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Climate change influences global distribution of alien tube worms

Hadiyanto Hadiyanto

Research Center for Oceanography, National Research and Innovation Agency

E-mail: hadi020@brin.go.id

Abstract. Alien tube worms have been introduced outside their original distribution areas via international shipping and have become invasive in these areas. Climate change has been acknowledged to redistribute both native and alien species; however, the effect of climate change on the global distribution of alien tube worms is unknown. This study predicts the global distribution patterns of alien tube worms (*Hydroides elegans*, *Sabella spallanzanii*, and *Ficopomatus enigmaticus*) and projects how climate change influences these patterns using species distribution modelling. Sea surface temperature, salinity, primary productivity, phosphate, nitrate, and current velocity are selected as the predictors. The models predict species occurrences well, with AUC values greater than 0.95. Under the present climate scenario, the occurrence probability of alien tube worms is high (>0.9) within the temperate Atlantic Ocean, Persian Gulf, Sea of Japan, Yellow Sea, Southern China, and Southern Australia. The probability of occurrence is expected to increase across oceans by 2100, suggesting that alien tube worms will be more common in the future. Increases in occurrence probability are also projected at higher latitudes (e.g., Barents Sea) by 2100, indicating poleward shifts of these species. This study highlights the urgency of incorporating climate change into the management of alien invasive species.

1. Introduction

Invasive alien species are the drivers of changes in marine ecosystems. These species affect the biodiversity (e.g., species composition, richness, abundance, and genetic composition) and ecological processes (e.g., nutrient cycling, hydrodynamics, and habitat structures) of local assemblages [1]. The ecological impacts of marine alien species are more significant on continental margins than on islands and are similar over latitudes [2]. These species are currently reported in 84% of marine ecoregions with the highest level of invasion occurring in Northern California [3]. However, new records of alien species tend to increase over time [4] because of the acceleration of international shipping, socioeconomic changes, and climate change [5], suggesting that their effects on marine ecosystems are more common.

Climate change has occurred since the 1860s, with the elevation of sea surface temperature by 0.61°C between 1861 and 2000 [6]. It is also projected that sea surface temperature will continue to rise by 2–4.5°C by 2100, depending on the climate scenario [7, 8]. Climate change may increase the abundance and distribution of alien species [9, 10], particularly warm stenothermal species, as the marine environment becomes more similar to its original range [11]. Therefore, climate change is a major issue in the management of invasive alien species, especially for strategic planning, preventive management, treatment, and education [12]. In the future climate, the ecological impacts of marine alien species are probably largest in the recipient areas that are currently 2.2°C cooler than the original areas of those



species [13], suggesting that projections of present and future distribution of these species are beneficial for early detection and rapid response measures [14].

Aline tube worms, such as *Hydroides elegans* (Serpulidae), *Ficopomatus enigmaticus* (Serpulidae), and *Sabella spallanzanii* (Sabellidae), are introduced outside their original distribution areas via international shipping [15]. In the new areas, they alter soft-bottom (e.g., estuaries and harbor habitats) and hard-bottom (e.g., artificial substrates) communities [16-18]. *H. elegans* tubes are more compact, harder, and more elastic at an elevated temperature of 6°C with a pH reduction of 0.3 and a salinity reduction of 7‰, suggesting that they may be resilient to climate change [19]. Nevertheless, the influence of climate change on the global distribution of these species remains unknown.

Species distribution modelling (SDM) provides projections of species distributions based on correlation between species data (occurrences or abundance) and environmental predictors under different climate scenarios using machine-learning, statistical, or similarity-based and expert-rule methods [20]. Previous studies have used this approach to project the distribution of marine alien species, including the lionfish *Pterois volitans* and *P. miles* [21], the Atlantic common starfish *Asterias rubens* [22], and the green crab *Carcinus maenas* [23]. Similarly, this study uses this method to predict the global distribution patterns of alien tube worms (*Hydroides elegans*, *Ficopomatus enigmaticus*, and *Sabella spallanzanii*) and to project how climate change shifts these patterns.

2. Materials and Methods

2.1. Species data

Presence data for *H. elegans*, *F. enigmaticus*, and *S. spallanzanii* are obtained from Ocean Biodiversity Information System (OBIS) (<https://obis.org>) and Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org>) on 25th March 2023. After duplicate records are removed, the total number of records is 555 for *H. elegans*; 1,093 for *F. enigmaticus*; and 2,441 for *S. spallanzanii*.

2.2. Environmental data

Sea surface temperature, salinity, primary productivity, phosphate, nitrate, current velocity, and their derivatives (mean, minimum, maximum, and range) are selected as environmental predictors. Environmental data at the resolution of 5-arc minutes are obtained from Bio-ORACLE [24, 25]. Changes in species distributions by 2100 are predicted using the future conditions of sea surface temperature, salinity, and current velocity, whereas those of other predictors are assumed to remain stable. These projections are based on the fifth phase of the Coupled Model Intercomparison Project (CMIP5) [26] and two representative concentration pathway scenarios (RCP): peak and decline (RCP 2.6) and increase (RCP 8.5) in emissions [27].

2.3. Species distribution modelling

A generalized linear model with binomial distribution is used to perform species distribution modelling. This algorithm requires both presence and absence data; thus, 10,000 pseudo-absences are randomly generated for each species [28]. The model is developed based on 80% of randomly selected data and evaluated using the remaining 20%. Automatic forward stepwise iteration based on the lowest Akaike's information criterion (AIC) is used to select the best model. The area under the receiver operating characteristic curve (AUC) is calculated to evaluate the predictive power of the model. The value of AUC ranges from 0 to 1, with a value of 0.5 indicating that the model is not better than a random guess and a value of 1.0 indicating that the model is perfectly fit [29]. Predicted distribution maps show the probability of occurrence of alien tube worms, ranging from 0 to 1. A probability of close to 0 means that alien tube worms are likely to be absent, while a probability of close to 1 means that alien tube worms are likely to be present. These maps are presented by marine ecoregions [30], which have been used as the smallest spatial units for regional risk assessment of marine invasive species [3].

3. Results

3.1. Model evaluation

Based on the most parsimonious models, there are 18 environmental predictors for *H. elegans* (AIC= 1427.89, $R^2= 0.61$), 14 for *F. enigmaticus* (AIC= 1186.93, $R^2= 0.75$), and 19 for *S. spallanzanii* (AIC= 1460.61, $R^2= 0.85$) (Figure 1). The occurrence of all tube worms increase with mean temperature, mean primary productivity, minimum nitrate, nitrate range, and mean current velocity. Temperature range and mean salinity show positive associations with *F. enigmaticus* occurrence but negative associations with *H. elegans* and *S. spallanzanii* occurrence. The occurrence of *H. elegans* and *S. spallanzanii* increases with salinity range and mean nitrate, but *F. enigmaticus* occurrence shows the opposite trend. The value of AUC is 0.97 for *H. elegans* and 0.99 for *F. enigmaticus* and *S. spallanzanii*, indicating that models predict well species occurrence.

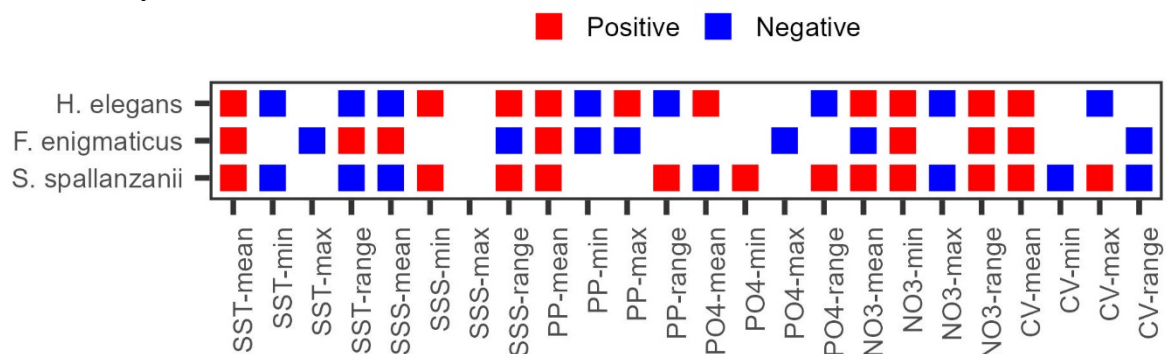


Figure 1. Responses of species occurrence to temperature (SST), salinity (SSS), primary productivity (PP), phosphate (PO4), nitrate (NO3), and current velocity (CV) changes.

3.2. Predicted distribution areas

Under the present climate scenario, the probability of occurrence for all tube worms is high (>0.90) within the temperate Atlantic Ocean, Persian Gulf, Sea of Japan, Yellow Sea, Southern China, and Southern Australia (Figure 2a-c). However, there are also differences in occurrence patterns among the species. The North Patagonia Gulf and Patagonia Shelf (temperate Southern America) show a high probability of occurrence for *H. elegans* but not for *F. enigmaticus* and *S. spallanzanii*. Namib and Namaqua (temperate Southern Africa) have a high probability of occurrence for *H. elegans* and *F. enigmaticus* but not for *S. spallanzanii*. In contrast, the Barents Sea (Arctic) tends to show a high probability of occurrence for *S. spallanzanii* but not for *H. elegans* and *F. enigmaticus*.

The probability of *H. elegans* occurrence is expected to change by 2100, depending on climate change scenarios. Under the RCP 2.6 scenario, the probability of occurrence is projected to increase within the Gulf of Alaska, Cortezian (Northeast Pacific), Northern Atlantic, Gulf of Oman, and Northeastern Honshu, by more than 0.30 (Figure 3a-b). Increases in the probability of occurrence are also predicted to occur under the RCP 8.5 scenario, especially within Northern America and Barents Sea by more than 0.30 (Figure 3c-d). Nevertheless, the North Sea and Celtic Seas have opposite trends, with a declining probability of occurrence of less than 0.25.

The probability of *S. spallanzanii* occurrence is expected to increase by 2100 (RCP 2.6), especially within the Northern Atlantic, Barents Sea, Gulf of Oman, and Northeastern Honshu but at a lower rate than that of *H. elegans* (less than 0.1) (Figure 4a-b). Occurrence patterns under the RCP 8.5 scenario are not much different from those under the RCP 2.6 scenario, except that the occurrence probability decreases by less than 0.03 found within the North Sea and Celtic Seas (Figure 4c-d).

The probability of *F. enigmaticus* occurrence within most ecoregions is predicted to remain stable by 2100 under the RCP 2.6 scenario, with a decrease in occurrence probability (less than 0.30) observed within the Scotian Shelf and Gulf of Maine (Figure 5a-b). Nevertheless, under this scenario, the probability of occurrence within the Barents Sea, Baltic Sea, and Northeastern Honshu will increase by

more than 0.30. Occurrence patterns under the RCP 8.5 scenario are predicted to be the same as those under the RCP 2.6 scenario, except that the North Sea and Celtic Seas will show declines in the probability of occurrence by less than 0.03 (Figure 5c-d).

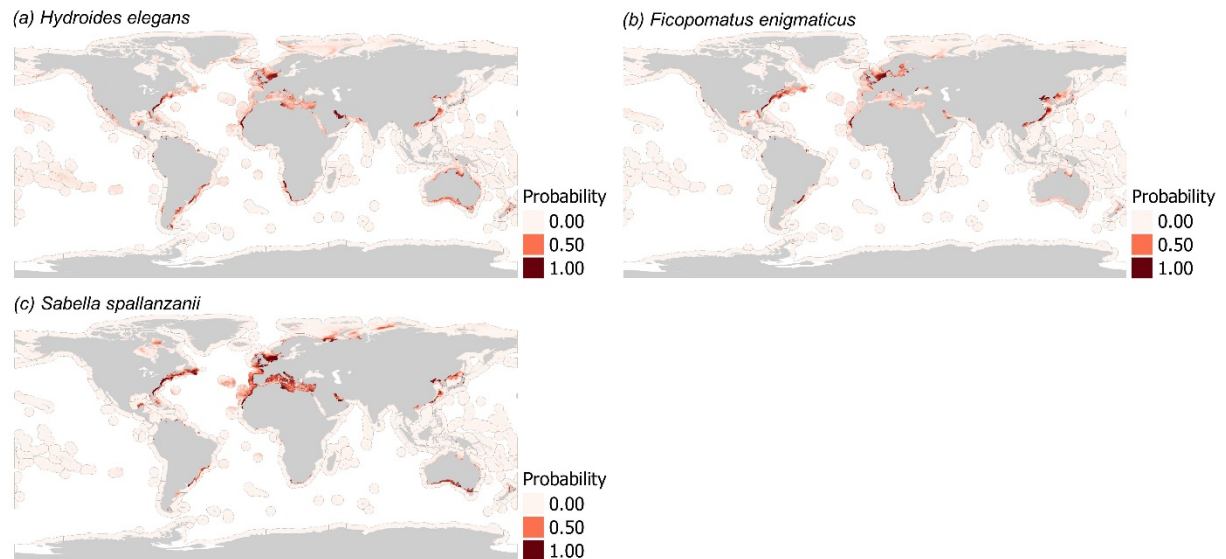


Figure 2. Occurrence probability of alien tube worms under the present climate scenario: (a) *Hydroides elegans*, (b) *Ficopomatus enigmaticus*, and (c) *Sabella spallanzanii*.

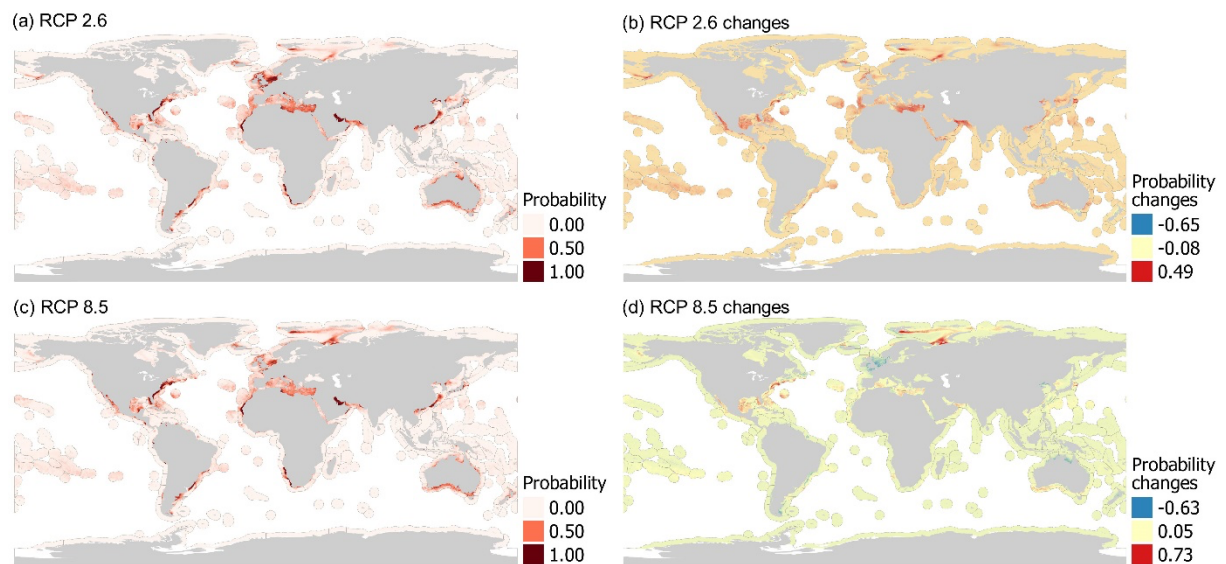


Figure 3. The probability of occurrence of *Hydroides elegans* by 2100 RCP 2.6 and 8.5.

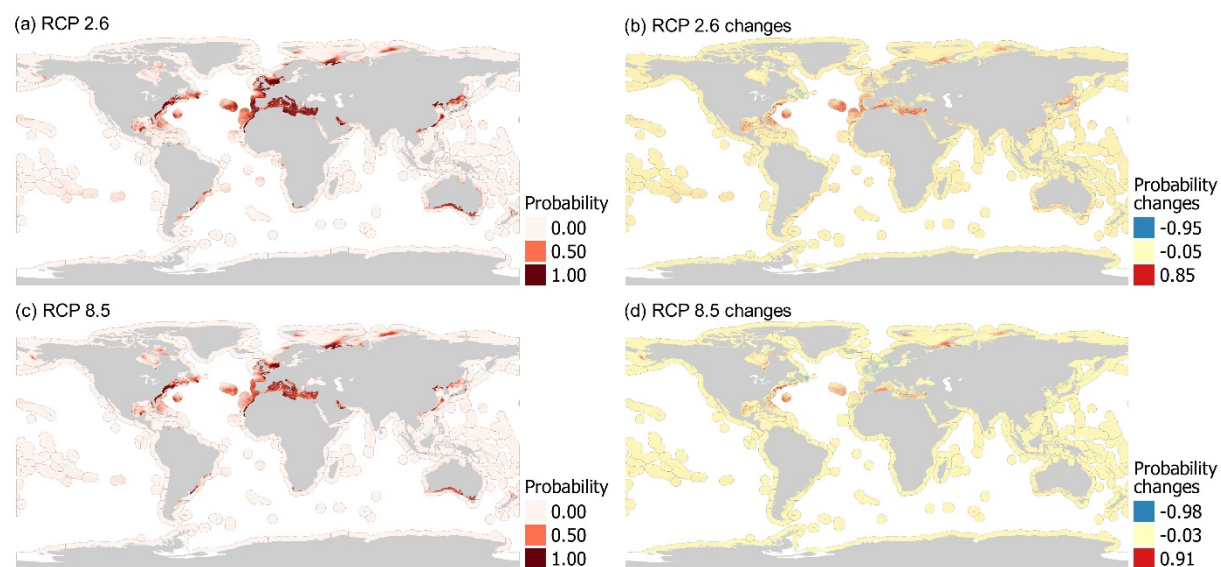


Figure 4. The probability of occurrence of *Sabella spallanzanii* by 2100 RCP 2.6 and 8.5.

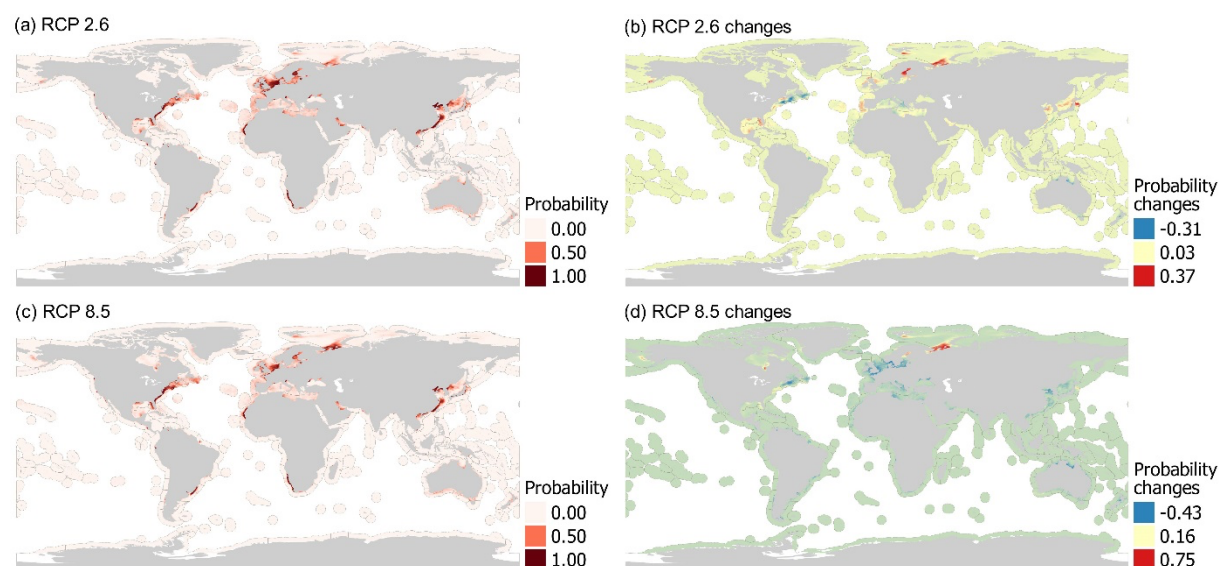


Figure 5. The probability of occurrence of *Ficopomatus enigmaticus* by 2100 RCP 2.6 and 8.5

4. Discussion

Tube worms, such as *H. elegans*, *S. spallanzanii*, and *F. enigmaticus*, have been well established outside their original distribution areas and have become invasive in these areas [16-18]. Climate change influences the global distribution of marine species [31-33], yet its effects on the global distribution of alien tube worms are still unknown. The present study predicts present and future distribution of these species using a set of environmental factors. Globally, *H. elegans*, *S. spallanzanii*, and *F. enigmaticus* have different distribution patterns. Climate change will affect these patterns and allow them to occupy new regions at higher latitudes.

Hydroides elegans, *S. spallanzanii*, and *F. enigmaticus* are predicted to share some distribution areas, including the temperate Atlantic Ocean, Persian Gulf, Sea of Japan, Yellow Sea, Southern China, and Southern Australia. These species are originally from different regions, i.e., *H. elegans* from Indo-Pacific, *S. spallanzanii* from the Mediterranean Sea, and *F. enigmaticus* from Australia [15], but previous studies have also found them within our predicted distribution areas, including Southern

Atlantic for *H. elegans* and *F. enigmaticus* [16, 17] and Southern Australia for *S. spallanzanii* [34]. Our model also identifies regions for a particular species. Patagonia (temperate Southern America), Namib, and Namaqua (temperate Southern Africa) are probably suitable areas for *H. elegans* but not for *S. spallanzanii*. Occurrences of *H. elegans* within these regions have been reported in Argentina [35] and Angola [36]. The Barents Sea (Arctic) appears to be suitable area for *S. spallanzanii* but not for *H. elegans* and *F. enigmaticus*. However, this prediction must be confirmed through field observations.

The present distribution patterns of alien tube worms will change due to climate change, as found for marine worms in the Pechora Sea during ocean warming in the Arctic between 1959 and 2000s [37] and the Tropical Eastern Pacific during the climatic variability of 2004-2012 [38]. Increases in the occurrence probability of *H. elegans* and *S. spallanzanii* within their current distribution areas (e.g., Mediterranean Sea) by 2100 indicate that alien tube worms will be more common in the future. Indeed, rapid increases in the recruitment of marine alien species due to climate change have been found for the Pacific oyster *Crassostrea gigas* in the northern Wadden Sea between 1995 and 2003 [39], the antipodean cirripede crustacean *Austrominius modestus* in the North Sea from 1955 to 2007 [40], and the star tunicate *Botryllus schlosseri* due to an increased water temperature of 4°C during laboratory experiments [41].

Some regions (e.g., the North Sea and Celtic Seas) are unsuitable for alien tube worms, but higher latitudes (e.g., Barents Sea) can be new suitable regions, indicating poleward shifts of these species. In fact, a poleward shift of marine alien species has been recorded for the fireworm *Hermodice carunculate* in the Mediterranean Sea between 1967 and 2019 [42]. Previous studies have also projected poleward shifts of other alien species by 2100, including the lionfish (*Pterois volitans* and *P. miles*) in the Northwest Atlantic [21], the Atlantic common starfish (*Asterias rubens*) in the Black Sea [22], and the green crab (*Carcinus maenas*) in the Canadian Arctic [23].

Two climate change scenarios, i.e., RCP 2.6 and RCP 8.5, with increases in mean temperature by 2°C and 4.5°C by 2100, respectively [7, 8], apparently provide similar effects on the distribution patterns of *H. elegans*, *S. spallanzanii*, and *F. enigmaticus*. This indicates that alien tube worms respond rapidly to small changes in environmental factors, especially mean sea surface temperature, primary productivity, and current velocity. Significant effects of these factors on the distribution patterns of marine worms have also been reported in previous studies [43-45]. Nevertheless, alien tube worms may respond differently to other factors, including temperature range, mean salinity, salinity range, and mean nitrate. These responses may explain differences in present and future distribution patterns of *H. elegans*, *S. spallanzanii*, and *F. enigmaticus*.

One potential limitation of this study is the use of occurrence data in modelling species distributions. Species abundance data provide information on total abundance and evenness of abundance [46]; thus, these data can show the pattern of species commonness and rarity [47], which are critical components in assessing the invasiveness of alien species [48-50]. However, species abundance often shows a positive correlation with species occurrence [51], making occurrence data a feasible alternative for analysing the distribution patterns of marine alien species when abundance data are not available. Indeed, occurrence data have been used in previous studies to predict the biogeographical distribution of marine alien species [21-23] and quantify the invasiveness of these species [52].

Regardless of this limitation, the models predict the global distribution patterns of alien tube worms well and show how climate change influences these patterns. The identification of distribution area of alien tube worms is an important component in mitigating their impacts [1, 53]. Projecting the future distribution of these species under different climate scenarios highlights the urgent need to incorporate climate change into the management of alien invasive species [12].

5. Conclusion

H. elegans, *S. spallanzanii*, and *F. enigmaticus* show differences in global distribution patterns. The occurrence of these species is predicted to increase by 2100 under RCP 2.6 and 8.5 climate change scenarios.

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