Lag times in Lessepsian fish invasion

E. Azzurro, F. Maynou, J. Belmaker, D. Golani & J. A. Crooks

Biological Invasions

ISSN 1387-3547

Biol Invasions
DOI 10.1007/s10530-016-1184-4

Springer

Your article is protected by copyright and all rights are held exclusively by Springer International Publishing Switzerland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com”.

Springer

Author's personal copy

Biol Invasions
DOI 10.1007/s10530-016-1184-4

PERPECTIVES AND PARADIGMS

Lag times in Lessepsian fish invasion

**E. Azzurro · F. Maynou · J. Belmaker ·
D. Golani · J. A. Crooks**

Received: 21 July 2015 / Accepted: 30 May 2016
© Springer International Publishing Switzerland 2016

Abstract Insight from theory has shown the usefulness of considering time lags in both plant and animal invasions, but this topic has yet to be fully explored with real examples. Here we define and investigate several types of lags using Red Sea fish invasions of the Mediterranean as a case study. By exploring both conceptual and analytical aspects of time lags, we suggest that this concept can be applied to both the ecology and management of invasions. Through the review of available literature and by compiling a comprehensive geo-referenced database, we show that our understanding of the temporal nature of invasion can be confounded by our varying capability to perceive it. This deep, sometimes inextricable, connection between the temporal nature of a process and its observation represents a critical issue for our understanding of the Lessepsian phenomenon, and is a challenge for invasion biology more generally. While our case study is associated with a very specific date in which the Suez Canal opened, our framework is expected to broaden the notion of time lags in bioinvasions research.

Keywords Red Sea · Mediterranean · Fish · Time lags · Detection · Monitoring

Introduction

Time lags are an increasingly recognized aspect of both plant and animal invasions (Crooks 2005; Daehler 2009; Essl et al. 2011). The term *lag* is generally used to indicate a 'relative slowness' (Crooks 2005), and this concept often refers to a period of slow growth of an invader preceding the

---

Electronic supplementary material The online version of this article (doi:10.1007/s10530-016-1184-4) contains supplementary material, which is available to authorized users.

E. Azzurro (✉)
ISPRA, Institute for Environmental Protection and Research, Piazzale dei Marmi 2, 57128 Leghorn, Italy
e-mail: eazzurr@gmail.com

F. Maynou
Institut de Ciències del Mar (CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

J. Belmaker
Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, 69978 Tel Aviv, Israel

D. Golani
Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel

J. A. Crooks
Tijuana River National Estuarine Research Reserve, Southwest Wetlands Interpretive Association, 301 Caspian Way, Imperial Beach, CA 91932, USA

Published online: 06 June 2016

Author's personal copy

onset of population outbreaks (e.g. Mack et al. 2000; Rilov et al. 2004). These seemingly dormant periods may range from a few years to several centuries (Whitney and Gabler 2008) and they have been documented in taxa such as plants (Larkin 2012), invertebrates (Rilov et al. 2004; Witte et al. 2010), and vertebrates (Aagaard and Lockwood 2014). The notion of lag, however, has been used in different ways among authors, and it broadly refers to either the delayed onset or relatively slow rate of an invasion process (Crooks 2011). In theory, this concept can be applied across all the subsequent phases of the invasion, from the arrival of a new invader up to its ecological integration in the new environment (Crooks 2011). Time lags can be also related to the human-dimension of invasions (Ricciardi 2013), including our readiness to note, monitor, and manage invasions, but so far very few studies have investigated these topics (Crooks 2005). Despite the importance of time lags for understanding and managing invasions (e.g. Bellard et al. 2016) these are seldom documented or quantified, and our understanding of lags is largely shaped by anecdotal observations (Larkin 2012).

Here we explore these temporal aspects of biological invasions using the Lessepsian fishes as a case study. Lessepsian species are Red Sea organisms, which have entered the Mediterranean via the Suez Canal (Por 1971). This process is one of the most important biogeographic events of modern history and is emblematic of the contemporary "Anthropocene" (Zalasiewic et al. 2010). Red Sea species entering the Mediterranean are causing major ecological and economic impacts (Galil 2009), and increasing scientific attention is devoted to explore patterns and processes associated with this invasion (for fish species, see Belmaker et al. 2009, 2010; Ben Rais Lasram et al. 2010; Azzurro et al. 2014; Bernardi et al. 2016; Parravicini et al. 2015). With respect to the difficulties to quantify invasion dynamics, Lessepsian species present some distinct advantages for research. The invasion vector is assumed to be the Suez Canal, and the place where the migrants arrive is known, being the opening of the Canal at Port Said. Also, the date of vector initiation is known, corresponding to the opening of this maritime route in 1869. Moreover, in comparison with other marine introductions, exotic fish species in the Mediterranean are quite well-tracked, due to their conspicuous appearance and their importance in eastern Mediterranean fisheries. Our goal here is to capitalize on these advantages to examine time lags throughout the invasion process and identify challenges in operationalizing the concept, including intersections with the human dimensions of invasion detection and management. Using this insight from the Lessepsian fishes, we aim to address the more general concept of lag (Crooks 2011), which has remained relatively underexplored in invasion biology.

Conceptual framework

Time lags were investigated across both the ecological and the human dimensions of Lessepsian invasions. The latter relates to those aspects of the invasions that are influenced by social factors and/or human actions in our society (McNeely 2001). Three consecutive phases of the invasion process were considered: *Arrival* (consisting of transport and introduction), *Establishment* of permanent populations, and *Geographic spread*, drawing on the invasion stages suggested by Blackburn et al. (2011) (Table 1). For each of these stages, time lags were analysed for both: *Onset*—The temporal offset between discrete events, and *Rate*—Changes of the same process at different times (Crooks 2011). Considering that our perception of the temporal nature of all these phases depends on our ability to identify and quantify invasion, we also focused on the implications of *Detection lags* across these invasion phases (sensu Crooks 2011). A conceptual scheme of the relationships between the onset of the above mentioned phases of an invasion and their detection is presented in Fig. 1. Finally, *Response lags* were taken into consideration to define and to evaluate aspects related to the communication, awareness and management of biological invasions.

Database of Lessepsian fish

Mediterranean records of Lessepsian fish species were compiled from published sources and grey literature. These were used to compile a geo-referenced database, which includes data on the recorded species, year of detection, year of publication, and other relevant information (see Azzurro et al. 2013 for an earlier version of the database). The list of species was extracted from Golani et al. (2013) plus other recent

Author's personal copy

Table 1 Definitions of lag times for Lessepsian fish invasion

Kind of lag		Definition
Detection		**Detection lags may be applied to all the stages of invasion: *Arrival*: Time between the actual arrival of a species and its first detection; *Establishment:* Time between the actual establishment of a permanent population and its detection; *Geographical spread*: Time between actual onset of geographical spread and its detection**
Arrival or introduction	*Onset*	Time between the vector initiation (the opening of the Suez canal in 1869*) and the species arrival
	Rate	Change in the rate of arrivals with time
Establishment	*Onset*	Time between arrival of a species and the establishment of a permanent population
	Rate	Change in the rate of establishment with time
Geographical spread	*Onset*	Time between the establishment of a permanent population and the subsequent geographical spread
	Rate	Difference in the rates of dispersal (speed)
Response		**Response lags are defined as the time between the detection of a discrete event and a subsequent action of society. It may concern the time needed to *Communicate* (this include publication lags) and *Manage* these events**

Lags related to our capacity to perceive and to respond to invasions ('the human dimension') are highlighted in bold

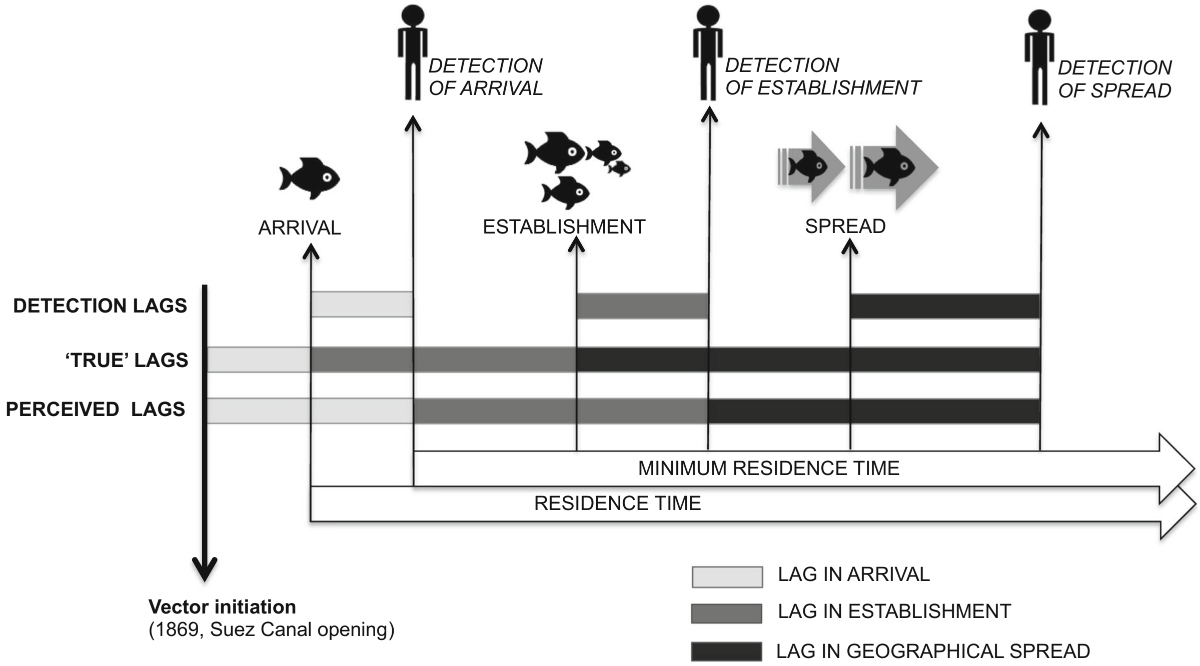

Fig. 1 Schematic illustration of our conceptual framework for lag times in Lessepsian fish species according to the onset of three subsequent stages of an invasion: (i.e. arrival; establishment of a self sustaining population; geographical spread). *Detection lag* is the time spanning the real onset of a new stage and its detection; *'True' lags* are the real, often unmeasured time needed for the onset of a new stage; *Perceived lags* are the way in which we usually measure time lags, based on the assumption that the onset of a new stage corresponds to its detection. The term "minimum residence time" typically indicates the length of time since detection, explicitly recognizing that this might be an underestimate

publications, which provided records of Lessepsian fish species. We considered 96 fish species in the analyses, which represent all the likely Lessepsian migrants (see Supplementary information Table 1). This number includes also species (e.g. *Abudefduf vaigiensis, Champsodon nudivittis, Champsodon*

Author's personal copy

vorax, Iniistius pavo, Parablennius thysanius, Platex teira, Terapon theraps) whose migration through the Suez Canal is considered plausible but not completely ascertained, as other means of transport, such as ballast water, are also possible vectors. Unconfirmed species or records of doubtful origin (e.g. *Champsodon capensis, Omobranchus punctatus, Istiblennius edentulous, Priacanthus hamrur, Tylosurus crocodilus, Chirocentrus dorab*) were not considered. Overall, the total number of geo-referenced observations included into the database was of 2164. Out of these, 1363 were extracted from published sources and the remaining 821 records from grey literature, unpublished sources, and existing databases.

Lags in detection

For an invader to appear in a system, it first must arrive and then it must be documented (Crooks 2005), therefore some lapse of time will nearly always exist between the first entrance and the subsequent discovery of the new Lessepsian species. All non-intentional invasions are likely to suffer from this kind of *Detection lag* (Crooks 2011) and *Perceived lags* are the way in which we usually measure time lags, based on the assumption that the onset of a new stage corresponds to its detection. The term "minimum residence time" (Simberloff and Rejmánek 2010) typically indicates the length of time since detection, explicitly recognizing that detection lags might make these underestimates of the residence time (Table 1; Fig. 1).

Lessepsian species provide a variety of examples of how detection lags might arise. One example is mistaken identity. For example, the Arabian scad, *Trachurus indicus* was identified for the first time from Iskenderun Bay in 2004 but this species was probably conflated with native *Trachurus* spp. due to similar morphologies (Bilecenoglu 2010). Similarly, the ocean anchovy *Stolephorus insularis*, first recorded along Israeli shores in 2009, has been overlooked for years due to its external similarities with the native *Engraulis encrasicolus* (Fricke et al. 2012). Other remarkable misidentifications, such as those related to *Pempheris rhomboidea* and *Saurida lessepsianus,* did not generate detection lags, since the species were immediately recognized as exotic even if with a different name (e.g. Azzurro et al. 2015; Russell et al. 2015). Detection lags might also tend to be more frequent or prolonged for relatively inconspicuous species. Small, non-commercial fishes have more chances to pass unnoticed, especially in poorly monitored areas of the Mediterranean. On the contrary, eye catching characteristics, such as the tubular shape of *Fistularia commersonii,* the prominent fins of *Pterois miles*; or the bright colors of *Heniochus intermedius* are certainly of great help to spot a newcomer (Golani 2010; Golani et al. 2013). These lags in detection are critical as they affect our ability to estimate the prevalence of other types of lags (Crooks 2005).

Sampling efforts typically vary through time, space, and taxonomic group. For example the improvement of sampling methods or more scientists actively looking for introduced species increase the probability of detection of a species, reducing the detection lag trough time. Detection lags have probably been very significant during the onset of Lessepsian invasion, with a strong reduction in the length of this lag over the last three decades because of the increasing scientific efforts. This can lead to an accelerating pattern in the discovery record that does not necessarily reflect changes in the underlying introduction rates. Thus, the rate at which new exotic species are described does not always provide a realistic picture of introduction rates (Costello and Solow 2003; Belmaker et al. 2009). Considering the widespread concern on increasing introductions, recognizing the potential of detection lags to skew patterns is essential, especially with data based on discovery records.

Lags in arrival

A true lag in arrival can be defined as the time interval between the initiation of the vector—the opening of the Suez Canal in 1869—and the entry of a new species into Mediterranean waters. As highlighted above, however, species are only recorded when they are encountered and accurately documented by scientists. Therefore, an unknown detection lag between these non-intentional introductions and their subsequent discovery always exists, meaning that true lag times can be overestimated (Table 1; Fig. 1). Nonetheless, striking patterns emerge in both the appearance of individual species (onset lags) and the

Author's personal copy

accumulation of species appearances over time (rate lags).

Onset

The first Lessepian fish, *Atherinomorus forskalii*, was detected 33 years after the opening of the Suez Canal (Tillier 1902). This time lapse can be taken as the maximum lag for the onset of the entire Lessepian migration, but the actual date of first arrival (of this or some other species) is almost certainly earlier than this. Following the detection of *A. forksalii,* we had to wait 25 more years (58 years after the opening of the Suez Canal) for the detection of other Lessepian fishes (e.g. *Hemiramphus far, Alepes djedaba, Siganus rivulatus, Stephanolepis diaspros*, *Hyporhamphus affinis, Liza carinata* and *Corygalops ochetica*). The chronological order of all these introductions is a way to represent the individual lags in arrival (Table II): from the first species to be recorded *A. forksalii* up to the most recent ones e.g. *Epinephelus geoffroyi* (Golani et al. 2015) which took 146 years to cross the Canal and be observed. Given that detection lags have likely decreased in recent years, these newer reports indicate that even after one-and-a-half centuries, the Suez Canal continues to operate as a viable vector of invasion.

Rate

We can also consider how the rate of appearance of Lessepsian fish, expressed as the cumulative increase of species detections, has changed over time. In order to test for changes in the rate of arrival, we computed the slope of the cumulative curve in 5-year periods from 1930 to 2014 (85 years or 17 periods), and fitted a linear model of cumulative number of species per year within each 5-year period. Looking at the observed arrivals of Lessepsian fishes over time, changes seem to be obvious (Fig. 2). There was long early lag in invader appearance, and only after 1927 (Steiniz 1927) did new species begin to more regularly appear. During the period 1930–2014, the average number of new species detected per year is 1.02. Results of the linear model show that this background level was significantly higher in the second half of the 1970s (slope of the linear fit 1.2 new sp/year) and it is significantly higher every 5-year period from the early 1990s to the present (1.4–2.6 new sp/year).

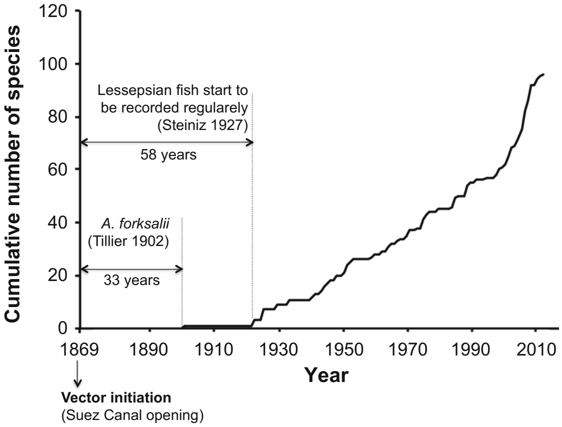

Fig. 2 Cumulative number of detected Lessepsian fish species in the Mediterranean Sea through time. Some major lags in the *onset* of Lessepsian fish migration are showed: Lag in the *onset* of Lessepsian fish migration (33 years after the opining of the Suez Canal); Lag in the *onset* of linear rate of recorded arrivals (58 years). These lags are calculated according to the assumptions made in Fig. 1

Although detection lags complicate efforts to disentangle true invasion patterns from our changing ability to perceive them, significant advances have been made in developing analytical tools to control for sampling effort in the estimation of introduction rates (Costello and Solow 2003; Solow and Costello 2004). Belmaker et al. (2009) used the discovery record of native species to control for sampling effort in Lessepsian fish migration and this analytical approach should represent an excellent example of how to potentially account for detection lags.

These observed changes in the rate of introductions are likely related to a variety of factors, including time needed for the species to become associated with the vector (enter the Canal), changes in characteristics of vector (changes in the Canal itself), and changes in receiving waters. We know little about the details of species entering the Canal, but modelling efforts like those described above (Belmaker et al. 2009) provide insight into possible dynamics associated with the pool of species in the Red Sea entering the Mediterranean. We know more about the characteristics and biological implications of changes in the Suez Canal. Due to its convoluted history, the Suez Canal has changed in its capacity as an effective vector of invasion, and changes are expected for the near future due to its expansion (Galil et al. 2015). It long remained inhospitable to marine organisms, mainly

Author's personal copy

due to two different salinity barriers: the hypersaline bitter lakes and the Nile dilution that constituted a barrier for Lessepsian passage. With the continuous dissolution of the salt beds and the construction of the Aswan Dam in 1965–1967, both barriers became weaker allowing Red Sea species to enter the Mediterranean with variable lags in their arrival (Galil 2006 for a review). More recently, the perceived intensification in the number of new arrivals has been mostly attributed to the temperature increase in the eastern Mediterranean (e.g. Raitsos et al. 2010). As already mentioned, all these conclusions would probably be refined by a realistic estimation of detection lags.

Lags in establishment

Establishment is related to the capacity of newly-arrived species to survive and reproduce in their new environment (Table 1; Fig. 1). While conceptually straightforward, operationally it is more difficult to assess than arrival, which can be documented by the appearance of a single individual. For this analysis, *Lags in establishment* were explored on the basis of the definition adopted by the CIESM atlas of exotic fish species in the Mediterranean Sea (Golani et al. 2013), that consider as established *those species that have self-maintaining populations as evidenced by a minimum of two (three for fishes) published records from either different localities or in different periods*. This choice was motivated by the lack of specific information regarding the time of establishment for all Lessepsian fish species. Then, the lag in the onset of establishment for each species can be quantified as the time elapsed between the first Mediterranean species record and the third observation (separated in space and time). This was calculated for the 69 species for which there were such 3 records.

Onset

Lags of establishment calculated with the 'third record criterion' vary from 0, as in the case of *Vanderhostia mertensi,* to several decades, as for *Etrumeus golanii* (see Supplementary information Fig. 1a, b). The bluespotted cornetfish *F. commersonii* was observed in the eastern Mediterranean (Bariche et al. 2013), 25 years before its establishment and concomitant invasion. Similarly, *E. golanii* was firstly recorded in the Mediterranean Sea in 1961, but no more sightings of this species were made until the nineties, when it reappeared in large numbers (Golani 2000). Other significant examples of lag in establishment can be given: An abundant population of *Sargocentron rubrum* was observed in Israel only in the 1980′s (Golani and Ben-Tuvia 1985; Spanier 2000), almost four decades after its first sighting in the same region. In the Levant Sea, *Scomberomorus commerson* was detected in the 30′s but it remained a rare species for more than half a century (Ben-Tuvia 1978), becoming one of the most abundant pelagic species only in the last two decades (Golani 2010). It is therefore possible that these earliest records represented abortive attempts of colonization, while the reappearance and subsequent success of these species at establishing a sustainable population were the result of further events of introduction. Thus, the failure of individuals or populations to establish at a given location does not preclude the possibility that a subsequent introduction of the same species at that location will succeed. As a matter of fact, a series of failed introductions have happened before establishment, with lags sometimes longer than the lifespan of an individual.

Rate

Potential lags in the rate of establishment, were examined using the cumulative increase of established species (3rd records) over time. This estimated lag in establishment significantly decreased along with time elapsed since the opening of the Suez Canal ($p < 0.001$; $R^2 = 0.3176$) (Fig. 3). Beyond changing detection lags, factors associated with changing Mediterranean climate (Macias et al. 2013) can act to modify survival or reproduction and influence the probabilities of establishment of exotic organisms. Specifically, increasing establishment rates are expected for warm adapted species in a warming Mediterranean environment (Jørgensen et al. 2012; Marras et al. 2015).

Lags in geographical expansion

Lags in geographical expansion were computed by calculating the distance of the first detection to the entry point at Suez and the distance between

Author's personal copy

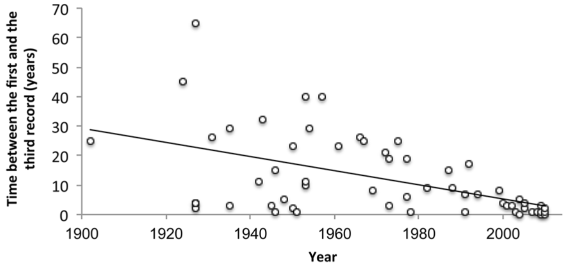

Fig. 3 The year of first species record in the Mediterranean Sea is plotted against the number of years until the third published record. According to (Golani et al. 2013), this gives us an indication of the time needed to establish a permanent population. N. species = 58

successive detections points against the time elapsed. To establish the distance travelled by fishes over successive detection points, we projected the geographic positions of detection points over the 50 m depth contour, as an approximation to the complexity of Mediterranean coastlines. We explored differences across species within the same geographical sector, and sectors for the same species. Two main Mediterranean sectors were considered: The Asian—European shores (AEU) and the African shores (AF) and twelve species for which at least 3 records were available for both the AEU and the AF sectors. Differing patterns of geographical expansion were also exemplified by comparing spread rates of two very abundant species, *F. commersonii* and *S. luridus,* based on: (a) the maximum distance travelled each year, and (b) by only plotting the maximum recorded spread (front of the invasion).

Onset

Once a species arrives in a new environment it may spread across that environment and a variable amount of time can go by between the establishment of a permanent population and its further geographical expansion. This lapse of time is what we define as *lag in the onset of geographical expansion* (Table 1). Some species started to expand their range immediately after their establishment. This is the case of *F. commersonii,* which reached the western limits of the Mediterranean Sea in only 7 years (Azzurro et al. 2012). Similarly, other species such as the silver-cheeked toadfish *Lagocephalus sceleratus*, the threadfin bream *Nemipterus randalli,* and the Indian scad *Decapterus russelli* spread soon after their first detection (Akyol et al. 2005; Lelli et al. 2008, Bilecenoglu and Russell 2008). In other cases, Lessepsian species remained confined for years in small sectors of the Eastern Mediterranean before starting to spread. This is the case of *E. golanii*, *S. rubrum, Lagocephalus guentheri,* and *Upeneus moluccensis,* which did not show signs of westward expansion for decades (Golani 2010).

Rate

Rates of geographical expansion may vary among species and across space and time. The analysis of dispersal rates (Fig. 4) show that they vary strongly according to Lessepsian fish species. For instance *F. commersonii* was detected at subsequent distances of more than 1000 km from one year to the next in Asian-European shores (AEU), while *L. guentheri* was always detected in nearby areas in African shores (AF) (Fig. 4). The comparison of the rate of expansion through the Asian—European shores (AEU) and the African shores (AF) did not result in any clear geographical pattern. In fact, out of 12 Lessepsian

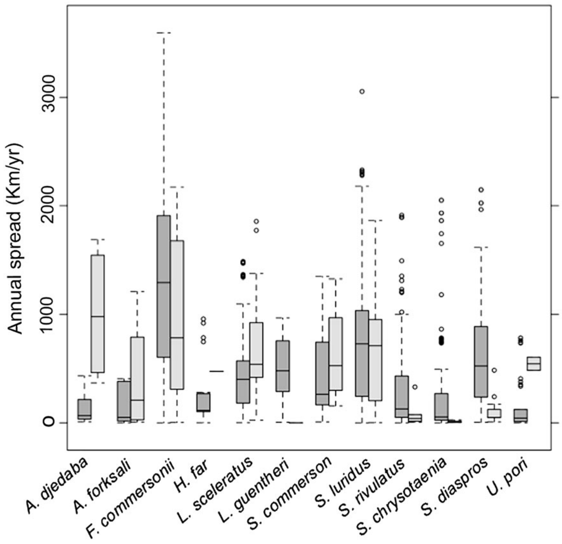

Fig. 4 Boxplots with estimates of distances travelled by 12 selected Lessepsian fishes along the Asian-European (*dark grey*) and the African (*grey*) margins. *Boxplots* show summary statistics of distances travelled between consecutive detection points (leading edge of the invasion): average, 25 and 75 percentiles; 10 and 90 percentiles and outlying values. Outliers shown as *open circles*

Author's personal copy

fish included in the analysis, 6 species progress faster on the North African shores, while exactly the same number of species progress faster along the Asian—European shores. Note also that the same species may show very different rates of dispersal along the southern shores or along the northern shores (e.g. *A. djedaba, L. guentheri, S. chrysotaenia, U. pori*), while in other cases the speed is quite similar (*F. commersonii, S. commerson*). The speed of dispersal is around 500 km/year on average.

Examining the time course of spread for individual species can also be used to detect potential intraspecific lags in geographic expansion. This can be exemplified by the differing patterns of spread of two abundant Lessepsian fishes, *F. commersonii* and *S. luridus*, away from the Suez Canal along Asian—European shorelines (Fig. 5). As noted earlier, *F. commersonii* exhibited a consistent, and rapid spread away from Suez. The pattern for *S. luridus*, however, differs in that there appeared to be a 30-year lag and relatively low spread rates until 2004. Looking at Fig. 5 (right panels), we can estimate that the invasion front expanded at a rate of ca 3000 km/50 years = 60 km/year in *S. luridus* and ca 3500 km/7 years = 500 km/year in *F. commersonii*, where the front is defined as the non-decreasing distance of subsequent observations It is also worth noting the intriguing spread pattern for the latter species. After the initial sprint (Fig. 5, top left), the speed of *F. commersonii* showed an apparent decrease corresponding to the crossing of the Sicily Strait in 2003–2004 and then it increased again until 2007, when the species reached its maximum distance from the entry point.

As seen with the spread of *F. commersonii,* geography and transitional areas might serve as important controls on spread rates (Azzurro et al. 2012). According to Ben Rais Lasram et al. (2010), the speed of dispersal increased over time for species restricted to the Levantine basin such as *Apogonichthyoides pharaonis, Callionymus filamentosus, Hemiramphus far, Herklotsichthys punctatus,*

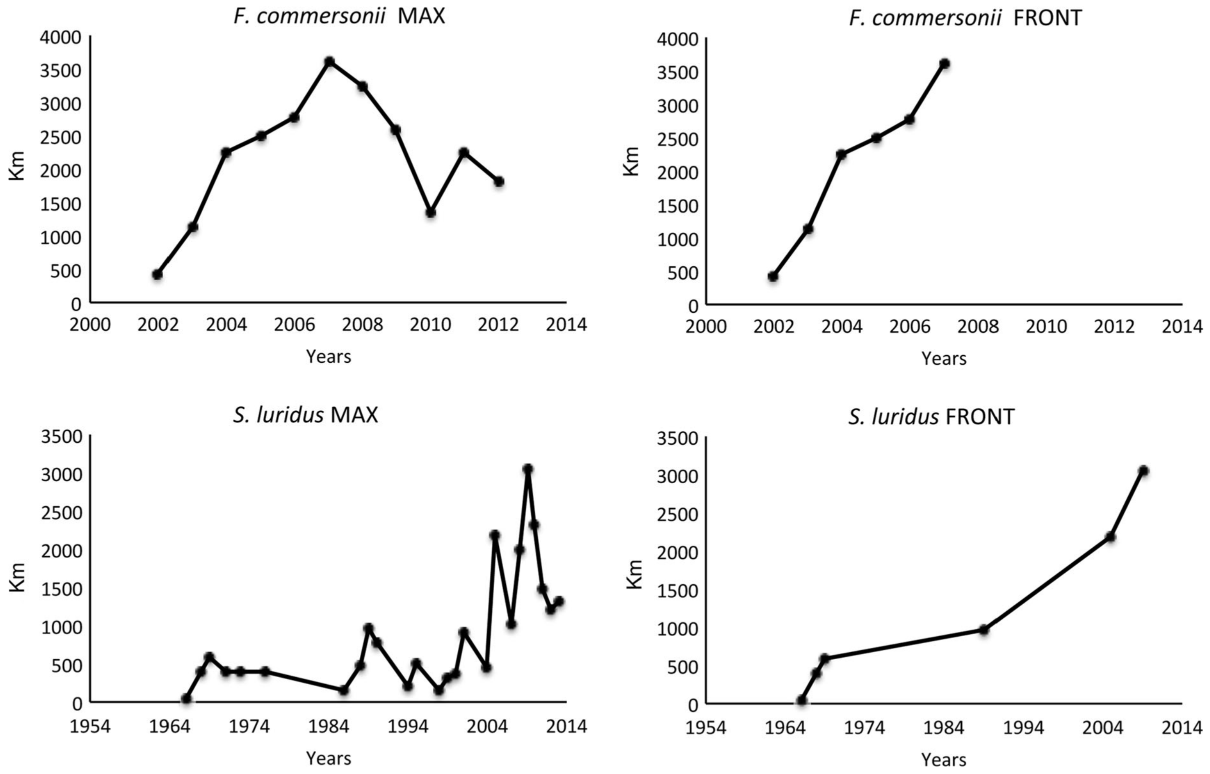

Fig. 5 Geographic spread of *Fistularia commersonii* and *Siganus luridus* along the northern rim of the Mediterranean calculated as the maximum observed distance from the point of introduction (i.e. Port Said at the opening of the Suez Canal) in each given year. Speeds were computed according to both the maximum distance travelled each year (MAX) and by only plotting the maximum recorded extents (FRONT)

Author's personal copy

Lagocephalus suezensis and *Petrocirtes ancylodon.* Conversely for species that spread beyond the Levant, the speed of dispersal can decrease at transitional zones e.g. *Equulites kluntzingeri, Parexocoetus mento, Siganus luridus, Siganus rivulatus* when they reached the Adriatic and Tyrrenian seas. The factors that could explain the observed patterns merit more study, but likely include species-specific population dynamics and biogeographic patterns in dispersal within the new environment. Also, as highlighted throughout, an accurate estimation of expansion rates would necessitate that human-related factors such as sampling probabilities and detection rates be disentangled from spread dynamics, but this remains difficult to do.

Lags in human response

Lag in response pertains to the human dimension of the invasions and can be defined as the time between the detection of a discrete event and a subsequent action of society. The detection lag, discussed above, is of primary importance but difficult to know. Related to this, however, it is possible assess the time needed to publish the occurrence of a new exotic species in

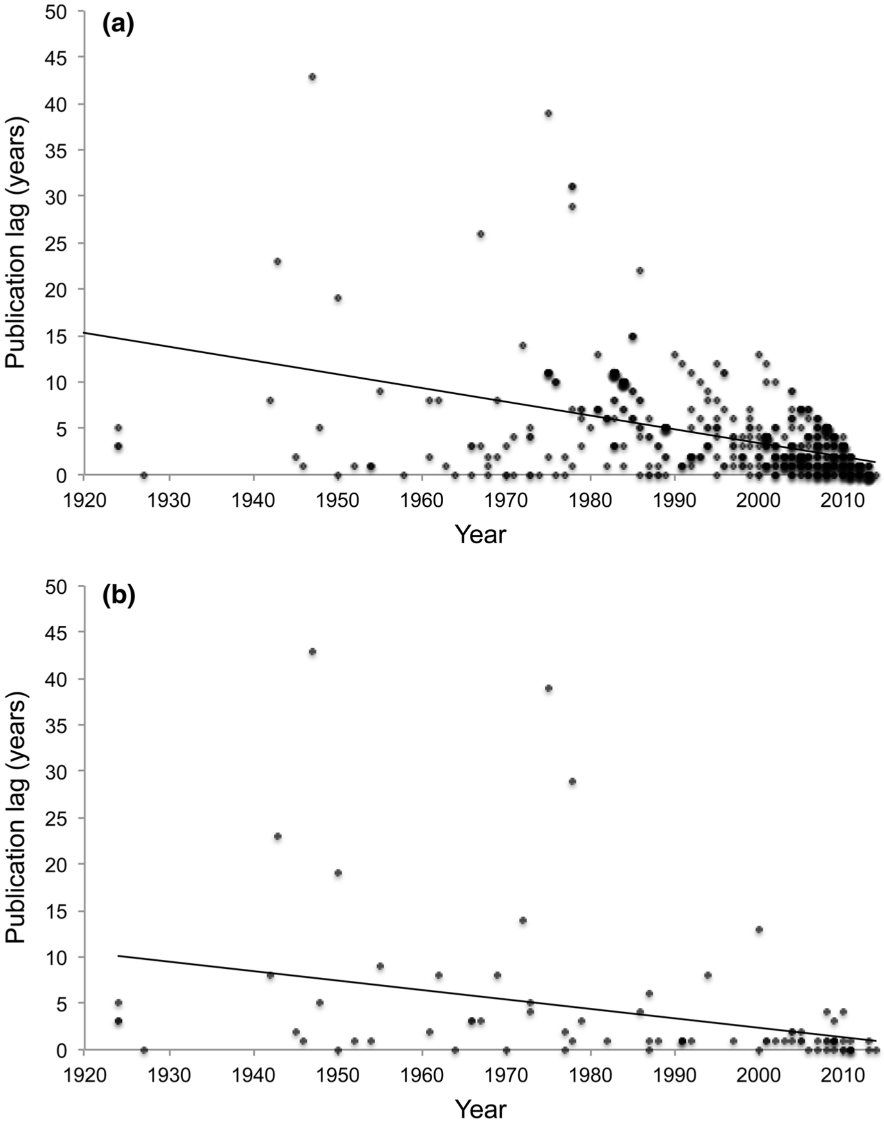

Fig. 6 Publication lag of (**a**) all Lessepsian fish records (N = 1011 observations) and (**b**) first Mediterranean records only (N = 83 observations)

Author's personal copy

scientific journals. These *publication lags* (the lapses of time between the detection of a Lessepsian species and its publication) were calculated using every point in the dataset for which both the year of detection and the year of publication were available (N observations = 1011 out of 2022). Publication lags were also calculated for a subset of occurrences represented by the first species records (N observations = 83).

Among Lessepsian fishes, this *publication lag* ranged from 0 to 38 years. Plotting every published record along the temporal axis (Fig. 6a, b), we observe a significant reduction of this time lapse, from early records to recent ones. This trend is visible both if we consider our entire set of observations (N = 1011; $R^2 = 0.26$, $p < 0.001$) or only the first Mediterranean records (N = 75; $R^2 = 0.11$, $p < 0.005$). The reasons for this trend are likely related to the expedited publication process and to the increasing scientific attention devoted to biological invasions. Interestingly, the slope of the linear regression between publication lag and time is comparable to what we observed for establishment lag estimated through publications records (Fig. 3).

Other important response lags include the time needed to set management actions or for promoting public awareness. The timing of these responses is a key component of our ability to react to the problems raised by biological invaders and the development of early warning and rapid response policies is in general the most efficient approach to manage these invasions (Genovesi et al. 2010). This temporal aspect of the human dimension clearly influences the success of actions aimed to control unwanted invaders before they become irreversible (Barbour et al. 2011). Public awareness is especially important when some risks are posed by a newly introduced exotic species. This is the case of the toxic *Lagocephalus sceleratus*, which has already caused fatal accidents when consumed by unaware people in the eastern basin. Differential distribution and efficacy of communication efforts among the stakeholders generate a different consciousness of people with respect to this phenomenon (Ben-Souissi et al. 2014) and this is a further outcome for lags in human response.

Conclusions

Time is an important parameter in biological invasion and the case of Lessepsian fishes gave us the opportunity to tackle some general and unexplored aspects of time lags. Every stage of an invasion has an initiation and it may proceed at a certain rate that is expected to change according to both spatial and temporal factors. Being informed on temporal aspects of an invasion is crucial not only for the development of more effective policy but is also valuable for testing the efficacy of efforts invested in response to the invasion problem. Using the example of Lessepsian fishes, we showed that the notion of lags can be theoretically applied to different stages of invasions and to the way in which we monitor, understand and manage them. These latter aspects, which belong to the human dimension, are certainly complex but sometimes tractable, as in the case of a correct estimation of introduction rates. In many other cases, however, it is extremely difficult to approach this subject in a quantitative way, given the nature of available information. Thus the observed picture is the product of the interaction between the dynamics of invaders and our capability to perceive it, and disentangling these aspects is one of the major challenges to understanding and managing invasions. Humans are both the cause and, potentially, the solution for biological invasions and we showed how the human dimension penetrates the various aspects of lag times, adding new layers of complexity to an already multifaceted problem (Le Maitre et al. 2004). As the human dimension is one of the most unpredictable variables for management (McNeely 2001; Bellard et al. 2016), bringing attention to this factor is expected to be more effective than focusing primarily on exotic species themselves as the problem. The way in which we deal with biological invaders will undoubtedly change over time, and the methods to monitor and manage these species are evolving. Hopefully, both detection and response lags can be gradually reduced by increasing research efforts and also better harmonizing strategies to address the need for early warning and rapid response policies.

References

Aagaard K, Lockwood J (2014) Exotic birds show lags in population growth. Divers Distrib 20:547–554

Akyol O, Ünal V, Ceyhan T, Bilecenoglu M (2005) First confirmed record of the silverside blaasop, *Lagocephalus sceleratus* (Gmelin, 1789), in the Mediterranean Sea. J Fish Biol 66:1183–1186

Author's personal copy

Azzurro E, Soto S, Garofalo G, Maynou F (2012) *Fistularia commersonii* in the Mediterranean Sea: invasion history and distribution modeling based on presence-only records. Biol Invasions 15:977–990

Azzurro E, Soto S, Bariche M, Fanelli E, Maynou F (2013) Exotic fish species in the Mediterranean Sea: analysis of occurrence records. Rapp Comm Int Mer Médit 40:598

Azzurro E, Tuset VM, Lombarte A, Maynou F, Simberloff D, Rodríguez-Pérez A, Solé RV (2014) External morphology explains the success of biological invasions. Ecol Lett 17:1455–1463

Azzurro E, Goren M, Diamant A, Galil B, Bernardi G (2015) Establishing the identity and assessing the dynamics of invasion in the Mediterranean Sea by the dusky sweeper, *Pempheris rhomboidea* Kossmann & Räuber, 1877 (Pempheridae, Perciformes). Biol Invasions 17:815–826

Barbour AB, Allen MS, Frazer TK, Sherman KD (2011) Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. PLoS ONE 6(5):e19666

Bariche M, Kazanjian G, Azzurro E (2013) A lag of 25 years: evidence from an old capture of *Fistularia commersonii* Rüppell, 1838 from Lebanon (Mediterranean Sea). J Appl Ichthyol 3:535–536

Bellard C, Genovesi P, Jeschke JM (2016) Global patterns in threats to vertebrates by biological invasions. Proc R Soc B 283:20152454. doi:10.1098/rspb.2015.2454

Belmaker J, Brokovich E, China V, Golani D, Kiflawi M (2009) Estimating the rate of biological introductions. Ecology 90:1134–1141

Belmaker J, Brokovich E, China V, Golani D, Kiflawi M (2010) Introduction rates of Lessepsian fishes in the Mediterranean. In: Golani D, Applebaum-Golani B (eds) Fish invasions of the Mediterranean Sea, change and renewal. Pensoft, Sofia, pp 35–56

Ben Rais Lasram F, Guilhaumon F, Mouillot D (2010) Global warming and exotic fishes in the Mediterranean Sea: introduction dynamic, range expansion and spatial congruence with endemic species. In: Golani D, Applebaum-Golani B (eds) Fish invasions of the Mediterranean Sea, change and renewal. Pensoft, Sofia, pp 35–56

Ben-Souissi J, Rifi M, Ghanem R, Ghozzi L, Boughedir W, Azzurro E (2014) *Lagocephalus sceleratus* (Gmelin, 1789) expands through the African coasts towards the Western Mediterranean Sea: a call for awareness. Manag Biol Invasions 5:357–362

Ben-Tuvia A (1978) Immigration of fishes through the Suez Canal. Fishery Bull 76:249–255

Bernardi G, Azzurro E, Golani D, Miller M (2016) Genomic signatures of rapid adaptive evolution in the bluespotted cornetfish, a Mediterranean Lessepsian invader. Mol Ecol. doi:10.1111/mec.13682

Bilecenoglu M (2010) Alien marine fishes of Turkey-an updated review. In: Golani D, Applebaum-Golani B (eds) Fish invasions of the Mediterranean Sea, change and renewal. Pensoft, Sofia, pp 189–217

Bilecenoglu M, Russell BC (2008) Record of *Nemipterus randalli* Russell, 1986 (Nemipteridae) from Iskenderun Bay, Turkey. Cybium 32:279–280

Blackburn TM, Pisek P, Bacher S, Bacher S, Carlton JT, Duncan RP, Jarosik V, Wilson JRU, Richardson D (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Costello CJ, Solow AR (2003) On the pattern of discovery of introduced species. Proc Natl Acad Sci 100:3321–3323

Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. Ecoscience 12:316–329

Crooks JA (2011) Lag times. In: Simberloff D, Rejmánek M (eds) Encyclopedia of Biological invasions. University of California Press, Oakland, pp 404–410

Daehler CC (2009) Short lag times for invasive tropical plants: evidence from experimental plantings in Hawai'i. PLoS ONE 4(2):e4462

Essl F, Dullinger S, Rabitsch W, Hulme PE, Hülber K et al (2011) Socioeconomic legacy yields an invasion debt. Proc Natl Acad Sci 108:203–207

Fricke R, Golani D, Appelbaum-Golani B (2012) First record of the Indian Ocean anchovy *Stolephorus insularis* Hardenberg, 1933 (Clupeiformes: Engraulidae) in the Mediterranean. BioInvasions Rec 1(4):303–306

Galil BS (2006) The marine caravan – the Suez Canal and Erythrean invasion. In: Gollasch S, Galil BS, Cohen AN (eds) Bridging divides. Maritime canals as invasion corridors. Springer, Dordrecht, pp 207–300

Galil B (2009) Taking stock: inventory of alien species in the Mediterranean sea. Biol Invasions 11:359–372

Galil BS, Boero F, Campbell ML, Carlton JT, Cook E, Fraschetti S et al (2015) 'Double trouble': the expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. Biol Invasions 17:973–976

Genovesi P, Scalera R, Brunel S, Roy D, Solarz W (2010) Towards an early warning and information system for invasive alien species (IAS) threatening biodiversity in Europe. EEA, Technical Report 5:1–49

Golani D (2000) The Lessepsian migrant, the Red-eye Round Herring, *Etremeus teres* (DeKay, 1842), a new record from Cyprus. Zool Middle East 20:61–64

Golani D (2010) Colonization of the Mediterranean by Red Sea fishes via the Suez Canal—Lessepsian migration. In: Golani D, Appelbaum-Golani B (eds) Fish invasions of the mediterranean sea: Change and reneval. Pensoft Publishers, Sofia, pp 145–188

Golani D, Ben-Tuvia A (1985) The biology of the Indo-Pacific squirrelfish, *Sargocentron rubrum* (Forsskål), a Suez Canal migrant to the eastern Mediterranean. J Fish Biol 27:249–258

Golani D, Massutí E, Orsi-Relini L, Quignard JP, Dulčić J, Azzurro E. (2013) CIESM atlas of exotic fish species. http://www.ciesm.org/atlas/appendix1.html Accessed 28 June 2015

Golani D, Askarov G, Dashevsky Y (2015) First record of the Red Sea spotted grouper, *Epinephelus geoffroyi* (Klunzinger, 1870) (Serranidae) in the Mediterranean. BioInvasion Records 2:143–145

Jørgensen C, Myron E, Peck A, Antognarelli F, Azzurro E et al. (2012) Conservation physiology of marine fishes: advancing the predictive capacity of models. Biol Lett. 8: 900–903. rsbl20120609

Larkin DJ (2012) Lengths and correlates of lag phases in upper-Midwest plant invasions. Biol Invasions 14:827–838

Le Maitre DC, Richardson DM, Chapman RA (2004) Conservation Physiology of Marine Fishes: advancing the

Author's personal copy

predictive capacity: working for water. S Afr J Sci 100:103–112

Lelli S, Colloca F, Carpentieri P, Russell BC (2008) The threadfin bream *Nemipterus randalli* Russell, 1986 (Perciformes; Nemipteridae) in the eastern Mediterranean Sea. J Fish Biol 60:1326–1330

Macias D, Garcia-Gorriz E, Stips A (2013) Understanding the causes of recent warming of Mediterranean waters. How much could be attributed to climate change? PLoS ONE 8(11):e81591

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Marras S, Cucco A, Antognarelli F, Azzurro E, Milazzo M, Bariche M, Butenschön M, Kay S, Di Bitetto M, Quattrocchi G, Sinerchia M, Domenici P (2015) Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. Cons Physiol 3.1:cou059. doi:10.1093/conphys/cou059

McNeely JA (ed) (2001) The great reshuffling: human dimensions of invasive alien species. Gland, Switz./Cambridge, UK: IUCN

Parravicini V, Azzurro E, Kulbicki M, Belmaker J (2015) Niche shift can impair the ability to predict invasion risk in the marine realm: an illustration using Mediterranean fish invaders. Ecol Lett 18:246–253

Por FD (1971) One hundred years of Suez Canal: a century of Lessepsian migration. Syst Zool 20:138–159

Raitsos DE, Beaugrand G, Georgopoulos D, Zenetos A, Pancucci-Papadopoulou AM, Theocharis A, Papathanassiou E (2010) Global climate change amplifies the entry of tropical species into the Eastern Mediterranean Sea. Limn Ocean 55:1478–1484

Ricciardi A (2013) Invasive species. In: Leemans R (ed) Ecological systems. Springer, New York, pp 161–178

Rilov G, Benayahu Y, Gasith A (2004) Prolonged lag in population outbreak of an invasive mussel: a shifting-habitat model. Biol Invasions 6:347–364

Russell BC, Golani D, Tikochinski Y (2015) *Saurida lessepsianus* a new species of lizardfish (Pisces: Synodontidae) from the Red Sea and Mediterranean Sea, with a key to Saurida species in the Red Sea. Zootaxa 3956:559–568

Simberloff D, Rejmánek M (eds) (2010) Encyclopedia of biological invasions, vol 3. University of California Press, Oakland

Solow AR, Costello CJ (2004) Estimating the rate of species introductions from the discovery record. Ecology 85:1822–1825

Spanier E (2000) Changes in the ichthyofauna of an artificial reef in the southeastern Mediterranean in one decade. Sci Mar 64:279–284

Steinitz W (1927) Beitrage zur Kenntnis der Küstenfauna Palästinas. Pubblicazioni della Stazione Zoologica di Napoli 8:311–353

Tillier JE (1902) Le Canal de Suez et sa faune ichthylogique. Mémoires de la Société zoologique de France 15:279–318

Whitney KD, Gabler CA (2008) Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. Divers Distrib 14:569–580

Witte S, Buschbaum C, Van Beusekom JE, Reise K (2010) Does climatic warming explain why an introduced barnacle finally takes over after a lag of more than 50 years? Biol Invasions 12:3579–3589

Zalasiewic J, Williams M, Steffen W, Crutzen P (2010) The new world of the Anthropocene. Environ Sci Technol 44:2228–2231