Ecological correlates of dispersal success of Lessepsian fishes

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ABSTRACT: Despite the importance of Lessepsian invasion by migrant fish species from the Red Sea into the Mediterranean Sea via the Suez Canal, determinants of invasive success have been poorly investigated. In this study, we reconstructed the spatio-temporal dynamics of all Lessepsian fish species in the Mediterranean Sea and analysed the relationship between ecological variables and dispersal rate. We created a database on species occurrences based on historical data (1869 to 2005) and estimated the dispersal rate of each species. Overall, 30% of the Lessepsian species succeeded in colonizing the Mediterranean Sea. On average, the 43 Lessepsian species not included in the category 'absence of dispersal' disperse at a rate of 221 ± 5.4 km yr^{-1} (SE) on the northern side and 70 km yr^{-1} (SE = 3 km yr^{-1}) on the southern side. Among the ecological variables studied, climate match, the year of introduction and interactions of both factors were significantly correlated with dispersal success. According to our observations, subtropical species introduced before 1980 have an advantage in the dispersal process. The transition from the Levantine basin to the western basin is clearly associated with a deceleration in dispersal rate that is likely due to a thermal barrier. In addition, we showed that species with pelagic propagules (eggs) tend to disperse more on the northern side (in comparison to the southern side) than do species with benthic propagules. This pattern was related to the counterclockwise surface circulation in the Levantine basin. We concluded that crossing the Suez Canal does not guarantee successful invasion and widespread dispersal of fish populations and that species ecology is a key determinant for dispersal success.

KEY WORDS: Lessepsian fish · Climate match · Exotic · Dispersal · Suez Canal · Mediterranean Sea · Propagules · Year of introduction

INTRODUCTION

Dispersal of exotic species has produced marked changes in the distribution of fish species all over the world. Some 'winner' species have expanded their geographic range to the detriment of many 'loser' species (McKinney & Lockwood 1999). Consequently, a worldwide homogenisation of biota has been observed for many taxonomic groups (Olden et al. 2004). Among the human influences on species dispersal, the creation of a canal connecting 2 marine biomes

that evolved independently is certainly one of the most spectacular. These large-scale experiments provide unique opportunities to study the processes that shape biodiversity patterns and, in particular, the rate of biotic exchanges and the determinants of invasive success for introduced species (Smith et al. 2004).

The Suez Canal, completed in 1869, was the first artificial connection between 2 naturally separated seas — the Mediterranean and Red Seas (Fig. 1). Hundreds of artificial canals have been created all over the world, but, with the exception of the Suez and Panama canals
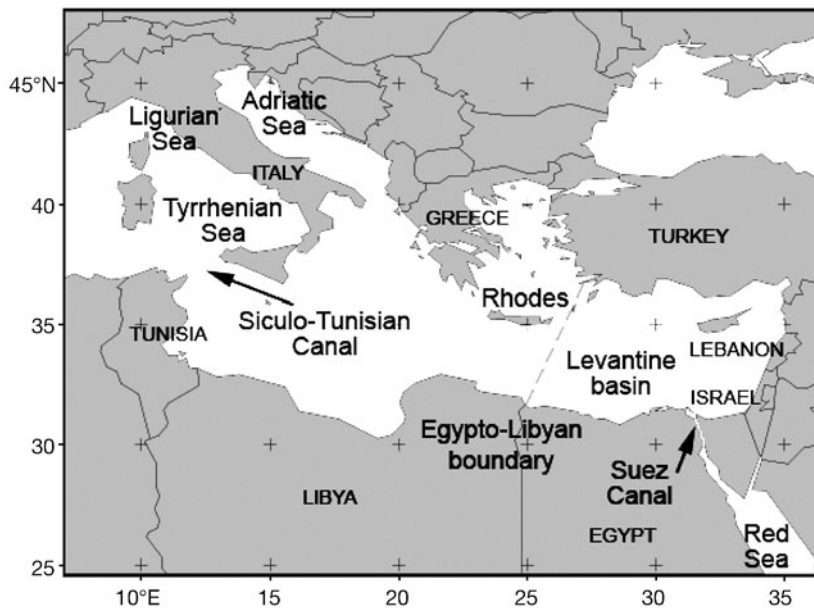
Fig. 1. Map of the Mediterranean Sea with the most important biogeo-
graphic features

(connecting 2 isolated seas), they connect a sea to a river
(e.g. Canal du Midi in France connecting the Mediter-
ranean Sea to the Garonne river), a sea to a lake (e.g.
Saint Lawrence Seaways in Canada connecting the
Atlantic Ocean to the Great Lakes), or 2 seas that are
already naturally connected (e.g. Corinth Canal connect-
ing the Ionian Sea and the Aegean Sea in Greece, Kiel
Canal in Germany connecting the North Sea and the
Baltic Sea) (The International Canal Monuments List
1996, www.icomos.org/ studies/canals-toc.htm).

Just after completion of the Suez Canal in 1869, mi-
gration of Red Sea species into the Mediterranean Sea
was blocked by the presence of hypersaline lakes in-
side the canal. After the salinity of these lakes equal-
ized, fish species began migrating into the Mediter-
ranean Sea (George & Athanassiou 1967), where 63
species were subsequently recorded. Species migrating
into the Mediterranean via the Suez Canal have been
termed Lessepsian species in reference to the canal's
architect, Ferdinand de Lesseps. In contrast, Goren &
Dor (1994) recorded only 15 anti-Lessepsian fishes.
According to some authors, it remains difficult to list
'anti-Lessepsian' fishes (Tortenese 1984). Lessepsian
flux of Red Sea fish species into the Mediterranean Sea
is favoured by the dominant current in the Suez Canal,
which flows South to North after the construction of the
Aswan Dam in 1965, because the Red Sea is higher
than the Eastern Mediterranean Sea (Hassan et al.
2003). In the context of global warming, most fish
species are expected to shift their ranges of distribution
polarwards, rather than adapt to warmer temperatures
in situ (Huntley 1991).

The Mediterranean and Red Seas had
very different faunal communities before
completion of the Suez Canal, because the
former is naturally connected to the Atlantic
Ocean, while the latter is under the influ-
ence of the Indo-Pacific Ocean. Moreover,
and in contrast to the Panama Canal (Smith
et al. 2004), the Suez Canal connects 2 semi-
closed seas with a high degree of endemism
(8.8% for the Mediterranean Sea) (Quig-
nard & Tomasini 2000). Thus, the impact of
the Suez Canal on the biodiversity of both
seas is potentially very important, because
species assemblages are likely to become
increasingly homogenised over time. In ad-
dition, local diversity loss can be expected if
native species are endangered by the
spread of exotic species. In our study, we
focussed exclusively on the ability of intro-
duced Lessepsian species to disperse in the
Mediterranean Sea, not on the initial
introduction of fishes from the Red Sea to
the Mediterranean Sea (Duncan et al. 2001).

Some fish species succeeded in the colonisation of the
entire Mediterranean, some remained limited to the
eastern part of the basin, and others have never been
recorded again after their first observation. Until
now, the majority of studies on Lessepsian migration
has been descriptive, reporting new occurrences of
Lessepsian species (e.g. Golani 2000, Corsini et al.
2005, Golani & Sonin 2006), setting up inventories (e.g.
Torcu & Mater 2000, Spanier 2000, Harmelin Vivien et
al. 2005, Golani 2005), or describing the ecological im-
pact of new arrivals on the Mediterranean fauna (e.g.
Goren & Galil 2005). A more challenging issue is to
search for either species or habitat characteristics that
can predict invasiveness (Goodwin et al. 1999, Colautti
et al. 2006, Strauss et al. 2006). For instance, recent
studies showed how some life history and ecological
traits predispose certain species to establish themselves
or to become invasive outside of their native range
(Ruesink 2005). Furthermore, the identification of such
biological traits common to invader species may allow
us to anticipate future colonisations. Few studies have
examined the factors determining the invasive success
of Lessepsian fishes in their new environment (Ben
Eliahu & Golani 1990), and none have included all of
the species ever recorded. In our study, we recon-
structed the spatio-temporal dynamic of all Lessepsian
fish species since their first record from the Mediter-
ranean, and we tested whether their dispersal success
can be related to functional traits (location in the water
column, body size), life history traits (reproduction,
growth), year of introduction into the Mediterranean,
confamilial resistance and climate match.

MATERIALS AND METHODS

Species list and calculation of dispersal rates. We compiled a list of Lessepsian fishes using and updating the CIESM Atlas (Golani et al. 2002). Our list includes 63 species (see Table 1 for the complete list). Since completion of this study, 3 new Lessepsian fishes have been recorded: *Iniistius pavo* (Corsini et al. 2006), *Apogon queketti* (Eryilmaz & Dalyan 2006) and *Decapterus russelli* (Golani 2006), increasing the total number of Lessepsian fishes to 66. These species were not included in our list or in our analysis, since they are less likely to have had enough time to spread along the Mediterranean coast and would consequently introduce bias into our analysis.

We compiled a bibliography of Lessepsian fish species recorded from the Mediterranean between 1896 and 2006 (Table 1). Each record was mapped using the Geographical Information System (GIS) software ArcView 3.3. Using this application, we measured the distance covered by each fish species along the coast line over a period of time, and then used this data to calculate their dispersal rate. Since it is not likely that

dispersal is achieved by swimming along the entire coast, we did not include the coastline in bays and along islands of the Aegean Sea and the Gulf of Taranto in the distance covered by each species. Instead, the distances were measured in direct lines. Because most of the species show an asymmetrical pattern of dispersal between the southern and the northern Mediterranean — i.e. they do not disperse equally on both sides — we calculated and analysed a propagation speed for these two regions separately. As the number of records was not the same for all the species, two dispersal rates were estimated:

$$S_T^n = \frac{d_T^n}{Y_f^n - Y_0}; \; S_T^s = \frac{d_T^s}{Y_f^s - Y_0} \tag{1}$$

$$S_t^n = \frac{d_{t+1}^n - d_t^n}{Y_{t+1}^n - Y_t^n}; \; S_t^s = \frac{d_{t+1}^s - d_t^s}{Y_{t+1}^s - Y_t^s} \tag{2}$$

where n is northern direction of dispersal, s is southern direction of dispersal, d_t^n is the total distance covered on the northern and d_t^s, the total distance covered on the southern side; Y_0 is the year of the first record in the Mediterranean Sea, Y_f^n, is the year of the record furthest

Table 1. Lessepsian species and their invasive success. YI: year of introduction, DS: dispersal success (1 = absence of dispersal, 2 = weak dispersal, 3 = strong dispersal), CM: climate match (t = tropical, st = subtropical), PWC: position in the water column (p = pelagic, b = benthic), ML: maximum total length (cm), Pr: propagule (p = pelagic, b = benthic), CR: confamilial resistance, ND: dispersal on the northern side (km), SD: dispersal on the southern side (km). Data for CM, PWC, ML, Pr and CR from FishBase unless otherwise indicated by superscripts

Species	Family	YI	DS	CM	PWC	ML	Pr	CR	ND	SD	Reference
Atherinomorus lacunosus	Atherinidae	1902	3	st	p	25	b	3	1213	1953	Tillier (1902)
Alepes djedaba	Carangidae	1927	2	st	b	40	p	15	2274	407	Steinitz (1927)
Hemiramphus far	Hemiramphidae	1927	2	st	p	45	b	1	2301	546	Steinitz (1927)
Coryogalops ochetica	Gobiidae	1927	1	t	b	6	b	49	0	0	Norman (1927)
Siganus rivulatus	Siganidae	1927	3	st	b	27	b	0	3680	1522	Steinitz (1927)
Stephanolepis diaspros	Monacanthidae	1927	3	t	b	25	p	0	2245	2548	Steinitz (1927)
Liza carinata	Mugilidae	1929	2	t	p	18	p	7	949	0	Norman (1928)
Lagocephalus spadiceus	Tetraodontidae	1930	2	st	b	20	b[B]	2	2343	23	Sanzo (1930)
Leiognathus klunzingeri	Leiognathidae	1931	3	t	b	110	p	0	5500	933	Spicer (1931)
Sphyraena chrysotaenia	Sphyraenidae	1931	3	t	p	30	p	3	5435	1702	Spicer (1931)
Parexocoetus mento	Exocoetidae	1935	3	t	p	11	b	4	3700	2834	Bruun (1935)
Scomberomorus commerson	Scombridae	1935	3	t	p	240	p	13	859	894	Hornell (1935)
Herklotsichthys punctatus	Clupeidae	1943	2	st	p	9	p	8	912	541	Bertin (1943)
Apogon pharaonis	Apogonidae	1947	2	st	b	10	b	2	1600	0	Haas & Steinitz (1947)
Sargocentrum rubrum	Holocentridae	1947	3	st	b	32	p	0	1666	1522	Haas & Steinitz (1947)
Upeneus moluccensis	Mullidae	1947	3	st	b	20	p	4	0	0	Haas & Steinitz (1947)
Sorsogona prionota	Platycephalidae	1947	1	t	b	22	p	0	3020	1862	Golani & Ben Tuvia (1990)
Dussumieria elopsoides	Dussumieriidae	1949	2	st	p	20	p	8	895	414	Lissner (1949)
Upeneus pori	Mullidae	1950	3	st	b	30	p	4	1600	2834	Kosswig (1950)
Callionymus filamentosus	Callionymidae	1953	2	st	b	20	p	7	1452	0	Ben Tuvia (1953)
Cynoglossus sinusarabici	Cynoglossidae	1953	2	t	b	10	p	3	895	592	Ben Tuvia (1953)
Platycephalus indicus	Platycephalidae	1953	2	st	b	100	p	0	572	420	Ben Tuvia (1953)
Saurida undosquamis	Synodontidae	1953	3	st	b	50	p	1	3434	1878	Ben Tuvia (1953)
Himantura uarnak	Dasyatidae	1955	2	st	b	200	b	6	912	0	Ben Tuvia (1955)
Siganus luridus	Siganidae	1955	3	st	b	30	b	0	4500	3407	Ben Tuvia (1964)
Etrumeus teres	Dussumieriidae	1963	2	st	p	30	p	8	2800	424	Whitehead (1963)
Hyporhamphus affinis	Hemiramphidae	1964	1	t	b	38	b	1	0	0	George et al. (1964)
Tylosorus choram	Belonidae	1967	1	t	b	120	b	3	0	0	Parin (1967)

Table 1 (continued)

Species	Family	YI	DS	CM	PWC	ML	Pr	CR	ND	SD	Reference
Epinephelus coïoïdes	Serranidae	1969	3	st	b	120	p	12	415	0	Ben Tuvia & Lourie (1969)
Epinephelus malabaricus	Serranidae	1969	1	t	b	234	p	12	0	0	Ben Tuvia & Lourie (1969)
Pomadasys stridens	Haemulidae	1969	3	t	b	20	p	1	8312	420	Torchio (1969)
Crenidens crenidens	Sparidae	1970	3	st	b	30	p	22	552	1522	Lourie & Ben Tuvia (1970)
Rastrelliger kanagurta	Scombridae	1970	1	t	p	35	p[A]	13	0	0	Collette (1970)
Terapon puta	Teraponidae	1976	2	t	p	16	p	0	744	580	Ben Tuvia (1976)
Lagocephalus suezensis	Tetraodontidae	1977	2	st	b[B]	18	b[B]	2	1806	28	Mouneimne (1977)
Pelates quadrilineatus	Teraponidae	1977	2	st	b	30	p	0	912	753	Ben Tuvia (1977)
Sillago sihama	Sillaginidae	1977	2	t	b	30	p	0	762	790	Mouneimne (1977)
Spratelloides delicatulus	Clupeidae	1978	1	t	p	7	b	8	0	0	Ben Tuvia (1978)
Lutjanus argentimaculatus	Lutjanidae	1979	1	st	b	150	p	0	0	0	Mouneimne (1979)
Pempehris vanicolensis	Pempheridae	1979	3	t	b	20	p	0	2153	2834	Mouneimne (1979)
Muraenesox cinereus	Muraenesocida	1982	1	st	b	16	p	1	0	0	Golani & BenTuvia (1982)
Oxyurichthys petersi	Gobiidae	1983	2	t	b	18	b	49	912	0	Ben Tuvia (1983)
Rachycentron canadum	Rachycentridae	1986	1	st	b	200	p	0	0	0	Golani & Ben Tuvia, (1986)
Silhouetta aegyptica	Gobiidae	1986	2	t	b	4	b	49	570	0	Miller & Fouda (1986)
Torquigener flavimaculosus	Tetraodontidae	1987	2	t	b	13	p	2	1327	0	Golani (1987)
Tetrosomus gibbosus	Ostraciontidae	1988	1	t	b	30	p	0	0	0	Spanier & Goren (1988)
Pteroscirtes ancylodon	Blenniidae	1989	2	t	b	11.5	b	20	1589	0	Goren & Galil (1989)
Papilloculiceps longiceps	Platycephalidae	1990	1	t	b	70	p	0	0	0	Golani & Ben Tuvia (1990)
Pteragogus pelycus	Labridae	1992	2	st	b	15	p	19	1666	0	Golani & Sonin (1992)
Pterois miles	Scorpaenidae	1992	1	t	b	35	p	8	0	0	Golani & Sonin (1992)
Rhabdosargus haffara	Sparidae	1992	1	t	b	35	p	22	0	0	Golani (1992)
Sphyraena flavicauda	Sphyraenidae	1992	3	t	b	60	p	3	1666	2209	Golani (1992)
Rhynchoconger trewavasae	Congridae	1993	1	st	b	57	p	3	0	0	Ben Tuvia (1993)
Chilomycterus spilostylus	Diodontidae	1993	1	t	b	34	p	0	0	0	Golani (1993)
Abudefduf vaigiensis	Pomacentridae	1998	3	t	b	20	b	2	8198	0	Goren & Galil (1998)
Fistularia commersonii	Fistulariidae	2000	3	t	b	160	p	1	3482	2153	Golani (2000)
Hippocampus fuscus	Syngnathidae	2001	2	t	b	14.4	b	12	1259	520	Golani & Fine (2002)
Plotosus lineatus	Plotosidae	2001	1	t	b	32	b	0	0	0	Golani (2002)
Heniochus intermedius	Chaetodontidae	2002	1	t	b	20	p	2	0	0	Gökoglu et al. (2003)
Scarus ghobban	Scaridae	2002	2	t	b	90	p	2	240	0	Goren & Aronov (2002)
Lagocephalus sceleratus	Tetraodontidae	2004	2	t	b	110	b[B]	2	1985	0	Filiz & Er (2004)
Nemipterus japonicus	Nemipteridae	2005	1	t	b	32	p	0	0	0	Golani & Sonin (2006)
Tylerius spinosissimus	Tetraodontidae	2005	1	st	b	12	p	2	0	0	Corsini et al. (2005)

[A]B. Colette pers. comm. (National Marine Fisheries Service Systematics Laboratory, Washington)
[B]Information not available for the species: we used information from the family level, making the assumption that co-familiar species are consistent for this trait

from the Suez Canal on the northern and Y_f^s on the southern side, respectively; and Y_t^n Y_{t+1}^n, Y_t^s, Y_{t+1}^s, are the record in year t and the following record ($t+1$) on the northern side and on the southern side, respectively.

Eq. (1) 1 was used to calculate the propagation speed S_T between the first record and that furthest from the Suez Canal, expressed in km yr^{-1}. Eq. (2) was used to reconstruct the chronological series of the dispersal speed S_t per record interval, i.e. at each new record.

Since dispersal rates were not accurate enough to be included in our statistical analysis, we used them only for a descriptive purpose. In order to provide a trend for the dispersal rate, we plotted the distance crossed against time. However, since this was only possible where the number of records was sufficient (at least 3) and this requirement was not met for the southern side of the Mediterranean, we produced the plots only for the northern side.

In order to investigate the ecological correlates of dispersal success, we built a categorical variable summarizing the species ability to spread over the Mediterranean Sea. The 63 fish species (Table 1) were assigned to 3 categories: (1) absence of dispersal, including the species that were recorded once and have never been recorded since; (2) weak dispersal, including species that were not able to spread beyond the biogeographical boundaries of the Levantine basin, i.e. the island of Rhodes (northern side) and the Egypto-Libyan boundary (southern side); and (3) strong dispersal, including species distributed beyond the above boundaries (Fig. 1). Dispersal success was estimated independently from observed abundances. We considered that even if a record includes only a small number of specimens, it reveals the spread of the species. Moreover, as most of the species follow a positive dispersal range–abundance

relationship (Gaston 2003), we hypothesized that spatial dispersal and total abundance in the Mediterranean Sea may evolve proportionally.

Ecological variables. We compiled a database containing variables that are likely to influence invasion success for each of the species: climate match, position in the water column, maximum length, presence of propagules, confamilial resistance, and year of introduction.

Climate match: Invasion success of some exotic species has been shown to be positively related to the match between native and colonised environment (Wolf et al. 1998, Duncan et al. 2001). As this information often lacks large-scale studies, the climate match has been explored by comparing the latitude of the native range to the introduction latitude (Blackburn & Duncan 2001). A species that is introduced at a latitude very close to its native latitude is more likely to experience rather similar thermal conditions, and thus more likely to establish successfully. Based on these assumptions, subtropical species are more likely to disperse over the Mediterranean Sea than tropical species because of the difference in their tolerance to cold water. For our study, each species was considered either as a tropical species, i.e. preferring water temperatures over 20°C, or as a subtropical species, i.e. preferring water temperatures between 10°C and 20°C, in their original environment. These temperature preferences were taken from FishBase (Froese & Pauly 2006).

Position in the water column: Pelagic fishes are more prone to undertaking migrations than benthic species. The former have a higher swimming performance than the latter, due to their hydrodynamic body shape (e.g. Bardin & Pont 2002). Thus, we hypothesized that pelagic species a have higher dispersal ability than benthic species. Information on the position in the water column of each species was taken from FishBase (Froese & Pauly 2006).

Maximum length: Fish species with rapid growth and a high reproduction rate may disperse better because invaders have to breed quickly to avoid extinction (McArthur & Wilson 1967). Thus, species with early sexual maturity are more likely to establish themselves in a new environment than others. Since sexual maturity is highly positively correlated to the maximum length (Peters 1983, Savage et al. 2004), we assumed that small species with earlier sexual maturity are more likely to disperse over the Mediterranean Sea than larger species. Maximum length data were taken from FishBase (Froese & Pauly 2006).

Propagules: Major oceanic currents may allow certain marine species to disperse over extremely long distances (Shanks et al. 2003). Species whose propagules have the ability to disperse more widely are expected to achieve a wider geographic range (Emlet 1995, Gaston 2003). Fish propagules are larvae and eggs. According to Leis

(1991), factors affecting larval dispersal are behaviour, swimming speed and duration of the pelagic larval phase. Because data for the larvae of all species in this study were not available, we considered only eggs, even though some demersal spawners have pelagic larvae and their dispersal ability is not less than that of pelagic spawners. We hypothesized that fish species with pelagic eggs have a wider geographic range than species with benthic eggs. Although some benthic fishes invest more in parental care, they are weak dispersers. Conversely, one may also argue that parental care increases larval survival and could therefore serve to enhance fish population establishment. Therefore, these 2 alternative hypotheses were tested. We also investigated which type of propagule, pelagic or benthic, disperses better in terms of distance covered by each species on the northern vs. the southern side of the Mediterranean. This method has the advantage of avoiding the bias of detectability, because species with pelagic propagules and species with benthic propagules have the same probability of being captured. Information about propagule type (pelagic or benthic) was taken from FishBase (Froese & Pauly 2006) and existing literature. Where data about fish propagules were not available for a species we used information from the family level, making the assumption that co-familiar species are consistent for this trait.

Confamilial resistance: We hypothesized that invading species with no or very few confamilial counterparts in the Mediterranean Sea would have a higher dispersal success rate than species which encounter close relatives because of the absence of competition for resources (habitat and food), based on observations by Davis et al. (2000) and Strauss et al. (2006). On the other hand, one could maintain that the dispersal potential of invasive species having confamilial species already installed in the Mediterranean Sea may be facilitated due to the availability of suitable habitats. This 'confamilial resistance' hypothesis was initially proposed by Darwin (1859). We tested these 2 opposite hypotheses by comparing the taxonomy of species coming from the Red Sea to the Mediterranean species pool. The confamilial resistance was estimated based on the number of Mediterranean species found in the family of each Lessepsian species.

Year of introduction: One potential confounding variable in our study is the year of introduction. Species introduced at the beginning of the century were more likely to disperse than more recently introduced species. For the purpose of our study, the year of first record was treated as the year of introduction into the Mediterranean.

Statistical analyses. We carried out 2 types of complementary analyses. First, we tested the effect of each variable on the dispersal success individually. Given

that our dataset was limited (63 species), and that the assumptions of parametric tests were not met by our data, we used a non-parametric chi-squared test for evaluating the qualitative relationships between ecological variables and dispersal success. We used the modalities 'tropical fish' (t) and 'subtropical fish' (st) for the climate match, the modalities 'benthic fish' (b) and 'pelagic fish' (p) for the position in the water column, and the modalities 'benthic eggs' (b) and 'pelagic eggs' (p) for the type of propagule. For the quantitative variables (mean values of maximum fish length: ML, confamilial resistance: CR, year of introduction: YI), we used the non-parametric Kruskal–Wallis test. This test was also used to analyse the influence of the propagule type on the relative dispersal on the northern and southern side of the Mediterranean Sea, using the difference $d^n - d^s$ as a predicted variable (where d^n is the distance covered on the northern side and d^s is the distance covered on the southern side). All statistical tests were performed using the software Minitab 12.2.

In order to prioritize the factors related to dispersal success (coded as a binary variable: absence or presence of dispersal), and to investigate potential subsequent interactions between factors, we followed a multiple logistic regression approach (Generalized Linear Model, GLM, with a binomial error and a logit link) in a second step. Starting with a maximal model including all 6 factors listed above and all second order interactions, the relative importance of factors was assessed using a backward selection procedure. The significance of the increase in deviance resulting from the deletion of a term in the model was estimated using chi-squared deletion tests (Crawley 2007). The minimal adequate model was selected as the one containing nothing but significant terms. We used the commands 'glm', 'summary' and 'anova' from the R statistical and programming environment (R Development Core Team 2007) to parameterize and select the models and to perform analyses of deviance.

Surface temperature map. Using the GIS software (ArcView 3.3), we generated a map using data from the National Climatic Data Center (NCDC) National Operational Model Archive and Distribution System Meteorological Data Server (NOMADS) of the US - National Oceanic and Atmospheric Administration (NOAA) Satellite and Information Service (at www. osdpd.noaa.gov/PSB/EPS/SST/al_climo_mon.html).

RESULTS

The first record of a Lessepsian fish species in the Mediterranean, *Atherinomorus lacunosus,* is attributed to Tillier (1902). The most recent record we took into account for our analysis is from 2005, *Tylerius*

spinosissimus (Corsini et al. 2005). The Lessepsian fish arrivals in the Mediterranean Sea continually increased between the 1930s and the 1950s (Fig. 2a). We observed another period of increased dispersal of Lessepsian species starting in 1980 from an average of 0.7 for the 1980s to 2 species yr^{-1} for the most recent years (Fig. 2a). Lessepsian species belonged to 45 families and 57 genera (Table 1). The most frequently represented families are the Tetraodontidae with 5 species, followed by the Clupeidae with 4 species and the Gobiidae and the Platycephalidae with 3 species each. Overall, 51 species are benthic while 12 are considered to be pelagic. The maximum size of these species varied from 4 cm to 240 cm, the most frequent maximum size (mode of distribution) being between 20 cm and 30 cm.

Dispersal rates of Lessepsian fishes

The western-most record of a Lessepsian species on the northern side of the Mediterranean was that of *Pomadasys stridens* in the Ligurian Sea (Torchio 1969). On the southern side of the Mediterranean Sea, the western most record was that of *Fistularia commersonii* in Sardinia (Pais et al. 2007). The species propagation rate analysis revealed that 20 species did not successfully
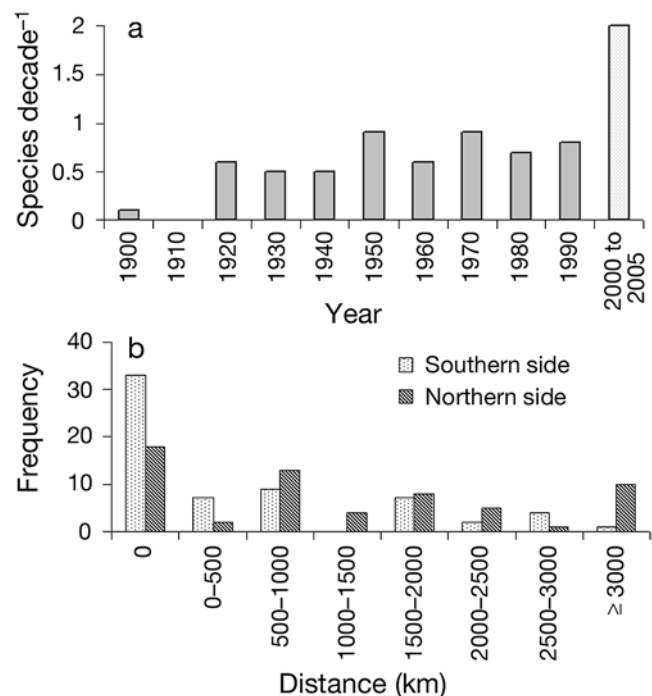

Fig. 2. (a) Introduction of Lessepsian fish species in the Mediterranean Sea over the study period. Bars represent the annual mean number of Lessepsian introductions per decade. The last column only includes values from 2000 to 2005; (b) Observation frequency (number of Lessepsian species) and distance from entry point (Suez Canal) on the northern and southern sides

disperse after they were first recorded. 24 species were limited to the coast of the Levantine basin while 19 species, corresponding to 30 % of the Lessespian pool, succeeded in dispersing beyond those limits.

The number of species observations and distance from their point of entry on the northern and southern sides of the Mediterranean are shown in Fig. 2b., illustrating the different dispersal rates for the two areas. We did not compare these 2 distributions statistically since fishing effort and scientific investigation are not comparable between the 2 sides. The dispersal rate was calculated for all species that were recorded at least 3 times (16 species): on average, Lessepsian species spread at a rate of 122 km yr^{-1} (SE = 2.1 km yr^{-1}) on the northern side of the Mediterranean Sea.

Dispersal rate appeared to increase over time for the species restricted to the Levantine basin, i.e. those assigned to the category 'weak dispersal' (e.g. *Apogon pharaonis* Fig. 3a, *Callionymus filamentus* Fig. 3i, *Hemiramphus far* Fig. 3c, *Herklotsichthys punctatus* Fig. 3d, *Lagocephalus suezensis* Fig. 3e and *Petroscirtes ancylodon* Fig. 3f). Conversely, for the species
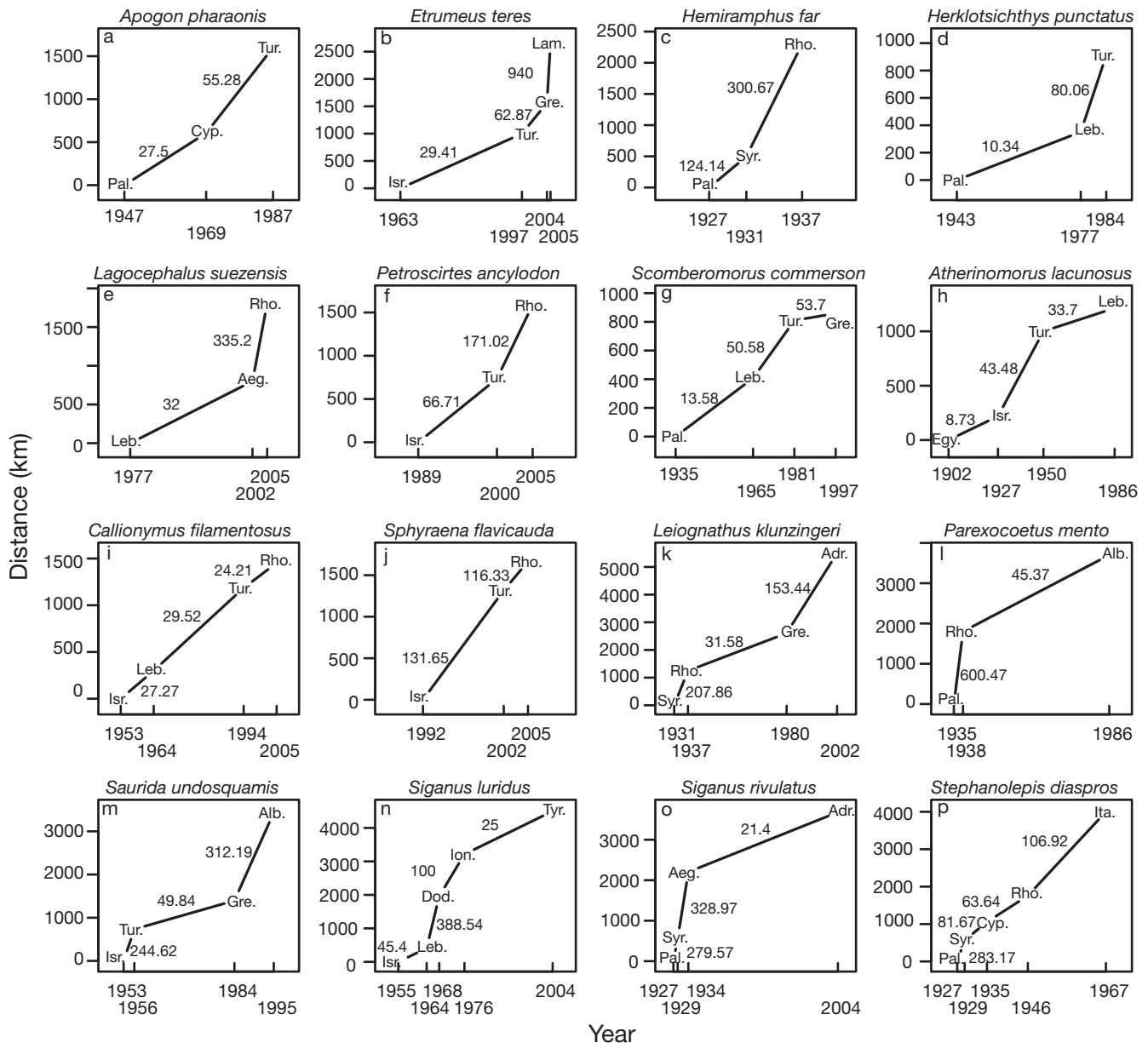
Fig. 3. Dipersal of 16 Lessepsian species recorded ≥ 3 times in the northern Mediterranean. Location of new records and average speed (km yr^{-1}) of dispersal between locations indicated within and beside curves, respectively. Places are: Adriatic Sea (Adr.), Aegean Sea (Aeg.), Albania (Alb.), Cyprus (Cyp.), Dodecanese (Dod.), Egypt (Egy.), Greece (Gre.), Ionian Sea (Ion.), Israel (Isr.), Italy (Ita.), Lampedusa (Lam.), Lebanon (Leb.), Palestine (Pal.), Rhodes (Rho.), Syria (Syr.), Turkey (Tur.) and Tyrrhenian Sea (Tyr.)

that spread beyond the limits of the Levantine (strong dispersal) towards the northern side of the Mediterranean Sea, the dispersal speed decreased at transitional zones between basins (e.g. *Leiognathus klunzingeri* Fig. 3k, *Parexocoetus mento* Fig. 3l, *Siganus luridus* Fig. 3n, and *Siganus rivulatus* Fig. 3o) when they reached the Adriatic and the Tyrrhenian seas. For instance, the dispersal rate of *L. klunzingeri* (Fig. 3k) was 207.8 km yr^{-1} until the species reached the island of Rhodes, and dropped to 31.6 km yr^{-1} between the island of Rhodes and the eastern coast of Greece while crossing the Aegean Sea. After this barrier was crossed, the speed increased again to 153.4 km yr^{-1} towards the Adriatic Sea. During the spread of *P. mento* from the island of Rhodes to Albania, the dispersal speed dropped from 600.4 km yr^{-1} to 72.9 km yr^{-1}. The same deceleration was observed for *S. luridus* during its transition from the Aegean Sea to the Adriatic Sea, where the dispersal rate decreased to less than a 7th of its previous value (Fig. 3n). It appears that the transition between different water bodies acts as a geographical barrier.

Of the 16 species for which dispersal rate trends were reconstructed, and excluding those that decelerated when crossing geographical barriers (6 species), 70% accelerated their propagation after the 1980s, with the average speed increasing about 5-fold. The species whose dispersal rate decelerated before reaching the island of Rhodes are *Atherinomorus lacunosus*, *Callionymus filamentus* and *Sphyraena flavicauda.*

Variables related to dispersal

Among the 6 variables tested, only the climate match (CM) and year of introduction (YI) were significantly correlated with the 3 dispersal success categories (absence, weak or strong dispersal, Table1). Tropical species spread less than expected by chance, while the spread of subtropical species, dispersing over areas outside of the Levantine basin, was greater than expected. For example, *Oxyurichthys petersi* (Fig. 4a), a tropical species, was limited to the eastern part of the Mediterranean Sea and showed weak dispersal, while the subtropical *Siganus luridus* (Fig. 4b) spread over the western part and showed strong dispersal. In addition, it appears that species that dispersed successfully were those that had been introduced a long time ago (Table 2). Species with pelagic propagules were more likely to disperse over the northern side than species with benthic propagules (Table 2).

The minimal adequate model from the logistic regression analysis predicted dispersal success (coded as a binary variable: absence or presence of dispersal)
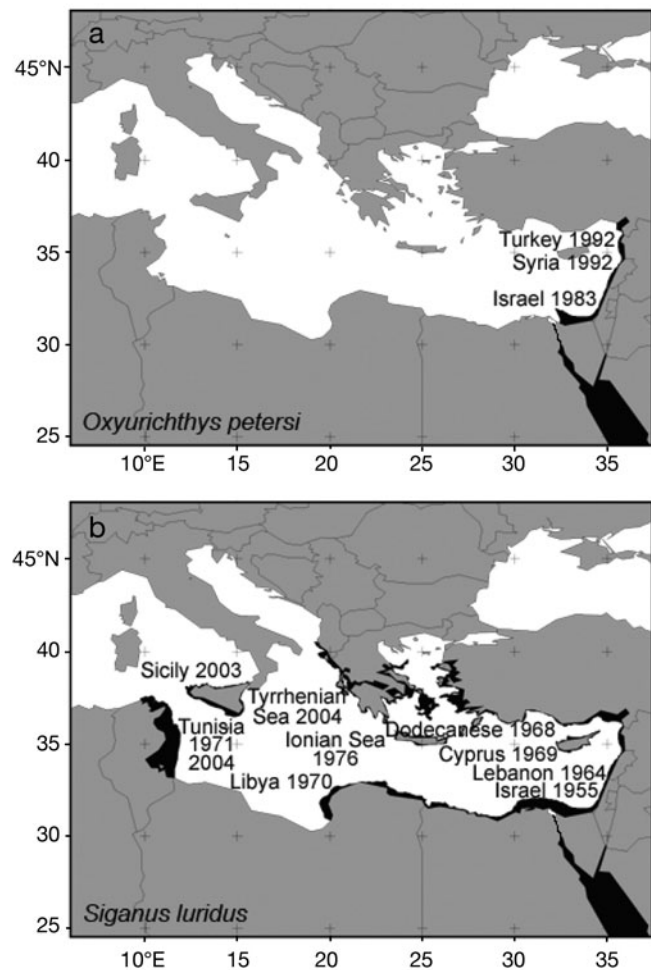

Fig. 4. *Oxyurichthys petersi* and *Siganus luridus*. Two examples of propagation (black shading) in the Mediterranean Sea: (a) *O. petersi*, a tropical species with weak dispersal limited to the eastern part, (b) *S. luridus,* a subtropical species with strong dispersal over the western Mediterranean

as a function of YI, CM, and the interaction between these 2 factors (CM:YI, Table 3). The 'interaction' term represents the joint multiplicative effect of the year of introduction and climate match and indicates the interactive influences of these variables on the dispersal rate beyond the corresponding main effects. These results corroborate and refine the conclusions from the independent tests for each factor: Lessepsian fishes with an earlier year of introduction and a subtropical origin are more likely to disperse successfully (Table 3). However, the GLM results (factor coefficients) reveal that climate match is the major influence on the dispersal success compared to the year of introduction. In addition, the significant interaction term showed that the year of introduction does not have the same effect on subtropical and tropical species: for tropical species, the year of introduction

Table 2. Chi-squared (CS) and Kruskal-Wallis (KW) tests for the effect of predictors on the dispersal success of Lessepsian fishes in the Mediterranean Sea. CM: climate match, PWC: position in the water column, ML: maximum total length, Pr: propagule type, Pr/NS: effect of the propagule type on the dispersal on the northern side versus the southern side, CR: confamilial resistance, YI: year of introduction. (ns) not significant, *p < 0.05, **p < 0.01

	CM	PWC	ML	Pr	Pr/NS	CR	YI
CS	7.48*	1.67ns		1.19ns			
KW			40.3ns		5.08*	5.9ns	10.6**

had a near to linear negative effect, whereas it had a logistic-type effect for subtropical species (Fig. 5). In summary, our results indicate that all subtropical species introduced before 1980 (Fig. 5: inflexion point of the logistic curve) have successfully dispersed, while the probability of tropical species to disperse through the Mediterranean decreases linearly with their date of introduction.

DISCUSSION

Dispersal rates

Our results revealed that, of the invasive species for which the dispersal rate could be assessed, the dispersal of 6 species had a logistic curve shape (*Leiognathus klunzingeri*, Fig. 3k; *Parexocoetus mento* Fig. 3l, *Saurida undosquamis* Fig. 3m, *Siganus luridus* Fig. 3n, *Siganus rivulatus* Fig. 3o and *Stephanolepis diaspros* Fig. 3p), which is typical for invasive species (Hengeveld 1989, Silva et al. 2002). The slowing of the dispersal rate near the inflexion in the curve happens around the island of Rhodes, which appears critical for Lessepsian species. The island of Rhodes lies at the transition between the warm Levant basin and the cooler western part of the Mediterranean Sea. At this point, the mean sea surface temperature drops from 20.8°C to 18.95°C (Fig. 6). The island of Rhodes represents a thermal barrier that decelerates species dispersal. This

Table 3. Selected logistic regression model relating dispersal success to climate match and year of introduction. df: degrees of freedom, Dev: deviance, %Exp: percent of explained deviance, RD: residual deviance, CM: climate match, YI: year of introduction

Factors	Estimate	df	Dev	%Exp	R df	RD	p(>|chi|)
Constant	349.02				62	78.74	
CM	−313.81	1	3.96	28.42	61	74.77	0.04
YI	−0.17	1	8.664	32.15	60	66.11	0.003
CM:YI	0.1584	1	8.49	36.89	59	57.61	0.004

hypothesis was consistently supported by our data, because most of the species reaching the western basin (*L. klunzingeri, P. mento, S. luridus* and *S. rivulatus*) slowed down during their passage from one basin to another (Fig. 3). This general trend supports the idea that observed decreases in dispersal rates are linked to the passage through thermal barriers. However, we used rough estimations of dispersal rates for our study that cannot be used to make predictions about future dispersal of Lessepsian fishes.

Variables correlated with dispersal

Six variables, potentially correlated with dispersal success, were examined: year of introduction, climate match, location in the water column, maximum fish length, propagule type and confamilial resistance. Among these ecological variables, climate match and year of introduction showed a significant relationship with dispersal success when split into 3 categories: subtropical species and species introduced early had an advantage in the dispersal. When we tested the relative dispersal on both sides of the Mediterranean, it appeared that species with pelagic propagules were more prone to disperse on the northern side than species with benthic propagules. By using logistic regression we showed that the dispersal success of Lessepsian fishes is significantly explained by the climate match (main factor), the year of introduction, and the interaction of these two factors (Table 3). More precisely, we demonstrated that the year of introduction does not have the same effect on subtropical and tropical species (Fig. 5).
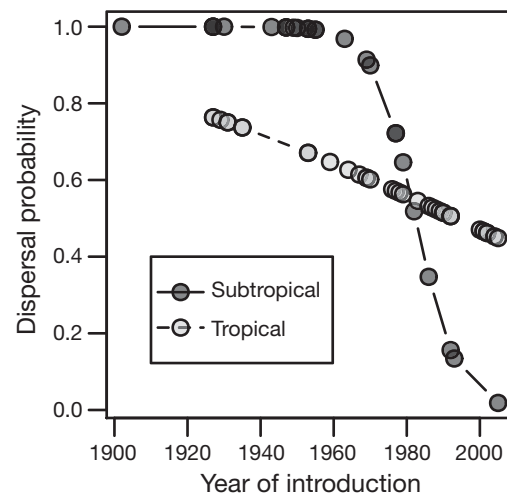

Fig. 5. Logistic model predicting probability of dispersal success for Lessepsian species by year of introduction and species origin (subtropical or tropical). The statistics of the model are summarized in Table 3
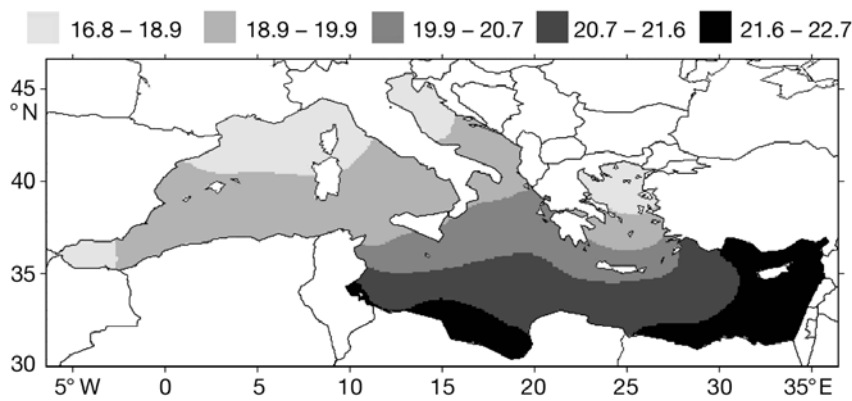
Fig. 6. Mean sea surface temperature (°C) in the Mediterranean Sea for the year 2000 (data from NCDC NOMADS Meteorological Data Server, NOAA)

Our results are in agreement with Blackburn & Duncan (2001), who also explored climate match by comparing the latitude of birds' native ranges to their introduction latitude. Their findings, as well as ours, suggest that dispersal success of exotic species depends on the suitability of the abiotic environment at their introduction site and that climate match is a useful tool for examining a species' potential success. Temperatures in the Mediterranean seem more suitable for subtropical than for tropical species. We found that subtropical fishes tend to spread more widely than tropical ones, which have more difficulties (more time needed) to extend away from their introduction site, due to minimal thermal tolerances.

The ability of species to establish themselves in new environments, to recover from disturbances and to adapt to varying environmental conditions, depends on their dispersal capacity and the amount of time passed since introduction. These are 2 fundamental elements of population ecology (Bobadilla & Santelices 2005). Dispersal capacity highly depends on the physical oceanographic processes, notably on the water circulation. In this study, we noticed that species with pelagic propagules tend to disperse more on the northern side (compared to the southern side) than do species with benthic propagules. This trend may be due to the general surface water circulation in the Eastern Mediterranean. The general surface circulation of the Mediterranean is strongly influenced by the circulation of the Atlantic current, whose counterclockwise trajectory has been studied since the beginning of the 20th century (Nielsen 1912, Ovchinnikov 1966). This current pattern was

confirmed by a recent study (Hamad et al. 2005) (Fig. 7). Pelagic propagules are more exposed to this pressure than benthic propagules, which may explain why species with pelagic propagules are more likely to disperse over the northern side, while species with benthic propagules disperse equally over the southern and northern sides. Therefore, the counterclockwise circulation in the Levantine basin appears to be the main forcing factor in the propagation of Lessepsian species with pelagic eggs.

Propagule pressure, in terms of size and number of individuals released, is emerging as a strong correlate of invasive success of organisms (Lockwood et al. 2005). In our study, we only considered the position of propagules (eggs) in the water column because data on larvae for all Lessepsian fishes included in this study was not available. We were also unable to control for phylogeny in our study because of the lack of molecular data on most of the species. Phylogenetic links between species may disrupt the observed distribution pattern when species are considered as independent while they are not (Ives & Zhu 2006). Phylogenetic control in correlative studies can be problematic when some genera are over-represented, given that traits are often conserved through lineages. However, most of the 63 Lessepsian species had very
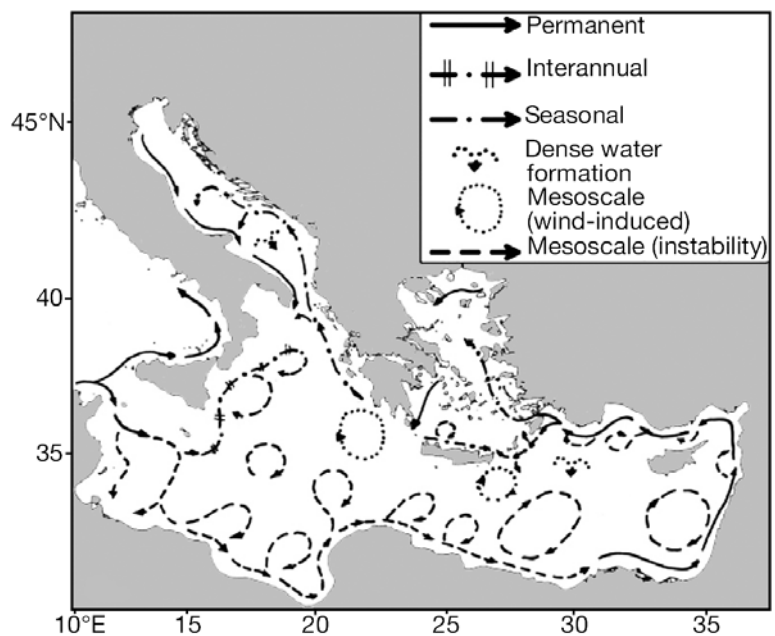

Fig. 7. Atlantic water circulation pattern of the eastern Mediterranean (from Hamad et al. 2005)

few co-genera and were divided into 45 families, diminishing the potential influence of phylogenetic links in our study.

Red herrings in inventorying Lessepsian fishes

Some records of Lessepsian species included in our database are somewhat odd. The first record of a species does not necessarily indicate that this species effectively arrived in the Mediterranean Sea at that date: it could have been caught and recorded many years after its first introduction. Moreover, after the reconstruction of dispersal rates, we noticed some unexpected 'jumps'. For instance, *Fistularia commersonii* (Fig. 8) was identified in the Mediterranean Sea for the first time in 2000 in Israel by Golani (2000). Two years later, it was recorded in Turkey by Gökoglu et al. (2002) and by Bilecenoglu et al. (2002) and around the Greek island of Rhodes by Corsini et al. (2002). In the summer of 2003, it was recorded in the northern Aegean by Karachle et al. (2004). One year later, it was recorded in Tunisia by Ben Souissi et al. (2004) and around the Italian island of Lampedusa by Azzurro et al. (2004), and in 2005 in Sardinia by Pais et al. (2007) (Fig. 8). This species is described as a 'Lessepsian sprinter' by Karachle et al. (2004). Indeed, we found that it progressed at the average speed of 1050 km yr^{-1} (SE = 154 km yr^{-1}) on the northern side. Another species, *Upeneus pori*, was recorded in Egypt by El Sayed (1994), then in southern Tunisia by Ben Souissi et al. (2005), without any intermediate record. *Pomadasys stridens* was recorded for the first time in the Gulf of Genoa by Torchio (1969) and then in Egypt by Ben Tuvia (1976).

The distribution of Lessepsian species may also be linked to species transport in ship's ballast waters, which represents an important vector for the introduction of non-indigenous species in marine environments (CIESM 2002, Streftaris et al. 2005). The potential influence of this vector is increasing because of the intense maritime traffic in the Mediterranean Sea (CIESM 2002). The contribution of shipping to the introduction of all alien species (fishes and other groups) into the Mediterranean has been estimated to be about 20% (Streftaris et al. 2005). However, ship-mediated introduction of fish into the Mediterranean Sea is surprisingly rare (Zibrowius 2002, Briggs 2007): among the Lessepsian fishes included in our study, only one record may have been ship-transported via ballast waters: *Epinephelus coioides* in the Adriatic Sea, recorded by Parenti & Bressi (2001). Thus, accidental introductions via ship ballast water did not affect our results.
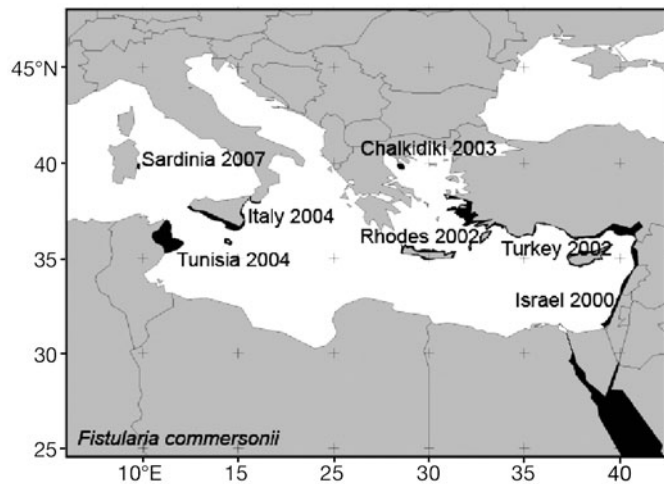

Fig. 8. *Fistularia commersonii.* An example of fast propagation (black shading)

CONCLUSIONS

Thirty percent of the Lessepsian species succeeded in dispersing over the Mediterranean Sea. Hence, crossing the Suez Canal does not guarantee the establishment and widespread dispersal of fish populations. Instead, it appears that time since introduction and climate match are key determinants for dispersal, while the type of propagule determines the main pathway of propagation within the Mediterranean. We also found that the transition from the Levantine basin to the western basin is clearly associated with a deceleration in propagation speed. Our study suggests that body size, position in the water column, confamilial resistance and interactions between these factors are all of secondary importance in explaining dispersal success when compared to history, climatic niche and propagule type. Many species accelerated their propagation in the 1980s: on average, the speed increased about 5-fold. This phenomenon could be directly related to the increase in sea surface temperatures observed during the same period. As Lessepsian fishes represent only 5.72% of the Red Sea fish fauna (Froese & Pauly 2006), we can expect that the risk of continuing fish invasion from the Red Sea is high, and that the phenomenon may accelerate with further sea surface warming. Similar to other regions, the Mediterranean basin is undergoing a warming trend (Bethoux & Gentili 1996, Diaz-Almela et al. 2007), and thus Lessepsian fishes that are favoured by warmer temperatures and selected according to their ecological attributes may get established to the detriment of Mediterranean species.

Predicting which Red Sea fishes are most likely to invade the Mediterranean Sea would require thorough knowledge of their ecology. Unfortunately, such data

are not available, as more than 1000 fishes are present in the Red Sea (Froese & Pauly 2006). However, our study suggests that basic biological information on fish species may help to predict future invaders. There is wide agreement that, on a global scale, invasive species constitute a major threat to biodiversity (Amborgi 2001, Bax et al. 2001, Perrings 2002, Dawson et al. 2005). However, some authors consider them to be clearly beneficial (Sax et al. 2002, Escapa et al. 2004, Briggs 2007). Regarding the increasing dispersal rate of Lessepsian fish species we can expect some major changes in fish assemblages of the Mediterranean Sea, especially considering global warming (Mandrak 1989, Chu et al. 2005), but the consequences are still challenging to predict.

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