The Mediterranean Sea as a 'cul-de-sac' for endemic fishes facing climate change

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Abstract

The Mediterranean Sea is a hotspot of biodiversity, and climate warming is expected to have a significant influence on its endemic fish species. However, no previous studies have predicted whether fish species will experience geographic range extensions or contractions as a consequence of warming. Here, we projected the potential future climatic niches of 75 Mediterranean Sea endemic fish species based on a global warming scenario implemented with the Mediterranean model OPAMED8 and a multimodel inference, which included uncertainty. By 2070–2099, the average surface temperature of the Mediterranean Sea was projected to warm by 3.1 °C. Projections for 2041–2060 are that 25 species would qualify for the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List, and six species would become extinct. By 2070–2099, 45 species were expected to qualify for the IUCN Red List whereas 14 were expected to become extinct. By the middle of the 21st century, the coldest areas of the Mediterranean Sea (Adriatic Sea and Gulf of Lion) would act as a refuge for cold-water species, but by the end of the century, those areas were projected to become a 'cul-de-sac' that would drive those species towards extinction. In addition, the range size of endemic species was projected to undergo extensive fragmentation, which is a potentially aggravating factor. Since a majority of endemic fishes are specialists, regarding substratum and diet, we may expect a reduced ability to track projected climatic niches. As a whole, 25% of the Mediterranean Sea continental shelf was predicted to experience a total modification of endemic species assemblages by the end of the 21st century. This expected turnover rate could be mitigated by marine protected areas or accelerated by fishing pressure or competition from exotic fishes. It remains a challenge to predict how these assemblage modifications might affect ecosystem function.

Keywords: BIOMOD, fragmentation, global warming, habitat suitability model (HSM), IUCN, species turnover, species vulnerability

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Introduction

Over the past 100 years, the worldwide climate has warmed by 0.61 °C and, by the end of the 21st century, the Intergovernmental Panel on Climate Change (IPCC) has projected that air temperatures will increase by 1.4–5.8 °C (IPCC, 2007). Recent investigations have shown that, although ambitious mitigation efforts can be implemented to reduce global warming, the inertia in climate and human systems will lead to increasing temperatures worldwide, even above those previously estimated (Van Vuuren et al., 2008).

A large body of evidence has accumulated that demonstrates the multiple impacts of climate warming on biodiversity. The expected responses to global warming include (i) a wide spectrum of taxa seeking cooler environments by shifting geographic distributions towards the poles or higher altitudes (Hickling et al., 2005; Parmesan, 2006; Lenoir et al., 2008), (ii) high global extinction rates (Thomas et al., 2001; Cheung et al., 2009), and (iii) marked reorganizations of local communities that have resulted, in some cases, from native population extinctions and the expansion of exotic thermophilic species (Mills et al., 2004; Olden et al., 2006). Moreover, global warming has a strong effect on the growth, survival, and reproduction rates of many species (e.g., Diaz Almela et al., 2007; Foden et al., 2007);

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this may, in turn, modify the size-based structures of communities (Blanchard *et al.*, 2005). The effects of these changes on the Earth's biota are currently under scrutiny; but 'winner' species that expand their geographical ranges can already be distinguished from 'loser' species that are subject to range contractions (Wilson *et al.*, 2004). Just as for their terrestrial counterparts, marine fish communities are changing markedly in response to climate changes (Attrill & Power, 2002; Genner *et al.*, 2004; Perry *et al.*, 2005; Hiddink & Hofstede, 2008). Indeed, southern fish species have shown increased abundance and a northward expansion of geographical ranges as a result of warming seas in the Northern hemisphere (e.g., Perry *et al.*, 2005; Hiddink & Hofstede, 2008; Cheung *et al.*, 2009).

The impacts of global warming are particularly critical in areas where range shifts are physically constrained, for example, in semienclosed areas (Pozdnyakov *et al.*, 2007) or polar regions (Cheung *et al.*, 2009). The Mediterranean Sea, an inland sea that comprises only 0.32% of the global oceanic volume, contains 4–18% of all known marine species (Bianchi & Morri, 2000), and nearly 10% of fishes are endemic to the Mediterranean Sea (Quignard & Tomasini, 2000). Over the past 30–40 years, water temperatures of the western Mediterranean Sea have been increasing at depth (Bethoux *et al.*, 1990; Rixen *et al.*, 2005) and at the surface (Diaz Almela *et al.*, 2007), and this reflects increased occurrences of thermophilic marine species (Goren & Galil, 2005) and shifts in fish geographic distributions (Sabates *et al.*, 2006; Ben Rais Lasram & Mouillot, 2009).

Fish geographic distributions are strongly clustered in the Mediterranean Sea: subtropical species occur in the south-eastern area, where water temperatures are higher than average (Theocharis *et al.*, 1993), whereas cold-adapted species inhabit northern areas (Bianchi & Morri, 2000). However, as a result of global warming, species that were typically found in the warm waters of the southern areas have been observed more frequently in the north, where waters are becoming warmer (Astraldi *et al.*, 1995; Bianchi & Morri, 2000; Sabatés *et al.*, 2006). In parallel, the abundance of some boreal species has markedly decreased since the 1980s (Quignard & Raibault, 1993).

Changes in thermal conditions have been documented to drive the reorganization of fish assemblages (Rahel & Hubert, 1991; Ben Rais Lasram & Mouillot, 2009). Thus, sea surface warming is expected to drive a general northward shift of fish ranges in the Mediterranean Sea leading to the gradual replacement of cold-temperate species by thermophilic species. Hence, the coldest parts of the Mediterranean Sea (Gulf of Lion and northern Adriatic, Fig. 1) could initially serve as a sanctuary for cold-temperate species; but, with intensified warming, those areas might become a 'cul-de-sac', from which cold-temperate species could not escape. This phenomenon would be critical to endemic species, because the trapping effect would lead to species extinction. The vulnerability of endemic Mediterranean Sea fishes is important because its surface waters are expected to warm by an average of 3.1 °C by the end of the 21st century (Somot *et al.*, 2006). Consequently, an assessment of future distributions of climatic niches for Mediterranean Sea endemic fishes is urgently needed to anticipate the potential biological response to the projected climate warming.

In addition to species geographic range shifts, climatic warming may also induce the fragmentation of suitable habitats. This issue has been largely neglected in studies that previously explored spatial responses to climate change. Indeed, there is a potential synergism
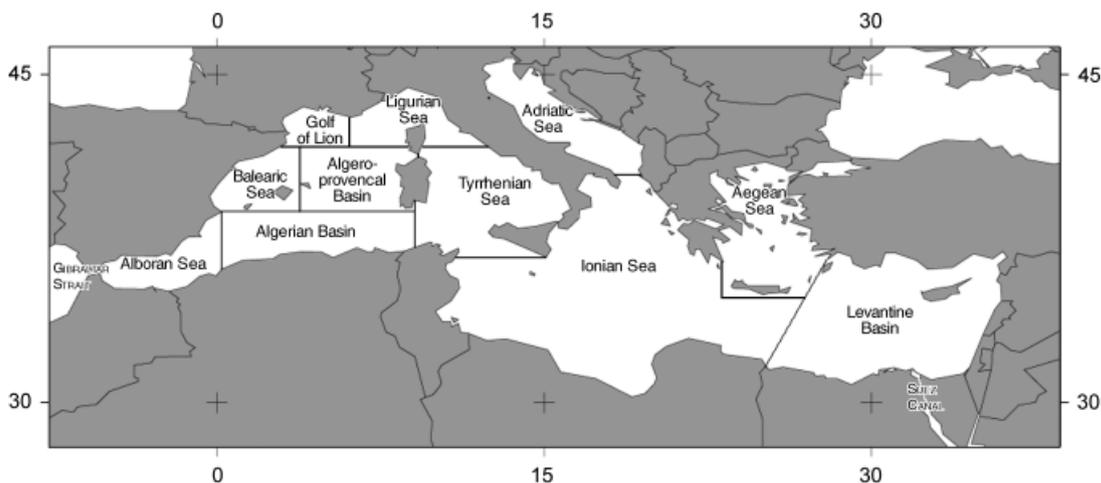

Fig. 1 Main geographical features of the Mediterranean Sea. The axes indicate degrees latitude (*x*-axis) and longitude (*y*-axis).

between climatic constraints and habitat fragmentation that may accelerate population decline and extinction rates (Opdam & Wascher, 2004). At the very least, habitat fragmentation can cause a loss of genetic diversity (Gibbs, 2001), and an increased population's vulnerability to extreme events and disturbances (Piessens *et al.*, 2009). The northern coast of the Mediterranean Sea is the more sinuous; the semiisolated basins (e.g., Adriatic Sea) and islands (Fig. 1) may promote increasing fragmentation of the geographic distributions of species as they move northward to seek cooler temperatures. Thus, to understand the total potential risk that climate change poses to Mediterranean Sea endemic fishes, consideration also must be given to the spatial fragmentation of thermally suitable habitats.

The degree of specialization is thought also to contribute strongly to extinction risk following climate change because specialist species require particular resources or habitats in addition to suitable thermal conditions in order to survive (e.g., Biesmeijer *et al.*, 2006). Here, we refer to the Grinnellian specialization, defined as the breadth of biotic and abiotic resources required for a species to survive (e.g., DeVictor *et al.*, 2010). Mediterranean Sea endemic fishes are more or less specialized in these resource requirements. This information must be considered for a precise interpretation of the predicted geographic range shift in response to the projected climate warming. Indeed, the most specialized fishes will face constraints in addition to simply seeking suitable thermal conditions; these fish may be considered at greater risk of population decline and extinction compared with the generalist species that are able to exploit a wide range of resources.

Here, we assessed the potential impacts of climate change on the spatial distribution of Mediterranean Sea endemic fish species. More precisely, we investigated the vulnerability of species to climatic niche reductions that might result from sea temperature changes predicted to occur by 2041–2060 and 2070–2099. Because the temperature of air and water are roughly correlated (Caissie, 2006), most forecasts of aquatic species range shifts consider air temperature to be a proxy of water temperature (e.g., Buisson *et al.*, 2008). This might be acceptable for inland water bodies, like rivers or lakes, but it is not appropriate for the marine habitat, where many forcing factors interact within a climate change context. For that reason, we calculated future sea surface temperatures (SST) using a Mediterranean Sea thermohaline circulation model that accounted for relevant forcing parameters, including river runoff, exchanges with connected water masses, and wind regimes (Somot *et al.*, 2006). These climatic data were combined with habitat suitability models (HSM) to obtain consensus forecasts of potential future climatic

niches (Araujo & New, 2007). For each species, we quantified the potential changes in geographic range and thermal habitat fragmentation. The potential effect of global change on Mediterranean Sea endemic fishes was summarized by assessing their potential endangerment according to their eligibility for Red Listing by the International Union for the Conservation of Nature and Natural Resources (IUCN). Finally, at the assemblage level, we mapped the expected temporal turnover in endemic species composition across the Mediterranean Sea and calculated a threat indicator based on the population status before and after climate warming.

Materials and methods

Species data

A database was generated for the geographic distributions of the 79 known endemic fish species in the Mediterranean Sea ('wide' and 'narrow' endemism, according to Quignard & Tomasini, 2000) using a Geographical Information System software package (ARCVIEW 3.3 by ESRI). Data were compiled from the atlas of Fishes of the Northern Atlantic and Mediterranean (FNAM; Whitehead *et al.*, 1986). That atlas is based on regional data sets and expert knowledge; it provides the only available basin-wide information on the geographic ranges of all Mediterranean Sea fish species (Ben Rais Lasram *et al.*, 2009). Four species were deleted from the dataset for the following reasons: *Tetrapturus belone*, because its presence throughout the Mediterranean Sea made discrimination between presence and absence impossible; *Gobius strictus*, *Microichthys sanzoi*, and *Nansenia iberica* because their extremely low prevalence might introduce bias in geographic range predictions (Stockwell & Peterson, 2002; Thuiller, 2004).

Over 93% of Mediterranean Sea endemic fish species are strictly confined to coastal waters; i.e., they do not live beyond the limits of the continental shelf. Thus, we restricted the dataset to the continental shelf (200 m depth limit). Our final dataset described the extent of occurrences for 75 endemic species on a 0.1° resolution grid covering the whole Mediterranean Sea continental shelf.

We collected ecological information for these 75 fish species to evaluate their degree of specialization in terms of habitat and feeding resources. First, we distinguished pelagic fish, with no substratum requirements, from benthic and demersal species, which require particular substrata (rocky shores, seagrasses). The former species were classified as habitat generalists (HG) while the latter were classified as habitat specialists (HS). Second, we classified fish species according to their feeding guild. Carnivorous fishes were considered to be diet specialists (DS) because they feed on particular prey while omnivorous and planktivorous fishes were considered diet generalists because they feed on a large range of resources. This information was obtained from FishBase (Froese & Pauly, 2009) and from the FNAM atlas (Whitehead *et al.*, 1986).

Temperature data

In terrestrial ecosystems, numerous environmental variables (temperature, rainfall, soil structure, and geochemistry, etc.) are required to make satisfactory predictions of species occurrences (e.g., Beaumont *et al.*, 2007). In contrast, marine ecosystems are constrained by fewer limiting factors. The main driver of fish geographic ranges was demonstrated to be water temperature (Sabates *et al.*, 2006; Dulvy *et al.*, 2008; Hiddink & Hofstede, 2008; Cheung *et al.*, 2009). In addition, the gradients and thresholds of SST have been shown to shape fish distributions in the Mediterranean Sea (e.g., Ben Rais Lasram & Mouillot, 2009). Thus, SST was used as the sole predictor of fish distribution patterns in this study.

The FNAM atlas used to digitize the spatial distributions of species was edited between 1984 and 1986. Therefore, we used the SST values averaged from an early period as a baseline to calibrate the species distribution models: weekly SST values on a 1° grid were taken for the period 1981–1984 from the National Climatic Data Center (NCDC) National Operational Model Archive and Distribution System of Meteorological Data Server (NOMADS) of the US National Oceanic and Atmospheric Administration (NOAA) Satellite and Information Service (www.osdpd.noaa.gov/PSB/EPS/SST/al_climo_mon.html). 0.1° resolution needed for analysis were interpolated by means of ordinary kriging (Diggle & Ribeiro, 2007). Fourteen variables were obtained – 12 monthly SST means, the absolute minimum SST, and the absolute maximum SST. All these variables were considered because some studies have reported the influence of winter, but not summer, conditions on fish composition assemblages (Henriques *et al.*, 2007), whereas others have emphasized the importance of surface temperature during particular life stages to predict fish spatial boundaries. For example, Sabates *et al.* (2006) demonstrated that the abundance of round sardinella (*Sardinella aurita*), in some parts of the Mediterranean Sea, was significantly correlated with the SST of the previous year recorded at the start of gonad maturation (April). However, species distribution models with too many predictive (and covarying) variables may overfit the data and show reduced predictive ability. To mitigate this problem, we reduced the set of predictive variables on the basis of a correlation analysis (Pearson's coefficient).

Future SST values were obtained for the middle (2041–2060) and the end of the 21st century (2070–2099) from the Mediterranean model OPAMED8, based on the IPCC A2 scenario (Somot *et al.*, 2006). OPAMED is a regional model (the Atlantic Ocean is considered only as a buffer zone) that accounts for the main drivers of SST, including air–water energy fluxes, river discharges, and water exchanges with the surrounding seas. Although widely used for regional scenarios of climate change (Christensen *et al.*, 2002), the A2 scenario is considered a conservative, but not the worst, future prediction of global warming. It assumes a very heterogeneous world that preserves local identities, and which results from a continuously growing human population and atmospheric CO_2 concentrations of ~815 ppm by 2099 (IPCC, 2007). The A2 scenario was chosen for OPAMED because it has become the standard for regional climate studies (Christensen *et al.*, 2002). Future climate data were averaged for the middle (2041–2060) and

the end of the 21st century (2070–2099). Maps were interpolated at 0.1° resolution using ordinary kriging.

Model calibration and evaluation

Equilibrium is a required assumption for predicting and projecting species distribution areas (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Indeed, to be reliable, models must capture the fully realized niche in order to avoid spurious results due to truncated responses (Thuiller *et al.*, 2004). Because our analysis was restricted to endemic species at a basin-wide scale, we assumed that the equilibrium condition was not violated.

Since there is still uncertainty in the modeling of climatic habitats that determine species geographic distributions, we implemented an ensemble forecasting method (Thuiller, 2004; Araujo & New, 2007; Buisson *et al.*, 2009; Marmion *et al.*, 2009). The 75 fish species distributions were modeled using seven of the techniques available in the BIOMOD package for ensemble forecasting of species distributions (Thuiller *et al.*, 2009). These HSM were implemented in R (R Development Core Team, 2008): (1) Generalized Linear Models (GLM), (2) Generalized Additive Models (GAM), (3) Classification Tree Analysis (CTA), (4) Random Forest (RF), (5) Boosted Regression Trees (BRT), (6) Mixture Discriminant Analysis (MDA), (7) Surface Range Envelope (SRE).

We implemented a cross validation procedure to avoid circular reasoning when the same data were used to construct and evaluate the model (e.g., Kohavi, 1995). For each species, models were calibrated using a random sample of the initial data (80%). Then, each model was evaluated on the remaining 20% of the initial data set for each species with the True Skill Statistic (TSS) criterion. Because AUC (Swets, 1988) and Kappa (Cohen, 1960) methods have been severely criticized (Termansen *et al.*, 2006; Austin, 2007; Peterson *et al.*, 2007; Lobo *et al.*, 2008), we based our evaluation on TSS, as recommended by Allouche *et al.* (2006) and used in some recent studies (e.g., Allouche *et al.*, 2008; Boitani *et al.*, 2008; Freeman & Moisen, 2008; La Morgia *et al.*, 2008). TSS scores were interpreted with the same classification as was used for Kappa, according to the Landis & Koch (1977) accuracy classification scheme: TSS > 0.8, excellent; 0.6 > TSS < 0.8, good; 0.4 > TSS < 0.6, fair; 0.2 > TSS < 0.4, poor; and TSS < 0.2, no predictive ability.

The predicted presence/absence of a species was derived from the predicted probability of occurrence using the threshold that maximized model accuracy; i.e., that maximized the percentage of presence and absence that could be correctly predicted (Thuiller, 2003).

Model projections

Alternative HSMs may provide markedly different projections for the same dataset, and model evaluations often cannot demonstrate which projection is superior (Araujo & New, 2007). To overcome these limitations, we used the Weighted Average Consensus (WAC) method (Marmion *et al.*, 2009; Thuiller *et al.*, 2009) that takes into account model-based uncertainty. Using the projected temperatures for 2041–2060

and 2070–2099, we projected the potential thermal habitat for each species according to each of the seven HSMs. We assumed no dispersal limitation towards new areas with suitable temperature conditions because recent invasions showed that Lessepsian fishes reach a mean dispersal rate of $221 \pm 5.4 \, \text{km yr}^{-1}$ on the northern side of the Mediterranean Sea, given favorable climatic conditions, regardless of their biological traits (Ben Rais Lasram *et al.*, 2008). Then, for each grid cell, we calculated a probability of occurrence (*W*) according to the weight of each model, based on TSS values

$$W_i^{\text{TSS}} = \frac{\sum_j (\text{TSS}_j \times m_{ji})}{\sum_j \text{TSS}_j}, \qquad (1)$$

where *i* is a given grid cell, *j* is a given model, and m_{ji} is the projected probability of occurrence in cell *i* according to model *j*. The future weighted probabilities of occurrence were then transformed into presence/absence values according to the same threshold values as were used for the current predictions (Thuiller *et al.*, 2009).

Species vulnerability

First, patterns of fragmentation in current and projected spatial distributions were measured for the 75 species. Fragmentation was calculated using the Fragstats Spatial Pattern Analysis Program for Quantifying Landscape Structure, Version 3.1 (McGarigal *et al.*, 2002). The term 'fragmentation' was reserved for the breaking apart of a habitat, independent of habitat loss; thus, we measured fragmentation in terms of the number of patches (NP). A myriad of fragmentation metrics are available, but most are highly redundant and would lead to similar results (McGarigal & Marks, 1995).

Second, the shift in a species' geographic range was calculated by subtracting the projected suitable habitat from the currently used habitat. Then, the species' vulnerability was assessed by identifying its IUCN Red List category (version 3.1 criterion A3c IUCN, 2001, following Bomhard *et al.*, 2005; Thuiller *et al.*, 2005), which depended on the projected reductions of suitable habitat:

- Extinct (Ex): a projected reduction of 100%
- Critically endangered (CE): a projected reduction between 80% and 100%
- Endangered (En): a projected reduction between 50% and 80%
- Vulnerable (V): a projected reduction between 30% and 50%
- No concern (NC): below 30% or expansion

Third, a composite threat indicator at the level of the entire endemic fish assemblage was calculated to determine whether a trend in global biodiversity threat could be expected following a given climate change. This indicator, introduced by Dulvy *et al.* (2006), is based on fish population status according to the IUCN list decline criteria. In summary, the indicator is a weighted average of species threat scores at the assemblage level. Species threat scores (according to Butchart *et al.*, 2004) include: 0 (no concern), 1 (vulnerable), 2 (endangered), or 3 (critically endangered). This indicator was estimated for the present range sizes and IUCN classifications, and for their projected status both in 2041–2060 and 2070–2099.

Species turnover

Beyond the conservation of individual species, scientists are increasingly concerned with the conservation of ecological assemblages and ecosystems. Assemblage degradation comprises at least three components: change in species composition, change in structure, and disruption of the ecological processes (Franklin *et al.*, 2002). However, current methods for assemblage level projections require scrutiny, and they have not proven to improve the accuracy of predictions for species range shifts due to climate changes (Baselga & Araujo, 2009). Hence, we quantified the level of endemic assemblage degradation by evaluating the expected turnover in each cell

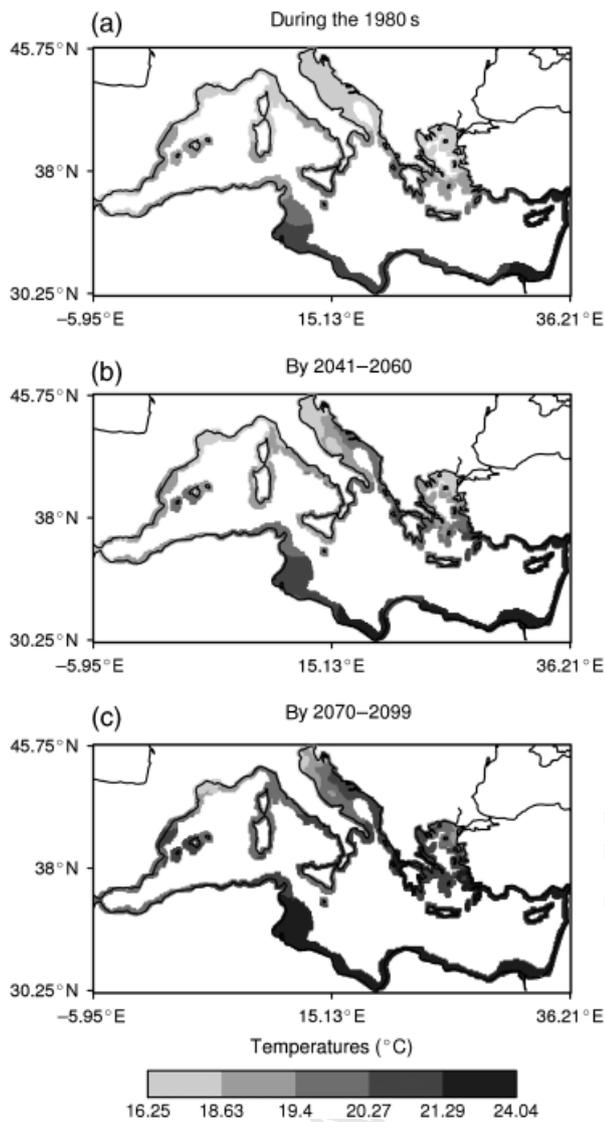$$\text{TO} = (P + G)/(\text{SR} + G)100, \qquad (2)$$

where TO is the turnover percentage, *P* is the number of species lost by a cell, *G* is the number of species gained per cell, and SR is the current species richness per cell (Peterson *et al.*, 2002; Thuiller *et al.*, 2006).

Results

Present and future climates

The map of the mean SSTs in the early 1980s (Fig. 2a) revealed that the warmest area of the Mediterranean Sea was the Levantine Basin, with a mean SST of 21.8 °C; the coolest areas were the Gulf of Lion and the Ligurian Sea, with a mean SST of 16.9 °C. By 2041–2060, the majority of the Mediterranean Sea is expected to become warmer, but the northern Adriatic is expected to become cooler; this is according to the OPAMED8 model, based on the A2 IPCC scenario (Fig. 2b). By 2070–2099, the Mediterranean Sea is projected to warm up by 3.1 °C (Fig. 2c); the last cool enclaves are expected to be the Gulf of Lion and the northern Adriatic, with a mean SST of around 18 °C.

Among the 14 SST values studied (one for each month, the maximum, and the minimum), there were very high correlations among the following groups: December, January, February, and March (all $r > 0.980$); July, August, and the absolute maximum (all $r > 0.980$); and September, October, and November (all $r > 0.989$). Accordingly, the number of predictor SST variables could be reduced to seven: April, May, June, the absolute minimum, the absolute maximum, the winter mean, and the autumn mean.

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Fig. 2 Sea surface temperature (SST) changes predicted on the continental shelf of the Mediterranean Sea. (a) SST during the 1980s [according to NOAA data; (www.osdpd.noaa.gov/PSB/EPS/SST/al_climo_mon.html)]; (b) SST predicted for 2041–2060 and (c) SST predicted for 2070–2099 (according to the OPAMED8 habitat suitability model, based on the A2 IPCC scenario). The axes indicate degrees latitude (*x*-axis) and longitude (*y*-axis).

Model prediction accuracies

The climatic niches of the 75 fish species were based on the fish distributions and SSTs collected in the early 1980s. These were modeled according to seven classical techniques. The predictive accuracy over all seven HSMs was classified as 'excellent', with a mean TSS criterion of 0.89. The least accurate model was the SRE, with a TSS = 0.56 whereas the most accurate model was the RF, with a TSS = 0.98. The TSS was insensitive to

prevalence since model accuracy was excellent even for species of low prevalence and fragmented habitats. However, no evidence of model superiority emerged; thus, we used the WAC method to project potential climatic niches.

Projected species vulnerability

According to the WAC method, by 2041–2060, 31 species (41%) were projected to gain geographic range (winners) whereas 44 species (59%) were projected to lose geographic range (losers) (Fig. 3a). Among the 44 loser species, 36 were expected to experience increased spatial fragmentation whereas six were projected to become extinct (Fig. 3a). The 31 winner species were predicted to experience higher fragmentation with more patches occupied (Fig. 3a). When species were classified into different specialization categories, the species classified as both habitat (pelagic) and diet (omnivorous or planktivorous) generalists were projected to become either more fragmented or extinct by 2041–2061 (Fig. 3b); those considered HG and DS were predicted to gain range size, but with more fragmentation (Fig. 3c); and those considered HS were projected to become either more fragmented or extinct (Fig. 3d and e).

By the end of the 21st century, only 25 species (33%) were projected to gain geographic range, and the remaining 50 endemic species (66%) were projected to lose geographic range (Fig. 3a). Among the 50 loser species, 23 were expected to become more fragmented and 14 were projected to become fully extinct (Fig. 3a). Among the 25 winner species, 23 were predicted to experience a more fragmented geographic distribution (Fig. 3a). As for the predictions for the middle of the century (2041–2060), by 2070–2099 all generalist species were predicted to become either more fragmented or extinct (Fig. 3b); those species considered to be HG and DS (Fig. 3c) were projected to gain range size compared with their present distributions. Only one benthic carnivorous species, *Solea aegyptiaca*, was predicted with a thermal suitable habitat spread almost all over the Mediterranean Sea continental shelf (Fig. 4a). Among the 14 species projected to become extinct (Fig 3a), 12 are HS. Of note, among the 49 species considered specialists in both HS and DS, only 14 were predicted to gain range size, and 13 of those would experience more fragmentation of suitable climate niches (Fig. 3e). For example, in the 1980s, the Scaldback (*Arnoglossus kessleri*) was continuously distributed throughout all Mediterranean Sea basins except the Alboran Sea; by the end of the 21st century, however, that species was expected to lose 90% of its potential suitable climatic habitat and its range would be restricted to the Gulf of
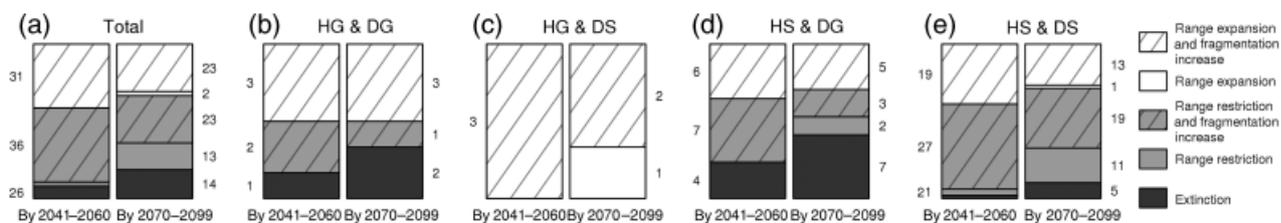
Fig. 3 Predicted changes in range size and habitat fragmentation of endemic fish species due to global warming at the middle (2050) and end (2100) of the 21st century. (a) Changes predicted for the entire assemblage of Mediterranean Sea fish species, and (b–e) for species categories: (b) Generalists in both habitat and diet (HG & DG); (c) generalists in habitat, but specialists in diet (HG & DS); (d) specialists in habitat, but generalists in diet (HS & DG); and (e) specialists in both habitat and diet (HS & DS). HG, habitat generalists (pelagic species); HS, habitat specialists (benthic and demersal species); DG, diet generalists (omnivorous and planktivorous species); DS, diet specialists (carnivorous species). The numbers on the y-axes indicate the numerators of the fraction of the given population that was predicted to undergo the indicated change.
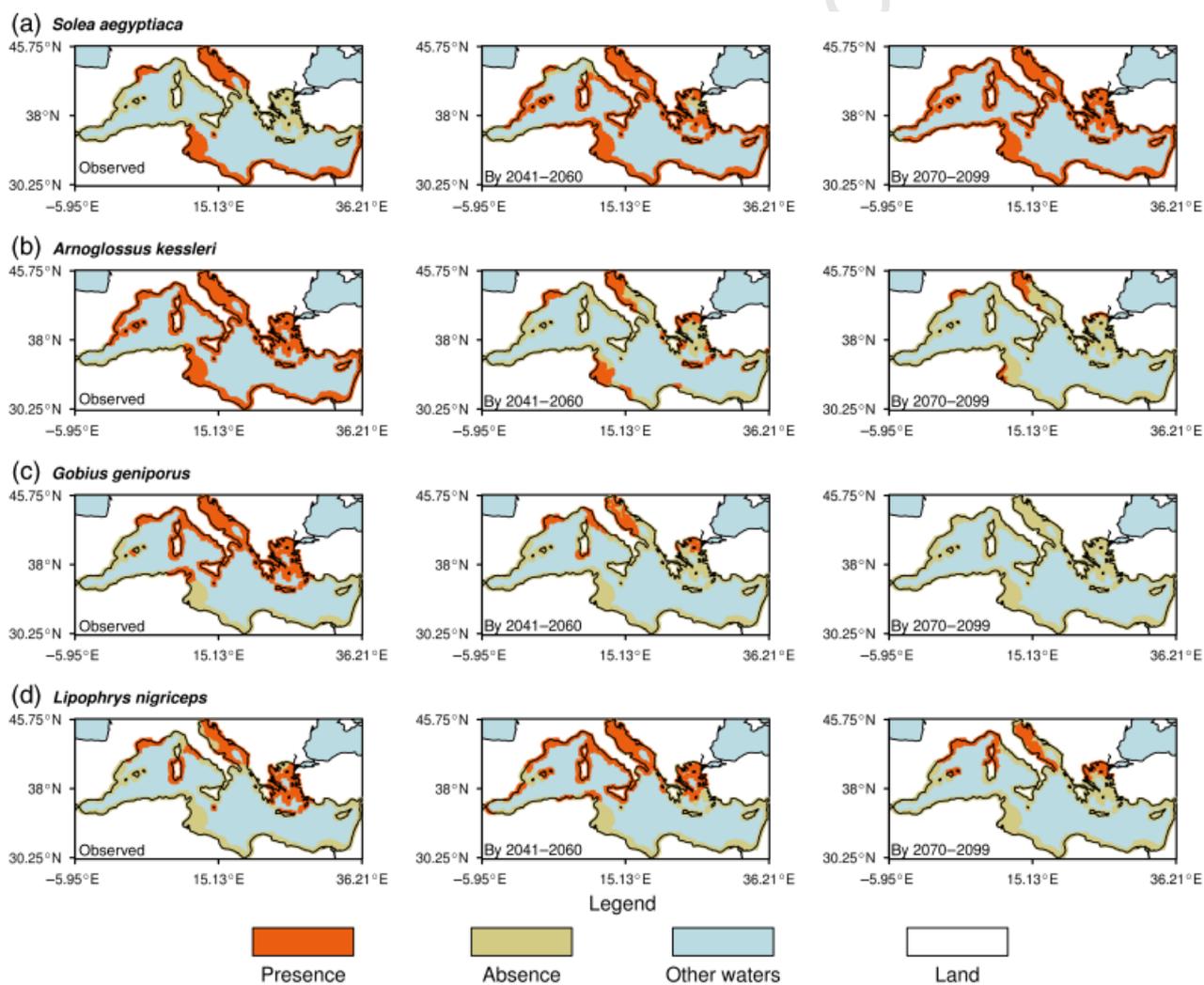
Fig. 4 Observed (1980s) and predicted (by 2040–2060; by 2070–2099) distribution areas of endemic Mediterranean Sea fish species, and potential future thermal habitats projected with a model-averaging approach. The axes indicate degrees of latitude (x-axis) and longitude (y-axis).

Lion, the northern Adriatic, and the northern Aegean (Fig. 4b). For the Slender goby (*Gobius geniporus*) a range reduction of 80% by the middle of the century is predicted, and for this species to be restricted to the Gulf of Lion, south Sardinia, the northern Adriatic, and the northern Aegean. Extinction by the end of the century is predicted for this species (Fig. 4c).

Other patterns were less obvious. Indeed, some species expected to be winners at the middle of the century might lose the gained suitable climate niche 50 years later. For instance, *Lipophrys nigriceps* was expected to extend its potential suitable climatic space by 73% at the middle of the century, but then, would lose it at the end of the century (Fig. 4d).

Changes in IUCN status and threat indicator

According to the WAC method, by 2041–2060, 31 endemic fish species were expected to qualify for the IUCN Red List; currently, only five species are on the list, according to geographic range sizes observed in the 1980s (Table 1). By 2070–2099, 45 species were projected to qualify for the IUCN Red List, and 42 species (56% of the total) would qualify as at least endangered.

The threat indicator increased for the whole assemblage, but also for each specialization category, except species considered HG and DS (Fig. 5). The 1980 values of the threat indicator were close to zero because most species were not on the IUCN Red List. This indicator was predicted to reach a maximum of 2.18 by 2070–2099 for the subset of endemic fish considered HS and diet generalists. For the whole assemblage, the threat indicator showed a 10-fold increase over the period of global warming.

Projected species turnover

By the middle of the 21st century, the Levantine Basin and the southern side of the eastern basin were

Table 1 Number of endemic fish species that qualify for each IUCN status according to current geographic range sizes (current) and projected range sizes, following climate changes by the middle of the 21st century (2041–2060) and by the end of the 21st century (2070–2099)

IUCN status	Current	2041–2060	2070–2099
Extinct (Ex)	0	6	14
Critically endangered (CE)	1	7	12
Endangered (En)	3	11	16
Vulnerable (V)	1	7	3
No concern (NC)	70	44	30

IUCN, International Union for the Conservation of Nature and Natural Resources.

expected to experience a turnover rate of 100% in species composition (Fig. 6a). That is, all endemic species in those areas would disappear (by extinction or migration) and would be replaced by different colonizing endemic species. By the end of the 21st century, 25% of the Mediterranean Sea continental shelf was predicted to experience a total modification of endemic species assemblages. At that point, global warming would be so marked that none of the endemic fish assemblages of the Mediterranean Sea would be identical to those of the 1980s (Fig. 6b).

Discussion

Taken together, our results showed that the endemic fish assemblage of the Mediterranean Sea would be under increasing threat during the 21st century, because, with sea surface water warming, species that tracked suitable climatic habitats were expected to move into constrained areas that could support only reduced populations. This predicted loss of biodiversity in a hotspot of endemism has strong conservation implications. Indeed, Tortonese (1985) and Quignard & Tomasini (2000) distinguished two kinds of endemism: 'narrow' endemism, which included taxa found strictly in the Mediterranean Sea and 'wide' endemism, which included taxa that reached the neighboring Atlantic Ocean and Black Sea. Clearly, the threat of
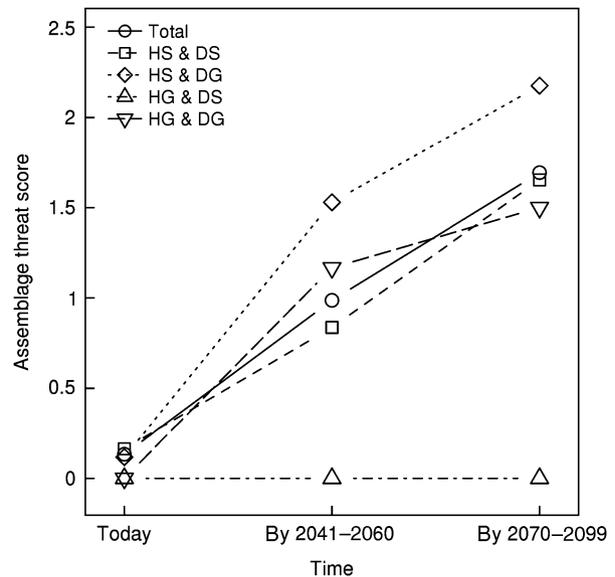
Fig. 5 Changes in IUCN endangerment qualification status based on threat indicator scores for the Mediterranean Sea endemic fish assemblage and for categories of species specialization from 1980 through the 21st century. HG, habitat generalists (pelagic species); HS, habitat specialists (benthic and demersal species); DG, diet generalists (omnivorous and planktivorous species); DS, diet specialists (carnivorous species).
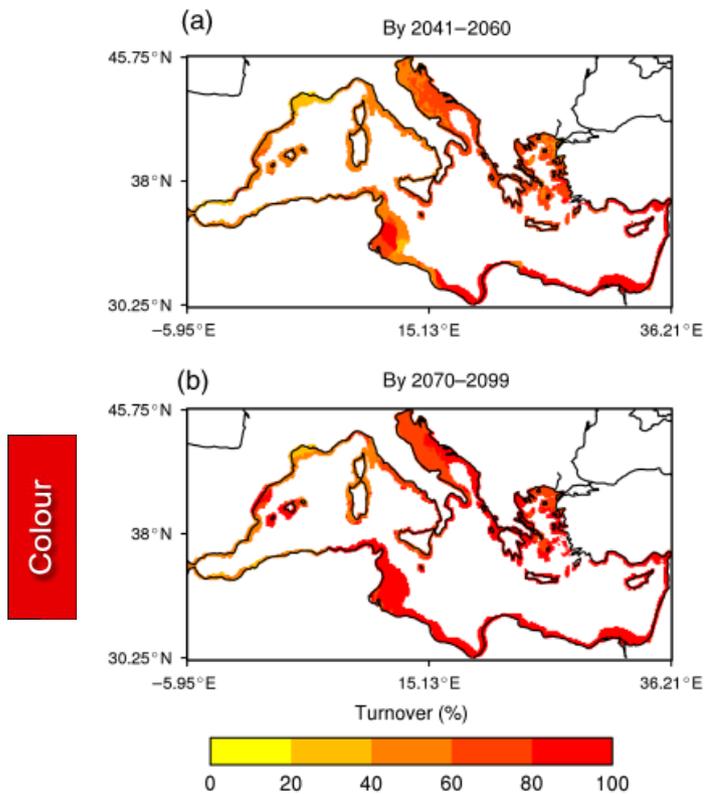
Fig. 6 Predicted percent turnover in endemic fish species of the Mediterranean Sea due to projected sea surface temperature. The percent of species replacement (turnover) predicted to occur by (a) 2040–2060 and (b) 2070–2099. The axes indicate degrees of latitude (*x*-axis) and longitude (*y*-axis). The color range legend indicates the percent of turnover of the assemblage of Mediterranean Sea fish species.

extinction is more critical for narrow than for wide endemic species. Indeed, in the event of extinction in the Mediterranean Sea, wide endemic species may continue to survive elsewhere; in contrast, narrow endemic species would face irreversible extinction. At the end of the 21st century, *Acipenser stellatus* and *Huso huso* are projected to be extinct in the Mediterranean Sea, but they could continue to survive in the Black Sea, where they are currently abundant (Froese & Pauly, 2009). Similarly, *Gobius fallax*, *Gymnammodytes cicerelus*, and *Lipophrys adriaticus* all are projected to be extinct in the Mediterranean Sea, though they may continue to survive around the Canary Islands, from coastal Morocco to Angola, and in the Black Sea; thus, they might avoid global extinction. Conversely, the extinction of *Acipenser naccarii*, *Buenia affinis*, *Corcyrogobius liechtensteini*, *Didogobius schlieweni*, *Gobius geniporus*, *Microichthys coccoi*, *Opeatogenys gracilis*, *Paralepis speciosa*, and *Speleogobius trigloides* in the Mediterranean Sea would represent irreversible extinction, because these species are strictly endemic.

We distinguished four scenarios for species predicted to lose part of their geographic range size and hence, qualify for the IUCN Red Listing: (i) a high probability of immediate extinction (e.g., *Corcyrogobius liechtensteini*), (ii) a high probability of extinction by the end of the 21st century, after severe climatic niche reduction (e.g., *Gymnammodytes cicerelus*), (iii) severe habitat fragmentation (e.g., *Arnoglossus kessleri*) (Fig. 4b), and (iv) migration to the coldest areas, associated with habitat reduction (e.g., *Cyclothone pygmaea*). In contrast, among the species projected to gain range, thermophilic species, such as *Solea aegyptiaca*, are predicted to experience the widest extensions, with up to 80% increases (Fig. 4a). Thus, by the middle of the 21st century, the coldest areas of the Mediterranean Sea (Adriatic Sea and Gulf of Lion) might serve as a sanctuary for cold-water species, but by the end of the century, they are likely to become 'cul-de-sacs', which would drive those species to extinction. This scenario is similar to that described as the upward altitudinal response of terrestrial organisms to global warming; initially, mountains might serve as refuges, but later, they are likely to become potential traps (e.g., Parmesan & Yohe, 2003; Chen *et al.*, 2009). Considering all the Mediterranean Sea fish species of this study, over 19% (14 species) were predicted to completely lose their ranges by 2070–2099, independently of habitat and diet considerations. This is a high extinction rate compared with, for example, the <5% extinction expected for the endemic Namibian flora following similar climate change (Thuiller *et al.*, 2006).

For many species, range size contraction may occur faster than predicted by models, because HSMs are likely to be too conservative (Lawler *et al.*, 2009). For example, HSMs do not take into consideration the fact that warming can intensify the influence of other forcing factors, such as competition from exotic species. Indeed, flourishing thermophilic exotic species can directly compete with endemic species and thus accelerate their extinction (Olden *et al.*, 2006). This competitive pressure from exotic species is likely to occur in the Mediterranean Sea, where an increasing spatial overlap between exotic and endemic ichthyofauna has been observed previously (Ben Rais Lasram & Mouillot, 2009). Endemic Mediterranean Sea species are thus likely to undergo both biotic and abiotic stress as a consequence of warming. Moreover, warming often is related to other changes; for example, acidification might affect the survival of many fish species by impacting the survival of invertebrate prey (Dupont *et al.*, 2008), the quality of fish growth, and the ability of fish to reproduce (Ishimatsu *et al.*, 2008). However, there is no consensus on these impacts, and the biological consequences remain challenging to predict (Bernhard *et al.*, 2009).

Our models are likely also to be conservative in predicting the outcomes for species that were expected to track their climatic niche without other limitations and to colonize new areas in the Mediterranean Sea. Indeed, the main weakness of HSMs resides in the fact that they do not consider several biotic aspects (Heikkinen *et al.*, 2006). For example, in this study, we made the assumption that all species were able to migrate towards any suitable temperature condition; this may be an over-optimistic assumption. Migration is particularly important for low prevalence species, because they generally exhibit a lack of dispersion ability (Gaston, 1994); thus, they are unlikely to fill the entire potential niche projected by HSMs. Moreover, a species might become extinct because its migration rate is too slow to track the optimum temperature. Dispersion is very difficult to model, especially at the leading edge of a species range shift (Midgley *et al.*, 2006; Thuiller *et al.*, 2008). However, adequate dispersion is less difficult for marine fish than for other organisms, such as butterflies, which are also affected by global warming (Parmesan *et al.*, 1999). Indeed, butterflies are unable to cross physical barriers such as open seas or mountains to seek suitable habitats (Menendez *et al.*, 2006). Conversely, marine fishes are less restricted and can undertake long migrations without obstacles, due to the continental shelf providing a more or less continuous habitat (Hiddink & Hofstede, 2008). For example, Lessepsian fishes (exotic species from the Red Sea invading the Mediterranean Sea) successfully dispersed in the Mediterranean Sea at a mean annual rate of $221 \pm 5.4 \, \text{km yr}^{-1}$ (Ben Rais Lasram *et al.*, 2008) which, at the temporal scale of our study, is fast enough to track potential changes in climatic habitats along the coast. Moreover, fish propagules (eggs and larvae) have the possibility to disperse with marine currents regardless of the depth and cross the barrier of the continental shelf (Gaston, 2003; Shanks *et al.*, 2003).

A species may also be limited by its degree of specialization in its ability to track a climatic niche. Indeed, the majority (49 out of 75 species) of endemic fishes are here considered specialists both in substratum (benthic and demersal species) and dietary (carnivorous) requirements whereas only six species were considered generalists for these two attributes (Fig. 3). Specialization may add constraints that accelerate range size decline and extinction; for example, in present terrestrial assemblages, specialist species are severely threatened (Biesmeijer *et al.*, 2006; DeVictor *et al.*, 2010). Although the Mediterranean Sea coast has highly patchy substrata (e.g., Garcia-Charton *et al.*, 2004), at the scale of observation used in this study ($0.1° \times 0.1°$), it was unlikely that a primary substratum (rock, seagrass, or sand-mud) would be absent in any cell or not within

fish swimming distance. It was more likely that climate change and subsequent range shifts would induce a spatial mismatch between carnivorous fish species and their prey (Durant *et al.*, 2007); however, this is not possible to predict, because geographic distributions of small prey and trophic links are only partially known.

An issue that has been largely overlooked in studies that explored spatial responses to climate change is the potentially synergistic effect of climatic constraint and habitat fragmentation. Indeed, habitat fragmentation, through a loss of connectivity between local populations, is known to reduce genetic diversity (Gibbs, 2001) and lower resistance to extreme events and disturbances (Piessens *et al.*, 2009). Thus, thermal habitat fragmentation, which may lead to species range fragmentation, is an aggravating factor for species survival. Connectivity among local populations plays a key role in species persistence: recolonization by individuals from neighboring areas is enhanced by a continuous distribution area, but may be difficult between fragmented areas (e.g., Fagan *et al.*, 2005). In this study (Fig. 3), both loser and winner species were predicted to undergo increased fragmentation of their suitable climatic habitats, due to global warming and the sinuosity of the northern Mediterranean Sea coast (e.g., *Arnoglossus kessleri*, Fig. 4b; *Lipophrys nigriceps*, Fig. 4d). Hence, climate change and habitat fragmentation could be expected to have negative synergistic effects on species survival (Opdam & Wascher, 2004); however, this was not taken into account in the present study.

Other factors may accelerate species decline and loss of biodiversity. For example, human activities, like pollution and overfishing, can aggravate an already declining population. Because overfishing remains a common practice in the Mediterranean Sea (FAO, 2006), the extinction rates revealed by this study are likely to be underestimates. Indeed, Hsieh *et al.* (2008) demonstrated that exploited fish populations are more vulnerable to climate variability than unexploited fish populations. Accordingly, marine protected areas, in addition to their benefit to coastal ecosystems (Garia-Charton *et al.*, 2008), may also mitigate the effect of climate warming in the Mediterranean Sea. Finally, the combination of biotic interactions, abiotic constraints, and human pressures or protection can markedly impact the vulnerability of fish species to climate change; thus, more investigations are merited in this area, particularly in potential antagonistic or synergistic relationships. Unfortunately, the modeling of these relationships is still in its infancy and requires advancement to be able to provide a broader understanding of biodiversity threats in marine ecosystems.

Despite the potentially confounding effects of many biotic and abiotic factors and their interactions, our

HSMs performed projections based only on temperature conditions, which were taken as proxies for all niche components (Lawler *et al.*, 2009). This simplification is acceptable only for species with ranges and shifts that are strongly determined by climatic constraints. This is certainly the case for many species at a coarse spatial scale, because environmental filters are assumed to overcome competitive interactions (Angermeier & Winston, 1998). In the case of fish species that invade the Mediterranean Sea, Ben Rais Lasram *et al.* (2008) have previously shown that the directions and rates of fish dispersal are primarily driven by thermal conditions. Sabates *et al.* (2006) also correlated the distribution of round sardinella to April temperatures, during the initiation of gonad maturation. The assumption was thus made that the thermal niche was the main driver of fish species distributions in the Mediterranean Sea. To reinforce this assumption, we showed that HSMs based only on SST could very accurately predict the geographic distribution of the current niches of Mediterranean Sea endemic species. Counter-intuitively, these models were accurate even for species of low prevalence and fragmented habitats; this result could be explained by the marked spatial heterogeneity of SST in the Mediterranean Sea (Ben Rais Lasram *et al.*, 2009).

There is accumulating evidence that many species expand or shift their distribution areas pole-ward rather than adapt to warmer temperatures (Hickling *et al.*, 2005; Perry *et al.*, 2005; Parmesan, 2006). Other terrestrial species undertake altitudinal migrations to reach suitable conditions (Parmesan & Yohe, 2003). Similarly, some marine species seek deeper water in response to climate warming. This hypothesis has been confirmed by Dulvy *et al.* (2008), who presented evidence for North Sea fish migrations to deeper water in response to climate change (3.6 m decade^{-1}). This issue was considered less critical in the present study because (i) deeper waters are limited in availability, and the focus is on the continental shelf, (ii) many species are unable to survive in deeper water (Dulvy *et al.*, 2008), and (iii) endemic species would have colonized other deeper habitats at equilibrium. Hence, although we cannot reject the issue of seeking deeper water in response to global change for Mediterranean Sea endemic fish, we are confident that northward migrations along the coast are more plausible, because adaptation to deeper water is usually detrimental to growth and survival rates (Sogard & Olla, 1996; Lloret *et al.*, 2005). In a similar vein, a number of researchers have argued for substantive roles of evolution to mitigate the influence of global warming and adaptation to buffer geographic range shifts (e.g., Rowan, 2004). However, both fossil records and contemporary data show little evidence for the evolution of novel phenotypes; instead they support

shifts in geographical distributions after climate changes (Parmesan, 2006). Under that assumption, our study predicted that 14 endemic fish species would become extinct (19% of the total endemic assemblage), and over half of the endemic species would shift in their qualifications for IUCN status by the end of the 21st century. In addition, the average turnover rates in endemic fish assemblages could exceed 64% by 2041–2060 and 79% by 2070–2099. These rates are exceptionally high; they surpass the typical predicted turnover rates of terrestrial species (e.g., Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Broennimann *et al.*, 2006) and other aquatic species (e.g., Buisson *et al.*, 2008). This implies that endemic assemblages would be markedly modified; in turn, these modifications could have consequences on ecosystem functioning. Indeed, we know that fish communities strongly shape trophic cascades in the Mediterranean Sea (Guidetti, 2006). Our results support the notion that the ecosystem-level impact of the predicted changes in species composition is indisputable and requires further investigation.

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