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Range contractions, fragmentation, species extirpations, and extinctions of commercially valuable molluscs in the Mediterranean Sea—a climate warming hotspot

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The Mediterranean Sea is a global hotspot of climate warming and biodiversity loss where molluscs have provided valuable ecosystem services, such as provisioning and cultural value, since pre-historic times. A high rate of warming and range shift limitations due to the semi-enclosed nature of the basin raise concerns about molluscan population persistence in future climate scenarios. We modelled the future distribution of 13 Mediterranean species of molluscs subject to industrial fisheries exploitation on both the Mediterranean and Atlantic European coasts. We tested the hypothesis that range contractions, fragmentation, and species extirpations will become increasingly severe in the Mediterranean by modelling mid-century and end-century species distributions for four IPCC climate change scenarios. Already under mild emissions scenarios, substantial range contractions and fragmentation are projected in the Mediterranean, suggesting global extinctions by end-century for most endemic species. Colder deep waters do not act as refugia, contrary to expectations. Species also occurring along the Atlantic European coasts may benefit from warming through range expansions to higher latitudes or deeper waters. Most of the modeled species are already over-exploited, but their eradication from the Mediterranean will imply substantial financial losses and a profound cultural change in coastal communities.

Keywords: clams, fisheries, global warming, scallops, species distribution modelling.

Introduction

Abiotic factors largely define the distributions of marine ectotherm species (Cahill *et al.*, 2014). Consequently, climate change is a primary driver of their shifting ranges (Poloczanska *et al.*, 2013). Increasing global temperatures cause species ranges to expand at the leading (poleward) edge and retract at the rear (equatorward) edge, where, in the absence of local adaptation and acclimatization, populations may experience temperatures close to or beyond their thermal tolerance limits (Hampe and Petit, 2005; Bennett *et al.*, 2015). When such range changes occur in semi-enclosed basins, where coastline obstructs latitudinal range shifts, global warming can be especially critical as it can restrict species to few colder areas. Such "cul-de-sacs" result in fragmented populations, reducing gene flow, and genetic diversity (Ben Rais Lasram *et al.*, 2010). If continued warming leads even these areas to become climatically unsuitable, species may go locally and then globally extinct (Cheung *et al.*, 2009; Ben Rais Lasram *et al.*, 2010).

The Mediterranean Sea is one such semi-enclosed basin and a climate change hotspot (Giorgi, 2006; Diffenbaugh and Giorgi, 2012). The semi-enclosed nature limits hydrological exchange with adjacent oceans resulting in a long water residence time and consequent heat storage (Marbà *et al.*, 2015). Due to its geographic position in the transition zone of two climatic regimes, this sea is warming at two to three times the rate of the global ocean (Vargas-Yáñez *et al.*, 2008), making it a hotspot of climate warming globally. This sea is also a biodiversity hotspot as 45% of its marine species are endemic (Costello *et al.*, 2017). Due to this high rate of endemism, the risk of global extinctions following biodiversity loss in the Mediterranean is high (Cahill *et al.*, 2013; Shaltout and Omstedt, 2014). Biodiversity loss ultimately implies a loss in the ecosystem services that benefit the ca. 130 million people inhabiting the Mediterranean coasts (European Environmental Agency, 2014).

Fisheries provide valuable nutritional and economic resources for coastal populations. Molluscs represent ∼8% of global marine capture production, promoting food and nutritional security for many coastal communities (FAO, 2020). The estimated global value of marine bivalve production for food is USD 23.9 billion per annum (van der Schatte Olivier *et al.*, 2020), with 11% of this production coming from wild-harvested populations (Wijsman *et al.*, 2019). As low trophic level organisms, mollusc consumption has a lesser environmental impact than high trophic level fishery resources (Ferreira *et al.*, 2019; Khan and Liu, 2019). Additionally, the cultural value of molluscs is deeply rooted in the historical context of the Mediterranean. Their exploitation by humans in the region is dated as early as the Lower Palaeolithic (ca. 300 ka; Colonese *et al.*, 2011). During the Mid- and Upper Palaeolithic, species such as the scallops *Pecten maximus* and *P. jacobaeus* and the clams *Callista chione*, *Chamelea gallina*, and *Ruditapes decussatus* were amongst the most commonly exploited molluscs for food and, in the case of *Callista chione*, as raw material for tools (Colonese *et al.*, 2011). More recently, the classical works of Greek antiquity described the exploitation of *P. jacobaeus*, the razor clam *Solen marginatus*, and the clams *Venus verrucosa* and *Chamelea gallina*

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Table 1. Target species by family and distribution.

Family	Mediterranean endemic	Atlanto-Mediterranean	Atlantic
Cassidae (helmet snails)	*Galeodea echinophora* (Linnaeus, 1758) (139)		
Muricidae (murex snails)	*Bolinus brandaris* (Linnaeus, 1758) (339)		
Nassariidae (dog whelks)	*Tritia mutabilis* (Linnaeus, 1758) (239)		
Pectinidae (scallops)	*Flexopecten glaber* (Linnaeus, 1758) (234) *Pecten jacobaeus* (Linnaeus, 1758) (201)	*Aequipecten opercularis* (Linnaeus, 1758) (2243)	*Pecten maximus* (Linnaeus, 1758) (1761)
Veneridae (clams)	*Chamelea gallina* (Linnaeus, 1758) (319)	*Callista chione* (Linnaeus, 1758) (285) *Polititapes aureus* (Gmelin, 1791) (432) *Ruditapes decussatus* (Linnaeus, 1758) (597) *Venus verrucosa* (Linnaeus, 1758) (657)	*Chamelea striatula* (da Costa, 1778) (1808)
Solenidae (razor shells)		*Solen marginatus* (Pulteney, 1799) (314)	
Pharidae (razor shells)		*Ensis ensis* (Linnaeus, 1758) (669)	

Distribution is defined as those species only occurring in the Mediterranean basin ("Mediterranean endemic"), those with broad distributions along Atlantic coasts and in Mediterranean Sea ("Atlanto-Mediterranean"), and those only occurring in the "Atlantic". The number of presence cells used for modelling are in parentheses.

for food and medicine (Voultsiadou *et al.*, 2009). Descriptions of the harvest of the gastropod *Bolinus brandaris* occur in works of the same era for the extraction of purple dyes (Vasconcelos *et al.*, 2008) used to colour textiles and paint, first by the Phoenicians (1570 BCE) and later by the Greeks and Romans, with the quality of such dyes holding economic and political implications (Susmann, 2020; Sukenik *et al.*, 2021).

The vulnerability of these resources in the Mediterranean will increase as socio-economic demands and the impacts of climate change conflict, with negative consequences for human populations (Cramer *et al.*, 2018). In the context of this long-lasting human–ocean relationship, the cost of climate-driven species extinctions in the region becomes evident.

To assess the risk of such climate-related losses, we projected the distribution of 13 commercially valuable Mediterranean molluscs under all four IPCC climate change scenarios (IPCC, 2013). We modelled two additional species distributed exclusively on the European Atlantic coast to compare with two closely related endemic species of the same genus. Because all modelled species proved to be endemic or of cold-temperate affinity (Fischer *et al.*, 1987), we hypothesize that the Mediterranean will become progressively less suitable for these species as scenario severity increases, resulting in range reductions, retraction in refugia in the coldest areas of the basin, and, eventually, global extinctions of endemic species.

Methods

Species data

We selected the 13 native Mediterranean molluscs because they are exploited industrially and reported as frequent in fish markets by the FAO (Fischer *et al.*, 1987; Table 1). Two of these species, *Callista chione* and *Tritia mutabilis*, were included as they are relevant local resources despite only semi-industrial exploitation. We included two additional Atlantic species, *Chamelea striatula* and *Pecten maximus* that are cogeneric and closely related to the Mediterranean endemic, *C. gallina* and *P. jacobaeus*, respectively (Backeljau *et al.*, 1994; Wilding *et al.*, 1999).

Despite heavy exploitation in the Mediterranean, two native species, the mussel *Mytilus galloprovincialis* and the oyster *Ostrea edulis*, were excluded from this analysis because they are extensively cultured across the basin with consequent release from predators and competitors. The subsequent expansion of the realized niche violates the assumption of correlative species distribution models that species niches remain unchanged (Wiens and Graham, 2005). For similar reasons, we did not consider occurrences in areas where target species are known to be introduced (e.g. *Bolinus brandaris* in Galicia, northern Spain; Bañón *et al.*, 2008). We also excluded *Ensis minor* and *E. siliqua* due to their similarity and thus the potential for misidentification errors in public databases (Von Cosel, 2009). Nomenclature follows the World Register of Marine Species (WoRMS Editorial Board, 2022).

The outcome of this selection process was a total of 15 mollusc species, comprised three gastropods, four scallops (Pectinidae), six clams (Veneridae), and two razor clams (Solenidae and Pharidae; Table 1 and ESM 1, Supplementary Table S1). These 15 species comprise three distinct biogeographic affinities. The first group, termed "Atlanto-Mediterranean", includes seven species with broad distributions along the Mediterranean and Atlantic coasts. Second, the group "Mediterranean endemic" includes six species endemic to the Mediterranean Sea. Finally, "Atlantic" includes two species present exclusively in the Atlantic.

We obtained occurrence records across the species' entire ranges from the Global Biodiversity Information Facility (GBIF.org, 2022; ESM 1, Supplementary Table S2). We controlled for the accuracy of species locations by cleaning the data manually in QGIS and removing unlikely occurrences, including those on land or clearly outside a species' known range (Fischer *et al.*, 1987). *Chamelea gallina* and *C. striatula* have distinct distributions in the Mediterranean and along the European Atlantic coast, respectively, with some overlap in the Alboran Sea, the Strait of Gibraltar, Southern Portugal, and the Gulf of Cadiz (Backeljau *et al.*, 1994). Based on this known distribution, occurrence data were polished, i.e. Mediterranean and Atlantic occurrences were assigned to *C. gallina* and *C. striatula*, respectively, with records in the region of overlap left unchanged, noting that the accuracy of these identifications is not verifiable. We applied the same method to *P. jacobaeus* and *P. maximus*, with known distributions in the Mediterranean and the Atlantic, respectively (Wilding *et al.*, 1999).

Although GBIF facilitates access to global biodiversity data and large datasets that may otherwise be too costly to obtain, we recognize the potential for spatial bias due to the lack of design in data collection. We addressed this bias in four ways. First, we applied a systematic sampling approach of occurrences to address the lack of sampling design resulting in incomplete or uneven spatial coverage. This method consistently reduces unequal sampling intensity across different bias types, bias intensities, and species (Fourcade *et al.*, 2014). Thus, we applied a grid with a spatial resolution of 5 arcmins (~9.2 km) and randomly sampled one occurrence from each grid cell. All occurrence records must match a cell of the environmental layer; therefore, mismatches were moved to the nearest cell by applying the function *points2nearestcell* (Pakillo/rSDM package; Rodriguez-Sanchez, 2021) with a maximum shift of 9000 m to approximate the 5 arcmin (~9.2 km) spatial resolution of the environmental layers (described in the following section). We checked all occurrence records beyond this 9000 m limit manually. This process resulted in 139 to 2243 cells per species, from 44201 cleaned occurrences overall (ESM 1, Supplementary Table S3). Second, we compared the occurrences with the known range of the species obtained from the literature (Fischer *et al.*, 1987) (ESM 1, section 4.2), noting that, in general, the overlap was very good, possibly because being of fisheries interest, these species have been broadly monitored, over most of the study area. Third, we constrained the study area to a realistic realm, selected for each species individually, as unnecessarily large areas may lead to potentially adverse effects on the model and the predictions (VanDerWal *et al.*, 2009; Elith *et al.*, 2010). This process resulted in a defined study area of 0°–80° latitude and −20°–52° longitude for most species. For the deep-dwelling Galeodea echinophora, we extended the study area to 20°–70° latitude and −15°–50° longitude. The intertidal bathymetry layer applied to *R. decussatus* resulted in a study area of 4°–70° latitude and −20°–52° longitude. To account for the distribution of *V. verrucosa* in both hemispheres, we selected a study area of −40°–80° latitude and −20°–52° longitude. Last, we selected pseudo-absences in a purely random way, as this method induces the least bias (Barbet-Massin *et al.*, 2012) (see also section "Model parameterization").

Environmental data

Environmental data were obtained from Bio-Oracle v.2.1 as raster grid layers at a spatial resolution of 5 arcmins (~9.2 km; Tyberghein *et al.*, 2012; Assis *et al.*, 2018). These environmental layers included the "current" period (based on monthly averages of satellite and *in situ* data from 2000 to 2014) and future conditions (monthly averages for 2040–2050 and 2090–2100) based on data from the IPCC's Representative Concentration Pathways (RCP) 2.6, 4.5, 6.0, and 8.5 as introduced and defined in the fifth Assessment Report of the IPCC (IPCC, 2013). Bio-ORACLE marine data layer construction, including climatic data sources, applied atmosphere ocean general circulation models, and statistical downscaling to final resolution, are discussed in detail by Assis *et al.* (2018). Six environmental predictors (maximum temperature, temperature range, minimum salinity, salinity range, maximum chlorophyll, and chlorophyll range), each measured at the sea surface and maximum depth, were selected based on their known importance in defining the ecological niche of molluscs (Guisan *et al.*, 2017). Temperature is an important environmental predictor, as it explains most of a marine ectotherm's distribution (Pinsky *et al.*, 2019). Salinity is relevant for mollusc physiological processes (Pourmozaffar *et al.*, 2019), while chlorophyll is a proxy for nutrient availability (Moraitis *et al.*, 2018). We selected species-specific variables (ESM 1, Supplementary Table S4) by pairwise correlation tests with a Pearson's correlation coefficient cut-off value of 0.7 to identify non-correlated relevant predictor variables and decrease model uncertainty (Guisan *et al.*, 2017). We cropped all environmental layers to the appropriate study area extent for each individual species.

Model parameterization

We applied an ensemble forecasting method using the Biomod package (Thuiller *et al.*, 2009) in R (R Core Team, 2019). We constructed the ensemble models from the default settings of four algorithms: generalized linear model (GLM), generalized additive model, generalized boosting model, and random forest (RF). These models require presence–absence data; therefore, we generated three sets of 10000 pseudo-absences selected in a completely random way across the complete study area. Equal weighting of pseudo-absences to presences ensured appropriate ratios across statistical modelling algorithms and, thus, robust ensemble modelling outputs (Barbet-Massin *et al.*, 2012). We repeated an 80/20 (model calibration/evaluation) data splitting procedure three times for each species, then evaluated each cross-validation with the true skill statistic (TSS) and area under the curve (AUC). The evaluation scores and graphical visualization provided an evaluation of the predictive power of each model. We also calculated variable importance to quantify the influence of each environmental variable on the model. We defined a TSS threshold of 0.6 as the minimum for model inclusion in the final ensemble models (Guisan *et al.*, 2017).

Ensemble model evaluation, projection, and visualization

The final ensemble models were evaluated using three common measures of accuracy: TSS, Cohen's Kappa, and the Receiver Operator Characteristic (ROC) curve (Guo *et al.*, 2015). TSS is calculated as sum of the true positive and true negative rates (TPR and TNR, respectively) minus 1 and thus ranges from −1 to 1. Values approaching 1 indicate model accuracy, while those <0 indicate models performed no better than random (Guo *et al.*, 2015). Accuracy overestimation was assessed with Cohen's Kappa, which measures the degree to which the agreement between observed and predicted values is better than expected by chance. On the scale from 0 to 1, values approaching 1 indicate increased reliability (Cohen, 1960). Finally, ROC is calculated by plotting sensitivity (TPR) against 1 minus specificity (false positive rate). The AUC thus provides a measure of accuracy ranging from 0 to 1. Scores between 0.9 and 1 are classified as excellent, while those between 0.5 and 0.6 are considered no better than random (Fielding and Bell, 1997). These ensemble models were then used to project each species' current distribution (2000–2014) and all four-climate change scenarios to 2050 and 2100. We quantified the uncertainty of predictions by computing the standard deviation per cell of the model predictions included in the ensemble. Then, we averaged these across the complete mapping area.

Projection visualization was conducted in QGIS using a colour gradient representing the probability of occurrence (0–100%) for each species in a given cell. Species range changes, defined as the difference between percent gain and percent loss of cells when comparing current and future projections, were quantified under each scenario with the *Biomod_RangeSize* function using binary presence/absence projections. Binary projections were calculated by applying the threshold that maximizes TSS (Liu *et al.*, 2005; ESM 1, Supplementary Table S6). Range change calculations were performed over each species' complete range, for the Mediterranean basin separately, and for vertical habitat <50 m depth after first applying a depth mask. Species range change assumed the hypothesis that species can disperse to any climatically suitable cell, given the high mobility of molluscs at the larval stage. Range change calculations were visualized in boxplots, distinguishing between Mediterranean (sub)endemic and Atlanto-Mediterranean species. Due to the small sample size and lack of *a priori* assumptions on distributions, we tested for differences in range change with a randomization test. First, we pooled the range change values of all species into a single set. Then, we resampled it 10000 times without replacement to build two groups of the same sample size as the pooled groups and computed the difference between the medians. Finally, under the null hypothesis of no difference between groups (difference between the medians equals zero), we calculated the *p*-value as the number of resampled values more extreme than the ± absolute value of the observed difference between the medians ($\alpha = 0.05$).

The projected range change of the Atlantic-only species, *P. maximus* and *C. striatula*, were compared directly to the Mediterranean endemic species of the same genus, *P. jacobaeus* and *C. striatula*, respectively. Species probability maps were layered for each scenario and year to provide a comprehensive view of diversity loss and a mean probability of occurrence for all species in the Mediterranean. We calculated the centroid of each species distribution under all future scenarios with the function *gCentroid* in the rgeos package (Bivand and Rundel, 2021). The difference in present-day and future distribution centroids provided latitudinal range shifts (Saupe *et al.*, 2014). Finally, we quantified fragmentation for each species by applying the "clump" function in the R package "raster" (Hijmans, 2021). This function clustered continuous presence cells in all eight directions as habitat patches (Halstead *et al.*, 2019). Then, we calculated the average minimum edge-to-edge distance between neighbouring patches.

Results

Predictor importance, single model evaluation, and ensemble model uncertainty

Temperature was the most influential environmental predictor in model construction for most species. For two venerid bivalves, *Ruditapes decussatus* and *Venus verrucosa*, temperature range at the sea surface had the highest average predictor importance across all models at 0.674 and 0.606, respectively. Benthic maximum temperature was most influential for the three other venerids [*Callista chione* (0.647), *Chamelea striatula* (0.729), and *Polititapes aureus* (0.788)] and the Atlantic scallop *Pecten maximus* (0.671). Maximum temperature at the sea surface was most important for *Aequipecten opercularis* (0.618), *Chamelea gallina* (0.633), *Ensis ensis* (0.794), *Flexopecten glaber* (0.654), and *Solen marginatus* (0.561). Benthic minimum salinity was most important for all three gastropods [*Bolinus brandaris* (0.717), *Galeodea echinophora* (0.887), and *Tritia mutabilis* (0.753)], and the Mediterranean scallop *Pecten jacobaeus* (0.807). Chlorophyll was the least influential environmental predictor for the majority of species.

The RF method preformed best for all species, while the GLM method consistently performed worst (ESM 1, Supplementary Table S5). Evaluation of the final ensemble models showed high performance, ranging from a maximum TSS score of 0.953 (*P. jacobaeus* and *V. verrucosa*) to a minimum of 0.819 (*C. striatula*). Kappa values ranged between 0.622 (*G. echinophora)* and 0.835 (*R. decussatus*) indicating model reliability. ROC values >0.9 for all ensemble models indicate excellent fit and high model accuracy (ESM 1, Supplementary Table S6).

The standard deviation of the ensemble models ranged from 3.6% [*T. mutabilis*, RCPs 6.0 and 8.5 (2100)] to 15.4% [*E. ensis*, RCP 8.5 (2100)]. Agreement between single models in the final ensembles was best for endemic species such as *B. brandaris*, *T. mutabilis*, and *P. jacobaeus*, as standard deviations remained <5% for most RCP scenarios and years. Uncertainty was higher mostly for species with broader distributions, such as *R. decussatus*, *V. verrucosa*, and *E. ensis*, with values near or above 10% (ESM 1, Supplementary Table S7).

Range variation in future climate scenarios

Range variation in the Mediterranean basin

Range contractions were projected for both endemic and Atlanto-Mediterranean species at the Mediterranean basin scale under all future scenarios (Figure 1; detailed results per species in ESM 1, Supplementary Table S8). For 2050 projections, median range loss for endemic species increased from −57.4% for RCP 2.6 to −67.5% for RCP 4.5, −59.3% for RCP 6.0, and −67.5% for RCP 8.5. This non-linear trend with scenario severity reflects the different emission reduction pathways whereby mid-century emissions are lower than present under RCP 2.6, experience their peak under RCP 4.5, and are on rising trends under RCPs 6.0 and 8.5 (van Vuuren *et al.*, 2011; IPCC, 2021). Median range loss increased further for all 2100 projections to −64.4% for RCP 2.6, −76.2% for RCP 4.5, −78.1% for RCP 6.0, and −94.6% for RCP 8.5, illustrating the consequences of carbon dioxide accumulation in the atmosphere even decades after the emission reduction efforts considered by some scenarios (IPCC, 2021). For individual species, range loss was projected for all endemics in all scenarios, ranging from a minimal −24.2% for *B. brandaris* in RCP 2.6 (2100) to a maximum of −98.4% for *Chamelea gallina* in RCP 8.5 (2100; ESM 1, Supplementary Table S8).

Range loss for Atlanto-Mediterranean species in the Mediterranean Sea is only marginally lower than for endemics (*p*-values in ESM 1, Supplementary Table S11), increasing in 2050 with scenario severity from −44.4% for RCP 2.6, −46.8% for RCP 4.5, −47.5% for RCP 6.0, and −50.7% for RCP 8.5 (Figure 1). Greater range contractions were projected for the year 2100 at −49.5% for RCP 2.6, −60.3% for RCP 4.5, −59.1% for RCP 6.0, and −73.5% for RCP 8.5. Of all seven Atlanto-Mediterranean species, models projected a minimal range loss of −27.0% for *S. marginatus* under RCP 2.6 (2100). Models predicted complete eradication from the Mediterranean for *A. opercularis* under RCP 8.5 (2100) and for *E. ensis* under RCP 2.6 (2100), RCP 4.5 (2050), RCP 6.0 (2100), and RCP 8.5 (2100; ESM 1, Supplementary Table S8).

Range contractions in the Mediterranean translate to loss of diversity in many regions (Figure 2; ESM 1, Supplemen-

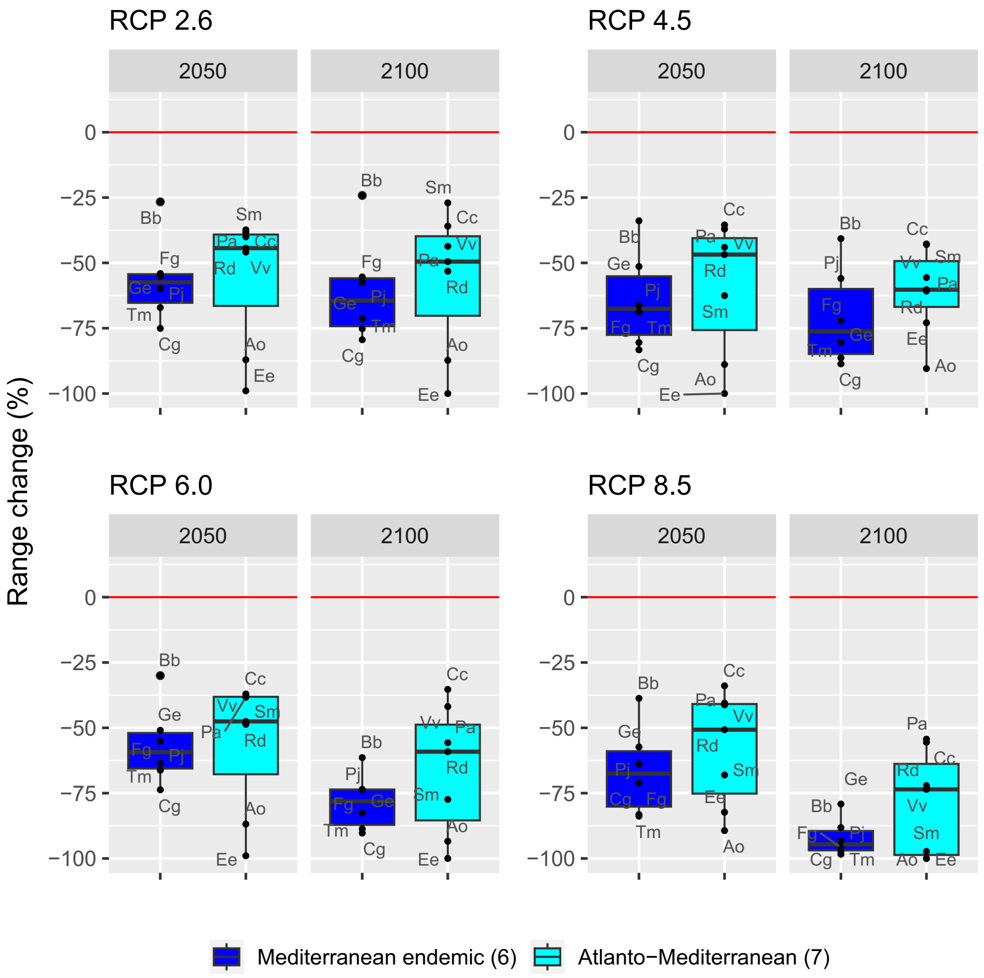


Figure 1. Projected range change in the Mediterranean Sea. Species labelled as "Mediterranean endemic" include those occurring in the Atlantic Ocean just off Gibraltar (*Bolinus brandaris*). Those labelled as "Atlanto-Mediterranean" mostly have broad distributions over the European Atlantic coasts. Labels are the initials of the species name. The red line indicates no change. Models project range loss for all species and scenarios, with complete eradication for some Atlanto-Mediterranean species (e.g. *Aequipecten opercularis* and *Ensis ensis*) under some scenarios. Projected range changes for Mediterranean endemic and Atlanto-Mediterranean species are non-significantly different under most scenarios (ESM 1, Supplementary Table S11), except RCP 8.5 (2100; $p = 0.029$).

tary Figures S2–S17). Currently, the mean probability of occurrence of the modelled species is high in the northwest regions of the basin, in the Adriatic Sea, and the north Aegean, a proxy for the diversity gradient of Mediterranean biodiversity. Under future scenarios, large areas are impoverished, including those currently rich in diversity. By mid-century, under the least severe scenario RCP 2.6, the spatial extents of the most diverse regions become reduced. In the worst-case scenario RCP 8.5, by end-century, the only pockets of high diversity remain in the Alboran Sea and southern France (Figure 2).

Range variation at a broad Atlantic and Mediterranean scale

In striking contrast with projections at the Mediterranean scale, models projected median range expansions for Atlanto-Mediterranean species in most scenarios when the full extent of species ranges in the Atlantic Ocean was also considered, with a maximum median increase of 27.7% projected for RCP 2.6 (2100; Figure 3; detailed results per species in ESM 1, Supplementary Table S9).

Range expansions were the greatest for *V. verrucosa* under all future scenarios, ranging from 291.3% under RCP 6.0 (2050) to 437.6% under RCP 4.5 (2100). Models projected that *E. ensis* and *R. decussatus* will also benefit from range expansions under all future scenarios. In contrast, *S. marginatus* will expand its range under most future scenarios, except in the most severe RCP 6.0 (2100) and RCP 8.5 (2100), when it will contract by −39.4% and −74.6%, respectively. Models projected minimal range expansions for *A. opercularis* for 2050 under RCPs 4.5 and 6.0 (11.7%, and 17.3%, respectively), but range contractions for all 2100 scenarios (−26.2% to −96.1% for RCPs 2.6 to 8.5, respectively; ESM 1, Supplementary Table S9).

Some Mediterranean endemic species showed range expansions into the nearby Atlantic Ocean. However, such range changes are unlikely for the same barriers to dispersal that made these species endemic.

A comparison of Mediterranean and Atlantic species couples

Comparing Mediterranean and Atlantic species couples, the clams *Chamelea gallina* and *C. striatula* and the scallops *P. jacobaeus* and *P. maximus*, offered mixed results (Figure 4). We observed range contractions for both species of

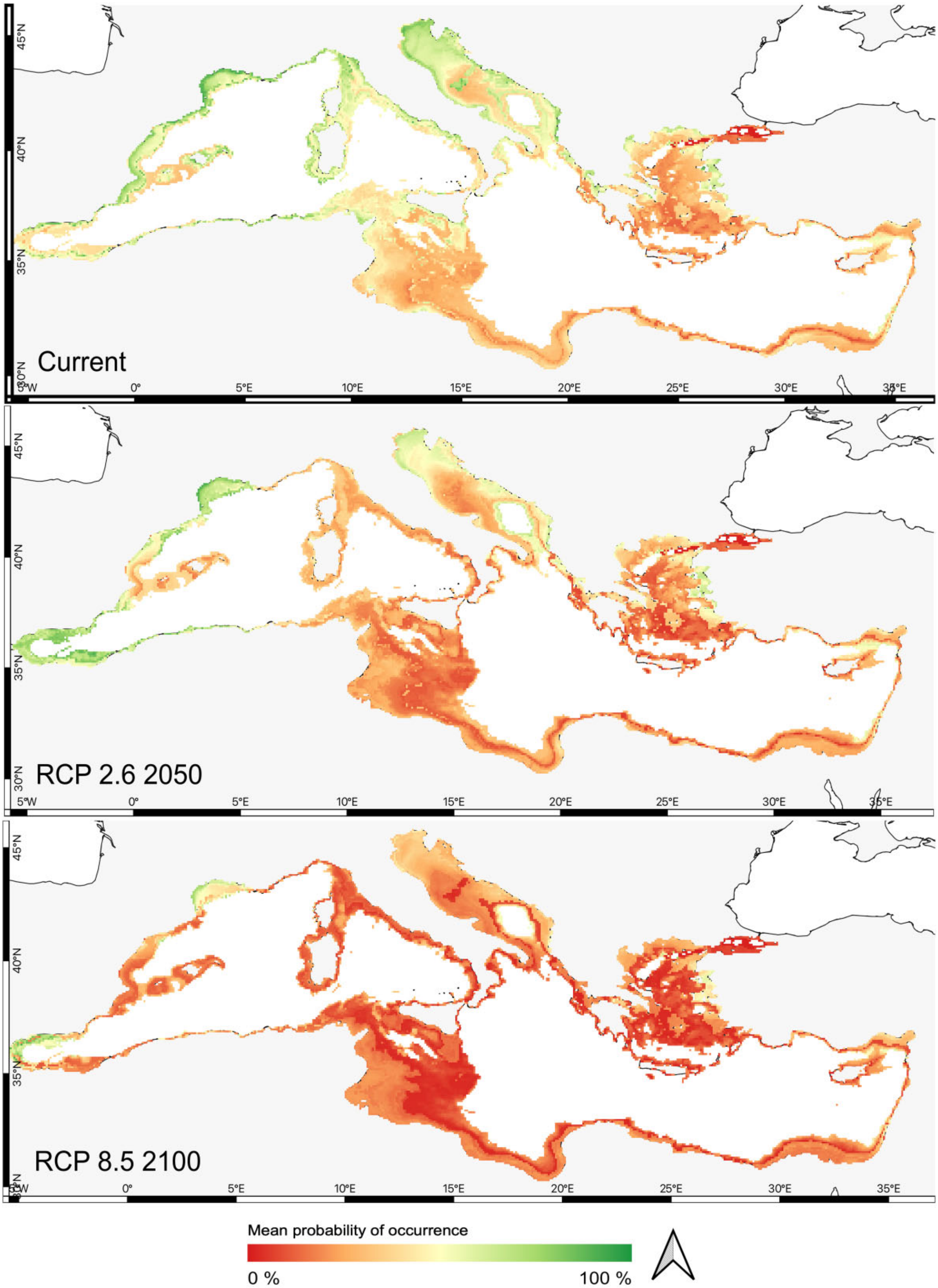


Figure 2. Mean probability of occurrence maps for the modelled species in the Mediterranean basin. Dark green indicates the highest diversity. In the "Current" scenario, the colour gradient provides a proxy of general diversity patterns in the basin, with high species richness in the northwest and low richness in the southeast. In future scenarios, the colour gradient highlights the occurrence of refugia in the northwest Mediterranean, the Adriatic, and the northern Aegean Sea (in the mildest RCP 2.6 for 2050). These regions become restricted to the Alboran Sea and southern France in the highest emissions scenario (RCP 8.5 for 2100).

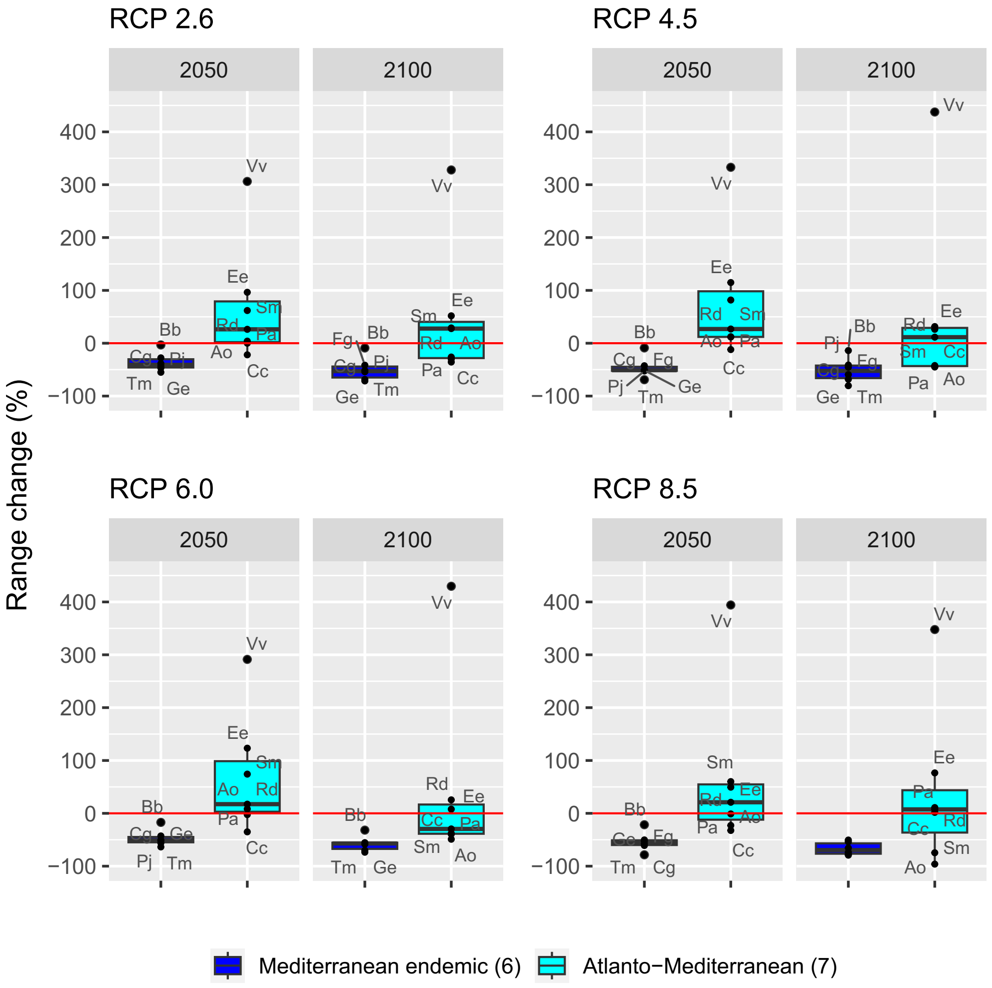


Figure 3. Projected change over the full extent of species ranges. Species labelled as "Mediterranean endemic" include those occurring in the Atlantic Ocean just off Gibraltar (*Bolinus brandaris*), and those labelled as "Atlanto-Mediterranean" mostly have broad distributions over the European Atlantic coasts. Labels are the initials of the species name. The red line indicates no change. The difference in range changes between Atlanto-Mediterranean and endemic species are significant (ESM 1, Supplementary Table S11).

Chamelea for 2050; however, those for the Mediterranean endemic *C. gallina* were twice as large as for the Atlantic *C. striatula*. By the end-century, range loss for *C. gallina* will remain higher than for *C. striatula* under RCPs 2.6 and 4.5 (−54.1% vs. −33.9% and −59.3% vs. −44.7%, respectively); however, range loss for *C. gallina* will be surpassed by *C. striatula* under RCPs 6.0 and 8.5 (−58.4% vs. −61.1% and −65.6% vs. −67.7%, respectively; ESM 1, Supplementary Table S9).

Under all scenarios, range contractions were projected for the Mediterranean endemic scallop *P. jacobaeus*, while range expansions occur for the Atlantic *P. maximus*, except in RCP 6.0 (2100) when range contractions of −20.4% were observed (Figure 4). Range contractions for *P. jacobaeus* remained close to −50% under most scenarios, except the most severe RCP 8.5 (2100), with a loss of −77.4%. In contrast, mid-century projections for *P. maximus* suggested stability under RCP 6.0 (4.2%) to a maximal range expansion under RCP 8.5 (21.9%). By end-century, projected range expansions remained high under the RCP 4.5 (57.2%), moderate under RCP 2.6 (23.3%) and RCP 8.5 (24.9%), but contract under RCP 6.0 (−20.4%; ESM, Supplementary Table S9).

Direction of range shifts

Changes in distributional centroids from present to all future scenarios (ESM 1, Supplementary Figure S1) showed marked differences for Mediterranean endemic and Atlanto-Mediterranean species. Endemic species showed a shift towards the western (cooler) regions of the Mediterranean basin but limited northward movement due to the barrier of the southern European coastline (Figure 5). In contrast, wider-ranging species with Atlanto-Mediterranean distributions generally experience poleward shifts in distributional centroids.

Habitat fragmentation

By 2050, the number of habitat patches by species generally decrease with scenario severity, ranging from a median of −23.3% (RCP 4.5) to −34% (RCP 8.5). The same pattern is more distinct for projections to 2100, whereby the median loss of habitat patches ranges from −31.2% (RCP 2.6) to −64% (RCP 8.5; Figure 6a; ESM 1, Supplementary Table S12). The observed increase in the minimum distance between neighbouring patches further exemplifies fragmentation. By mid-century (2050), the increase in minimum

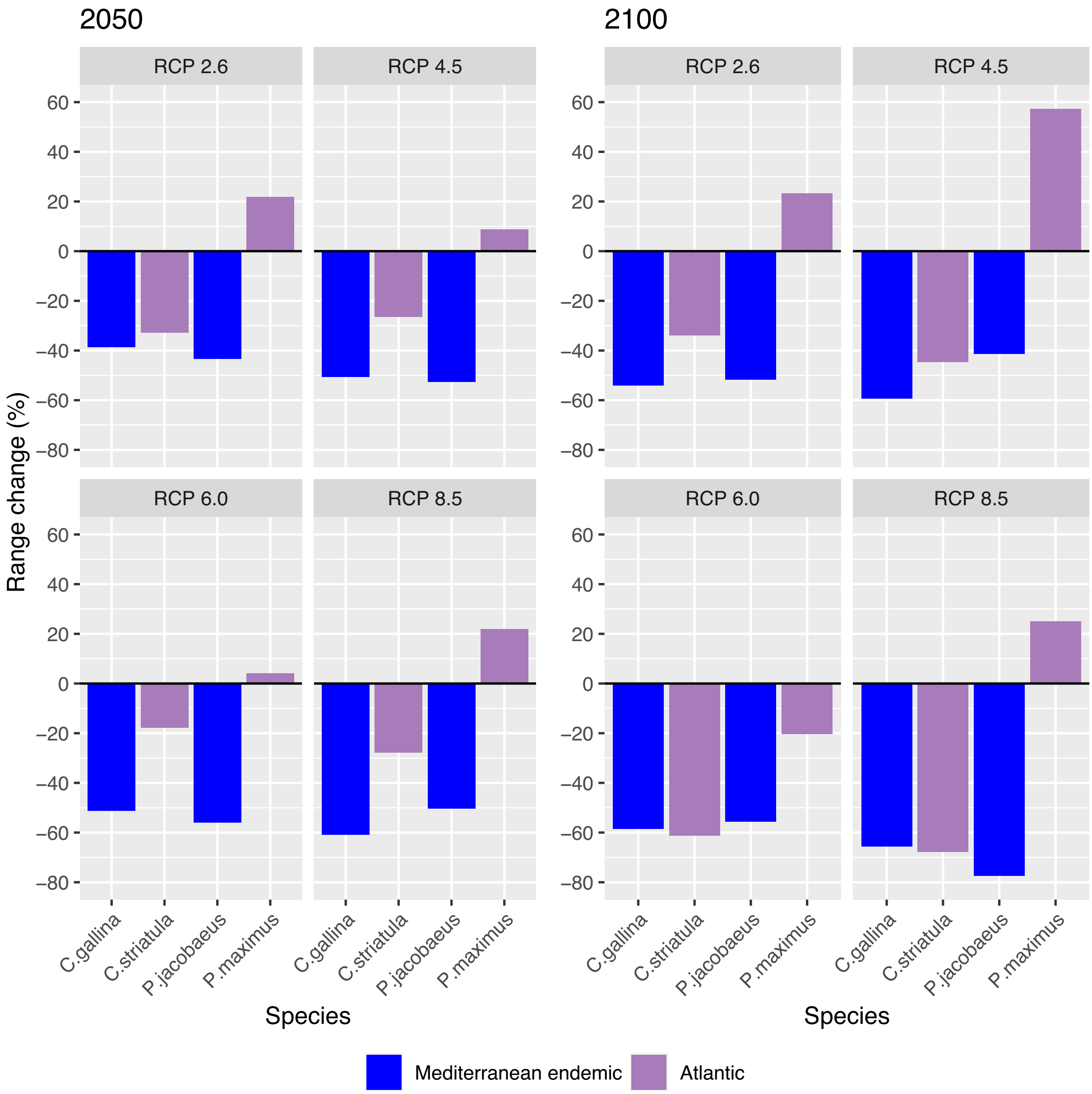


Figure 4. A comparison of projected range changes of Mediterranean endemic and Atlantic representatives of the genera *Chamelea* (clams) and *Pecten* (scallops). Whereas range loss is consistently projected for the Mediterranean endemic species *C. gallina* and *P. jacobaeus*, the Atlantic species either experience reduced range losses (*C. striatula*) or range expansions (*P. maximus*).

edge-to-edge distance ranges from a median of 6.7% (RCP 4.5) to 22.7% (RCP 8.5). Projections to 2100 indicate considerable changes in the minimum distance between patches, with median values ranging from 15.8% (RCP 2.6) to 61.6% (RCP 8.5; Figure 6b; ESM 1, Supplementary Table S13).

Vertical range change in future climate scenarios

Models projected range expansions into waters <50 m for species with broad Atlanto-Mediterranean distributions under all future scenarios (Figure 7). The median of such range expansion was highest for Atlanto-Mediterranean species under RCP 6.0 (2050) at 150.4%; however, for the same scenario, projections to the year 2100 resulted in the lowest median range expansion (16.7%). Under the most severe RCP 8.5, median vertical range expansions remained high for 2050 and 2100 (139.4% and 126.5%, respectively). *Venus verrucosa* and *E. ensis* will benefit from range expansions into deeper waters under all scenarios, ranging from 408.9% (RCP 6.0, 2050) to 646.3% (RCP 6.0, 2100) and 286.6% (RCP 6.0, 2050) to 625.1% (RCP 8.5, 2100), respectively. Models projected range expansion across most scenarios for *S. marginatus*, except under RCP 8.5 (2100), when the species will lose 60% of its range. *Aequipecten opercularis* and *C. chione* were the only two Atlanto-Mediterranean species projected to experience vertical range loss across most scenarios; however, in the most extreme RCP 8.5 (2100), models project opposite responses with an expansion of 45.3% for *C. chione* and a contraction of −94.5%, the most severe vertical range loss of all species, for *A. opercularis* (ESM 1, Supplementary Table S10).

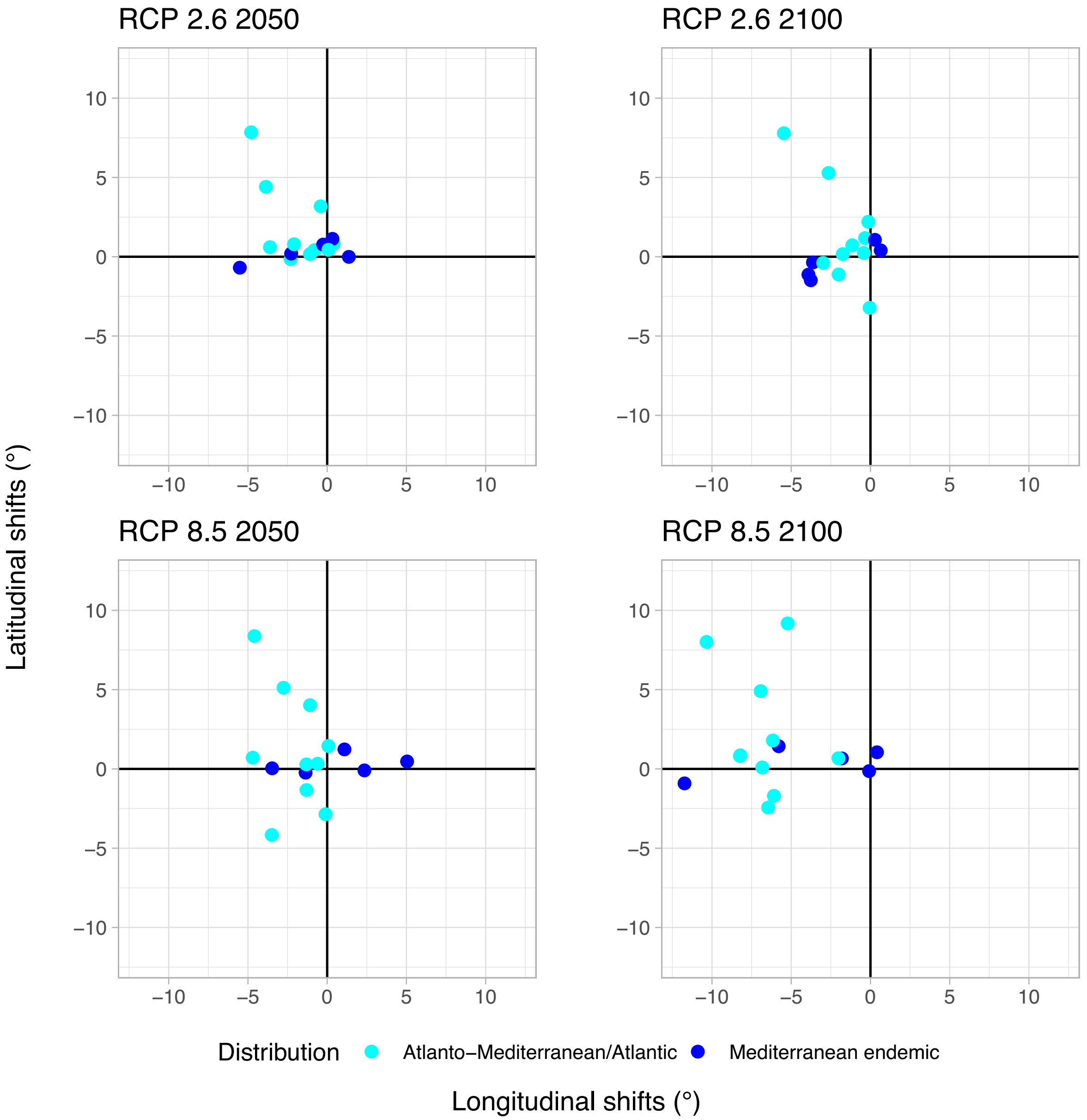


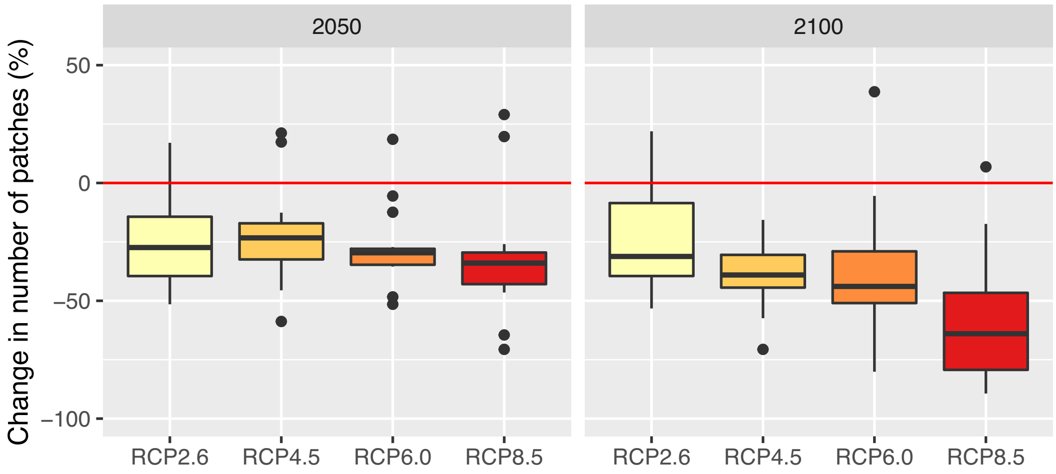
Figure 5. Latitudinal and longitudinal shifts (in degrees) of species distribution centroids under the least and most severe emissions scenarios, RCPs 2.6 and 8.5, for 2050 and 2100. Species with Atlanto-Mediterranean distributions (light blue) show larger poleward shifts than Mediterranean endemic species (dark blue). The latter tend to shift longitudinally due to constrained poleward movement by the northern Mediterranean coast. Thus, the mean latitudinal and longitudinal coordinates for endemic species change from (0.28°, −1.27°) under RCP 2.6, 2050 to (0.42°, −3.80°) under RCP 8.5, 2100, while those for Altanto-Mediterranean species change from (1.85°, −1.85°) under RCP 2.6, 2050 to (2.28°, −6.65°) under RCP 8.5, 2100.

Mediterranean endemic species experienced median vertical range contractions under all future scenarios (Figure 7). Median vertical range change for endemics varied from a minimum loss of −33.9% under the least severe RCP 2.6 (2050) to a maximum of −69.9% (RCP 8.5; 2100). Additional end-century projections remained close to 50% (−52.0%, −47.1%, and −54.5% for RCPs 2.6 to 6.0, respectively). Models project that the deep-dwelling *G. echinophora* will lose the greatest vertical range among the endemic species, ranging from −59.8% (RCP 4.5; 2050) to near-complete extirpation at −91.8% under RCP 8.5 (2100). Conversely, models projected minimal vertical range loss for *B. brandaris* as it remained relatively unchanged under RCPs 2.6 and 4.5 for 2050 (6.2% and 0.8%, respectively), while a maximum loss of −48.6% for RCP 8.5 (2100; ESM 1, Supplementary Table S10).

Discussion

Range shifts and contractions in the Mediterranean sea

Our models predicted major range shifts for all modelled species. The location of range centroids of endemic species primarily shifts longitudinally towards the western sectors of the basin (Figure 5). This is only in apparent contrast to the expectation of poleward shifts for marine ectotherm species (Perry *et al.*, 2005; Parmesan, 2006; Cheung *et al.*, 2009; Poloczanska *et al.*, 2013, 2016) because the Mediterranean


(a) Number of habitat patches

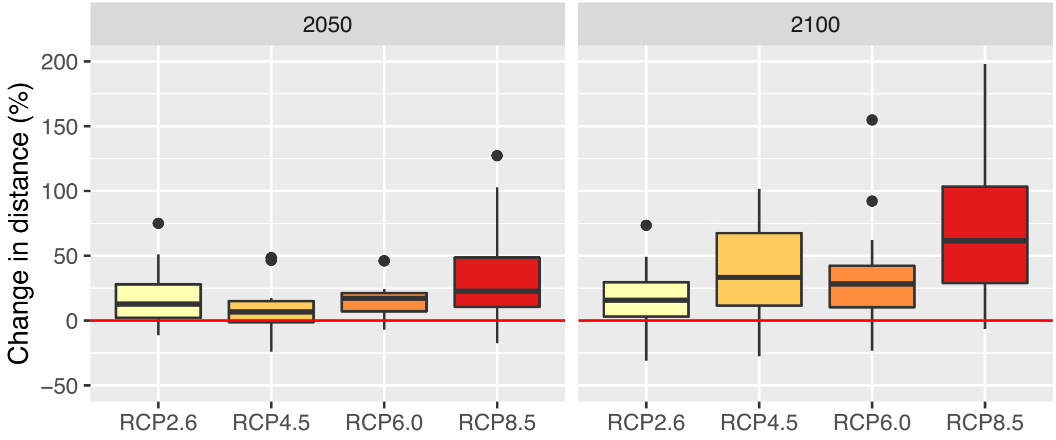

(b) Minimum edge−to−edge distance between patches

Figure 6. (a) The percent change in the total number of habitat patches by species between present and future scenarios for 2050 and 2100. (b) The percent change in the minimum edge-to-edge distance between neighbouring patches when the current scenario is compared to all future scenarios for the years 2050 and 2100. The red line indicates no change. Fragmentation becomes more severe over time and with scenario severity as the number of patches generally decreases, while the distance between neighbouring patches increases.

has a strong temperature gradient, with cooler western and warmer eastern sectors (Bianchi, 2007). Additionally, northern landmasses physically constrain the potential for significant poleward shifts. Most species also occurring in the Atlantic Ocean, thus having no such constraints, show the expected poleward shifts in future scenarios. Few species (e.g. *Callista chione*, *Polititapes aureus*, and *E. ensis*) show southern shifts, but this is due to the colonization of the northwest African coast, a cool area due to strong seasonal upwelling (Klenz *et al.*, 2018) that becomes more suitable in some scenarios.

All modelled species will experience substantial range contractions in the Mediterranean. For the six endemic species, median range loss of at least 65% is projected by end-century, with a median range contraction of 95% in the most severe RCP 8.5. Crucially, the predicted near complete range contractions by end-century for the endemic *Tritia mutabilis* (RCP 8.5), *Flexopecten glaber* (RCP 8.5), *Pecten jacobaeus* (RCP 8.5), and *Chamelea gallina* (RCP 6.0 and 8.5) indicate global extinctions. Additionally, complete extirpation from the Mediterranean was projected for the Atlanto-Mediterranean species *Aequipecten opercularis* (RCPs 4.5, 6.0, and 8.5), *E. ensis* (RCPs 2.6, 6.0, and 8.5), and *Solen marginatus* (RCP 8.5). Contrary to the expected expansion of species into deeper waters in response to warming sea temperatures (Dulvy *et al.*, 2008; Nye *et al.*, 2009; Pinsky *et al.*, 2013; Frade *et al.*, 2018), endemic species will not benefit from this potential refugium. Even *Galeodea echinophora*, a shelf species occurring down to several hundred meters, will experience substantial vertical range contractions. Indeed, vertical range changes will likely be complex and highly dependent on species-specific climatic and depth preferences (Chaikin *et al.*, 2022). These results are also a consequence of the temperate-cold affinity of the modelled species. Despite being selected exclusively based on their interest for fishery industrial exploitation, the Mediterranean is the most southern and warmest part of their current distribution (Fischer *et al.*, 1987).

Models projected suitable range for some endemic species outside the Strait of Gibraltar in the most extreme scenarios suggesting potential refugia outside the Mediterranean. For example, occurrences in northwest Africa and the North Sea are predicted for *F. glaber*, in southern Mauritania for *P. jacobaeus*, and in Mauritania for *C. gallina*. However, such expansions are unlikely due to the same

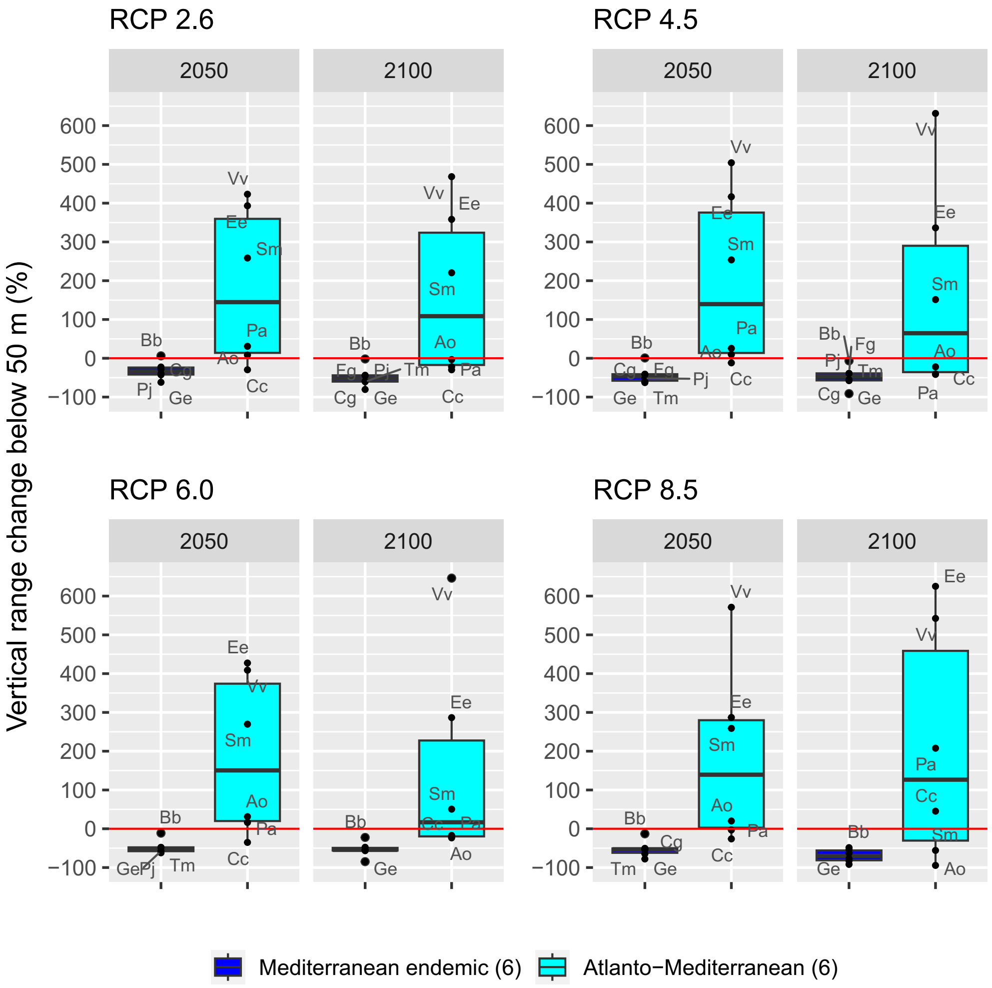


Figure 7. Projected vertical range change into waters deeper than 50 m. Species labelled as "Mediterranean endemic" include those occurring in the Atlantic Ocean just off Gibraltar (*Bolinus brandaris*), and those labelled as "Atlanto-Mediterranean" mostly have broad distributions over the European Atlantic coasts. Labels are the initials of the species name. The red line indicates no change. While Atlanto-Mediterranean species may find refuge in colder, deeper waters through range expansions below 50 m, expansion into deeper waters does not buffer range contractions for endemic species under all scenarios. The difference in range change for Atlanto-Mediterranean and Endemic species is significant for all scenarios ($p < 0.05$; ESM 1, Supplementary Table S11).

barriers that made them endemic. Indeed, for both *P. jacobaeus* and *C. gallina*, genetic discontinuities from their sister species *Pecten maximus* and *Chamelea striatula* were detected at the Almeria Oran Front (Ríos *et al*., 2002) and in the Gibraltar area (Backeljau *et al*., 1994), respectively. These areas represent barriers to gene flow, causing genetic differences among populations (Patarnello *et al*., 2007; Calderón *et al*., 2008; Evangelisti *et al*., 2017). The fossil record may help in testing hypotheses on the reliability of extra-Mediterranean distributions in future climate scenarios by searching for species occurrences in climate analogues of predicted future conditions (e.g. Pleistocene interglacial intervals).

Biotic attrition in the south-eastern Mediterranean

A consequence of the projected poleward retraction of trailing edges will be the impoverishment of the southern and eastern sectors of the Mediterranean Sea (Figure 2). This model result matches predictions for other taxa, such as fish (Ben Rais Lasram *et al*., 2010; Albouy *et al*., 2012) and copepods (Benedetti *et al*., 2019). Moreover, current field observations of regional-scale collapses of native biodiversity and community shift in favour of species of warm affinity on the Israeli shelf, among the warmest parts of the basin (Rilov, 2016; Givan *et al*., 2018; Albano *et al*., 2021), empirically confirm this trend. This part of the basin hosts hundreds of non-indigenous species that entered through the Suez Canal. However, findings suggest that native biodiversity loss was not caused by direct competition for resources or by overexploitation (Givan *et al*., 2018; Steger *et al*., 2021), pointing at climate warming as a primary driver. Such changes are likely already occurring in other south-eastern Mediterranean countries, as predicted by our models, but insufficient monitoring hampers mapping this pattern in detail.

Of course, the quality of available data and the subsequent risk of compounded error in ensemble modelling are important considerations in evaluating model reliability (Manel *et al*., 2001; Segurado and Araújo, 2004). However, ensemble models, in taking the average consensus outcome of many models, offer a powerful approach to increase the robustness of the predicted distribution (Araújo and New, 2007) and reduce the rates of false positives and negatives, thereby improving model-based conservation and policy decisions (Araújo *et al*., 2005; Pearson *et al*., 2006; Grenouillet *et al*., 2011).

Notably, ensemble SDMs may underestimate climate-induced biodiversity changes as they do not account for biotic factors, such as trophic interactions (Moullec *et al*., 2022), or acute and extreme anomalies resulting in mass mortality events (Garrabou *et al*., 2022). Our projected species range contractions, extirpations, and ultimately, extinctions may thus be conservative (Vargas-Yáñez *et al*., 2008; Marbà *et al*., 2015).

Range fragmentation in the Mediterranean Sea

Species ranges in the Mediterranean will experience extensive fragmentation, even in the mildest future scenarios, as expressed by the decreased number but increased distance between suitable habitat patches (Figure 6). The presence of many islands and the Italian and Hellenic peninsulas create disconnect between areas of the north Mediterranean. The retraction of most species to northern refugia, including southern France, the north Adriatic, and the north Aegean, will thus result in heavily fragmented ranges with limited connectivity among suitable range patches. Such "cul-de-sacs" increase extinction risk (Ben Rais Lasram et al., 2010; Albouy *et al*., 2012) and require adaptive marine spatial planning strategies to effectively reduce the consequences of such risk (Rilov *et al*., 2019).

A restricted range is one of the best indicators of extinction risk and is often used to define species of conservation priority (Roberts and Hawkins, 1999). The reduced population size generally associated with small geographic distributions may further limit species dispersal ability and result in low genetic diversity or genetic bottlenecks, further increasing the vulnerability of populations to localized impacts of climate change (Gerber *et al*., 2014). When cul-de-sacs eventually become thermally unsuitable, basin-scale extinctions occur, as shown by our data and predicted for fish (Ben Rais Lasram et al., 2010; Albouy *et al*., 2012).

Range changes in the Atlantic Ocean

In contrast to the results for endemic species, those that also occur in the Atlantic Ocean will show range expansions in several cases due to gaining new ground in northern latitudes. Moreover, models predict range expansions into deeper water for these species. These findings generally align with the expectation that cold-water tolerant species experience more substantial deepening (Chaikin *et al*., 2022), and with observations of North Atlantic invertebrates shifting to deeper waters under the pressure of climate warming (Beukema and Dekker, 2005; Hiddink *et al*., 2015).

In the Atlantic Ocean, where the open continental margins enable responses unconstrained by the morphology of continents, the predicted poleward shifts are consistent with the observed northward shifts of multiple species on European continental coasts over the last few decades (Lima *et al*., 2006; Mieszkowska *et al*., 2006; Lima *et al*., 2007; Mieszkowska *et al*., 2007). However, changes in range size are idiosyncratic: e.g. *P. maximus*, *Ruditapes decussatus*, *Venus verrucosa*, and *E. ensis* consistently increase their range, sometimes multiplying in size (*V. verrucosa* will also take advantage of range expansion in the southern hemisphere), whereas *A. opercularis*, *C. chione*, *C. striatula*, and *P. aureus* contract in most scenarios. These results align well with findings describing the varied responses to climate change within and between taxonomic groups, ocean basins, and regions (Saupe *et al*., 2014; Poloczanska *et al*., 2016). The greater ensemble model uncertainties for these species with broad distributions, including in the Atlantic Ocean, compared to Mediterranean endemics are consistent with similarly wide-ranging taxa and geographic extents (McPherson and Jetz, 2007; Marmion *et al*., 2009), as species with broader ranges have more complex ecological niches that are more difficult to model (Marmion *et al*., 2009).

The consequences of species range changes for fisheries potential

Range shifts of Mediterranean molluscs under climate change may result in varied consequences at the Mediterranean, European, and global scales. For example, a comparison of the sister scallop species, *P. jacobaeus* and *P. maximus*, illustrates the loss of fisheries potential in the Mediterranean through climate-driven range contractions. *Pecten jacobaeus* currently provides income to fishers throughout the North Adriatic (Mattei and Pellizzato, 1996; Koutsoubas *et al*., 2007), a region expected to become unsuitable to this species by end-century (RCP 8.5), with reduced occurrence under milder scenarios. The recorded susceptibility to overfishing (Mattei and Pellizzato, 1996, 1997; Armelloni *et al*., 2021) further exacerbates harvest pressures, with consequences for local economies. In contrast, the high-value Atlantic scallop *P. maximus*, which comprises 67% (2013) of European scallop landings (Cortés *et al*., 2021), will maintain and expand its current range along the Atlantic coasts of Europe (Mattei and Pellizzato, 1996; Duncan *et al*., 2016; Morvezen *et al*., 2016), suggesting the persistence of associated ecosystem services. However, this assumes sustainable management of *P. maximus* fisheries under growing concern over many fully or overexploited populations in Europe (Duncan *et al*., 2016; Cortés *et al*., 2021), a pattern that may intensify with future declines in the fisheries potential of other scallops. End-century range contractions for the clams *Chamelea gallina* and *C. striatula* will impact bivalve fisheries at a European scale, as clams are among the most exploited bivalve species in European waters, contributing 28.9% of annual bivalve fisheries production (0.18 million tonnes; Baeta *et al*., 2021). Concentrated impacts may occur in the Mediterranean and Black Sea where *C. gallina* comprises, on average, over 90% of clam landings annually (2000–2014; FAO, 2016) but will lose 60% of its range (RCP 8.5, 2100).

For Atlanto-Mediterranean species, the impacts of projected range changes are likely to vary by region. For example, models predict the scallop *A. opercularis* to lose 87% of its Mediterranean range under the lowest emissions scenario (RCP 2.6), with end-century global extinction under RCP 8.5 at the scale of this species full extent. Consequences of this species extinction would be concentrated around the Irish Sea, a region that produces 80% of annual European landings (Duncan *et al*., 2016; Outeiro *et al*., 2021). Mediterranean extirpations of the razor clams *S. marginatus* and *E. ensis* by end-century under high emissions scenarios are contrasted by range expansions outside the Mediterranean, with benefits for Scottish (Tuck *et al*., 2000) and Welsh (Fraser *et al*., 2018) fisheries and global benefits to foreign markets where these species are increasingly demanded (da Costa and Martínez-Patiño, 2009; Fraser *et al*., 2018). Similarly, although models predicted range expansions outside the Mediterranean for *V. verrucosa*, with potential benefits for existing fisheries along the European Atlantic coast (Tirado *et al*., 2003), range contractions in the Mediterranean may have consequences for commercial fisheries in the South Adriatic and Aegean Seas (Arneri *et al*., 1998).

The remaining Atlanto-Mediterranean species support clam fisheries in the Mediterranean (Gaspar *et al*., 2001; Metaxatos, 2004; Ezgeta-Balić *et al*., 2011). *Ruditapes decussatus* and *Polititapes aureus* are locally critical resources in Tunisia, where most fishers are women, and clams offer an important low-cost protein source (Derbali and Jarboui, 2021). Our models predict the southern Mediterranean coast, including Tunisia, will become unsuitable for *R. decussatus* under low emissions scenarios, with reduced occurrence of *P. aureus*. As such, our models highlight vulnerable species and regions of the Mediterranean. In the context of each bordering country's vulnerability to climate-induced changes in fisheries production, measured by exposure (physical climate variables influencing fisheries), sensitivity (relative fisheries dependence for food security and national economy), and adaptive capacity (Allison *et al*., 2009), the national economies of Algeria, Morocco, and Turkey are highly vulnerable to climate-driven fisheries impacts (Allison *et al*., 2009). Although the primary focus of this approach is fish catch vulnerability, it is critical to recognize the connection between marine natural resources, as declines in one resource may lead to increased pressure on another or vice versa (Beukema and Dekker, 2005). The vulnerability of these southern Mediterranean countries coincides with high rates of local molluscan extirpation, potentially amplifying socio-economic vulnerabilities (Cheung *et al*., 2010).

Although industrially exploited species were our primary focus, many of these molluscs are also exploited in small-scale and artisanal fisheries, which in the Mediterranean and Black Sea, represent 84% of the total fishing fleet and employ 62% of fishers (Baeta *et al*., 2021), with valuable localized benefits (Garcia *et al*., 2008; Guyader *et al*., 2013; Baeta *et al*., 2021). For example, the predicted extirpation of the locally important endemic gastropods, *B. brandaris* and *T. mutabilis* (Martín *et al*., 1995; Ramón and Amor, 2001; Vasconcelos *et al*., 2008, 2008; Katsanevakis *et al*., 2011; Elhasni *et al*., 2013; Cocci *et al*., 2021) from the southern Mediterranean under low emissions scenarios followed by reduced occurrence in northern regions under high emissions scenarios, raises concerns, especially in the context of recently recorded population declines of *T. mutabilis*, possibly due to overexploitation (Caprioli and Giansante, 2018).

Fisheries policy and marine resource management that aims to minimize the socio-economic and ecological consequences of molluscan species distribution shifts are needed (García Molinos *et al*., 2016), in combination with efforts to reduce greenhouse gas emissions and limit the effects of other anthropogenic impacts (Brander, 2008; Cheung *et al*., 2009).

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest

The authors have no conflicts of interest to declare.

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Author contributions

K.M.G. contributed to data curation, formal analysis, visualization, and writing of the original draft, review, and editing. K.M.G. acquired the Erasmus+Traineeship Grant. P.G.A. conceptualized the study, supervised data curation, formal analysis and visualization, and contributed to writing the original draft, its review, and editing.

Data availability

Occurrences derive from the GBIF. Electronic Supplementary Material 2 contains the occupied cells used as model input.

References

Albano, P. G., Steger, J., Bošnjak, M., Dunne, B., Guifarro, Z., Turapova, E., Hua, Q. *et al.* 2021. Native biodiversity collapse in the Eastern Mediterranean. Proceedings of the Royal Society B: Biological Sciences, 288: 1–9.

Albouy, C., Guilhaumon, F., Araújo, M. B., Mouillot, D., and Leprieur, F. 2012. Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages. Global Change Biology, 18: 2995–3003.

Allison, E. H., Perry, A. L., Badjeck, M-C., Neil Adger, W., Brown, K., Conway, D., Halls, A. S. *et al.* 2009. Vulnerability of national economies to the impacts of climate change on fisheries. Fish and Fisheries, 10: 173–196.

Araújo, M. B., Whittaker, R. J., Ladle, R. J., and Erhard, M. 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography, 14: 529–538.

Araújo, M. B., and New, M. 2007. Ensemble forecasting of species distributions. Trends in Ecology & Evolution, 22: 42–47.

Armelloni, E. N., Scanu, M., Masnadi, F., Coro, G., Angelini, S., and Scarcella, G. 2021. Data poor approach for the assessment of the main target species of rapido trawl fishery in Adriatic Sea. Frontiers in Marine Science, 8: 552076.

Arneri, E., Giannetti, G., and Antolini, B. 1998. Age determination and growth of *Venus verrucosa* L. (Bivalvia: veneridae) in the southern Adriatic and the Aegean Sea. Fisheries Research, 38: 193–198.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., and De Clerck, O. 2018. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography, 27: 277–284.

Backeljau, T., Bouchet, P., Gofas, S., and Bruyn, L. D. 1994. Genetic variation, systematics and distribution of the venerid clam *Chamelea gallina*. Journal of the Marine Biological Association of the United Kingdom, 74: 211–223.

Baeta, M., Solís, M. A., Ballesteros, M., and Defeo, O. 2021. Long-term trends in striped venus clam (*Chamelea gallina*) fisheries in the western Mediterranean Sea: the case of Ebro Delta (NE Spain). Marine Policy, 134: 104798.

Bañón, R., Rolán, E., and García-Tasende, M. 2008. First record of the purple dye murex *Bolinus brandaris* (Gastropoda: muricidae) and a revised list of non native molluscs from Galician waters (Spain, NE Atlantic). Aquatic Invasions, 3: 331–334.

Barbet-Massin, M., Jiguet, F., Albert, C. H., and Thuiller, W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution, 3: 327–338.

Ben Rais Lasram, F., Guilhaumon, F., Albouy, C., Somot, S., Thuiller, W., and Mouillot, D. 2010. The Mediterranean Sea as a "cul-de-sac" for endemic fishes facing climate change. Global Change Biology, 16: 3233–3245.

Benedetti, F., Ayata, S-D., Irisson, J-O., Adloff, F., and Guilhaumon, F. 2019. Climate change may have minor impact on zooplankton functional diversity in the Mediterranean Sea. Diversity and Distributions, 25: 568–581.

Bennett, S., Wernberg, T., Arackal Joy, B., de Bettignies, T., and Campbell, A. H. 2015. Central and rear-edge populations can be equally vulnerable to warming. Nature Communications, 6: 10280.

Beukema, J. J., and Dekker, R. 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Marine Ecology Progress Series, 287: 149–167.

Bianchi, C. N. 2007. Biodiversity issues for the forthcoming tropical Mediterranean Sea. Hydrobiologia, 580: 7–21.

Bivand, R., and Rundel, C. 2021. Rgeos: interface to geometry engine—open source ("geos"). https://CRAN.R-project.org/package=rgeos (last accessed 31 December 2022).

Brander, K. 2008. Tackling the old familiar problems of pollution, habitat alteration and overfishing will help with adapting to climate change. Marine Pollution Bulletin, 56: 1957–1958.

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., Sbeglia, G. C. *et al.* 2013. How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences, 280: 20121890.

Cahill, A. E., Aiello-Lammens, M. E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C. J., Ryu, H. Y., Sbeglia, G. C. *et al.* 2014. Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. Journal of Biogeography, 41: 429–442.

Calderón, I., Giribet, G., and Turon, X. 2008. Two markers and one history: phylogeography of the edible common sea urchin *Paracentrotus lividus* in the Lusitanian region. Marine Biology, 154: 137–151.

Caprioli, R., and Giansante, C. 2018. Preliminary investigation on the use of artificial substrates to favor *Tritia mutabilis* (Linnaeus, 1758) spawning in Central Adriatic Sea: a possible contribution to stock maintenance. Acta Adriatica, 59: 141–148.

Chaikin, S., Dubiner, S., and Belmaker, J. 2022. Cold-water species deepen to escape warm water temperatures. Global Ecology and Biogeography, 31: 75–88.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., and Pauly, D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries, 10: 235–251.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., and Pauly, D. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Global Change Biology, 16: 24–35.

Cocci, P., Troli, E., Angeletti, M., and Palermo, F. A. 2021. Field monitoring of *Tritia mutabilis* (Linnaeus, 1758) egg capsule deposition and intracapsular embryonic patterns using artificial substrates and machine learning-based approaches. Frontiers in Marine Science, 8: 755.

Cohen, J. 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement, 20: 37–46.

Colonese, A. C., Mannino, M. A., Bar-Yosef Mayer, D. E., Fa, D. A., Finlayson, J. C., Lubell, D., and Stiner, M. C. 2011. Marine mollusc exploitation in Mediterranean prehistory: an overview. Quaternary International, 239: 86–103.

Cortés, A., González-García, S., Franco-Uría, A., Moreira, M. T., and Feijoo, G. 2021. Evaluation of the environmental sustainability of the inshore great scallop (*Pecten maximus*) fishery in Galicia. Journal of Industrial Ecology, 26: 1920–1933.

Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z., and Chaudhary, C. 2017. Marine biogeographic realms and species endemicity. Nature Communications, 8: 1–10.

Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J-P., Iglesias, A., Lange, M. A. *et al.* 2018. Climate change and interconnected risks to sustainable development in the Mediterranean. Nature Climate Change, 8: 972–980.

da Costa, F., and Martínez-Patiño, D. 2009. Culture potential of the razor clam *Solen marginatus* (Pennánt, 1777). Aquaculture, 288: 57–64.

Derbali, A., and Jarboui, O. 2021. Stock mapping, size structure and biological parameters of the clam *Polititapes aureus* in the shellfish production area of the southern Tunisian waters (Central Mediterranean). Oceanological and Hydrobiological Studies, 50: 128–136.

Diffenbaugh, N. S., and Giorgi, F. 2012. Climate change hotspots in the CMIP5 global climate model ensemble. Climatic Change, 114: 813–822.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., and Skjoldal, H. R. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology, 45: 1029–1039.

Duncan, P. F., Brand, A. R., Strand, Ø., and Foucher, E. 2016. Chapter 19—The European scallop Fisheries for *Pecten maximus*, *Aequipecten opercularis*, *Chlamys islandica*, and *Mimachlamys varia*. *In* Developments in Aquaculture and Fisheries Science, pp. 781–858. Ed. by S. E. Shumway, and G. J. Parsons, Elsevier, Amsterdam.

Elhasni, K., Vasconcelos, P., Ghorbel, M., and Jarboui, O. 2013. Reproductive cycle of *Bolinus brandaris* (Gastropoda: muricidae) in the Gulf of Gabès (southern Tunisia). Mediterranean Marine Science, 14: 24–35.

Elith, J., Kearney, M., and Phillips, S. 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution, 1: 330–342.

European Environmental Agency. 2014. Horizon 2020 Mediterranean Report. European Environment Agency, Copenhagen.

Evangelisti, F., Bellucci, A., Sabelli, B., and Albano, P. G. 2017. The periwinkle *Echinolittorina punctata* (Mollusca: gastropoda) tracked the warming of the Mediterranean Sea following the last glacial maximum. Marine Biology, 164: 34.

Ezgeta-Balić, D., Peharda, M., Richardson, C. A., Kuzmanić, M., Vrgoč, N., and Isajlović, I. 2011. Age, growth, and population structure of the smooth clam *Callista chione* in the eastern Adriatic Sea. Helgoland Marine Research, 65: 457–465.

FAO. 2016. The state of Mediterranean and Black Sea fisheries 2016. https://www.fao.org/fishery/en/publications/3002 (last accessed 11 March 2022).

FAO. 2020. The state of World Fisheries and Aquaculture: Sustainability in Action. FAO, Rome. 244pp. https://doi.org/10.4060/ca9229en.

Ferreira, J. G., Grant, J., Petersen, J. K., Smaal, A. C., and Strand, Ø. (Eds.). 2019. Goods and Services of Marine Bivalves. Springer International Publishing, Germany. 591pp.

Fielding, A. H., and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24: 38–49.

Fischer, W., Schneider, M., and Bauchot, M. L. 1987. FAO Species Identification Guide for Fisheries Purposes: Mediterranean and Black Sea—Fishing Area 37. Food and Agriculture Organization of the United Nations, Rome. https://www.fao.org/3/x0169f/x0169f00.htm (last accessed 27 April 2022).

Fourcade, Y., Engler, J. O., Rödder, D., and Secondi, J. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS One, 9: e97122.

Frade, P. R., Bongaerts, P., Englebert, N., Rogers, A., Gonzalez-Rivero, M., and Hoegh-Guldberg, O. 2018. Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching. Nature Communications, 9: 3447.

Fraser, S., Shelmerdine, R. L., and Mouat, B. 2018. Razor clam biology, ecology, stock assessment, and exploitation: a review of *Ensis* spp.

in Wales. Welsh Government. https://www.nafc.uhi.ac.uk/research/ (last accessed 11 March 2022).

García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., Pandolfi, J. M. *et al.* 2016. Climate velocity and the future global redistribution of marine biodiversity. Nature Climate Change, 6: 83–88.

Garcia, S. M., Allison, E. H., Andrew, N., Béné, C., Bianchi, G., de Graaf, G., Kalikoski, D. *et al.* 2008. Towards integrated assessment and advice in small-scale fisheries: principles and processes. Report. https://digitalarchive.worldfishcenter.org/handle/20.500.12348/1532 (last accessed 11 March 2022).

Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R., Bensoussan, N. *et al.* 2022. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. Global Change Biology, 28: 5708–5725.

Gaspar, M. B., Dias, M. D., Campos, A., Monteiro, C. C., Santos, M. N., Chicharo, A., and Chicharo, L. 2001. The influence of dredge design on the catch of *Callista chione* (Linnaeus, 1758). In Coastal Shellfish—A Sustainable Resource, pp. 153–167. Ed. by G. Burnell, Springer, Germany.

GBIF.org. 2022. GBIF Home page. https://www.gbif.org/(last accessed 10 May 2022).

Gerber, L. R., Mancha-Cisneros, M. D. M., O'Connor, M. I., and Selig, E. R. 2014. Climate change impacts on connectivity in the ocean: implications for conservation. Ecosphere, 5: 1–18.

Giorgi, F. 2006. Climate change hot-spots. Geophysical Research Letters, 33: L08707.

Givan, O., Edelist, D., Sonin, O., and Belmaker, J. 2018. Thermal affinity as the dominant factor changing Mediterranean fish abundances. Global Change Biology, 24: e80–e89.

Grenouillet, G., Buisson, L., Casajus, N., and Lek, S. 2011. Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography, 34: 9–17.

Guisan, A., Thuiller, W., and Zimmermann, N. E. 2017. Habitat Suitability and Distribution Models: With Applications in R. Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge. 10.1017/9781139028271

Guo, C., Lek, S., Ye, S., Li, W., Liu, J., and Li, Z. 2015. Uncertainty in ensemble modelling of large-scale species distribution: effects from species characteristics and model techniques. Ecological Modelling, 306: 67–75.

Guyader, O., Berthou, P., Koutsikopoulos, C., Alban, F., Demanèche, S., Gaspar, M. B., Eschbaum, R. *et al.* 2013. Small scale fisheries in Europe: a comparative analysis based on a selection of case studies. Fisheries Research, 140: 1–13.

Halstead, K., Alexander, J., Hadley, A., Stephens, J., Yang, Z., and Betts, M. 2019. Using a species-centered approach to predict bird community responses to habitat fragmentation. Landscape Ecology, 34: 1919–1935.

Hampe, A., and Petit, R. J. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters, 8: 461–467.

Hiddink, J. G., Burrows, M. T., and García Molinos, J. 2015. Temperature tracking by North Sea benthic invertebrates in response to climate change. Global Change Biology, 21: 117–129.

Hijmans, R. J. 2021. raster: Geographic Data Analysis and Modeling. R package version 3.4-10. https://CRAN.R-project.org/package=raster (last accessed 31 December 2022).

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

IPCC. 2021. Summary for policymakers. In Climate change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge. 10.1017/9781009157896.001

Katsanevakis, S., Poursanidis, D., Issaris, Y., Panou, A., Petza, D., Vassilopoulou, V., Chaldaiou, I. *et al.* 2011. "Protected" marine shelled molluscs: thriving in Greek seafood restaurants. Mediterranean Marine Science, 12: 429–438.

Khan, B. M., and Liu, Y. 2019. Marine mollusks: food with benefits. Comprehensive Reviews in Food Science and Food Safety, 18: 548–564.

Klenz, T., Dengler, M., and Brandt, P. 2018. Seasonal variability of the Mauritania current and hydrography at 18°N. Journal of Geophysical Research: Oceans, 123: 8122–8137.

Koutsoubas, D., Galinou-Mitsoudi, S., Katsanevakis, S., Leontarakis, P., Metaxatos, A., and Zenetos, A. 2007. Bivalve and gastropod molluscs of commercial interest for human consumption in the Hellenic Seas. *In* State of the Hellenic Fisheries, pp. 70–84. Ed. by E. Papathanassiou, A. Zenetos, V. Vassilopoulou, and G. Tserpes HCMR, Athens.

Lima, F. P., Queiroz, N., Ribeiro, P. A., Hawkins, S. J., and Santos, A. M. 2006. Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. Journal of Biogeography, 33: 812–822.

Lima, F. P., Ribeiro, P. A., Queiroz, N., Hawkins, S. J., and Santos, A. M. 2007. Do distributional shifts of northern and southern species of algae match the warming pattern? Global Change Biology, 13: 2592–2604.

Liu, C., Berry, P. M., Dawson, T. P., and Pearson, R. G. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography, 28: 385–393.

Manel, S., Williams, H. C., and Ormerod, S. J. 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. Journal of Applied Ecology, 38: 921–931.

Marbà, N., Jordà, G., Agustí, S., Girard, C., and Duarte, C. M. 2015. Footprints of climate change on Mediterranean Sea biota. Frontiers in Marine Science, 2. http://journal.frontiersin.org/Article/10.3389/fmars.2015.00056/abstract (last accessed 1 December 2021).

Marmion, M., Luoto, M., Heikkinen, R. K., and Thuiller, W. 2009. The performance of state-of-the-art modelling techniques depends on geographical distribution of species. Ecological Modelling, 220: 3512–3520.

Martín, P., Sánchez, P., and Ramón, M. 1995. Population structure and exploitation of *Bolinus brandaris* (Mollusca: gastropoda) off the Catalan coast (northwestern Mediterranean). Fisheries Research, 23: 319–331.

Mattei, N., and Pellizzato, M. 1996. A population study on three stocks of a commercial Adriatic pectinid (*Pecten jacobaeus*). Fisheries Research, 26: 49–65.

Mattei, N., and Pellizzato, M. 1997. NOAA Technical Report NMFS. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. 600pp.

McPherson, J. M., and Jetz, W. 2007. Effects of species' ecology on the accuracy of distribution models. Ecography, 30: 135–151.

Metaxatos, A. 2004. Population dynamics of the venerid bivalve *Callista chione* (L.) in a coastal area of the eastern Mediterranean. Journal of Sea Research, 52: 293–305.

Mieszkowska, N., Kendall, M. A., Hawkins, S. J., Leaper, R., Williamson, P., Hardman-Mountford, N. J., and Southward, A. J. 2006. Changes in the range of some common rocky shore species in Britain—a response to climate change? *In* Marine Biodiversity: Patterns and Processes, Assessment, Threats, Management and Conservation, pp. 241–251. Ed. by K. Martens, H. Queiroga, M. R. Cunha, A. Cunha, M. H. Moreira, V. Quintino, A. M. Rodrigues, J. Serodio, and R. M. Warwick, Springer, Dordrecht. https://doi.org/10.1007/1-4020-4697-9_20 (last accessed 6 May 2022).

Mieszkowska, N., Hawkins, S. J., Burrows, M. T., and Kendall, M. A. 2007. Long-term changes in the geographic distribution and population structures of *Osilinus lineatus* (Gastropoda: trochidae) in Britain and Ireland. Journal of the Marine Biological Association of the United Kingdom, 87: 537–545.

Moraitis, M. L., Tsikopoulou, I., Geropoulos, A., Dimitriou, P. D., Papageorgiou, N., Giannoulaki, M., Valavanis, V. D. *et al.* 2018. Molluscan indicator species and their potential use in ecological status assessment using species distribution modeling. Marine Environmental Research, 140: 10–17.

Morvezen, R., Charrier, G., Boudry, P., Chauvaud, L., Breton, F., Strand, Ø., and Laroche, J. 2016. Genetic structure of a commercially exploited bivalve, the great scallop *Pecten maximus*, along the European coasts. Conservation Genetics, 17: 57–67.

Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Hattab, T., Peck, M. A., and Shin, Y-J. 2022. Using species distribution models only may underestimate climate change impacts on future marine biodiversity. Ecological Modelling, 464: 109826.

Nye, J. A., Link, J. S., Hare, J. A., and Overholtz, W. J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series, 393: 111–129.

Outeiro, L., Otero, J., Alonso-Fernández, A., Bañón, R., and Palacios-Abrantes, J. 2021. Quantifying abundance trends and environmental effects on a population of queen scallop *Aequipecten opercularis* targeted by artisanal fishers in a coastal upwelling area (Ría de Arousa, NW Spain) using a bayesian spatial model. Fisheries Research, 240: 105963.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics, 37: 637–669.

Patarnello, T., Volckaert, F. A. M. J., and Castilho, R. 2007. Pillars of Hercules: is the Atlantic–Mediterranean transition a phylogeographical break? Molecular Ecology, 16: 4426–4444.

Pearson, R. G., Thuiller, W., Araújo, M. B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L. *et al.* 2006. Model-based uncertainty in species range prediction. Journal of Biogeography, 33: 1704–1711.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. Science, 308: 1912–1915.

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., and Levin, S. A. 2013. Marine taxa track local climate velocities. Science, 341: 1239–1242.

Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L., and Sunday, J. M. 2019. Greater vulnerability to warming of marine versus terrestrial ectotherms. Nature, 569: 108–111.

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K. *et al.* 2013. Global imprint of climate change on marine life. Nature Climate Change, 3: 919–925.

Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V. *et al.* 2016. Responses of marine organisms to climate change across oceans. Frontiers in Marine Science, 3: 62.

Pourmozaffar, S., Jahromi, S., Rameshi, H., Sadeghi, A., Bagheri, T., Behzadi, S., Gozari, M. *et al.* 2019. The role of salinity in physiological responses of bivalves. Reviews in Aquaculture.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. Vienna. https://www.R-project.org/ (last accessed 31 December 2022).

Ramón, M., and Amor, M. J. 2001. Increasing imposex in populations of *Bolinus brandaris* (Gastropoda: muricidae) in the north-western Mediterranean. Marine Environmental Research, 52: 463–475.

Rilov, G. 2016. Multi-species collapses at the warm edge of a warming sea. Scientific Reports, 6: 36897.

Rilov, G., Mazaris, A. D., Stelzenmüller, V., Helmuth, B., Wahl, M., Guy-Haim, T., Mieszkowska, N. *et al.* 2019. Adaptive marine conservation planning in the face of climate change: what can we learn from physiological, ecological and genetic studies? Global Ecology and Conservation, 17: e00566.

Ríos, C., Sanz, S., Saavedra, C., and Peña, J. B. 2002. Allozyme variation in populations of scallops, *Pecten jacobaeus* (L.) and *P. maximus* (L.) (Bivalvia: pectinidae), across the Almeria–Oran front. Journal of Experimental Marine Biology and Ecology, 267: 223–244.

Roberts, C. M., and Hawkins, J. P. 1999. Extinction risk in the sea. Trends in Ecology & Evolution, 14: 241–246.

Rodriguez-Sanchez, F. 2021. rSDM: species distribution and niche modelling in R. https://github.com/Pakillo/rSDM (last accessed 31 December 2022).

Saupe, E. E., Hendricks, J. R., Townsend Peterson, A., and Lieberman, B. S. 2014. Climate change and marine molluscs of the western North Atlantic: future prospects and perils. Journal of Biogeography, 41: 1352–1366.

Segurado, P., and Araújo, M. B. 2004. An evaluation of methods for modelling species distributions. Journal of Biogeography, 31: 1555–1568.

Shaltout, M., and Omstedt, A. 2014. Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. Oceanologia, 56: 411–443.

Steger, J., Bošnjak, M., Belmaker, J., Galil, B. S., Zuschin, M., and Albano, P. G. 2022. Non-indigenous molluscs in the Eastern Mediterranean have distinct traits and cannot replace historic ecosystem functioning. Global Ecology and Biogeography, 31: 89–102.

Sukenik, N., Iluz, D., Amar, Z., Varvak, A., Shamir, O., and Ben-Yosef, E. 2021. Early evidence of royal purple dyed textile from Timna Valley (Israel). PLoS One, 16: e0245897.

Susmann, N. M. 2020. Tyrian, true, royal, or real: archaeological assumptions about the Roman murex dye industry. Journal of Eastern Mediterranean Archaeology and Heritage Studies, 8: 159–173.

Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M. B. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography, 32: 369–373.

Tirado, C., Salas, C., and Márquez, I. 2003. Reproduction of *Venus verrucosa* L., 1758 (Bivalvia: veneridae) in the littoral of Málaga (southern Spain). Fisheries Research, 63: 437–445.

Tuck, I. D., Bailey, N., Harding, M., Sangster, G., Howell, T., Graham, N., and Breen, M. 2000. The impact of water jet dredging for razor clams, *Ensis* spp., in a shallow sandy subtidal environment. Journal of Sea Research, 43: 65–81.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., and De Clerck, O. 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Global Ecology and Biogeography, 21: 272–281.

van der Schatte Olivier, A., Jones, L., Vay, L. L., Christie, M., Wilson, J., and Malham, S. K. 2020. A global review of the ecosystem services provided by bivalve aquaculture. Reviews in Aquaculture, 12: 3–25.

van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C. *et al.* 2011. The representative concentration pathways: an overview. Climatic Change, 109: 5.

VanDerWal, J., Shoo, L. P., Graham, C., and Williams, S. E. 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecological Modelling, 220: 589–594.

Vargas-Yáñez, M., Jesús García, M., Salat, J., García-Martínez, M. C., Pascual, J., and Moya, F. 2008. Warming trends and decadal variability in the Western Mediterranean shelf. Global and Planetary Change, 63: 177–184.

Vasconcelos, P., Carvalho, S., Castro, M., and Gaspar, M. B. 2008. The artisanal fishery for muricid gastropods (banded murex and purple dye murex) in the Ria Formosa lagoon (Algarve coast, southern Portugal). Scientia Marina, 72: 287–298.

Von Cosel, R. 2009. The razor shells of the eastern Atlantic, part 2. Pharidae II: the genus *Ensis Schumacher*, 1817 (Bivalvia, Solenoidea). Basteria, 73: 9–56.

Voultsiadou, E., Koutsoubas, D., and Achparaki, M. 2009. Bivalve mollusc exploitation in Mediterranean coastal communities: an historical approach. Journal of Biological Research, 13: 35–45.

Wiens, J. J., and Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics, 36: 519–539.

Wijsman, J. W. M., Troost, K., Fang, J., and Roncarati, A. 2019. Global production of marine bivalves. Trends and challenges. *In* Goods and Services of Marine Bivalves, pp. 7–26. Ed. by A. C. Smaal, J. G. Ferreira, J. Grant, J. K. Petersen, and Ø. Strand, Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-96776-9_2 (last accessed 13 March 2022).

Wilding, C. S., Beaumont, A. R., and Latchford, J. W. 1999. Are *Pecten maximus* and *Pecten jacobaeus* different species? Journal of the Marine Biological Association of the United Kingdom, 79: 949–952.

WoRMS Editorial Board. 2022. WoRMS—World Register of Marine Species. doi: 10.14284/170 (last accessed 7 May 2022).

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