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## ***Fistularia commersonii* in the Mediterranean Sea:**

### **Invasion history and distribution modeling based on presence-only records**

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## **Abstract**

The bluespotted cornetfish (*Fistularia commersonii*) (Osteichthyes, Fistulariidae) is considered to be one of the most invasive species of the Mediterranean Sea and Europe but only scattered information exists on its distribution and abundance. Here we collated the available species records, following its first detection in the Mediterranean Sea, in January 2000, until October 2011. A total of 191 observations were used to reconstruct the invasion sequence, to provide estimates of the rate of spread and to construct an environmental suitability model based on six biophysical variables and the maximum entropy approach (MaxEnt). The results showed that colonization of the Mediterranean Sea proceeded in parallel along the southern and northern rim of the Basin at speeds that reached 1000-1500 km · yr<sup>-1</sup> with a clear decrease in the rate of spread at the Sicily Strait. The most important explanatory variables for describing the distribution of *F. commersonii* were mean depth (explaining 32.4% of the data variance), chlorophyll-a (29.3%), and salinity (18.4%). Coastal areas with relatively low chlorophyll-a concentrations and high salinity were the preferred habitat of the bluespotted cornetfish in its invaded range. Conversely, extreme productivity (highly eutrophic or highly oligotrophic), low salinity and cold temperatures provided abiotic resistance to this invasion. Areas of high environmental suitability were identified along the northern coasts of the Levantine Sea, Dodecanese, Sicily Strait and Tyrrhenian Sea. In contrast, the north Aegean Sea, the Adriatic and the Alboran Sea, the Nile Delta, the western coasts of Egypt and Cyrenaica were unfavourable for the invasion. Despite some limits due to the model's resolution scale, these general predictions provide new insights into the *F. commersonii* invasion, indicating abiotic factors of primary importance in shaping the distribution of this species in its invaded range.

**Keywords:** Bluespotted cornetfish, Lessepsian migration, GIS, maximum entropy model, rate of spread, presence-only data

## Introduction

The bluespotted cornetfish, *Fistularia commersonii* Rüppell, 1838, originally distributed in the Indian and Pacific Oceans (Fritzsche 1976; Froese and Pauly 2011), is today one of the most successful invaders of the Mediterranean Sea (Streftaris and Zenetos 2006) and European waters (DAISIE 2008). Twelve years ago, in January 2000, this species was recorded for the first time along the Mediterranean coasts of Israel, entering from the Red Sea via the Suez Canal (Golani 2000). Since then, it has spread rapidly all over the Mediterranean, across the eastern (Bilecenoglu et al. 2002; Corsini et al. 2002; Karachle et al. 2004), central (Azzurro et al. 2004; Ben Souissi et al. 2004) and western sectors of the Basin (Garibaldi and Orsi-Relini 2008; Kara and Oudjane 2008). In 2007 it reached the Alboran Sea (Sanchez-Tocino et al. 2007), which is the farthest a Lessepsian fish migrant has ever been recorded from its entry point (CIESM 2009).

Genetic studies demonstrated that this successful invasion was the result of a single introduction episode that produced a severe bottleneck in the Mediterranean population (Golani et al. 2007). However, there is little further information on the biology and ecology of the bluespotted cornetfish and the available data are mainly limited to its predatory feeding behaviour (Corsini et al. 2002; Takeuchi et al. 2002; Nakamura et al. 2003; Kalogirou et al. 2007; Bariche et al. 2009; Takeuchi 2009) and reproduction (Bariche et al. 2012). Nevertheless, the conspicuous size of this species and its peculiar elongated shape make this fish clearly recognizable when captured or observed. Consequently, there is a good set of occurrence records of *F. commersonii* scattered in the scientific literature, together with other reliable point observations in unpublished sources. This therefore provides an ideal system in which to reconstruct the chronology of the invasion and to investigate distribution-related aspects in the newly colonized environment.

In recent years, species distribution models (SDMs) have been widely used to predict ecologically suitable areas for invasive species to become established under current and future climate projections (Nori et al. 2011). Due to the nature of the observations made of invasive species, only the presence of individuals is reported in the literature, while absences are usually not reported and are certainly difficult to verify. When sightings have such an incidental character, they are known as *presence-only records* (Elith and Leathwick 2007). Records in presence-only form are widespread, such as those derived from ad-hoc compilations, made during scientific expeditions or those reported by atlases, museums, collections and any other kind of occasional or non-systematic observations. In recent years, due to the increasing need for managing, mapping and predicting biodiversity, this kind of data has been increasingly used, providing new possibilities to map and model the spatial distribution of biological invaders (Gormley et al. 2011). However, presence-only records may be subject to major spatial and detection biases (Stockwell and Peterson 2001; Gu and Swihart 2004; Araújo and Guisan 2006) and they cannot be used directly to estimate occupancy and introduction rates (Gu and Swihart 2004; Belmaker et al. 2009). In fact, the likelihood of reporting an occurrence varies from place to place depending on both population density and the efficiency of the sampling approaches and effort. This kind of bias is exactly what is expected for the Mediterranean records of *F. commersonii*, because of the chance nature of these observations (Azzurro 2010) and the substantial differences in scientific effort among the various sectors of the Mediterranean Sea (Coll et al. 2010). However, new methodological approaches that overcome these biases have emerged in the last decade, and have made it possible to quantify the potential distribution of invasive species and predict ecologically suitable areas for them to become established (Elith et al. 2006; Anderson and Gonzalez 2011). As in other modeling approaches (Guisan et al. 2002; Scott et al. 2002, Franklin 2010; Nori 2011), these tools make it possible to correlate environmental variables with observed distributions without taking into account the physiological aspects of species, adopting the general assumption that the best indicator of a species' climatic requirements is its

current distribution. Therefore, the realized niche of the species can be estimated (Austin 2002). From among the models that have been developed to predict species range expansions (reviewed by Koike and Iwasaki 2011), we chose the maximum entropy (MaxEnt) approach (Phillips et al. 2006). This method is being increasingly applied to model species niches and distributions based on presence-only data (Phillips et al. 2006; Phillips and Dudík 2008; Anderson and Gonzalez 2011).

We used records of the presence of *F. commersonii* in the Mediterranean Sea, from January 2000 (first detection) to October 2011 to address three objectives: (1) To reconstruct the chronology of the invasion; (2) To assess spread rates; and (3) To estimate the environmental suitability of different areas in the Mediterranean to this Lessepsian invasion. To achieve this last objective, we used our presence-only data set in combination with biophysical variables to fit a ‘niche-based model’.

## Methods

The available presence records of the bluespotted cornetfish in the Mediterranean Sea were collected by means of an exhaustive bibliographic search based on scientific journals, grey literature and trustworthy personal communications updated in October 2011. This last information was only included after expert validation by the first author. Each point observation was associated with information on the sampling date, latitude, longitude, habitat and depth, when available.

In order to follow the progress of the invasion and update the distribution of *F. commersonii*, point data were imported into ArcGIS 10 (ESRI 1999) and geographically represented as cumulative occurrences for each calendar year, from 2000 to 2011. To provide a realistic reconstruction of the advance of this species, the observations from the southern Mediterranean rim (i.e. from the Suez Canal opening to Gibraltar, along the African Mediterranean coast (AfMed)) were analysed separately from the observation made in the northern Mediterranean rim (i.e. from the Suez Canal opening to Gibraltar, along the Asiatic and European coasts (AsEuMed)). For each year, from 2000 to 2011, we calculated the centroid of the geographic positions. In this calculation we assumed that, once a given position was reached, only records implying a forward (northward or westward) movement were relevant for calculating the position for the following years and hence the speed of the invasion.

The rate of spread was estimated using two different methods: I) centroids were projected onto the 50 m depth contour to calculate the distance travelled (km) from one year to the next, assuming that the centroids represent the average locations of departure and arrival of the invader over time; and II) all possible distances between points were calculated between one year and the following year, without making *a priori* assumptions on the likely travel path. For each pair of consecutive years this last method produces a set of distances for which we calculated the modal (mean or median), minimum and maximum distances travelled.

In order to estimate the environmental suitability of areas for this Lessepsian invasion, we built a species distribution model (SDM) based on field observations of all the occurrences of *F. commersonii* coupled with environmental maps. From among the available techniques we chose to use the maximum entropy method (MaxEnt) for analysing *presence-only records* (Phillips et al. 2006). MaxEnt has been shown to outperform other occurrence-only methods in estimating SDMs (Phillips et al. 2006; Elith et al. 2006). An excellent introduction to MaxEnt for ecologists is found in Elith et al. (2011) and in the tutorial to the software, which is available at <http://www.cs.princeton.edu/~schapire/maxent/>. MaxEnt uses presence-only data and a user-defined number of randomly selected points (*pseudo-absences*) and combines these with the biophysical covariates to construct a habitat

suitability index for each cell ranging from 0 (least suitable habitat) to 1 (most suitable habitat). As a threshold, to differentiate *suitable* and *unsuitable* habitats, we chose a habitat index of 0.5. Briefly, the MaxEnt model minimizes the relative entropy between two probability densities: a first probability density estimated from the presence data and another estimated from the set of environmental variables or *landscape*. In MaxEnt, data pixels without presences are not interpreted as absences. We used predictive modelling to determine the potential distribution of the species in the Mediterranean based on the sites of known occurrence with the help of eight ancillary variables that provide the environmental conditions at these sites. High-resolution environmental variables (km scale) in the ocean are usually restricted to surface temperature, surface salinity and chlorophyll levels, and are generally from relatively recent periods (last 5-15 years). We chose a data set at a coarser scale (LOICZ data set, University of Kansas, [http://hercules.kgs.ku.edu/hexacoral/envirodata/hex\\_modfilt\\_firststep3dev1.cfm](http://hercules.kgs.ku.edu/hexacoral/envirodata/hex_modfilt_firststep3dev1.cfm)) because it provides a larger set of environmental variables, albeit at a coarser spatial scale (30' or 0.5° grid), and long-term (1950-present) average or climatic conditions. The environmental variables chosen are given in Table 1 and shown in Fig. 4. We chose three types of variables: i) environmental variables related to water temperature (and its variability), salinity and biological production (based on the average chlorophyll-a concentration and its variability), which are known to influence biological processes in the ocean; ii) geographical variables defining the mean depth and the length of the coastline in each cell, as a proxy for the complexity of the coastline, because *F. commersonii* is a shallow water species; and iii) human population density as a proxy for the human disturbance of the coastal zone, because one of the reasons that invaders become successfully established in a new geographical setting can be due to the ecological degradation of these locations resulting from human disturbance. We masked land areas, as well as the Atlantic Ocean, and the Red and Black Seas from the data sets of environmental variables. The model was built with an implementation of MaxEnt 3.3.3k provided by Phillips et al. (2006), and Phillips and Dudik (2008), available as a Java program at <http://www.cs.princeton.edu/~schapire/maxent/>. Model selection consisted in a backwards procedure, starting with the full set of eight explanatory variables, and taking away one variable at a time with the jackknife procedure available in MaxEnt (Elith et al. 2006; 2011). The goodness of fit of each model was assessed by a ROC (receiver operating characteristics) analysis, comparing the AUC (area under the ROC curve) of the model for presences against a purely random distribution model. A purely random distribution model would have an AUC = 0.5 and models whose AUC was not significantly different from this value were discarded. The significance of the AUC was tested by a cross-validation procedure involving 100 permutations. When the confidence intervals of the AUC included the value of 0.5 the model was rejected. We used the default parameters for the analysis, with default prevalence=0.5, convergence threshold=10<sup>-5</sup>, 500 training iterations of the optimization algorithm, regularization multiplier=1, and the use of “auto” features. The AUC test was computed with a random set of 20% of the points set aside for testing. The importance of the variables was measured with a jackknife procedure built into MaxEnt.

## Results

### Chronology of the invasion and distribution update

In total 191 Mediterranean presence records of *F. commersonii* were collated from January 2000 to October 2011. The chronological order of these sightings showed a progressive series of successful colonizations, with a clear spatio-temporal sequence directed westward from the entry point (Fig. 1). The invasion occurred in parallel along the southern and northern rims of the Mediterranean, without any apparent lag (*sensu* Crooks 2011) between these two routes (Fig.

2). According to the information associated with these Mediterranean records, the species has been encountered at shallow depths in many different habitats, including rocky, muddy and sandy bottoms, seagrass meadows and mixed environments (Corsini et al. 2002; Azzurro et al. 2004; Pais et al. 2007; Garibaldi and Orsi-Relini 2008; Kara and Oudjane 2008; Psomadakis et al. 2009). The species has also been caught offshore, up to depths of 40-60 m. In the islands of Rhodes (Kalogirou et al. 2007) and Malta (present study), juveniles have been observed on sandy bottoms rich in *Cymodocea nodosa* meadows, which could act as nursery grounds for the species in these areas. The temporal pattern of adult sightings was significantly skewed towards the cold season, with most of the records (75%) made during the late autumn and early winter, especially from October to December.

#### Speed of the invasion

The bluespotted cornetfish invasion is progressing very quickly, reaching rates of spread of around 1000-1500 km year<sup>-1</sup>, calculated either with 'method I' (the distance between two subsequent centroids) or with 'method II' (without making assumptions on the likely invasion path) (Fig. 3). *Fistularia* reached its maximum speed in 2003 along the northern (AsEuMed) rim of the Mediterranean and in 2002 along the southern (AfMed) rim. Both methods suggest a decrease in the rate of spread in 2003-2004, corresponding to the crossing of the Sicily Strait, slowing down to less than 250 km year<sup>-1</sup>. After crossing this area, the rate of spread increased again up to maximum levels of 800 km year<sup>-1</sup> (or as high as 2000 km yr<sup>-1</sup> in 2007 according to 'method II') in AfMed. This pattern was consistent between the southern and northern routes. Finally, in recent years the rate of spread has dropped again to minimum values, as shown in Fig. 3 with the speeds calculated according to both methods.

#### Environmental suitability model

The full model with eight variables was not significant (Table 2) and the jackknife estimates for regularized training gain suggested that the *human population density* could be eliminated without incurring a noticeable loss of gain. Likewise, in the model with seven variables, although statistically significant, we eliminated *coastline length* without incurring loss of gain. The final, reduced model was based on six explanatory variables (Table 2), corresponding to the last six variables in Table 1 (SST and its standard deviation, chlorophyll-a concentration and its standard deviation, SSS and mean cell depth; Fig. 4). The regularized gain was 0.643 on average, which results in an average likelihood of presence 1.9 times higher than the value of a random background grid cell (or pixel). This means that the cells with environmental conditions similar to the conditions in the presence samples have almost twice the probability of being invaded by *F. commersonii* than other cells. The marginal response of *F. commersonii* to the six selected variables is shown in Fig 5. The explanatory variable with the highest permutation importance was the mean cell depth (32.4%), with a higher likelihood of presence in cells shallower than 2000 m (cf with a maximum reported depth of 132 m in Fishbase; this apparent discrepancy is due to the coarse scale of the environmental data set used). The second variable in terms of permutation importance was chlorophyll-a concentration (29.3%): the species had a higher likelihood of presence at intermediate chlorophyll-a values (75-140 colour units). The third variable was SSS (18.4%) and showed that the cells with high salinity values (especially 38.5‰ and higher) are more likely to be invaded by the species. The fourth variable was average SST (7.8%), and showed that cells between 19.5 and 21°C provide a suitable habitat for *Fistularia*, and that cells with the warmest waters do not, although the response to temperature was minor. The standard

deviation of the chlorophyll-a concentration and the standard deviation of SST also made minor contributions to the model (permutation importance of 5.4% and 6.7%).

#### Geographical projection of modelled suitability

The spatial model of the potential distribution of *F. commersonii* is shown as a continuous map in Fig. 6, which allowed us to make fine distinctions between the modelled suitability of different areas. In general, the environmental conditions are more suitable for the species along the coast, in relatively shallow water. The areas of highest environmental suitability are generally found in the eastern Mediterranean, from the Sinai peninsula eastwards, i.e. Israel, Lebanon, southern Turkey, Dodecanese, southern Peloponnese and locally, around Cyprus, Rhodes and Crete. In contrast, there were large sections of the North African coast that showed low suitability, such as in the area around the Nile Delta, along the western coasts of Egypt and in Cyrenaica. In the central Mediterranean, the conditions would generally be suitable along the coasts of Sicily, especially on its southern side, in Tunisia, and in the Tyrrhenian Sea, including Corsica and Sardinia. The western Mediterranean generally showed low suitability, especially at the western end of the Basin, in the Alboran Sea and along the coast of Spain, western Algeria and Morocco. Nevertheless, suitable areas would exist in the French Riviera, along the northeastern Spanish coast (including the Balearic Islands) and to a lesser extent on the Algerian coast, intermingled with low suitability areas. The Alboran Sea, north Aegean, north and central Adriatic, Gulf of Genoa and Gulf of Lion were found to be areas of extremely low suitability.

#### Discussion

The records of *F. commersonii* in the Mediterranean Sea significantly updated the information on its distribution (CIESM 2009), making it possible to reconstruct the spatial pattern and temporal rhythm of this invasion. The first sighting in 2000 (Golani 2002) of this species was immediately followed by its establishment and the rapid and progressive colonization of the Levantine Basin, without any apparent lag (*sensu* Crooks 2011) between arrival, establishment and subsequent spread. The absence of prolonged lags, as well as the quickness with which it spreads (Streftaris and Zenetos 2006; DAISIE 2008), could be related to high initial population growth rates, as highlighted for other invasive fish species by population dynamics models (Forsyth et al. 2012). The spatio-temporal linearity of the invasion sequence shown in Fig. 1 and Fig. 2 is astounding, being consistent with a single, spatially-limited invasion episode close to the Suez Canal followed by subsequent population expansion, as previously highlighted by the findings of a genetic study (Golani et al. 2007).

Remarkably, the colonization of the southern and northern rims of the Mediterranean, along the African (AfMed) and Asiatic and European Mediterranean (AsEuMED) routes, seems to have proceeded in parallel, regardless of the water circulation pattern. In fact, along the African shores of the eastern Mediterranean, major currents are directed eastward, whilst they run in the opposite direction along the Euro-Asiatic shores (Pinardi and Masetti 2000). Considering that surface currents are responsible for the drift of larvae, the spread of *Fistularia* could be better explained by active adult migration rather than larval dispersal. Recently, the changing surface circulation pattern in the eastern Mediterranean (reviewed by Briand 2000) has been considered the cause for the expansion of some warm-water fish species (Bianchi 2007), but specific studies are needed to clarify the importance of this factor for the dispersal of Lessepsian species.

Finally, at the intra-annual level, the distribution of our records was clearly skewed towards the cold-season, especially towards the period October-December, as already noted by Occhipinti-Ambrogi and Galil (2008) and by Bodilis et al. (2011). Sampling biases are not a possible explanation, since autumn and winter are the worst seasons for observing fish at sea. Alternatively, it is possible that *Fistularia* adults migrate preferably during these months, which leads to the increase in records. This hypothesis needs to be investigated further.

The speed of the *Fistularia* invasion has no equals among Mediterranean non-indigenous fish (Ben Rais Lasram et al. 2010), with the lowest values in the order of hundreds of km yr<sup>-1</sup> and the highest values around one thousand km yr<sup>-1</sup>. *F. commersonii* has been able to colonize almost the entire Mediterranean region in only seven years after its first sighting. To our knowledge few examples of this kind are available for marine fish worldwide. The lionfish (i.e. the complex *Pterois volitans*, *P. miles*) is one other example; it is an eye-catching invader with a large number of confirmed occurrence records (US Geological Survey Nonindigenous Aquatic Species database USGS-NAS; <http://nas.er.usgs.gov/>). This species was introduced into Florida waters as a result of aquarium releases and expanded rapidly throughout the Caribbean in less than a decade (Schofield 2009). Another example of a very quick invasion is the mitten crab *Eriocheir sinensis*, which dispersed along the UK coast reaching maximum rates of spread of 448 km yr<sup>-1</sup> (Herborg et al. 2005).

Despite the general success of *F. commersonii* in its new environment, it does not show an even rate of spread across the different sectors of the Mediterranean, with a clear decrease in the Sicily Strait, the major transitional sector of the Basin. Evidently, this bio-geographical barrier, considered once the western limit of Lessepsian migration (Por 1978; Quignard and Tomassini 2000), forced the species to decelerate its spread rate but did not stop it completely. In fact, once this barrier was crossed, the speed increased again. After 2007, the progressive decrease in the rate of spread to the minimum values indicates that no new areas of the Mediterranean have been colonized in recent years, which is probably because all suitable habitats have been colonized.

A spatial distribution model of *F. commersonii* was constructed with MaxEnt from a data set of presence-only records. The model determines the areas where the environmental conditions are most similar to the locations where the species has been recorded, making it possible to evaluate areas of high and low suitability (Fig 5). The three most important variables, explaining around 80% of the variance in the model, were depth, chlorophyll-a concentration and salinity, indicating that the bluespotted cornetfish invades coastal areas of average biological productivity and high salinity, and avoids highly productive areas, such as the northern Adriatic or the Gulf of Lions, as well as highly oligotrophic areas, such as the Libyan coasts. The probability of the presence of *F. commersonii* was also low in areas of low salinity with a continental (Gulf of Lions, northern Adriatic, northern Aegean) or Atlantic influence (Alboran Sea). Besides the specific relevance of these environmental factors, one general result is that the physical environment is an important limit to the progress of *F. commersonii* in the Mediterranean Sea. Actually, the inability of invaders to adapt to abiotic conditions is a common constraint in biological invasions (for fish species see: Baltz and Moyle 1993; Moyle and Light 1996) and this would make the above mentioned Mediterranean subregions resistant to the bluespotted cornetfish.

Several empirical observations can be used to validate our spatial predictions. Firstly, the eastern Mediterranean showed the highest values of suitability for *F. commersonii*, which obviously agrees with the general success of the species in this area (CIESM 2009; Golani 2010). However, within the same Levantine Basin the model identified areas of low suitability, such as the western Egyptian coasts and eastern Libya. This is confirmed by a recent study by Halim and Rizkalla (2011), which considered *F. commersonii* to be still absent on the eastern side of Mediterranean Egypt, and by Shakman and Kinzelbach (2007), which reported this species as rare along the Libyan

coasts. In the Aegean Sea, *F. commersonii* occurred from the south (Crete) up to the Chalkidiki Peninsula (north Aegean). Nevertheless, according to our findings, only the southern edge of the Aegean Sea would be suitable for *F. commersonii*. Por (1978) noted the limited success (in terms of abundance and distribution) that Lessepsian invaders have in the Aegean Sea, and this was later highlighted by Corsini and Economidis (2007) specifically for the bluespotted cornetfish. This ‘Aegean resistance’ is now fully confirmed by our model, but the most important abiotic factors limiting the success of *F. commersonii* were not only low temperatures and low salinity, as suggested by Por (1978), but also oligotrophy, which is an important ‘defence’ against the *F. commersonii* invasion. It is possible that other marked unfavourable situations exist in the north Adriatic, Gulf of Genoa, Gulf of Lions and Alboran Sea, which were the least favourable areas of the Mediterranean, due to their high levels of primary production (chlorophyll-a) and low salinity, or both. We therefore predict that in the near future *F. commersonii* will barely develop successful populations in these sectors, even if vagrant individuals are sporadically encountered. As shown by the overall distribution of sightings (Fig. 1) and by the most extreme records of this species (Fig. 2), incursions into habitats where conditions are outside the fundamental species niche are possible (Pulliam 2000), probably due to the great dispersal potential of the bluespotted cornetfish. Other comparisons with bibliographic information can be made for the Dodecanese, which resulted an area of high environmental suitability for this species. Corsini and Economidis (2007) reported that this area, which marks the eastern limit of the Aegean Sea, hosts large numbers of both adult and juvenile cornetfish throughout the year. These authors found Dodecanese to be a ‘refuge’ and a transitional sector for Lessepsian species, including *F. commersonii*. The Dodecanese is located at the boundary of an unfavourable area (Ben Rais Lasram et al. 2010), thus corroborating the results of our model. In the central and western Mediterranean, favourable conditions would exist along the coasts of Sicily and in the Tyrrhenian Sea. These sectors probably have the potential to support increasing abundances of the bluespotted cornetfish, even though currently populations can still be considered unstable in these areas (Azzurro et al. 2011). Conditions in Tunisia would also be favourable for the establishment of the species, as also confirmed by Ben Souissi et al. (2004).

## **Final remarks**

Besides the spectacular spread of *F. commersonii* in the Mediterranean Sea, our study highlights the importance of environmental barriers for setting limits to this invasion. Thus, the extent of its suitable environment determines its invasive range (Blackburn et al. 2011). Abiotic resistance has been very important in preventing some of the Mediterranean subregions from this invasion. Some of these areas, such as the north Adriatic Sea, the north Aegean Sea and the Gulf of Lion, are known to be endemism hotspots (Ben Rais Lasram and Mouillot 2009). Therefore, in terms of conservation, it is certainly desirable that these areas remain physically resistant to the settlement of this predatory species. However, changes in the salinity, productivity and temperature of the Mediterranean Sea (Briand 2008; Caddy et al. 1995) could increase the suitability of this area for the bluespotted cornetfish, increasing the niche overlap between this invader and native species and allowing *F. commersonii* to expand its exotic range further. The current challenges are therefore to keep monitoring this species and contrasting the invasion sequence with our spatial model predictions. Certainly, the present model was based on a set of environmental predictors at a relatively coarse scale (0.5°x0.5°, approx 2235 km<sup>2</sup>), which may limit its reliability. Environmental data at a finer scale (e.g. satellite derived data at a scale of 4x4 km or even 1x1 km) would be better suited for this coastal species that occupies highly heterogeneous habitats. These data are available but the choice of variables in these fine-scale data sets is usually



limited to SST, chlorophyll-a concentration and sometimes SSS. Further work is needed to assess the differences in models due to environmental data sets at different scales and employ the increasing number of presence-only records. In any case, it will be necessary to adapt the scale and the available variables to use SDMs for predicting the effects of climate change on the distribution of this species in future climate scenario projections.

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**Fig. 1** Cumulative occurrences of *Fistularia commersonii* in the Mediterranean Sea from December 2000 to October 2011. Data consisted of 191 georeferenced records pooled from both bibliographic sources and other confirmed observations.

**Fig. 2** Centroids of records (circles) and most extreme observations (stars) of *Fistularia commersonii* in the Mediterranean Sea with a reconstruction of the chronology of the invasion. \* The Suez Canal exit (Port Said, Egypt).

**Fig. 3** Spread rates of *Fistularia commersonii* along the northern (AsEuMed) and southern (AfMed) rims of the Mediterranean. Speeds were computed according to the distance between centroids and with all possible distances, resulting in minimum, median, mean and maximum speeds. Some of the lines in the upper graph (AsEuMed) are discontinued because there is not sufficient data to compute the min-median-mean-max statistics.

**Fig. 4** Environmental predictor variables from the LOICZ database (the Black and Red Seas and the Atlantic were masked for the MaxEnt analysis).

**Fig. 5** Partial dependence curves showing the marginal response (i.e. for constant values of the other variables) of *Fistularia commersonii* in the Mediterranean to the six explanatory variables of the final reduced model. The importance of the variable (as a percentage) obtained from a permutation procedure in MaxEnt is also given.

**Fig. 6** Predictions from the MaxEnt environmental suitability model for *Fistularia commersonii*. Colours denote the habitat suitability index for each cell, ranging from 0 (least suitable habitat) to 1 (most suitable habitat).