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

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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 & Rejma´nek 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 bottle-necked 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

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 wide-spread 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; Tenggardjaja *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 (F_{st} values) and realized dispersal in the new invasive range found that the best correlation was obtained between median pairwise F_{st} 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 sea-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 F_{st} 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 CO1 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.

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 Φ_{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).

Fig. 1. Collection localities for genetic samples of *Fistularia commersonii*. The color of each sampling location refers to the haplotype networks showed in Fig. 2.
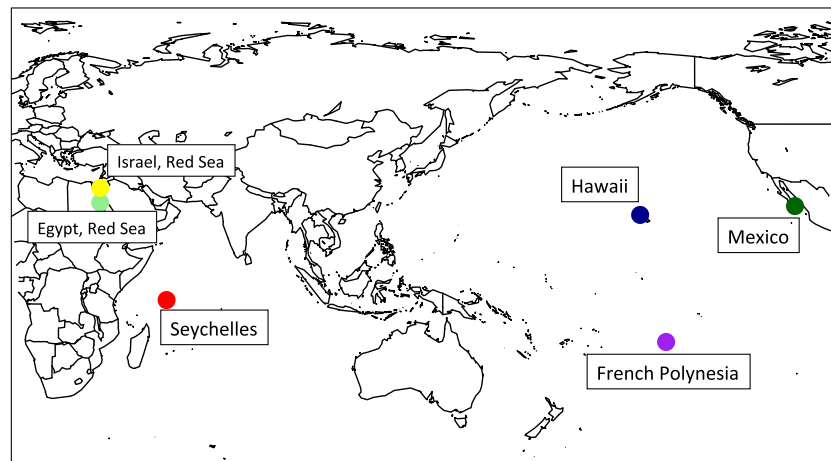
Table 1. Genetic characteristics of populations of *Fistularia commersonii* based on combined mitochondrial markers (first value in each entry) and the nuclear marker (second value).

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

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.

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 Dst 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 Θ theta = 2Nμ, where μ is the mutation rate for mtDNA, and g (the exponential growth parameter in units of μ) were estimated, the parameter Θ 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 (μ) as μ = 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 (8.24×10^{-8} to

9.30×10^{-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

Fig. 2. Haplotype networks of *Fistularia commersonii* based on the combined mitochondrial markers (control region, CR; cytochrome oxidase 1, CO1) on the left, and the nuclear marker (rhodopsin, ROD) on the right. 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. Haplotype networks for each mitochondrial marker are shown in Fig. S1.
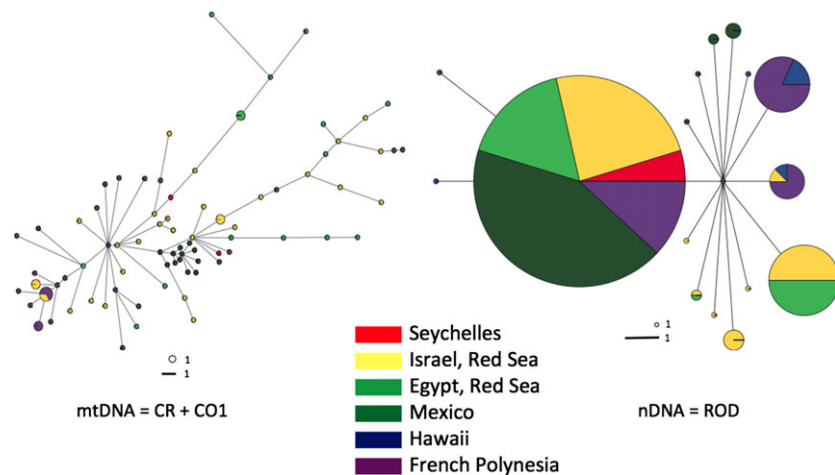
mtDNA = CR + CO1

nDNA = ROD

Seychelles
Israel, Red Sea
Egypt, Red Sea
Mexico
Hawaii
French Polynesia

Table 2. Population structure summary for *Fistularia commersonii*.

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

F_{st} values are given above the diagonal; Phist values are given below the diagonal. Asterisks indicate statistically significant values. Only populations with more than 15 individuals were used. A breakdown of values for each of the mitochondrial markers is given in Table S2. Localities 1,2,3,and 4, correspond to Eilat, Marsa Alam, French Polynesia, and Mexico, respectively.

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.

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

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

species	native range	population size	invasion spread	year of invasion	reference
Abudefduf vaigiensis	Indo-Pacific	large	eastern Mediterranean		Goren and Galil 1998
Ostracion cubicus	Indo-Pacific	small	eastern Mediterranean	2011	Bariche 2011
Plotosus lineatus	Indo-Pacific	large	eastern Mediterranean	2002	Golani 2002
Pomacanthus imperator	Indo-Pacific	small	eastern Mediterranean	2010	Golani 2010;
Terapon jarbua	Indo-Pacific	large	eastern Mediterranean	2009	Golani 2010;
Scarus ghobban	Indo-Pacific + TEP	small	eastern Mediterranean	2001	Goren and Aronov 2002
Fistularia commersonii	Indo-Pacific + TEP	medium	Mediterranean	2000	Golani 2000

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
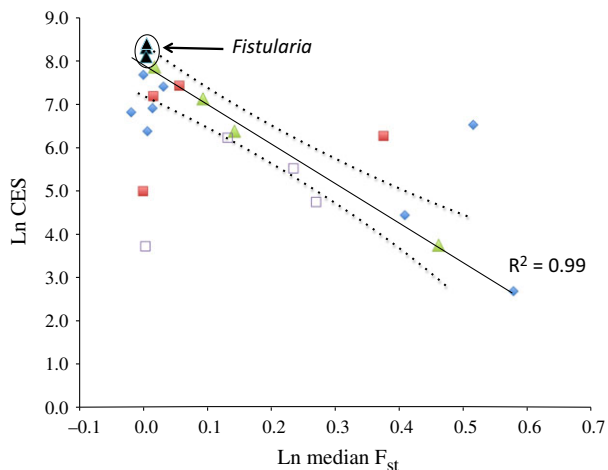
Fig. 3. Population genetic structure (F_{st}) based on mitochondrial markers *versus* continuous extent of spread (CES) for mollusks, blue; crustaceans, red; fishes, green; sponges + tunicates, open squares. Re-drawn from published data (Gaither *et al.* 2013). Data are natural log-transformed, CES is given in km and the value for population structure is the median of the population pairwise F_{st} + 1, as described in the Material and Methods. The regression line was plotted for the fish data set (solid line and its associated R^2) and 95% confidence intervals were calculated and plotted (dashed lines). Solid black triangles represent the data for *Fistularia commersonii*, with values corresponding to the three different CES (north, south and middle Mediterranean).

larvae, the long pelagic larval stage, large geographic range and rapid expansion in the Mediterranean, we predicted a very high capability of dispersal in this species. Such a capability usually translates into very low levels of population structure. Indeed, the median pairwise F_{st} values were found to be within the expected range under all of our spreading scenarios (northern, southern or intermediate route through the Mediterranean).

In contrast to our initial expectations, however, both mitochondrial and nuclear sequences showed some instances of structure for *F. commersonii* native populations. Yet, this structure was likely the result of time scales that are much larger than ecologically relevant scales such as the one observed over the course of a few years in the Mediterranean expansion, although the overall population structure of a species can shed light on the processes that occur at ecological scales (Bowen *et al.* 2014). Indeed, coalescent analyses estimated the age of the populations sampled here to be between 200,000 and 500,000 years old. Nevertheless, the Indo-Pacific population showed high levels of connectivity that would be consistent with the rapid dispersal of this species within the Mediterranean Sea. Therefore, the phylogeographic approach provided some potential predictive elements to predict the dispersal capabilities of this species in its invaded 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, *F. commersonii* became a formidable invader of the Mediterranean with a spectacular rate of dispersal.

Acknowledgements

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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.