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Looking at the Expansion of Three Demersal Lessepsian Fish Immigrants in the Greek Seas: What Can We Get from Spatial Distribution Modeling?

Maria Solanou [1,*], Vasilis D. Valavanis [2], Paraskevi K. Karachle [2] and Marianna Giannoulaki [1,*]

[1] Hellenic Centre for Marine Research, Institute of Marine Biological Resources and Inland Waters, P.O. Box 2214, 71003 Heraklion, Crete, Greece
[2] Hellenic Centre for Marine Research, Institute of Marine Biological Resources and Inland Waters, 46.7 km Athinon-Souniou Ave, P.O. Box 712, 19013 Anavyssos, Attika, Greece; vasilis@hcmr.gr (V.D.V.); pkarachle@hcmr.gr (P.K.K.)
* Correspondence: m.solanou@hcmr.gr (M.S.); marianna@hcmr.gr (M.G.)

Abstract: A big number of Red Sea species have entered the Mediterranean Sea since the opening of the Suez Canal. Some of them quickly establish local populations and increase their abundance, forming a potential threat for local biodiversity and fisheries. Here, we use habitat modeling tools to study the expansion of three alien, demersal fish species that entered the Mediterranean basin at different times: *Pterois miles*, *Siganus luridus* and *Siganus rivulatus*. Georeferenced occurrence data from the eastern Mediterranean over the past ten years were compiled using online sources, published scientific literature and questionnaires and were correlated with environmental and topographic variables. The maximum entropy modeling approach was applied to construct habitat suitability maps for the target species over all of the Greek Seas. Results emphasized the three species' strong coastal nature and their association with the presence of *Posidonia oceanica* meadows. Probability maps evidenced that for all species there is a higher likelihood of presence along the southeast and central Aegean and Ionian Sea coasts and a lower likelihood throughout the North Aegean Sea. For *Siganus* spp., predictions in the Thracian Sea were highlighted as highly uncertain, as the environmental conditions in this area partly fall outside the range of values occurring in locations of their current presence.

Keywords: habitat suitability; maximum entropy; invasive fish species; Greek Seas

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1. Introduction

Introductions of non-indigenous (also called "alien", a term hereafter used as synonym to "non-indigenous") species have been considered a major driver of change in the Mediterranean Sea [1], one of the most invaded marine basins worldwide [2]. To date, 183 documented alien, mainly thermophilic, fish species have entered through the Suez Canal [3], commonly called "Lessepsian immigrants" [4]. The number of alien species is higher in the eastern part of the basin [5], apparently due to the proximity to the canal and the propagule pressure exerted by it [6]. To give a sense of proportion, approximately 13% of the fish species recorded around Rhodes Island were found to be alien in a survey conducted more than a decade ago [7], while more recent studies found that alien species compromise more than 90% of the catch composition in trammel nets on the Mediterranean coasts of Turkey [8].

Given that their survival and reproductive rates are sufficient for establishment in the new areas [9], alien marine species can sometimes become invasive with severe ecological and socio-economic impacts ([10] and references therein), affecting biodiversity, ecosystem services (e.g., recreational activities, fisheries) and human health [11]. Some authors even came to compare the alteration that invasive species provoke in community composition with the perturbations caused by climate change, pollution or overexploitation [2,12]. In the current study we focus on three invasive Erythrean fish species: *Siganus luridus* (Rüppell, 1829) (dusky spinefoot), *Siganus rivulatus* (Forsskål & Niebuhr, 1775) (marbled spinefoot) and *Pterois miles* (Bennett, 1828) (devil lionfish). All three species have succeeded in expanding their distribution throughout the eastern Mediterranean and beyond, since they hold biological traits that enable them to be competitive [13,14], or take advantage of the limited presence of natural predators in the new ranges [15].

Both *S. luridus* and *S. rivulatus* are originally distributed in the western Indian Ocean and have more than fifty years of occurrence in the eastern Mediterranean [1]. They are herbivorous, usually playing a balancing role by controlling benthic primary producers [16]. However, their intense grazing habits in some regions of the Mediterranean seem to negatively affect the ecological community that depends on macroalgae and seagrass, by creating barren areas that replace algal forests [17,18]. Therefore, concerns have been expressed that the proliferation and expansion of the siganids may lead to the impoverishment of the biodiversity of sublittoral benthic communities [18]. *Pterois miles*, although native to the Indian Ocean, has entered and established a population in the eastern Mediterranean during the last decade [19], being one of the most recent Lessepsian fish immigrants. During this period, it has been considered the fastest spreading invasive fish species in the area [20], currently reaching as far north as the island of Vis, in Croatian waters [21]. Recent surveys from Turkey and Greece have recorded areas with *P. miles* densities as high as 30–40 individuals per 10 m^2 [19]. Concerns arise about the potential impacts, given the example of a previous well-documented invasion, together with the co-generic *P. volitans* (Linnaeus, 1758) in the western Atlantic, Caribbean Sea and the Gulf of Mexico [22]. They became a major problem for coastal environments of the aforementioned areas [23], constituting one of the most ecologically damaging marine fish invasions to date [24] by altering ecosystem structure and function [25].

All three species are edible and are slowly entering the commercial fisheries in Greece. *Siganus* spp., in particular, are the most popular and highly priced fishes in certain areas of the easternmost Mediterranean, such as the islands of Rhodes and Cyprus [26,27]. On the other hand, *P. miles* has a low (but constantly increasing) market price in the eastern Mediterranean, mainly due to its venomous spines that can injure the fishers or damage part of their gear [27]. Further efforts to introduce these species in the local menu could possibly serve as a mitigation measure for regional population control. Yet such initiatives should be planned with caution in order not to encourage intentional introductions to new areas and/or a fishery métier that might collapse and lead local fishers to economic losses (e.g., [28]).

Given the fast-spreading rate of many invasive species, marine spatial planning and management efforts have been undertaken to restrict their expansion. Under this framework, knowledge of the spatial expansion and assessment of the high-risk regions are of prime importance. Hence, despite being particularly challenging [29], predicting the potential geographic distributions of marine bioinvaders is currently one of the most crucial research objectives. Species distribution model (SDM) approaches are among the most common tools for predicting spatio-temporal range dynamics [30], relating species' presence/absence records to environmental predictor variables with a combination of statistically or theoretically derived response curves that best reflect their ecological requirements [31]. The ongoing development of powerful statistical tools and software encouraged the production of scientific papers orientated towards modeling the habitat suitability of invaders into the Mediterranean in an accelerating pace (e.g., *P. miles* [19,20,32,33]; *Siganus* spp. [32,34]; *Fistularia commersonii* [35]; *Lagocephalus sceleratus* [36]). Previous studies examined the potential expansion of invasive species across the entire Mediterranean, while more regional and fined-grained investigation in individual parts of the basin is generally lacking.

Hence, this study aims to assess the potential spatial distribution of the three target species in all of the Greek Seas using the maximum entropy approach. The selected models were used for quantifying species distribution along environmental gradients and assessing habitat maps to indicate those geographic areas where environmental variables, in the absence of explicit biotic interactions (such as competition or predation), are considered suitable for the presence of the particular species.

2. Materials and Methods

A spatial dataset on each species' occurrences was constructed based on georeferenced observations recorded from 2010 to 2022. Available *P. miles'* occurrences from the northern Red Sea were also incorporated in the analysis, as the area represents the marginal distribution of the species within its native range. The decision of incorporating only occurrences from the invaded ranges was based on the assumption that populations located away from the Mediterranean would probably share distinct ecological traits that differentiate them and would lead to misleading results. Although several studies obtained better results when integrating both native and invaded ranges [32,37,38], it is also proven that regionally fitted models often perform better than models derived from the entire range and subsequently fitted at marginal locations [39].

Data originating from various sources of information included: available databases (offline ELNAIS database [40]; www.gbif.org (accessed on 13 February 2023)), published scientific literature [19,41–43] and questionnaires filled in by local fishers [44]. Data were screened by retaining only the records from reliable sources (i.e., verified occurrence and georeferenced info available) for further analyses, excluding data characterized by a coordinate uncertainty greater than 400 m, based on the resolution of the raster environmental layers. Isolated occurrences of the species were removed in order to avoid sink population effects [45]. Species occurrences were subsequently filtered using the spThin R package [46] to retain the highest number of records being at least 9 km apart in order to condense any spatial autocorrelation issues in modeling. A total of 241, 253 and 262 georeferenced records were finally retained for *P. miles*, *S. luridus* and *S. rivulatus*, respectively.

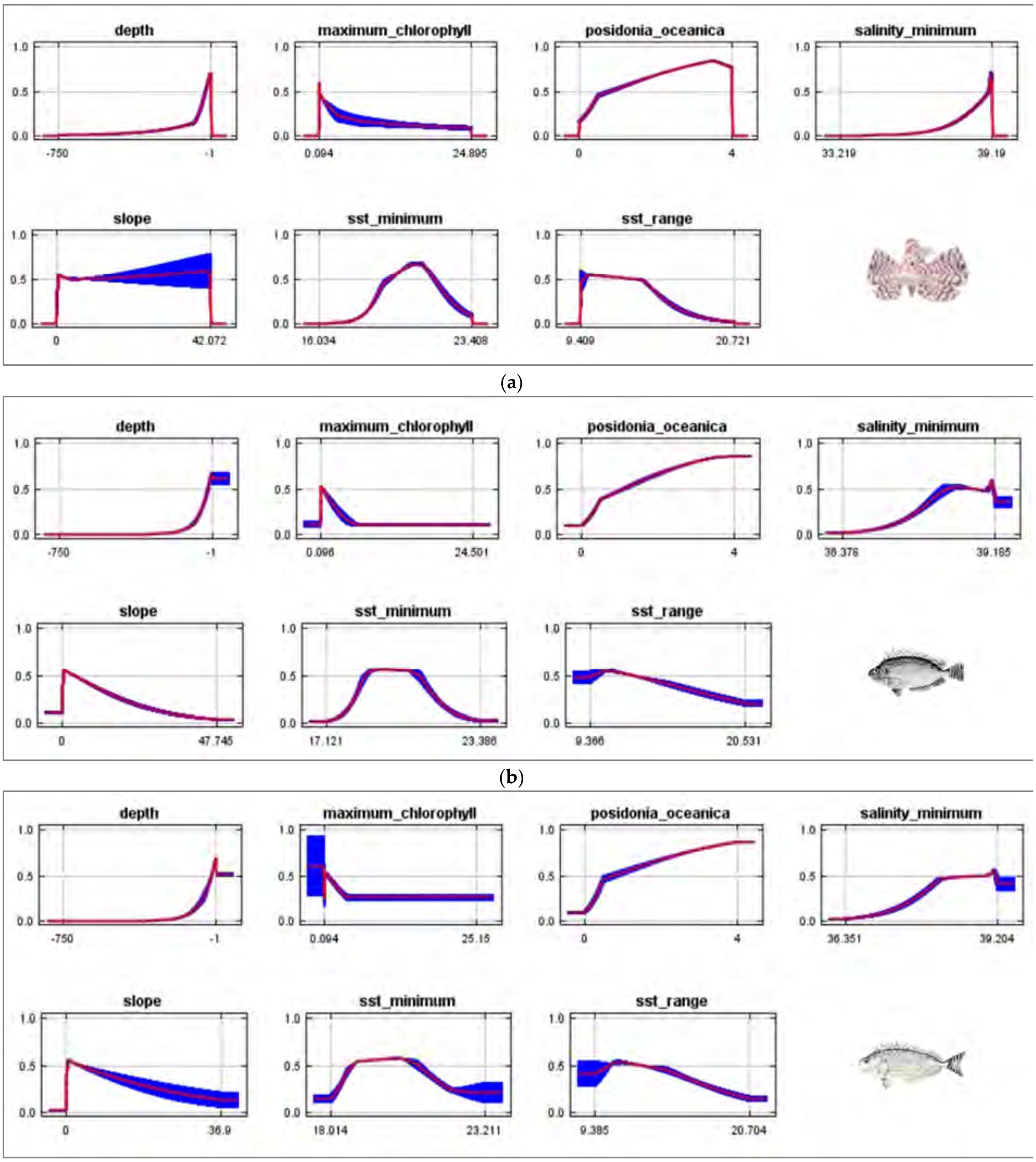
Satellite environmental data were used as explanatory variables to model the suitable habitat of the target species. Mean maximum sea surface temperature (SST in °C; hereafter "maximum SST"; oceancolor.gsfc.nasa.gov), mean minimum SST (hereafter "minimum SST"), mean annual SST range (hereafter "SST range"), mean minimum sea surface salinity (SSS in psu; hereafter "minimum salinity"; marine.copernicus.eu) and mean maximum sea surface chlorophyll (CHL in mg/m^3; hereafter "maximum chlorophyll"; oceancolor.gsfc.nasa.gov) were downloaded from the respective databases for the period 2010–2020, allowing for the use of reliable, standardized satellite environmental data and providing a snapshot of the most recent climatic condition in the eastern Mediterranean coastal seas. The selection of the above environmental variables was based on extensive study of the available literature and they were considered important either as a direct influence on the distribution of fish or as proxies for causal factors. All environmental variables were checked for multicollinearity issues using both correlation coefficients (Pearson or Spearman, depending on the variables) and variance inflation factor (VIF) index. Strong collinearity issues were detected between minimum SST and maximum SST for all the datasets and, subsequently, one of them should be excluded from further analyses. Since the studied species are invasive fishes coming from tropical or sub-tropical, warmer waters [47,48], it was considered that it would be more interesting and biologically meaningful to explore the effect of minimum (rather than maximum) SST as a limiting factor in the expansion of these species into the Greek Seas. Therefore, maximum SST was discarded and not included in further analyses. All monthly averaged satellite images from daily measurements were processed as regular grids in a geographic information system (GIS) environment using ArcInfo GRID software. Bottom depth was derived from the GEBCO portal (General Bathymetric Chart of the Oceans GEBCO_2021 Grid, DEP in m; www.gebco.net) along with bottom slope. Finally, a model-based distribution of *Posidonia oceanica* meadows was used (scale 0–4), as produced under the MediSeH [49] framework. The spatial resolution of the variables was set at 400 × 400 m^2. As all three fish species are mainly located in coastal waters, a depth limit of 750 m was applied to the environmental grids.

Maximum entropy, an SDM approach specialized for modeling species distributions from presence-only records [50], was applied using the MaxEnt ver. 3.4.4 software [51]. Models were trained using pooled data from the wider eastern Mediterranean Sea, while background points for modeling were selected solely within the current confirmed boundaries of the distribution of each species. This was specifically applied as the expansion of these species in the Greek Seas is still evolving and the model would fail to distinguish between areas where the species have not yet dispersed and unsuitable habitats. A large number (>10,000) of pseudo-absences were extracted for each species following the recommendations of Phillips and Dudík [52]. The SDMtune script in R [53] was used for model selection, opting for the parameters (features and regularization multiplier) indicated by the lowest AICc value. A 5-fold cross-validation method was selected in order to retain an adequate number of occurrences for each fold. The predictive accuracy of the models was evaluated using the receiver operating characteristic curve and the area under the curve (AUC) metric along with true skill statistics (TSS), a threshold-dependent indicator. The predictor importance was evaluated with jackknife analysis and a logistic output was selected. Finally, in order to evaluate the ability of the model to predict beyond the training conditions, we used multivariate environmental similarity surface (MESS) analysis and produced the corresponding maps. MESS is an index incorporated in the most recent versions of MaxEnt and represents how similar a point in space is to a reference set of points (the training area in our case), with respect to a set of predictor variables. Grid cells of negative values of the MESS index indicate areas where the values of the environmental variables fall outside the range of the environmental values of the training conditions. Associated maps that identify which environmental variable is driving the MESS value in each grid cell are also provided [54]. MESS analysis was applied only for *S. luridus* and *S. rivulatus*, since the training area of *P. miles* included the whole region of the Greek Seas.

3. Results

Bottom depth was the most important variable for all species for the given study area, followed by the occurrence of *P. oceanica* meadows (Supplementary Materials, Figures S1–S3). Specifically, the probability of presence for all species was exponentially increasing from -200 to 0 m, while it was also increasing with higher probabilities of occurrence of *P. oceanica* (Figure 1). On the contrary, SST range contributed the least to the models for all species. Similarly, bottom slope and maximum chlorophyll both had relatively limited contribution to all models. Minimum salinity seems to be an important factor to predict *P. miles* range in the Greek Seas (Supplementary Materials, Figure S1), as opposed to the *Siganus* species (Supplementary Materials, Figures S2 and S3). Interestingly, *P. miles* is found to reach its highest probability of presence (~50%) close to 39 psu (Figure 1). On the other hand, minimum SST proved to be a more successful predictor in the case of *S. luridus* but also *S. rivulatus* (Supplementary Materials, Figures S2 and S3).

Probabilities of the distribution of the target species are mapped in Figures 2–4, revealing quite similar spatial distributions for all species. Higher probabilities of presence were estimated throughout the coastal waters of the southern regions of the Greek Seas (i.e., Cretan Sea, Cyclades Plateau, Dodecanese Islands) and the eastern Ionian Sea. Furthermore, an expansion of the suitable habitat for these species is foreseen as far north as Lesvos Island in the North Aegean Sea. In general, *P. miles* showed higher probability of presence in some parts of the North Aegean Sea, such as the western part of Chalkidiki Peninsula and Pagasitikos Gulf, in comparison to *Siganus* spp. Furthermore, *P. miles* exhibited higher probabilities of presence in coastal areas of the southern Greek Seas. Areas with a low probability of presence for all species included North Evoikos, Maliakos, Thermaikos, Amvrakikos and Korinthiakos Gulfs and the Thracian Sea. Prediction accuracy was overall high, as AUC scored 0.938 (±0.015), 0.962 (±0.004) and 0.955 (±0.007) along with TSS: 0.78, 0.86 and 0.83 for *P. miles*, *S. luridus* and *S. rivulatus*, respectively.



(**a**)

(**b**)

(**c**)

Figure 1. Response curves for (**a**) *Pterois miles*, (**b**) *Siganus luridus* and (**c**) *Siganus rivulatus*. The X axes represent the values of the environmental variables and the Y axes represent the probability of presence of each species, as predicted from MaxEnt. The curves show how the predicted probability of presence changes as each environmental variable is varied. The mean response of the replicate runs is represented by the red line, while the standard deviation is represented by the blue shading. Variable explanation: depth = bottom depth (m); maximum_chlorophyll = mean maximum sea surface chlorophyll (mg/m^3); posidonia_oceanica = model-based distribution of *Posidonia oceanica* meadows (scale 0–4); salinity_minimum = mean minimum sea surface salinity (psu); slope = bottom slope (degree); sst_minimum = mean minimum SST (°C); sst_range = mean annual SST range (°C).

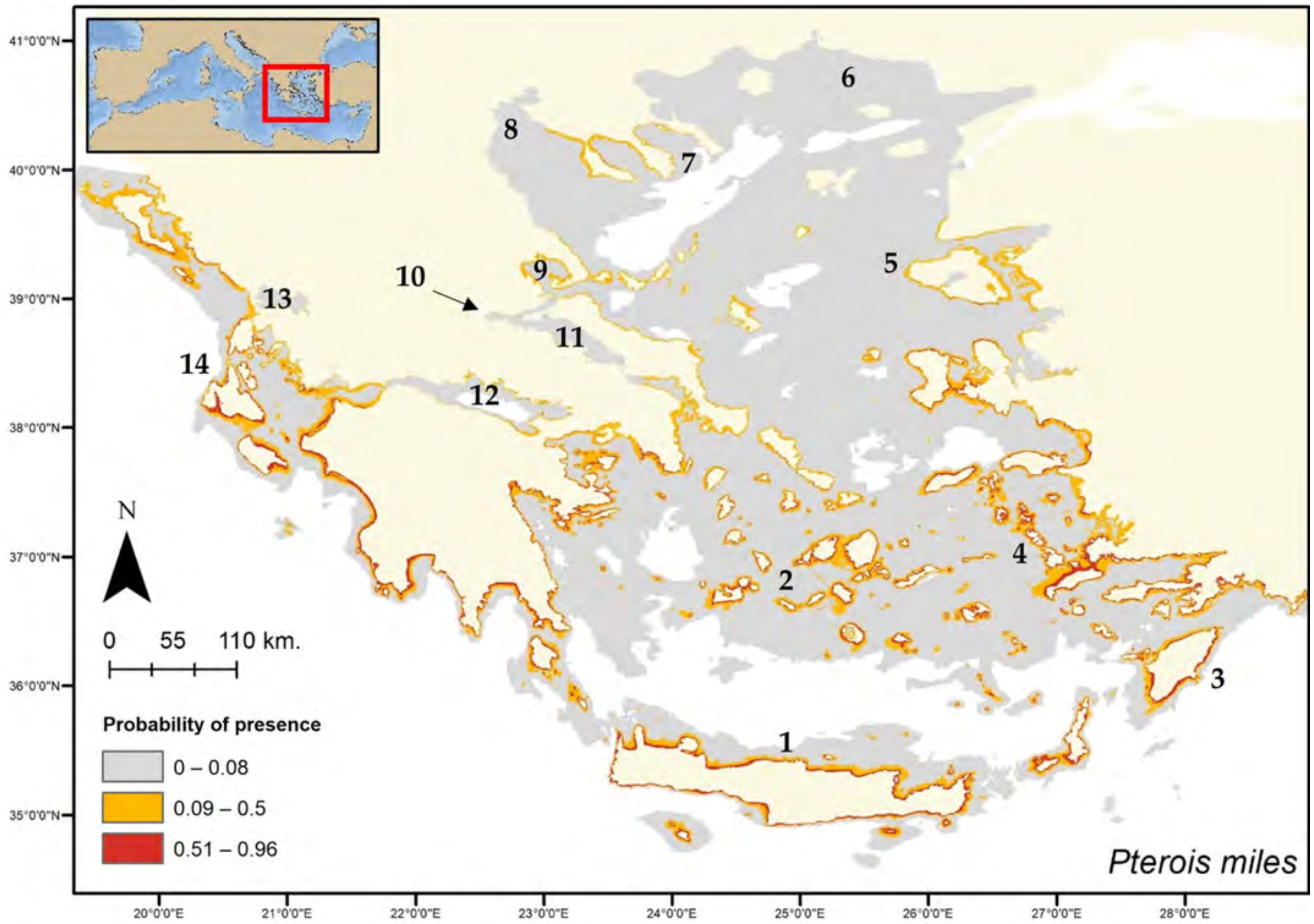


Figure 2. Probability of occurrence of *P. miles* in the Greek Seas (indicated by the red box in the map of the Mediterranean Sea in the upper left corner), as predicted by maximum entropy modeling approach. Numbers refer to the following toponyms mentioned in the text. 1 Cretan Sea; 2 Cyclades Plateau; 3 Rhodes Island; 4 Dodecanese Islands; 5 Lesvos Island; 6 Thracian Sea; 7 Chalkidiki Peninsula; 8 Thermaikos Gulf; 9 Pagasitikos Gulf; 10 Maliakos Gulf; 11 North Evoikos Gulf; 12 Korinthiakos Gulf; 13 Amvrakikos Gulf; 14 Ionian Sea.

Results of MESS analyses for *S. luridus* and *S. rivulatus* that evaluated the predicting ability of the model beyond the training environmental conditions are presented in Figure 5. Despite slight differences between the MESS maps of *S. luridus* and *S. rivulatus*, similar areas present novel (i.e., substantially different from the ones used to train the models) environmental conditions for the species. Grid cells with negative values of the MESS index are present mainly in some parts of the North Aegean Sea for both species. As noted in Figure 5, *S. rivulatus* is generally characterized by larger areas of new environmental conditions in comparison to *S. luridus*. The main variable that falls outside of the training range for *S. luridus* is the minimum salinity followed by minimum SST in a small region, while the opposite is observed for *S. rivulatus* with minimum SST being the most divergent variable in the majority of the areas.

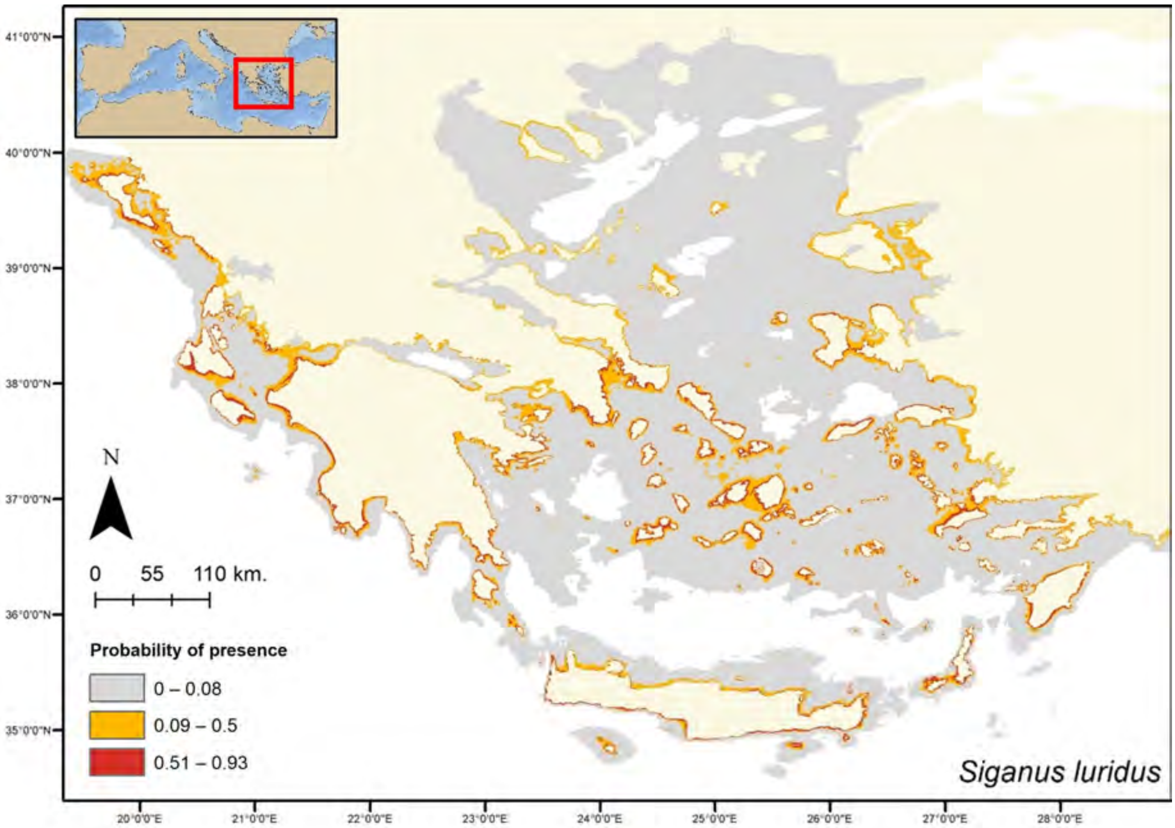


Figure 3. Probability of occurrence of *Siganus luridus* in the Greek Seas, as predicted by maximum entropy modeling approach.

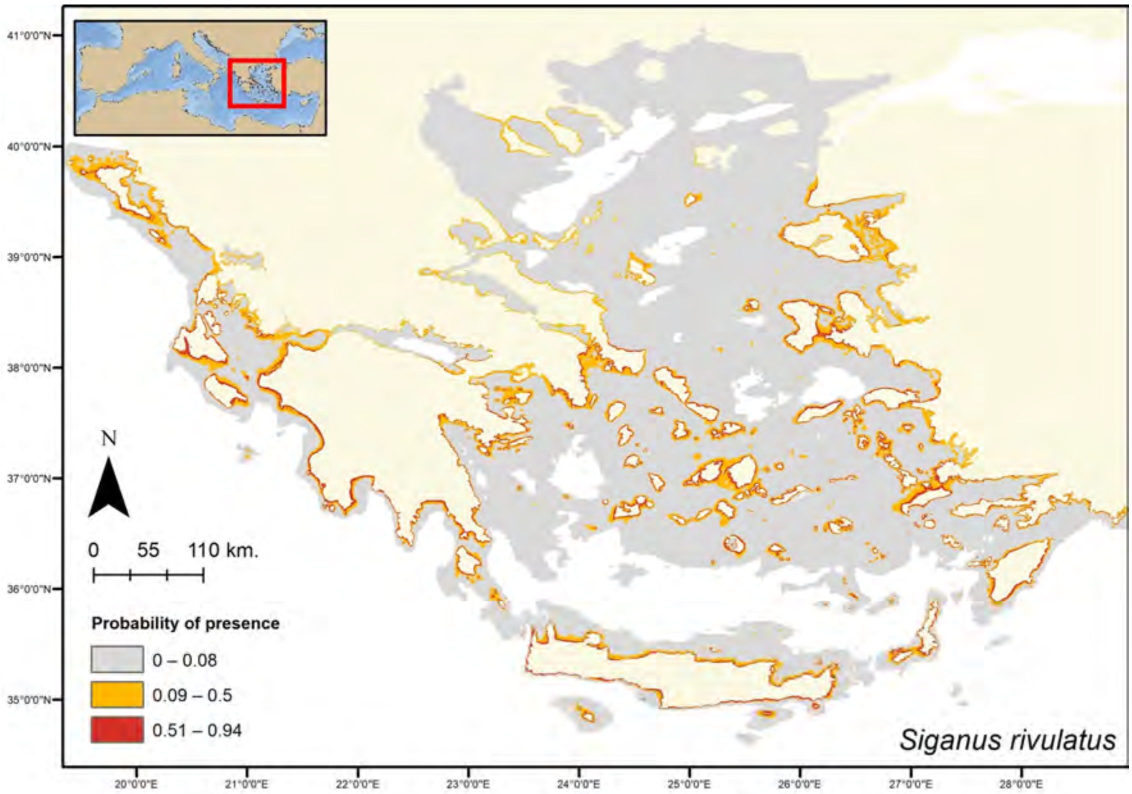


Figure 4. Probability of occurrence of *Siganus rivulatus* in the Greek Seas, as predicted by maximum entropy modeling approach.

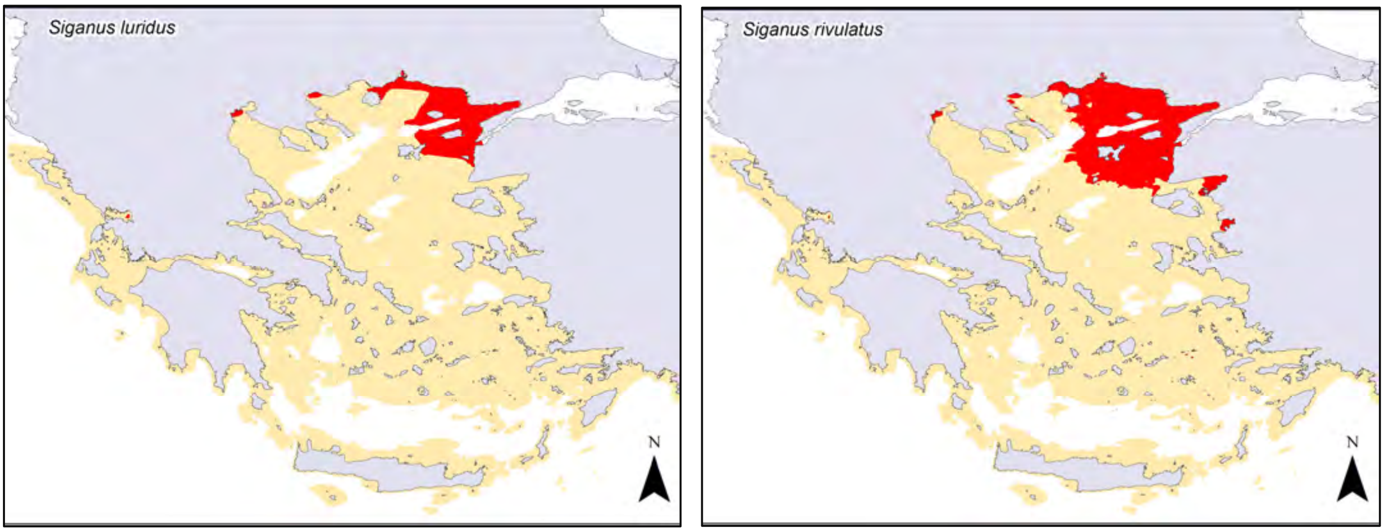


Figure 5. Results of MESS analysis conducted by MaxEnt software for *S. luridus* and *S. rivulatus*. Red areas indicate regions where at least one of the predictors falls outside of the training range.

4. Discussion

The Greek Seas are located close to the initial point of entrance of invasive species in the Mediterranean basin through the Suez Canal and form a transition area for their expansion towards the central and western Mediterranean. Therefore, the investigation of the potential expansion of invasive species in the Greek Seas using high-resolution environmental variables is of particular interest and could inform spatial planning and management.

Our results confirmed the already known extended presence of all three species mainly in coastal areas of the southern part of the Aegean and Ionian Seas. As noted elsewhere, the Ionian Sea serves as a bridge for the dispersion of numerous Lessepsian immigrants towards the western part of the Mediterranean basin [55]. Certain gulfs, such as Maliakos, North Evoikos and Amvrakikos, display very low probabilities of presence for all the studied species, demonstrating rather unfavorable conditions for their establishment. Very low or no presences are also predicted for all target species in the northern areas of the Island of Lesvos, with the exception of the westernmost and central peninsulas of Chalkidiki.

Regarding *P. miles*, past studies predict a much more confined expansion into the basin. For example, Johnston and Purkis [56] predict that a lionfish invasion in the Mediterranean is unlikely to occur, as oceanic conditions are far less favorable for larval dispersion over large distances in comparison to the Atlantic Ocean. Both D'Amen and Azzurro [32] and Poursanidis et al. [38] conclude that *P. miles*' distribution will remain restricted mainly in the easternmost section of the Mediterranean, excluding most parts of the Ionian Sea as regions subject to its expansion. However, as of this writing, *P. miles* individuals have been reported as far north as Croatia [21] and as far west as Sicily and Tunisia [19]. On the other hand, the results of most recent studies are generally in agreement with findings of the current study, such as Poursanidis et al. [20] who predict a potential distribution of *P. miles* mainly in areas already known in the eastern Mediterranean under current climatic conditions.

In general terms, the results of habitat modeling studies regarding *P. miles* seem to underestimate the expansion capacities of the species into the Mediterranean to date (e.g., [32,38]). This could be attributed mainly to niche unfilling or niche expansion that take place during a species invasion into new geographic areas (sensu [38]). Niche unfilling refers to the presence of favorable climate that is not yet occupied in the invaded domain while niche expansion refers to the environmental shift beyond the species climatic limits in their native ranges [29]. This commentary, along with the broad thermal tolerance of *P. miles* [57], also supported by the low contribution of SST range in the current study, could not exclude a further northward and westward expansion of the species. Parravicini et al. [29] also describe a tendency of several Lessepsian fish to expand their climatic niche and SDMs to usually underestimate the potential spread.

Attempts to model the potential distribution of the two siganids in the Mediterranean in current conditions are scarcer in the literature compared to *P. miles*. Our findings are in accordance with the potential spatial distribution of *S. rivulatus* predicted for the Greek Seas by D'Amen and Azzurro [34]. Regarding *S. luridus*, the south Aegean and Ionian Seas are also highlighted as areas with high probability of presence for the species, but slightly higher probabilities of presence are estimated at Thermaikos Gulf, in comparison to our results. The results of other scientific papers are also analogous to the findings of the present study. Namely, *S. luridus* displayed a gradient of decreased abundance from the southeastern to the northwestern islands of the Cyclades Archipelago [18], while Marras et al. [58] found relatively low thermal habitat suitability values for *S. rivulatus* in the northern Aegean Sea.

According to MESS analysis, the Thracian Sea and small parts of Thermaikos Gulf seem to accommodate novel conditions for the species and, subsequently, predictions in these areas are characterized by high uncertainty. However, while it is evident that the North Aegean Sea has marginal conditions for the studied species, it is also characterized by a relatively smooth temperature gradient throughout the year that would possibly allow for some over-wintering survival, potentially facilitating a northward spread [19]. In addition, the anticipated climate warming is expected to facilitate the expansion of the Red Sea, warm-adapted species towards sectors of the Mediterranean currently having unsuitable abiotic conditions for them [32,59], such as the ones highlighted by the MESS analysis.

Areas mostly favoring the occurrence of all three species coincide with shallow waters presenting high probability of the presence of *P. oceanica* meadows. Bottom depth proved to be a particularly strong predictor for all three species, exhibiting higher probabilities of presence (>50%) in depths ranging from 0 to approximately 30 m, highlighting their strong coastal nature (Figure 1). Azzurro et al. [23] also found that most sightings of *P. miles* in the Mediterranean occurred in waters 4 to 42 m deep, with a peak between 20 and 29 m. Likewise, Gavriel et al. [60] detected *P. miles* at depths of 0–64 m in a study conducted at the Gulf of Aqaba.

High occurrence of *P. oceanica* meadows favored the presence of all three species, leading us to make some relevant conjectures. Regarding *Siganus* spp., both species are herbivorous, feeding on the epiphytes associated with phanerogams (such as *P. oceanica*) and, to a lesser extent, on the phanerogams themselves [61,62]. Regarding *P. miles*, although most of its sightings are associated with hard substrata [14,19,23], it is also frequently observed in locations characterized by mosaics of rocky reefs, seagrass meadows and sand [14] while habitat complexity has sometimes been assumed to be the most important factor affecting its distribution [63]. Here, the high occurrence in relation to *P. oceanica* could be attributed to the species' feeding habits, as it is likely to feed on the fish and crustacean species associated with such meadows [64].

Regarding the climatic variables, *P. miles*' probability of presence increases with the increase in minimum salinity. The effect of salinity on habitat suitability of *P. miles* was also mentioned in other recent studies [20,38]. Although Turan [33] defines mean SST as a stronger predictor for the species' distribution in the Mediterranean, he also concludes that *P. miles* primarily prefers and persists in higher salinity habitats. Minimum SST also had an important effect on predicting *P. miles* distribution. It seems that although it is a tropical, thermophilic species, it is also capable of resisting much lower temperatures than the ones it experiences in its native habitat. Here, our results showed high probability of presence (>0.50) from 19 to 21.5 °C. The species is still expanding and exhibits a large thermal niche, allowing for the exploitation of a wide range of thermal habitats [65]. Thus, the lower limit of its thermal tolerance remains to be clarified, and this will depend on whether its future expansion and establishment of breeding populations towards the lower temperatures of the North Aegean Sea will succeed or not.

Minimum SST was among the most important abiotic factors influencing the distribution of *Siganus* spp., a finding also stated elsewhere ([66] and references therein). The probability of the presence of *S. luridus* sharply decreased below 19 °C and was zero for a temperature equal to 17 °C, while the probability of the presence *of S. rivulatus* also decreased from 19–17.5 °C. However, there are some indications that the species are less sensitive to low temperatures than expected. For example, *S. luridus* was present in areas with minimum winter SST below 14.5 °C and no clear minimum temperature threshold was revealed during a study conducted by Giakoumi [18] in the Cyclades Archipelago. The exact role of minimum temperatures as a limiting factor of the expansion of the siganids in the Greek Seas remains to be clarified in the near future. In contrast, SST range was not found to be important as a primary determinant, similar to the findings of D'Amen and Azzurro, [34], a fact possibly due to the large thermal tolerance of the species.

A further addition to the current study could involve the inclusion of biotic interactions. Biotic interactions such as predation rates, interspecific competition and feeding habits have been demonstrated to play a key role in predicting the invasion success [35]. For example, adding information on the probability of the presence of a predator or prey species, upon availability, could further enhance our knowledge on the spatial distribution of the target species. Another suggestion would be to take into account the presence of native, competitive fishes. For example, the native herbivores are assumed to compete for the same resources with *Siganus* spp. in the eastern Mediterranean Sea [67,68], especially under limiting trophic resources. Thus, the competitive displacement, decrease in the biomass and/or narrowing of the native species' trophic niche in the eastern Mediterranean have been proposed ([3] and references therein) but it has also been hypothesized that alien species might also occupy available and underexploited niches, due to stressors such as overfishing or a shift in environmental conditions [1,69], as has been suggested for both *S. luridus* and *S. rivulatus* [70]. Gut-content analysis has also shown different feeding preferences of *S. luridus* and the native herbivore *Sarpa salpa* (Linnaeus, 1758), indicating good resource partitioning [71]. After all, the native and non-indigenous herbivorous fishes co-occur and macrophytes are abundant in many regions of the Aegean and Ionian Seas [48,72]. To support this argument, a recent study from the Cretan Sea concluded that the presence of *S. rivulatus* did not significantly affect the grazing activity of *S. salpa* [73]. In conclusion, the biotic interactions between the native and alien species in the Mediterranean are complicated and further investigation, such as of specific local and regional species data, is needed for a proper incorporation into a modeling process.

An increasing number of publications predict that under various human-induced climatic change scenarios, a lot of regions of the Mediterranean will become more and more inhospitable for the native species, simultaneously facilitating the dispersion and establishment of warm-adapted Lessepsian species (e.g., [19,32,59,74]. It has also been proved that several alien species have already spread far beyond temperature conditions matching their native ranges [32,34], taking advantage of a wide niche breadth. At the same time, it has been assumed that the native biota will be less adaptable to climatic change [2], while stocks of many indigenous species which could be potential predators or competitors have been markedly reduced in the Mediterranean by overfishing [75]. Under these circumstances, several mitigation measurements have been proposed or applied for the restriction or reduction of the abundance of invasive species (e.g., [76]) and legislation on European or regional bases has been enacted. Proper review and interpretation of the results of habitat modeling approaches, such as the ones presented here, could provide an additional, extremely helpful tool towards these conservation efforts.

5. Conclusions

This study predicts the potential geographic distribution of three Red Sea invaders (*P. miles*, *S. luridus* and *S. rivulatus*) in the Greek Seas under current climatic conditions and in the absence of biotic interactions. The marine regions with the highest likelihood of presence for all species are the coastal areas of the southern and central Aegean Sea and the Ionian Sea. The limited presence of the studied species is predicted in a few locations, primarily enclosed gulfs (Amvrakikos, Maliakos, Korinthiakos, North Evoikos). The North Aegean Sea is predicted to have low presence probabilities, as well. However, uncertainty in this area is regionally high, especially in the Thracian Sea, due to novel climatic conditions and the results there should be speculated on with caution. Researchers, stakeholders and policy makers may find the spatial information generated by the current study useful in identifying locations that may soon experience expansion risk. The need for proper conservation measures becomes more and more important as a result of global warming climatic conditions that favor the tropical species at the expense of the natives. Additional research and effective management methods should additionally take into consideration other biological traits, such as the diet, reproduction and growth of the target species.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15060776/s1, Figure S1: The percent contribution (a) and the jackknife table (b) of variable importance for *Pterois miles* for both training and test datasets. The gain in the environmental variables when used in isolation is represented by the blue line while the decrease in the gain when the specific environmental variable is omitted is represented with the green line. Variable explanation: depth = bottom depth (m); maximum_chlorophyll = mean maximum sea surface chlorophyll (mg/m^3); posidonia_oceanica = model-based distribution of *Posidonia oceanica* meadows (scale 0–4); salinity_minimum = mean minimum sea surface salinity (psu); slope = bottom slope (degree); sst_minimum = mean minimum SST (°C); sst_range = mean annual SST range (°C). Figure S2: The percent contribution (a) and the jackknife table (b) of variable importance for *Siganus luridus* for both training and test datasets. The gain in the environmental variables when used in isolation is represented by the blue line while the decrease in the gain when the specific environmental variable is omitted is represented with the green line. Variable explanation: depth = bottom depth (m); maximum_chlorophyll = mean maximum sea surface chlorophyll (mg/m^3); posidonia_oceanica = model-based distribution of *Posidonia oceanica* meadows (scale 0–4); salinity_minimum = mean minimum sea surface salinity (psu); slope = bottom slope (degree); sst_minimum = mean minimum SST (°C); sst_range = mean annual SST range (°C). Figure S3: The percent contribution (a) and the jackknife table (b) of variable importance for *Siganus rivulatus* for both training and test datasets. The gain in the environmental variables when used in isolation is represented by the blue line while the decrease in the gain when the specific environmental variable is omitted is represented with the green line. Variable explanation: depth = bottom depth (m); maximum_chlorophyll = mean maximum sea surface chlorophyll (mg/m^3); posidonia_oceanica = model-based distribution of *Posidonia oceanica* meadows (scale 0–4); salinity_minimum = mean minimum sea surface salinity (psu); slope = bottom slope (degree); sst_minimum = mean minimum SST (°C); sst_range = mean annual SST range (°C).

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