Phylogeography of the bluespotted cornetfish, *Fistularia commersonii*: a predictor of bioinvasion success?

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biological invasions; continuous extent of spread; dispersal; *Fistularia commersonii*; Lessepsian migration; phylogeography.

Abstract
Biological invasions result in huge ecological and economic impacts; therefore, a great amount of effort is dedicated to predicting the potential success of newly established or candidate bioinvaders. Thus far, over 90 species of fish have entered the Mediterranean Sea via the Suez canal, the so-called Lessepsian bioinvaders. The bluespotted cornetfish, *Fistularia commersonii*, is remarkable in its ability to disperse within the Mediterranean and has been dubbed ‘the Lessepsian sprinter’. In just a few years, starting in 2000, it expanded over the entire area, from the Suez Canal to Gibraltar. Theoretical predictions correlate the dispersal capabilities of an invader in its native range (using the population genetic metrics, $F_{st}$, as a proxy) with its dispersal capability in its invading area (continuous extent of spread, CES). Here, we estimated the population genetic characteristics of Indo-Pacific native populations of *F. commersonii* in order to determine if this Lessepsian ‘sprinter’ fits the predictive model of dispersal. Indeed, we found that even in the case of such a very rapid range expansion, the predicted relationship between $F_{st}$ and CES is fulfilled in *F. commersonii*.

Introduction
Biological invasions are increasingly impacting ecological and economic balances in both terrestrial and marine habitats and, as such, are becoming the focus of scientific attention (Mack *et al.* 2000; Kolar & Lodge 2001; Simberloff & Rejmanek 2011). At the same time, invasive phenomena are seen as a unique opportunity to explore ecological (Lockwood *et al.* 2011) and evolutionary processes in the marine environment (Lee 2002; Sax *et al.* 2005, 2007). Much work has been dedicated to understanding the ecological consequences of introductions, and resources have been allocated to prevent and control invasions. Recently, genetic tools have been added to the approaches used to assess bioinvasions, and, together with new results, theoretical predictions have been formulated (Holland 2000; Gaither *et al.* 2013; Rius *et al.* 2015). Genetic studies have been employed to answer a variety of questions, such as determining invasive patterns by reconstructing the route, source and timing of invasion, and exploring the historical component of an invasion (Baker & Stebbins 1965; Gaither *et al.* 2010; Geller *et al.* 2010). Despite these concerted efforts, it remains very difficult to predict the potential for invasion success of a given organism, and a number of hypotheses have been formulated so far (Catford *et al.* 2009; Gaither *et al.* 2013). As the number of invaders is usually limited, in general the genetic pool of an invading population is a subset of the pool from the source population (founding effects), and this, in turn, is predicted to have negative effects on the invasion potential (Bernardi *et al.* 2010). However, in many cases small numbers of founding individuals have led to widespread invasions, and bottlenecked populations may still evolve rapidly, despite the negative effects of diminished diversity (Dlugosch & Parker 2008).

Invasions involve different essential stages, including introduction, establishment and regional spread from
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initial successful populations (Simberloff & Rejma’nek 2011). Additionally, dispersal potential can play a crucial role in the invading capacity of a species, at least in determining its spreading potential (Gaither et al. 2013). Here, we used phylogeographic characteristics of a widespread species, which provide an understanding of both dispersal potential and genetic diversity, to evaluate its invasion potential.

One of the major problems plaguing the study of bio-invasions derives from the fact that bioinvaders are usually observed a long time after their original invasion, and only once they successfully have colonized the new habitat. This detection lag (sensu Croock 2011) often impedes our ability to determine when the invasion initiated and whether it is the result of a single event or multiple successive ones. Furthermore, it is difficult to account for why some invasions have failed. In this respect, the case of the Lessepsian bioinvasions is unique.

Lessepsian bioinvaders are organisms originating from the Red Sea that entered the Mediterranean Sea through the Suez Canal, which opened in 1869 under the supervision of the engineer Ferdinand de Lesseps (thus the name). The Lessepsian migration represents the ‘most important biogeographic phenomenon witnessed in the contemporary oceans’ (Por 1978), adding more than 490 new species to the Mediterranean (Zenetos et al. 2012), including over 90 species of fishes (Fricke et al. 2012; Özbek et al. 2014), approximately a quarter to half of the world’s marine fish invaders (Lockwood et al. 2007). It is an ongoing process with new species regularly entering every year and certainly is a massive human-mediated ‘experiment’ (Féral 2002), with unique opportunities to study rapid evolutionary changes (Belmaker et al. 2009).

To date, Lessepsian fishes that have been the focus of genetic studies have exhibited patterns that were mostly consistent in showing a lack of the expected bottle-neck (Sax et al. 2005), with little difference in genetic diversity between the native Red Sea populations and the newly established Mediterranean populations (Bernardi et al. 2010). For these species, data showed that colonization had occurred by a large number of individuals, by multiple colonization events or by a combination of both (Golani & Ritte 1999; Bucciarelli et al. 2002; Hassan et al. 2003; Hassan & Bonhomme 2005; Azzurro et al. 2006). This pattern is in sharp contrast with what is observed for the bluespotted cornetfish, Fistularia commersonii.

The bluespotted cornetfish is a widely distributed species that is naturally found in the inter-tropical zone over the entire Indo-Pacific between the Tropical Eastern Pacific and the Red Sea. Since its introduction to the Mediterranean via the Suez Canal (Golani 2000), F. commersonii has rapidly spread westward to the southern shores of Italy, Sardinia, France and finally Spain, the furthest a Lessepsian fish species has ever been recorded (Azzurro et al. 2012). Work on F. commersonii based on mitochondrial and nuclear markers has shown that the genetic diversity of the Mediterranean population is greatly reduced compared with the naturally distributed Red Sea population (Golani et al. 2007; Sanna et al. 2010; Tenggadjaja et al. 2014). These results are consistent with few, highly dispersive individuals entering the Mediterranean.

The Mediterranean invasion of the bluespotted cornetfish proceeded rapidly, with the lowest values in the order of hundreds of km year⁻¹ and the highest values around 1000 km year⁻¹ (Azzurro et al. 2012). In only 7 years, this species colonized almost the entire Mediterranean. Very few examples of invasions of this kind are available for marine fishes worldwide. This remarkable dispersal capability of F. commersonii, accomplished either by passive larval drift or by active swimming of adult individuals (Merella et al. 2010; Azzurro et al. 2012), should be reflected in high connectivity among native populations and result in nearly panmictic populations at a larger scale (Gaither et al. 2013).

A study on marine organisms that specifically tested the relationship between gene flow in the native range (Fst values) and realized dispersal in the new invasive range found that the best correlation was obtained between median pairwise Fst of mitochondrial markers and the continuous extent of spread (CES; Gaither et al. 2013). In the case of F. commersonii, the CES may be calculated as a southern route (via the Northern Africa shore), a northern route (via Turkey and Greece) or a middle route (via the Greek Islands) (Azzurro et al. 2012). Using the correlation described above, these three routes (3300 to 4400 km) predict median pairwise Fst values between 0.01 and 0.04.

The goal of this work was to assess the structure of F. commersonii populations in their natural range on a global scale and determine if there was a correlation between phylogeographic patterns (population structure) and the success of the species (CES) as an effective and rapid bioinvader.

Material and Methods

DNA samples used in this study covered the range of the species, from the Eastern Pacific shores of Mexico to the Red Sea (Fig. 1, Table 1). Samples from Israel and Egypt were from a previous study (Golani et al. 2007). All other samples were collected by spear or hand nets. We genotyped all samples for two mitochondrial markers, control region (CR) and cytochrome oxidase 1 (CO1), and one nuclear marker, rhodopsin (ROD). CR is a commonly used locus in population genetics because its high variability is useful for population-level studies. The use
of COI and ROD is increasingly common because they are the loci of choice in barcode studies, which allows for direct comparison with a very large number of other studies. When heterozygous sites were found, they were coded following International Union of Pure and Applied Chemistry (IUPAC) ambiguity codes. The amplification of COI and ROD followed previously described protocols (Tenggardjaja et al. 2014). Sequence data for the Israel and Egypt samples were from previous publications (Golani et al. 2007; Tenggardjaja et al. 2014).

Sequence diversity and variability

Sequences were trimmed and aligned using the MAFFT routine (Katoh et al. 2002) implemented in GENEIOUS 5.0 (Biomatters, San Francisco, CA, USA). Sequence variability was estimated by computing haplotype diversity, Hd, and nucleotide diversity 'π' (Nei 1987) using ARLEQUIN (Excoffier & Lischer 2010). We used jModeltest 0.1.1 (Posada & Crandall 1998) on each data set to determine the substitution model that best fitted the data based on the corrected Akaike information criterion.

Table 1. Genetic characteristics of populations of *Fistularia commersonii* based on combined mitochondrial markers (first value in each entry) and the nuclear marker (second value).

<table>
<thead>
<tr>
<th>locality</th>
<th>n</th>
<th>nH</th>
<th>π</th>
<th>HD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Israel, Eilat, Red Sea</td>
<td>31/26</td>
<td>29/8</td>
<td>17.35/0.05</td>
<td>0.99/0.78</td>
</tr>
<tr>
<td>Egypt, Marsa Alam, Red Sea</td>
<td>14/15</td>
<td>13/3</td>
<td>21.23/0.07</td>
<td>0.99/0.60</td>
</tr>
<tr>
<td>Seychelles</td>
<td>2/2</td>
<td>2/1</td>
<td>19.00/0.00</td>
<td>1.00/0.00</td>
</tr>
<tr>
<td>Hawaii, Kauai, Maui</td>
<td>4/4</td>
<td>4/3</td>
<td>12.50/0.83</td>
<td>1.00/0.83</td>
</tr>
<tr>
<td>French Polynesia, Rangiroa, Moorea</td>
<td>21/23</td>
<td>19/6</td>
<td>14.99/0.76</td>
<td>0.99/0.41</td>
</tr>
<tr>
<td>Mexico, Baja California – La Paz</td>
<td>18/25</td>
<td>18/5</td>
<td>5.67/0.21</td>
<td>1.00/0.48</td>
</tr>
</tbody>
</table>

Number of samples (n), number of haplotypes (nH), molecular diversity (π) and haplotype diversity (HD) are given in columns from left to right. Data for each mitochondrial locus are provided in Table S1.

Haplotype networks

Relationships between intra-specific haplotypes within each species were assessed using a minimum spanning network (MSN) or haplotype network (Excoffier & Smouse 1994). Haplotype networks for the combined mitochondrial markers COI and CR and for ROD were generated in R using HaploNet in the APE package (Paradis et al. 2004) (R Development Core Team 2010) combined with pie diagrams of haplotype frequencies obtained with APE and ARLEQUIN (Excoffier & Lischer 2010).

Population structure

Population structure was evaluated using classical fixation indices ($F_{st}$ and $\Phi_{st}$ values) implemented in ARLEQUIN (Excoffier & Lischer 2010) based on pairwise genetic distances using unweighted transitions and transversions. Deviations from values expected under the null hypothesis of genetic homogeneity were tested using a non-parametric permutation approach using 10,000 replicates (Excoffier et al. 1992).
Simulations show that the power to detect population differentiation is reduced when some of the samples are very small (usually fewer than five individuals; Hudson et al. 1992; Pennings et al. 2011). We therefore conservatively removed all populations with fewer than 15 individuals from the analysis. For this study, our goal was to place our results within a previously established model of dispersal potential that is based on $F_{st}$ calculations (Gaither et al. 2013). However, in the case of high haplotype diversity, $F_{st}$ may underestimate the level of population structure, and a different metric, Jost’s $D_{st}$ should be used (Jost 2008; Bird et al. 2011). The value of $D_{st}$ was originally devised for genotypes, not sequences; therefore, our data could not be used directly but first needed to be derived into haplotypes (Pennings et al. 2011). In turn, haplotype diversity is vulnerable to sequence length; where $D_{st}$ values might be incorrectly estimated for shorter sequences (Pennings et al. 2011). We therefore simulated results with different sequence lengths, starting at 100 bp and increasing those lengths by 100 bp at a time and repeated these iterations 20 times for each fragment length to ensure that the length that we used accurately portrayed genetic differentiation. We then averaged these 20 values. All simulations were performed using a published R program (Pennings et al. 2011).

**Historical demography**

Population fluctuations were estimated using coalescent models, a powerful approach that allows the reconstruction of the size of a given population at a set date based on current population genetic signatures (Kingman 2000). Historical demography was evaluated using the program LAMARC (Kuhner 2006). Population parameters $\Theta \theta_\mu = 2N_\mu$, where $\mu$ is the mutation rate for mtDNA, and $g$ (the exponential growth parameter in units of $\mu$) were estimated, the parameter $\Theta$ being estimated with population growth (parameters estimated jointly) or with growth kept constant ($g = 0$). Both estimates were obtained by running 10 replicates, which generated a mean value and its associated standard deviation. Analysis of each data set was carried out with 10 short Monte Carlo chains of 4000 steps each and five long chains of 20,000 steps, with a sampling increment of 20.

Coalescence times were estimated by assuming that coalescence was reached when the population size was reduced to 1% of its present-day value (Wares & Cunningham 2001). In order to estimate coalescence time, we used a range of mutation rates ($\mu$) as $\mu =$ substitutions per site per generation obtained for a marine genus, *Chromis* (Domingues et al. 2005, 2006), and a guild of fresh-water cichlid species (Sturmbauer et al. 2001), thus providing a window of mutation rates ($8.24 \times 10^{-8}$ to $9.30 \times 10^{-8}$). Importantly, such data must be considered with much caution (Cárdenas et al. 2005; Ho et al. 2005). Indeed, neither fish group used to calibrate the molecular clock is closely related to *Fistularia*; however, these values provide some information on the relative times of coalescence within this study and some potential information on absolute times. Mediterranean populations were purposefully excluded from this study because these populations are not naturally in equilibrium and as such a coalescence study would not be appropriate.

**Relationships between $F_{st}$ and CES**

Following previous studies (Gaither et al. 2013), median $F_{st}$ values for the concatenated mtDNA data were natural log-transformed prior to analyses comparing $F_{st}$ values and geographic distances (km). CES was estimated using the path function of Google Earth. As values of $F_{st}$ can be zero or negative, a value of 1 was added to each $F_{st}$ prior to transformation [$\ln(F_{st} + 1)$] as per a previous study (Gaither et al. 2013). Marine animals (crustaceans, tunicates, sponges and fishes) used in that study were also included here for comparison. A regression for the fishes was used and its 95% confidence interval calculated and graphed in Microsoft EXCEL.

**Results**

**Sequence diversity**

We analysed 99, 105 and 95 individuals for the CR, CO1 and ROD markers, respectively (Tables 1 and S1). Sequences were deposited in GenBank with accession numbers KP052941 to KP053237. Haplotype diversity was high in all populations of *Fistularia commersonii*, averaging 0.992, 0.557 and 0.566 for CR, CO1, and ROD, respectively (averages did not include localities with sample sizes lower than 10 individuals, Table 1). In general, mitochondrial and nuclear markers showed similar patterns, with the exception of the French Polynesian and Mexican populations studied, which showed lower haplotype diversities in the nuclear locus relative to the mitochondrial markers.

**Haplotype networks**

As expected, the haplotype networks based on mitochondrial markers were more complex than the ones based on the nuclear marker ROD. The haplotype networks did not show striking geographic patterns. For the mitochondrial markers, the samples collected in Mexico tended to cluster together. For the haplotype network based on ROD, one haplotype was exclusively found in Hawaii and
French Polynesia, and one was exclusively found in Israel and Egypt, but for all four populations, samples were not restricted to those haplotypes, namely additional haplotypes from these localities were present (Fig. 2).

Population structure
As mentioned above, the haplotype networks did not show obvious geographic patterns. A similar trend was observed when looking at pairwise comparisons. For the nuclear marker, almost all pairwise comparisons were statistically significant (14 out of 15), both for Phist and \( F_{st} \) values, while for the mitochondrial markers, the Eilat, Marsa Alam and Mexican populations displayed significant values of pairwise Phists but not \( F_{st} \)s (Table 2). The difference in significance between \( F_{st} \) and Phist values for mitochondrial markers is likely to be due to the high haplotype diversity in the mtDNA markers (Bird et al. 2011). This is also corroborated by higher values of Jost’s \( D_{st} \) compared with \( G_{st} \) values (Fig. S2). Importantly, the simulations showed that the concatenated mitochondrial sequences (844 bp) were sufficiently long enough to obtain consistent results, as values of both \( G_{st} \) and \( D_{st} \) reached an asymptote around 600 bp (Fig. S2).

Demography
Coalescent approaches allowed us to estimate size, growth and age of different populations. Values of theta, which are proportional to population size, and population growth values, indicated that populations of Fistularia commersonii were not unusually expanding or contracting. Their estimated age was relatively recent, all within the last 500 kyr (278–501 kyr). There was no obvious trend of expansion or age among the different geographic locations.

Relationships between \( F_{st} \) and CES
In just a few years, Fistularia commersonii invaded the Mediterranean from the Suez Canal to Gibraltar. In order to estimate the CES for F. commersonii in the Mediterranean, we used three different potential routes to explain the current distribution of the invading species (Azzurro et al. 2012). The southern route of invasion, which follows the North African coastline, is approximately 4050 km long. The northern route, which follows the coastlines of the Levant, Turkey, Greece and Italy, is approximately 4750 km. Finally, an intermediate route that would have used stepping-stones, skipping among Greek islands, and is more direct, is approximately 3650 km. These values were then natural log-transformed and plotted against the median of pairwise \( F_{st} \)s among populations of concatenated mtDNA markers, as shown in Fig. 3. We found that the three F. commersonii points, corresponding to the three routes of invasions, clustered very tightly and were within the predicted 95% confidence interval of the regression previously published for fishes (Gaither et al. 2013).

Discussion
Population structure in natural ranges has been used to forecast the spread of invading species, with a negative correlation found between median \( F_{st} \) (a proxy for population structure) and invasive spread (Gaither et al. 2013). We have shown here that Fistularia commersonii represents an ideal case study to test the relevance of phylogeographic patterns as predictors of invasiveness. This species naturally inhabits a vast geographic range, from the Red Sea to the Mexican Eastern Pacific. Once introduced into the Mediterranean, it rapidly expanded over the entire basin from Israel to Gibraltar, and this spread...
The first six species are found in the Levant, occasionally including Turkey, and Fistularia commersonii is found in the entire Mediterranean. Population size denotes if only very few individuals have ever been sighted (for example fewer than 10 Ostracion cubicus have been sighted) or if large numbers of individuals are regularly observed (for example hundreds of Plotosus lineatus are regularly trawled). Fistularia commersonii is not uncommon but it is never an abundant species in its native range. TEP, Tropical Eastern Pacific.

was closely monitored as it was happening (Golani et al. 2007; Azzurro et al. 2012; Tenggardjaja et al. 2014). The goal of this study was to assess the population structure of F. commersonii in its natural range to shed light on its dispersal capabilities as it relates to the success of this invasion. Considering the large size of its recruiting

Table 2. Population structure summary for Fistularia commersonii.

<table>
<thead>
<tr>
<th>locality</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>mitochondrial markers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Israel, Eilat, Red Sea</td>
<td>–</td>
<td>0.007</td>
<td>0.005</td>
<td>0.002</td>
</tr>
<tr>
<td>Egypt, Marsa Alam, Red Sea</td>
<td>0.160*</td>
<td>–</td>
<td>0.009</td>
<td>0.005</td>
</tr>
<tr>
<td>French Polynesia, Rangiroa, Moorea</td>
<td>0.100*</td>
<td>0.272*</td>
<td>–</td>
<td>0.003</td>
</tr>
<tr>
<td>Mexico, Baja California – La Paz</td>
<td>0.284*</td>
<td>0.403*</td>
<td>0.456*</td>
<td>–</td>
</tr>
<tr>
<td>nuclear marker</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Israel, Eilat, Red Sea</td>
<td>–</td>
<td>0.301*</td>
<td>0.231*</td>
<td>0.371*</td>
</tr>
<tr>
<td>Egypt, Marsa Alam, Red Sea</td>
<td>0.038</td>
<td>–</td>
<td>0.313*</td>
<td>0.470*</td>
</tr>
<tr>
<td>French Polynesia, Rangiroa, Moorea</td>
<td>0.585*</td>
<td>0.553*</td>
<td>–</td>
<td>0.384*</td>
</tr>
<tr>
<td>Mexico, Baja California – La Paz</td>
<td>0.143*</td>
<td>0.237*</td>
<td>0.523*</td>
<td>–</td>
</tr>
</tbody>
</table>

Estimates of theta (θ) (compound parameter representing the effective population size and mutation rate) when growth is constant (θc) and variable (θv), and g (growth parameter), are given in the first three columns. Coalescence time (in thousands of years) based on mitochondrial control region data using mutation rates for that region is given in the last column. The standard deviations are presented in parentheses after each estimator when applicable. Only populations with more than 15 individuals were used.

Table 3. Demographic parameters of Fistularia commersonii based on mtDNA control region and on combined mtDNA (control region and cytochrome oxidase 1) and nuclear (rhodopsin) markers.

<table>
<thead>
<tr>
<th>species</th>
<th>θc</th>
<th>θv</th>
<th>g</th>
<th>coalescence time (kyr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mitochondrial control region</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Israel, Eilat, Red Sea</td>
<td>0.108 (±0.0062)</td>
<td>1.324 (±0.1527)</td>
<td>177.81 (±21.604)</td>
<td>278.5–314.3</td>
</tr>
<tr>
<td>Egypt, Marsa Alam, Red Sea</td>
<td>0.191 (±0.0045)</td>
<td>0.987 (±0.0461)</td>
<td>111.51 (±5.0412)</td>
<td>444.1–501.2</td>
</tr>
<tr>
<td>French Polynesia, Rangiroa, Moorea</td>
<td>0.167 (±0.0036)</td>
<td>0.739 (±0.0464)</td>
<td>147.01 (±6.312)</td>
<td>380.1–336.8</td>
</tr>
<tr>
<td>Mexico, Baja California – La Paz</td>
<td>0.059 (±0.0007)</td>
<td>0.112 (±0.0146)</td>
<td>115.08 (±27.206)</td>
<td>485.6–430.3</td>
</tr>
<tr>
<td>Combined mitochondrial and nuclear markers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Israel, Eilat, Red Sea</td>
<td>0.245 (±0.0034)</td>
<td>0.688 (±0.0710)</td>
<td>460.97 (±45.286)</td>
<td></td>
</tr>
<tr>
<td>Egypt, Marsa Alam, Red Sea</td>
<td>0.072 (±0.0012)</td>
<td>0.376 (±0.0170)</td>
<td>272.09 (±4.655)</td>
<td></td>
</tr>
<tr>
<td>French Polynesia, Rangiroa, Moorea</td>
<td>0.070 (±0.0029)</td>
<td>0.439 (±0.1360)</td>
<td>376.99 (±18.147)</td>
<td></td>
</tr>
<tr>
<td>Mexico, Baja California – La Paz</td>
<td>0.025 (±0.0008)</td>
<td>0.065 (±0.0307)</td>
<td>438.63 (±239.756)</td>
<td></td>
</tr>
</tbody>
</table>

Table 4. Lessepsian migrants with native ranges covering the entire Indo-Pacific and their spread and population size in the Mediterranean.

<table>
<thead>
<tr>
<th>species</th>
<th>native range</th>
<th>population size</th>
<th>invasion spread</th>
<th>year of invasion</th>
<th>reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abudefuf vaigiensis</td>
<td>Indo-Pacific</td>
<td>large</td>
<td>eastern Mediterranean</td>
<td>–</td>
<td>Goren and Galil 1998</td>
</tr>
<tr>
<td>Ostracion cubicus</td>
<td>Indo-Pacific</td>
<td>small</td>
<td>eastern Mediterranean</td>
<td>2011</td>
<td>Bariche 2011</td>
</tr>
<tr>
<td>Plotosus lineatus</td>
<td>Indo-Pacific</td>
<td>large</td>
<td>eastern Mediterranean</td>
<td>2002</td>
<td>Goren and Aronov 2010</td>
</tr>
<tr>
<td>Pomacanthus imperator</td>
<td>Indo-Pacific</td>
<td>small</td>
<td>eastern Mediterranean</td>
<td>2010</td>
<td>Goren and Aronov 2002</td>
</tr>
<tr>
<td>Terapon jarbua</td>
<td>Indo-Pacific</td>
<td>large</td>
<td>eastern Mediterranean</td>
<td>2009</td>
<td>Goren and Aronov 2010</td>
</tr>
<tr>
<td>Scarus ghobban</td>
<td>Indo-Pacific + TEP</td>
<td>small</td>
<td>eastern Mediterranean</td>
<td>2001</td>
<td>Goren and Aronov 2002</td>
</tr>
<tr>
<td>Fistularia commersonii</td>
<td>Indo-Pacific + TEP</td>
<td>medium</td>
<td>Mediterranean</td>
<td>2000</td>
<td>Goren and Aronov 2002</td>
</tr>
</tbody>
</table>

The first six species are found in the Levant, occasionally including Turkey, and Fistularia commersonii is found in the entire Mediterranean. Population size denotes if only very few individuals have ever been sighted (for example fewer than 10 Ostracion cubicus have been sighted) or if large numbers of individuals are regularly observed (for example hundreds of Plotosus lineatus are regularly trawled). Fistularia commersonii is not uncommon but it is never an abundant species in its native range.
Among the more than 90 fish species that have entered the Mediterranean through the Suez Canal (ÖZbek et al. 2014), *F. commersonii* is not the only one to exhibit a very large geographic range. In fact, five species have an Indo-Pacific distribution that goes from the Red Sea to the entire Pacific (but excluding the Tropical Eastern Pacific): *Abudefduf vaigiensis*, *Ostracion cubicus*, *Plotosus lineatus*, *Pomacanthus imperator* and *Terapon jarbua*. An additional species, the blue-barred parrotfish, *Scarus ghobban*, has the same range as *F. commersonii*, spanning the entire Indo-Pacific from the Red Sea to the Eastern Tropical Pacific (Bariche & Saad 2005; Bariche & Bernardi 2009). *Scarus ghobban* shows very strong population structure in its natural range (Bariche & Bernardi 2009; Visram et al. 2010). Yet, all seven species have shown a very modest expansion within the Mediterranean. For all of them, except *P. lineatus*, population sizes are very small, and only few documented records are currently available for these species (Golani 2010).

Our findings reinforce the idea that dispersal capability is only one aspect in the invasion potential equation that should be taken into consideration. Indeed, a combination of ecological, physiological and behavioral variables is considered to influence different phases of the invasion process. According to Belmaker et al. (2013), fish species that occupy a larger variety of environments in their native ranges have more probabilities to thrive in the seasonal Mediterranean Sea. Nevertheless, additional processes, primarily competitive interactions with resident species, can determine the success or the failure of these introductions. For example, the success in the Mediterranean of herbivorous rabbitfish (*Siganus luridus* and *Siganus rivulatus*) that come from the Red Sea, where abundance of herbivores is very high (Brokovich et al. 2010; Khalil et al. 2013), has been attributed to the lack of native competitors (only two native herbivorous species are found in the Mediterranean, *Sarpa salpa* and *Sparisoma cretense*).

Once success is demonstrated, it is also difficult to predict if the species will expand rapidly. For example, *Pl. lineatus*, a species that entered the Mediterranean in 2001, only one year after *F. commersonii*, is extremely successful in the eastern Mediterranean basin (Edelist et al. 2011). Yet, this species still has not expanded its range beyond the Levant. The stages of arrival, establishment of a self-sustaining population, ecological impact and further geographic spread should be investigated separately in order to appropriately test how dispersal potential contributes to the success of a given invasion (Johnston & Purkis 2013).

**Conclusions**

The genetic structure of *Fistularia commersonii* in its native range, estimated by $F_{st}$ metrics, was consistent with...
the high rate of spread of this invader in the Mediterranean Sea. Evidence of high connectivity among Indo-Pacific populations may agree with the rapid dispersal of this species within the Mediterranean Sea, but additional processes, such as competition release, may have contributed to its invasion success. Despite taking a long time to breach the barrier of the Suez Canal, \textit{F. commersonii} became a formidable invader of the Mediterranean with a spectacular rate of dispersal.

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**References**


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**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Fig. S1.** Haplotype networks of *Fistularia commersonii* based on the mitochondrial control region (CR, left panel) and cytochrome oxidase 1 (CO1, right panel). Legend indicates the color of each sampling location, the size of a pie diagram for one individual and the size of a junction proportional to one substitution. The areas of the pie diagrams are proportional to the number of individuals within each pie.

**Fig. S2.** Effect of the length of the mtDNA sequence on $D_{st}$ and $G_{st}$ using data from *Fistularia commersonii*. Circles: $D_{st}$ values; triangles: $G_{st}$ values. Each data point for $D_{st}$ and $G_{st}$ is based on 20 randomly chosen fragments of the total data.