growth rates of *Sebastes schlegelii*, *E. malabaricus*, *Centropristis striata*, and *Oplegnathus fasciatus* were relatively low, below 0.04 kg·month⁻¹. The optimal growth temperature for most species was above 15 °C (Figs. S1(b) and (c)), with most warm-water species having optimal growth temperatures above 25 °C (Fig. S1(c)). The optimal growth temperatures of the three representative cold-water fish species (*G. morhua*, *O. mykiss*, and *S. salar*) were all below 15 °C (Fig. S1(a)).

3.3. Global potential suitable areas and their response to climate change

Under the premise of considering the heterogeneity of the marine environment, the potentially suitable area for finfish mariculture refers to regions where the species can survive throughout the year and the growth rates are not lower than 50% of their maximum growth rates for at least six months.

Considering the premise of utilizing the heterogeneity of marine environments, the current size of potentially suitable areas was approximately $(8.00 \pm 0.30) \times 10^6$ km² (mean ± standard error). In the Northern Hemisphere, they were mainly found in the Atlantic and sub-Arctic regions, as well as the northern and western Pacific. In the Southern Hemisphere, they were primarily located in western and northern Australia and along the west coast of the Atlantic. Few potentially suitable areas for mariculture existed in the eastern Pacific and western Indian oceans. The average relative growth potential varied across latitudes in potentially globally suitable areas. Low latitudes had a higher average relative growth potential, whereas mid- and high-latitudes had a lower average relative growth potential (Fig. 3). Higher average relative growth potential occurred in Southeast Asia, northern Australia, and northern South America, whereas lower average relative growth potential was found in the Yellow Sea, East China Sea, northwestern part of the North Atlantic, and sub-Arctic regions (Fig. 3(a)).

Under the climate change scenarios, potentially suitable areas for finfish mariculture will gradually increase. By 2035, the sizes of suitable areas under the SSP1-2.6 and SSP5-8.5 scenarios will increase to $(8.29 \pm 0.32) \times 10^6$ and $(8.24 \pm 0.33) \times 10^6$ km², respectively. By 2050, the sizes of suitable areas under the SSP1-2.6 and SSP5-8.5 scenarios will further increase to $(8.44 \pm 0.41) \times 10^6$ (an increase of 2.55% compared to the current size) and $(8.63 \pm 0.42) \times 10^6$ km² (an increase of 5.47% compared to the current size), respectively.
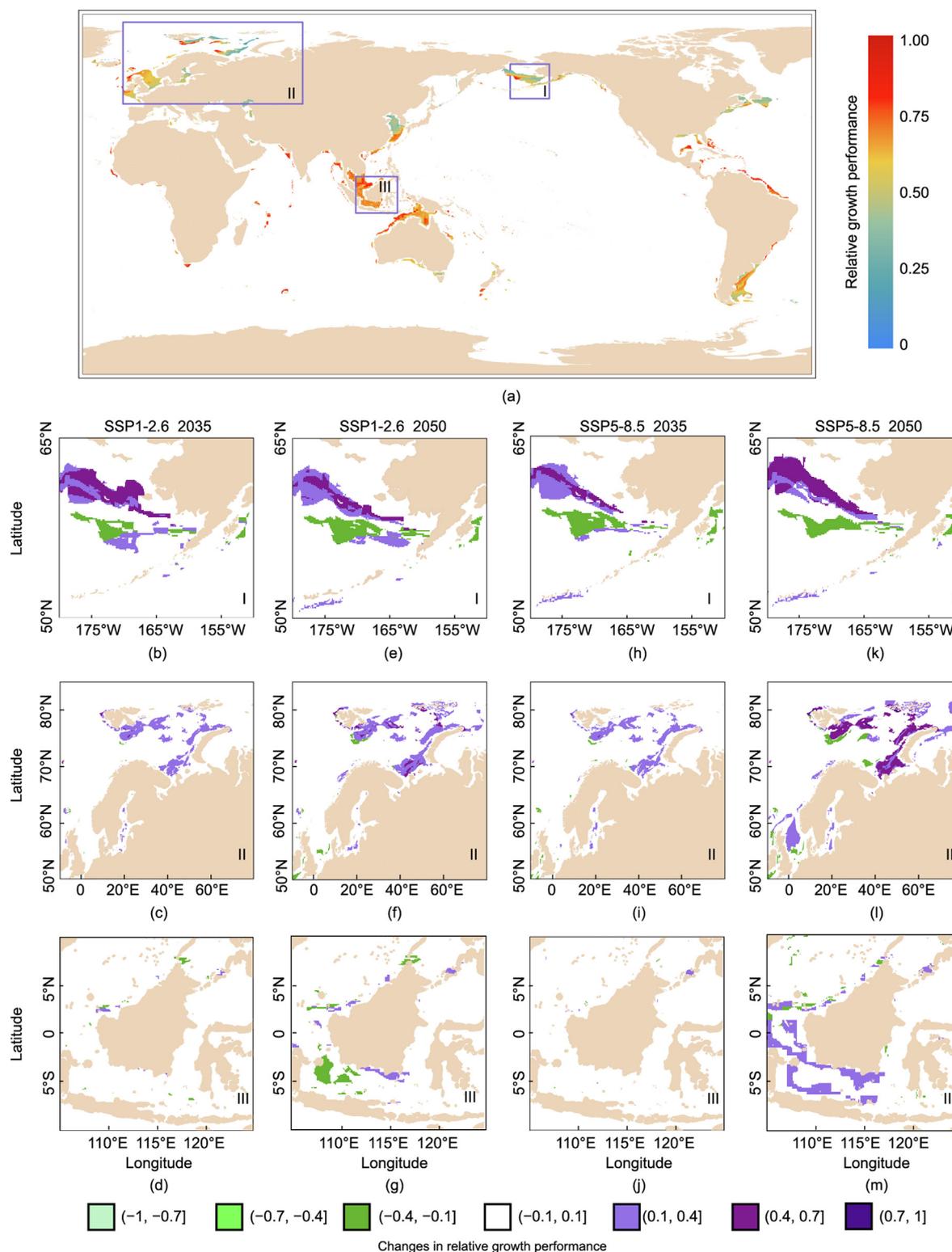
Under the two climate change scenarios, the distribution of potentially suitable areas in the future was similar to that under the current environmental conditions. Higher average relative growth potential was observed at low latitudes (Fig. S2 in Appendix A). In both scenarios, the average relative growth potential in the northeastern Bering Sea will increase in the future, whereas there will be a decrease in the southern growth regions (Figs. 3(b), (e), (h), and (k)). The average relative growth potential was also expected to increase in the Sea of Okhotsk, north of the Barents Sea, and near Newfoundland Island, Canada (Figs. 3(c), (f), (i), and (l)). By 2050, under the SSP1-2.6 scenario, there will be a decrease in the average relative growth potential in the southwest of Kalimantan (Fig. 3(g)), whereas under SSP5-8.5, there will be an increase in the average relative growth potential in this region (Fig. 3(m)).

3.4. Global potential high-yield areas and their response to climate change

Considering the heterogeneity of the marine environment, potential high-yield areas for finfish mariculture refer to regions where the growth rates of the species are not lower than 75% of their maximum growth rates throughout the year.

Under current environmental conditions, the distribution of high-yield areas was more concentrated than that of suitable areas and was primarily located in the North Sea, southern marine regions of Great Britain, mid- and low-latitudes of the western Pacific Ocean, and southeastern waters of South America (Fig. 4). The current size of potential high-yield areas was approximately $(5.96 \pm 0.13) \times 10^6$ km². Within these potential high-yield global areas for finfish mariculture, a high average relative growth potential occurred in the North Sea, eastern waters of Argentina, and East China Sea (Fig. 4(a)).
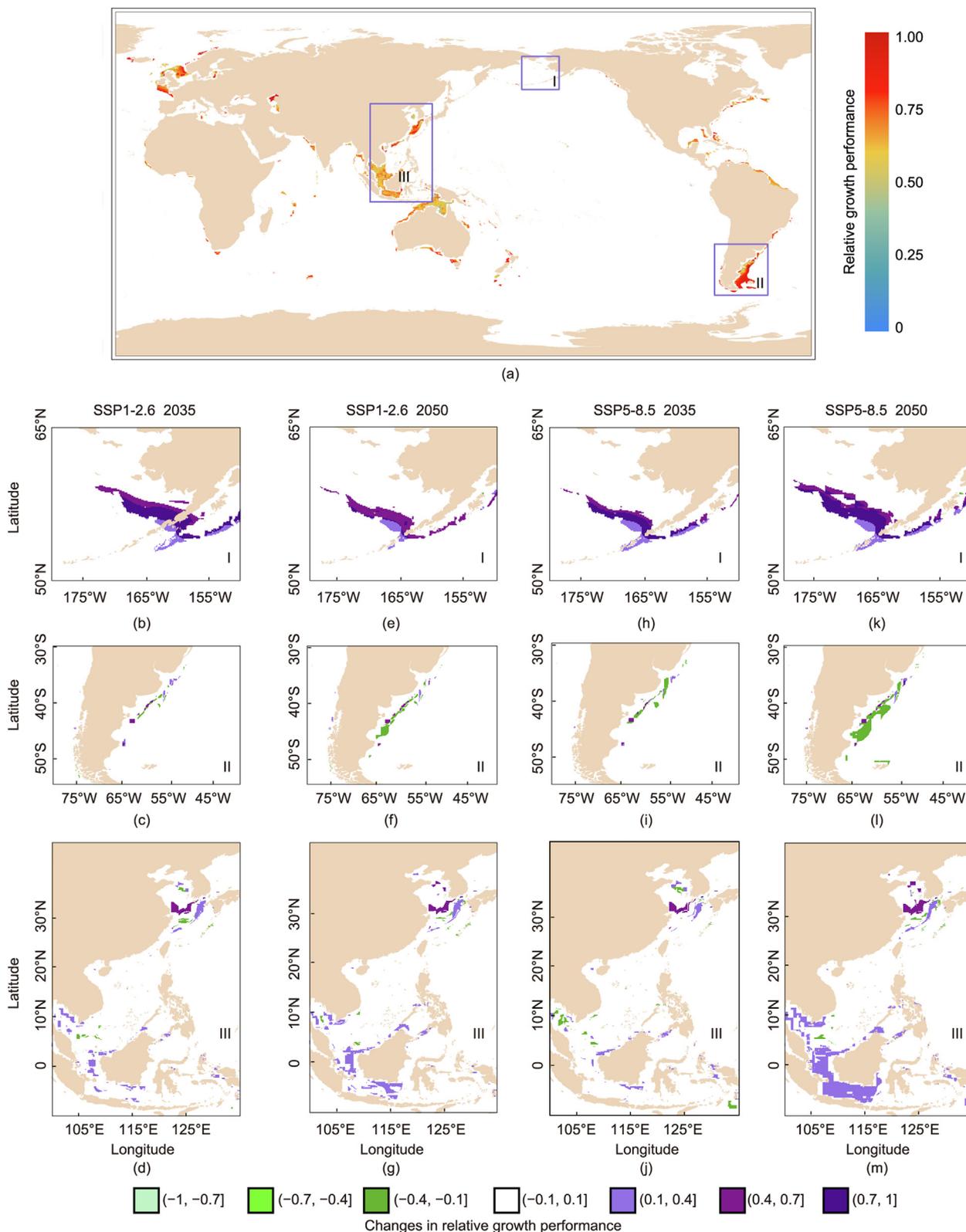
Under both climate change scenarios, potential high-yield areas for finfish mariculture gradually increased (Fig. 5). By 2035, the sizes of high-yield areas will increase to $(6.02 \pm 0.11) \times 10^6$ and $(6.11 \pm 0.11) \times 10^6$ km², respectively. By 2050, the sizes of high-yield areas will further increase to $(6.12 \pm 0.12) \times 10^6$ (an increase of 5.59% compared to the current size) and $(6.30 \pm 0.15) \times 10^6$ km² (an increase of 7.87% compared to the current size), respectively.

Fig. 3. Potential suitable areas and the changes in average relative growth potential for mariculture. (a) The potential suitable areas and average relative growth potential for mariculture under the current conditions. Low-latitudes have higher average relative growth potential, whereas mid- and high-latitudes have lower average relative growth potential. (b–m) Changes in the average relative growth performance of mariculture species in potentially suitable areas in the context of climate change. The average relative growth potential in (b, e, h, k) the northeast of the Bering Sea and the Sea of Okhotsk, (c, f, i, l) the north of the Barents Sea, and (d, g, j, m) Indonesiais provided across two shared socioeconomic pathway scenarios (SSP1-2.6 and SSP5-8.5) and averaged across four ESMs (ACCESS-ESM1-5, CanESM5, CMCC-ESM2, and IPSL-CM6A-LR) for 2035 and 2050.

Under SSP1-2.6 and SSP5-8.5, the distribution of potential high-yield areas in the future was similar to that under current environmental conditions (Fig. S3 in Appendix A). In both scenarios, the average relative growth potential of high-yield areas in the north-
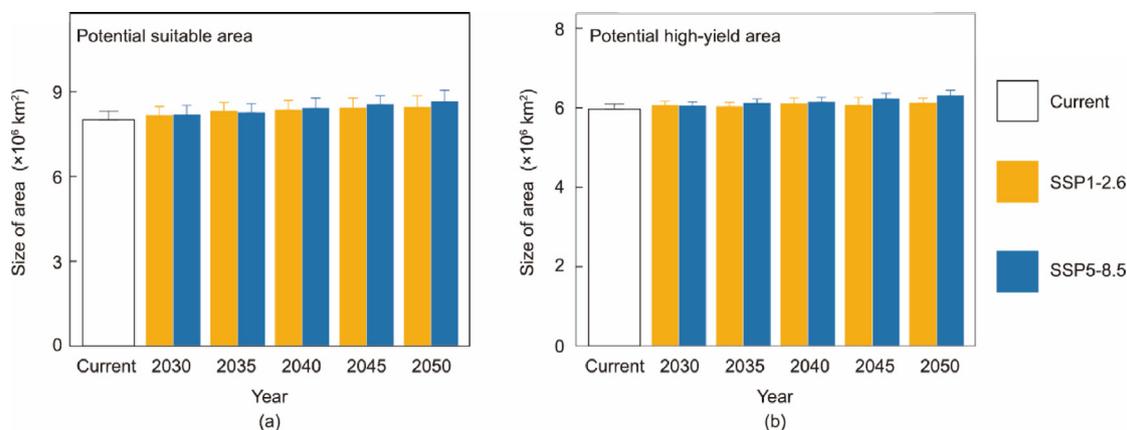
east of the Bering Sea and around Newfoundland Island will increase (Figs. 4(b), (e), (h), and (k)). The average relative growth potential in the eastern waters of Argentina decreased (Figs. 4(c), (f), (i), and (l)). By 2035, the average relative growth potential in

Fig. 4. Potential high-yield areas and the changes in average relative growth potential for mariculture. (a) The potential high-yield areas and average relative growth potential for mariculture under the current conditions. Higher average relative growth potential occurs in the North Sea, the eastern waters of Argentina, and the East China Sea. (b–m) Changes in the average relative growth performance of mariculture species in potential high-yield areas in the context of climate change. The average relative growth potential in (b, e, h, k) the northeast of the Bering Sea, (c, f, i, l) the eastern waters of Argentina, and (d, g, j, m) Southeast Asian seas is provided across SSP1-2.6 and SSP5-8.5 and averaged across four Earth system models (ACCESS-ESM1-5, CanESM5, CMCC-ESM2, and IPSL-CM6A-LR) for 2035 and 2050.

the Yellow Sea, East China Sea, southern waters of Vietnam, and Indonesian waters is expected to change slightly. However, by 2050, the average relative growth potential in these areas will increase, particularly under the SSP5-8.5, where the trend of increased average relative growth potential is more prominent (Figs. 4(d), (g), (j), and (m)).

Fig. 5. Sizes of potential suitable and high production areas for mariculture. (a) The sizes of areas potentially suitable for mariculture under the influence of climate change. (b) The sizes of potentially high-yield areas for mariculture under the influence of climate change. Results are provided across SSP1-2.6 and SSP5-8.5 and averaged across four ESMs (ACCESS-ESM1-5, CanESM5, CMCC-ESM2, and IPSL-CM6A-LR).

3.5. Responses of different mariculture species to climate change

The future global development of finfish mariculture will benefit from climate change according to the sizes of potentially suitable and high-yield areas. However, the size of the mariculture areas varied among different species (Figs. S4 and S5 in Appendix A). The *Lateolabrax maculatus* had the largest potential suitable area, exceeding 6.0×10^6 km^2 (Fig. S4). Most warm-water fish species had relatively large potential high-yield mariculture areas, with sizes all exceeding 1.5×10^6 km^2 (Fig. S5). Changes in the size of potentially suitable and high-yield areas under global climate change differed among species (Figs. S6–S8 in Appendix A). Among warm-water species such as *R. canadum*, an increase in the potentially suitable and high-yield areas was observed, whereas for species such as *L. crocea*, the suitable and high-yield areas were expected to decrease. Under SSP5-8.5, by 2050, the sizes of the suitable and high-yield areas for *R. canadum* mariculture are projected to increase by approximately 3.26% and 115.16%, respectively, whereas those for *L. crocea* are expected to decrease by approximately 25.72% and 31.22%, respectively (Fig. S6). The reasons for the differences among warm-water species may include the following: ① Thermal ecological niches do not entirely overlap. For example, according to the modeling results, the optimal temperature for *R. canadum* was 33.2 °C, whereas the optimal temperature for *L. crocea* was 26.7 °C. ② The shapes of thermal growth curves of different species also lead to differences in their physiological responses to climate change. ③ The study limited the depth to within 200 m. Water depth information from different regions was also an important factor. Cold-water mariculture species such as *S. salar* are expected to benefit from climate change, with suitable and high-yield areas expanding under both climate scenarios. Under the SSP5-8.5 scenario, by 2050, the sizes of suitable and high-yield areas for *S. salar* mariculture are predicted to increase by approximately 15.31% and 8.71%, respectively (Fig. S6). By contrast, the sizes of the mariculture areas for temperate species were expected to experience a decreasing or relatively stable trend (Figs. S6–S8). For *S. aurata*, under SSP5-8.5, the sizes of suitable and high-yield areas are projected to decrease by approximately 17.20% and 26.73% by 2050, respectively (Fig. S6).

4. Discussion

Our model integrated nonlinear TPCs for the growth of mariculture finfish and the spatiotemporal heterogeneity of the marine environment and was used to accurately assess the growth poten-

tial of global mariculture. Our TPCs for growth addressed the limitations inherent in previous simplified TPCs. We also improved the mathematical model using the parameter r_{max}, representing the maximum growth rate at the optimal temperature. Contrastingly, the depth-adjustable mariculture approach enabled us to better use suitable marine environmental conditions at different depths and times. Using this integrated model, we assessed potentially suitable and high-yield areas for global finfish mariculture, quantified the regional growth potential, estimated the mariculture area, and predicted the response of regional growth potential to climate change. We provided growth-based mapping for high-efficiency production in global finfish mariculture.

We improved the global mariculture potential assessment by developing a physiological model and using a list of representative species. Limited by the difficulties in obtaining experimental physiological data on mariculture species, simplified TPCs have always been used to assess mariculture potential [8,12,15]. We made notable efforts to collect physiological data from typical mariculture species to construct nonlinear models. In addition, we developed TPCs for 27 mariculture species, accounting for approximately 70% of the global mariculture fish production in the past five years.

The spatiotemporal heterogeneity of marine environments, particularly offshore environments, may present new opportunities for mariculture [11,13,36]. In this study, we established a mariculture model with net cages adjustable to four depths to provide the environmental conditions necessary for fish to achieve high growth rates in different months. Notably, using more water layers may help improve the accuracy of the assessments. Adjusting cages among the different water layers may help identify more high-yield mariculture areas. We also set criteria for potentially suitable areas ($\geq 50\%$ of maximum growth rate and ≥ 6 months) and high-yield areas ($\geq 75\%$ of maximum growth rate throughout the year); however, in practical mariculture activities, the time and growth rate thresholds can be set according to different species characteristics, costs, and economic benefits. Notably, in large mariculture net cages, factors such as uneven feed distribution and individual growth disparities often lead to significant differences in size and weight within the same batch at harvest. Therefore, grading and harvesting equipment are necessary [111,112], and environmental conditions must ensure the survival or continued growth of the remaining fish or new seedlings within the cages.

Changes in the potential high-yield areas under climate change are species-specific. In a previous study, the area of high growth potential mariculture (the threshold for monthly average growth

rate used was the top 25% of the maximum growth rate) for *S. aurata* will decrease by 15.3%, whereas for *S. salar*, it will increase by 5.6%, and for *R. canadum,* it will increase by 4.3% by 2050 [8]. However, some differences were observed in the magnitudes of these changes. The main reasons for this are as follows: ① The simplified growth performance using cold tolerance, hot tolerance, and optimal growth temperature [8] cannot effectively describe the growth patterns of fish. The missing parts between cold tolerance and optimal growth temperature, as well as between hot tolerance and optimal growth temperature, were directly simplified to straight lines (linear functions). This leads to inaccurate results when calculating the actual growth potential of fish in different thermal environments. In this study, we used the physiological data collected at multiple temperatures, which can accurately describe the nonlinear relationship between fish growth performance and temperature. ② Spatiotemporal heterogeneity of marine environments should not be ignored. Compared to assessment models that only consider sea surface temperature, utilizing dynamic marine environmental conditions enables some areas to meet the requirements for farming certain fish [11,13,36]. ③ Different depth limitations led to different results. The development of single-point mooring systems has enabled the fixation of cages in large marine areas. Klinger et al. [8] used a maximum depth of 2000 m. However, for depth-adjustable cages, no case studies that can be applied to deep-sea mariculture have been found [113]. Following the methods referenced in other global-scale studies, we adopted a depth limit of 200 m [7]. For example, in the offshore areas of the West Coast of the United States, according to our study and other global-scale studies, few areas are suitable for offshore mariculture [7,10]. However, Klinger et al. [8] highlighted extensive mariculture potential for *S. salar*.

The increase in global potentially suitable areas and high-yield areas under climate change indicates that the newly obtained mariculture area (after overlaying all mariculture area layers) was larger than the lost area. The reasons for these results are complex. First, the shapes of the thermal growth performance curves (such as width and height) of the different species vary significantly (Fig. S1), leading to diverse responses of the growth rates of various species to climate change (Fig. S6). Second, some overlap was observed among the thermal ecological niches of different species (Fig. S1). Thus, climate change may not lead to the complete loss of all mariculture species in some regions. Third, when certain aquaculture species become locally unsuitable, other species may gain mariculture potential, thereby offsetting some of the global losses in mariculture areas. Fourth, ocean topography can also influence research results, as this study set the maximum depth at 200 m [7–9,114]. With climate change, the dynamics of mariculture zones are constrained by depth. In summary, various complex factors may contribute to increasing the global potential suitable and high-yield areas.

Several considerations must be considered when using our model for local-scale assessments. ① Determine the target species for mariculture in a given country or region. In addition to environmental requirements, the selection of mariculture species is influenced by local demands and techniques. ② Local policies and socioeconomic considerations. Active policies can considerably encourage farmers and local economic investment to engage in mariculture and related industries, including equipment development, seedling cultivation, logistics transportation, feed production, and more [115]. Public acceptance also influences the future growth of mariculture, and attitudes toward mariculture may vary greatly between countries and regions [116]. ③ Fine-scale environmental data were used to accurately assess potential mariculture areas. Global-scale Ocean environmental data have relatively low spatial resolution [8,9], and climate models at regional scales often rely on local historical environments [117].

Our assessment of the global maricultural potential has a few limitations. First, we did not consider selective breeding of mariculture fish. Fish with high growth rates or broad thermal windows can be cultivated via selective breeding (the thermal-growth performance curve of a species can be transformed). Selectively bred mariculture species show an increasing growth performance [118,119]. Second, our integrated model provides valuable information based on heterogeneous marine environments and physiological performances. Socioeconomic backgrounds (local mariculture technologies, marine protected areas, policies, and other uses of marine space) are not involved [9] because these factors are difficult to project in different regions. Light and other environmental variables can influence the growth of mariculture fish. However, some depth-adjustable mariculture cages (such as Deep Blue 1) contain supplemental lighting systems or other functional components [113]. Therefore, light and other factors were not considered in the present study. However, our model provides a valuable method for assessing the growth potential of mariculture finfish. The results of high-yield mariculture areas under current conditions and future climate scenarios provide valuable insights for effective planning in mariculture engineering.

5. Conclusions

We integrated nonlinear TPCs for the growth of mariculture finfish and the marine environment's spatiotemporal heterogeneity and accurately assessed the growth potential of global mariculture. The TPCs for growth addressed the limitations of the previously simplified TPCs. The depth-adjustable mariculture approach enabled us to better use suitable marine environmental conditions at different depths and times. Our findings indicate that the total potential for globally suitable and high-yield mariculture areas will continue to increase in the future, whereas different species and regions will respond differently to climate change. Overall, we provide growth-based mapping for high-efficiency production of global finfish mariculture.

CRediT authorship contribution statement

Shuang-En Yu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Xin Qi:** Formal analysis, Data curation. **Yun-Wei Dong:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Formal analysis, Data curation, 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.eng.2025.01.023.

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