


# Parasites and Lessepsian migration of *Fistularia commersonii* (Osteichthyes, Fistulariidae): shadows and light on the enemy release hypothesis

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**Abstract** According to the enemy release hypothesis, one of the reasons for the successful establishment of non-indigenous species in a new habitat is the liberation from natural enemies, and among them the parasites. The rapid spread of the Red Sea/Indo-Pacific fish *Fistularia commersonii* in the Mediterranean Sea, which in just 7 years (2000–2007) invaded nearly all of the basin, gives an opportunity to study the dynamics of the host and its parasites in its recently invaded range. Information on the parasites of this fish in its original habitat is quite scarce. The present study describes the metazoan parasites of 40 specimens of *F. commersonii* (total length range 73–107 cm) caught in the Mediterranean Sea (Sardinia, Tunisia, Libya) from 2005 to 2015. The parasite fauna of this migrant in the recently invaded range is mainly a combination of generalist juvenile/larval species (probably acquired in the new habitat) with some of its adult natural parasites (probably co-introduced during migration). The results indicate that a non-indigenous species is not always released from its natural parasites

and that its success is not simply associated with such liberation. Actually, the parasite fauna of *F. commersonii* increased along its migration path, acquiring new generalist species, but also conserving a subset of natural parasites. These data suggest caution in the uncritical acceptance of the enemy release hypothesis, because the different phases of the invasion process and establishment of a non-indigenous species appear to be related to a combination of ecological, physiological and behavioural factors.

## Introduction

The opening of the Suez Canal in 1869 has to be considered an important event from a biogeographical perspective (Galil 2007). Actually, it caused dramatic changes in the eastern Mediterranean Sea, in particular by facilitating marine faunal migrations from the Red Sea into the Mediterranean Sea (Por 1971). Fish have been involved in this so-called “Lessepsian migration”, and just over 30 years from the reconnection of the two seas (they were in fact connected about ten million years before) the occurrence of several Indo-Pacific fish was reported off the Mediterranean coast of Egypt (Tillier 1902). During the following decades, an astonishing number of Lessepsian fish has been recorded throughout the Mediterranean Sea (Golani and Appelbaum-Golani 2010), and many of them have quickly become well-established also spawning in different parts of the eastern basin (Golani 1998; Bariche et al. 2013).

Among them, the bluespotted cornetfish *Fistularia commersonii* Rüppel 1838 (Osteichthyes, Fistulariidae), originally distributed in the Red Sea and the Indian and Pacific Oceans (Fritzsche 1976; Froese and Pauly 2011)

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is considered as one of the most invasive species of the Mediterranean Sea (Streftaris and Zenetos 2006) and of European waters (DAISIE 2008). The rapid and successful spread of *F. commersonii* in the Mediterranean Sea was predicted by Karachle et al. (2004), giving this species the nickname “Lessepsian sprinter.” Fifteen years ago, this species was registered for the first time off the Mediterranean coasts of Israel (Golani 2000). Since then, it has spread rapidly all over the Mediterranean Sea, across the eastern (Bilecenoglu et al. 2002; Corsini et al. 2002; Karachle et al. 2004), central (Azzurro et al. 2004; Ben-Souissi et al. 2004) and western sectors of the basin (Pais et al. 2007; Garibaldi and Orsi Relini 2008; Kara and Oudjane 2008). In 2007, it also reached the Alboran Sea (Sanchez-Tocino et al. 2007), which is the farthest a Lessepsian fish migrant has ever been recorded from its entry point (CIESM 2009).

Genetic studies based on mitochondrial markers showed that this invasion produced a severe bottleneck in the Mediterranean population, with a great decrease of genetic diversity in comparison with the natural one (Golani et al. 2007; Sanna et al. 2015). Recently, Azzurro et al. (2013) showed that colonisation of the Mediterranean Sea proceeded in parallel along the southern and northern rim of the basin at speeds that reached 1000–1500 km per year, with a clear decrease at the Sicily Strait. This biogeographical barrier, once considered the western limit of Lessepsian migrations (Por 1978; Quignard and Tomasini 2000), forced the species to decelerate but did not stop it completely. In fact, once it was crossed, the speed increased again.

The success of a non-indigenous species (NIS) in a new habitat is often explained with the so-called enemy release hypothesis (ERH). According to this theory, during the process of biological invasion, NIS are released from the effects of their natural enemies (competitors, predators, pathogens and parasites) which control their population in the native region. The idea that exotic species may leave their natural enemies behind has a long history (Darwin 1859; Elton 1958), and initially it was focused on species escaping from herbivores and predators (Keane and Crawley 2002), but recently it has been suggested that the escape from parasites may have a great relevance (Torchin et al. 2002; Colautti et al. 2004; Hänfling 2007; Vignon and Sasal 2010). Parasites can directly affect their hosts, reducing growth, reproduction, and survivorship or, indirectly, by influencing behaviours and interacting with predation and competition to increase the likelihood of parasite transmission to the next host (Møller 2005). Thus, like most natural enemies, and analogously to predator–prey interactions, parasites are able to regulate the host population in a density dependent way (Anderson and May 1978; May and Anderson 1978).

Although this theory is becoming increasingly popular, particularly for plant species and terrestrial animals, the

few studies that try to evaluate its significance for aquatic animal invasions deal mainly with invertebrates and freshwater fish, whereas those on marine fish are scarce (see Torchin et al. 2002, Colautti et al. 2004, Hänfling 2007, Vignon and Sasal 2010, and references therein).

At present, few data have been published on the parasites of *F. commersonii* from its natural range, and all of them are simple faunistic reports or new species descriptions. The parasite fauna of *F. commersonii* (Table 1) is mainly characterised by various species of trematodes and caligid copepods, reported from the eastern, southern and western Pacific Ocean. In addition, the myxozoan *Ceratomyxa hurghadensis* Abdel-Ghaffar et al. 2008, was described from the Red Sea off Egypt, and sporadic records of monogeneans, larval stages of cestodes and adult and larval stages of nematodes have been reported from the southern Pacific Ocean.

The first parasitological study of *F. commersonii* in the Mediterranean Sea was published by Pais et al. (2007), when the following parasites were found in a single specimen caught off the eastern coast of Sardinia: adults of *Allolepidapedon fistulariae* Yamaguti 1940 (Trematoda), plerocercoid larvae of *Nybelinia africana* Dollfus 1960 and of Phyllobothriidae (Cestoda); a preadult female of *Spinitectus* sp. (Nematoda); and pranzia larvae of Gnathiididae (Crustacea). Subsequently, Merella et al. (2007, 2015) reported partial information on the parasites of this fish from Sardinia and some localities off Tunisia and Libya. These contributions added several generalist juvenile/larval parasites and some adult parasites to the Mediterranean parasite list, among them the Indo-Pacific trematode *Neoallopepidapedon hawaiiense* Yamaguti 1965 which, along with *A. fistulariae*, had been described exclusively in *Fistularia* spp. from the Indo-Pacific Region (Bray 2005).

The present study describes the metazoan parasites of 40 specimens of *F. commersonii* from the Mediterranean Sea, adding new information on the parasite fauna of this migrant fish in the recently invaded range. The qualitative and quantitative comparison between the parasite assemblages of this fish from the Mediterranean Sea and the Red Sea/Indo-Pacific area will be used to evaluate the importance of the ERH in the success of a marine fish species invasion.

## Materials and methods

The fish samples considered in this study comprise all the specimens of *Fistularia commersonii* examined by the authors during the 11 years between 2005 and 2015, including the data published by Pais et al. (2007). Sampling was carried out with the occasional aid of sport and professional

**Table 1** Previous studies on the parasites of *Fistularia commersonii* in its natural range

Reference (*)	1	2	3	4	5	6	7	8	9	10
Locality (**)	SEP	EP	SCP	SWP	RS	WP	SWP	SWP	WP	SWP
Parasite\N. hosts	3	1	2	2	40	3	1	1	1	1
Class Myxozoa										
<i>Ceratomyxa hurghadensis</i> <sup>a</sup>					30 %					
Class Monogenea										
Monogenea (juvenile) <sup>a</sup>								X		
Class Trematoda										
<i>Ectenurus virgulus</i>		1								
<i>Lecithochirium microstomum</i>		1								
<i>Allolepidapedon fistulariae</i> <sup>a</sup>			32	39						
<i>Neoalolepidapedon hawaiiense</i> <sup>a</sup>			13							
Bucephalidae			3							
Hemiuridae			1							
<i>Stephanostomum fijiensis</i> <sup>a</sup>				31						
Class Cestoda										
Phyllobothriidae (plerocercoid)								X		
<i>Dasyrhynchus basipunctatus</i>										1
Phylum Nematoda										
Capillariidae							1			
Anisakidae (larvae)								X		
Class Hirudinea										
Hirudinea								1		
Subphylum Crustacea										
<i>Caligus fistulariae</i> <sup>a</sup>	34					26		10	3	
<i>Caligus flexispina</i> <sup>a</sup>	4									
Copepoda			30							

For each reference and locality there are reported the number of hosts examined and the number (or prevalence %, or presence “X”) of the parasites found. Supposed specific and/or frequently occurring parasites are mentioned with superscript a

(\*) 1 Fernández and Villalba (1986); 2 Pérez-Ponce de León et al. (1998); 3 Rigby et al. (1999); 4 Nahhas et al. (2004); 5 Abdel-Ghaffar et al. (2008); 6 Ho et al. (2008); 7 Moravec and Justine (2010); 8 Justine pers. comm.; 9 Moon et al. (2012); 10 Beveridge et al. (2014)

(\*\*) *SCP* southern central Pacific Ocean, *EP* eastern Pacific Ocean, *SEP* southeastern Pacific Ocean, *SWP* southwestern Pacific Ocean, *RS* Red Sea, *WP* western Pacific Ocean

fishermen who, after catching this “strange pipe fish”, sent specimens to the authors for examination.

A total of 40 specimens of *F. commersonii* from the Mediterranean Sea were analysed: 34 were caught off the coasts of Sardinia, and six off the North African coast (Tunisia and Libya). Table 2 shows the length–weight data of the hosts examined (total length range 73–107 cm; total weight range 227–1000 g). Fish were caught mainly during the cold seasons (autumn and winter) in shallow waters ranging 5–50 m, on sandy or rocky bottoms, or *Posidonia oceanica* (Linnaeus) sea beds. For parasitological analysis, body surface, mouth, gills, body cavity and all internal organs were examined for metazoan parasites with the naked eye and under a stereomicroscope. The parasites collected were stored in

70 % ethanol and processed for identification according to standard protocols (Kennedy 1979; Berland 1984).

Due to the opportunistic sampling strategy, the size of samples according to year and locality was stochastic, and all specimens were examined after freezing, with not all of them fully intact and preserved in an optimal condition for parasitological analysis. Therefore, it is possible that some parasites were lost or displaced during transportation or preservation and also that parasite species richness and levels of infections could have been subject to some bias (i.e. underestimated). However, the opportunistic sampling is the only approach that can be adopted for the study of marine species that are difficult to collect or not subject to commercial fishery (Santoro et al. 2010; Aznar et al. 2012).

**Table 2** Data of the examined specimens of *Fistularia commersonii*

N.	Locality	Date	TL (cm)	TW (g)	Sex
<i>Sardinia</i>					
1	Arbatax	27/10/2005	82	411	F
2	Gulf of Cagliari	19/09/2007	79	350	F
3	Capo Comino	22/09/2007	93	646	–
4	Gulf of Cagliari	23/09/2007	84	440	–
5	Gulf of Cagliari	27/09/2007	80	400	F
6	Gulf of Cagliari	12/10/2007	75	292	M
7	Gulf of Cagliari	12/10/2007	75	308	F
8	Gulf of Cagliari	12/10/2007	81	394	M
9	Sant'Antioco	15/10/2007	89	517	F
10	Sant'Antioco	15/10/2007	79	340	–
11	Su Pallosu	05/11/2007	86	526	F
12	Arbatax	05/11/2007	78	339	F
13	Gulf of Oristano	15/11/2007	82	365	F
14	Gulf of Cagliari	15/11/2007	85	446	F
15	Capo Malfatano	26/12/2007	86	436	F
16	Torre delle Stelle	06/01/2008	86	395	F
17	Arbatax	06/01/2008	84	402	F
18	La Maddalena	01/04/2010	73	227	F
19	Gulf of Orosei	26/09/2010	80	303	F
20	Gulf of Orosei	27/09/2010	107	1000	F
21	Golfo Aranci	16/10/2010	85	324	F
22	Punta Tramontana	20/10/2010	80	306	F
23	Castelsardo	20/10/2010	80	314	F
24	Cala Sinzias	02/01/2011	85	337	F
25	Teulada	31/01/2011	81	267	M
26	Castelsardo	01/09/2011	92	394	F
27	Su Pallosu	01/12/2011	98	656	F
28	Su Pallosu	01/12/2011	82	433	F
29	Su Pallosu	02/12/2011	90	579	F
30	Stintino	01/10/2012	86	227	F
31	Santa Teresa di Gallura	01/10/2014	83	328	F
32	Gulf of Orosei	30/10/2014	76	258	M
33	Gulf of Orosei	31/10/2014	94	630	M
34	Isola Rossa	01/04/2015	89	440	F
<i>North Africa</i>					
35	Sfax	06/12/2006	96	717	M
36	Tboulba	13/12/2006	81	371	F
37	Tboulba	18/12/2006	85	415	F
38	Tboulba	23/12/2006	85	478	F
39	Tripoli	28/12/2006	89	585	M
40	Tripoli	28/12/2006	90	542	F

TL total length, TW total weight

Prevalence, mean intensity and mean abundance of each parasite species were calculated according to Bush et al. (1997). Differences were evaluated using the Fisher exact test for prevalence and the bootstrap rank Welch test for

mean abundance and mean intensity (2000 replications). Correlation between the abundance of the parasite species and host size was evaluated using the Spearman rank correlation coefficient. Statistical analyses were carried out with the free software QPweb (Reiczigel et al. 2013).

Infracommunity dissimilarity was evaluated according to Mele et al. (2014). The vegan library of the R-software (R Development Core Team 2015) was used to compute a two-dimensional non-metric multidimensional scaling (NMDS) based on a Bray–Curtis distance matrix of infracommunity richness, previously square root transformed (Oksanen 2015). Three geographical areas were considered a priori: the native range, excluding the eastern Pacific samples (51 infracommunities, see Table 1); Sardinia (24 infracommunities, excluding ten because samples were damaged and parasitological data were incomplete, see Table 3); North Africa (six infracommunities, see Table 3). Accidental parasite species (i.e. only one specimen collected or only one host infected) were not included in the analysis. Vectors of each variable were included in NMDS graphs in order to determine the principal factors driving the separation of the infracommunities. Only the vectors with significant Pearson  $r^2$  values ( $p$  value  $\leq 0.05$ ) were showed in the plots. Kruskal stress was calculated to estimate the goodness of fit of the NMDS graphs.

## Results

The parasitological analysis of 40 specimens of *Fistularia commersonii* from the Mediterranean Sea retrieved 22 species/taxa of metazoan parasites (Table 3). Some parasites were not identified at the species level, because they were juvenile or larval stages, or also because of the poor quality of some samples.

Adults of six species/taxa were recovered: the lepidapedid trematodes *Allolepidapedon fistulariae* and *Neoallopepidapedon hawaiiense* in the digestive tract; a male philometrid nematode in the stomach; males and females of the arhythmacanthid acanthocephalan *Breizacanthus ligur* Paggi et al. 1975 in the intestine; the piscicolid hirudinean *Trachelobdella lubrica* (Grube 1840) on the gills and in the mouth; and a female of the caligid copepod *Caligus minimus* Otto 1821 in the mouth. The remaining 16 taxonomical groups of juvenile/larval stages belonged to trematodes, cestodes, nematodes and crustaceans. Among the trematodes, seven taxa of barely identifiable juvenile/larval stages were found in the digestive tract. Concerning cestodes, three different types of plerocercoid stages were recognised: unidentified phyllobothriids in the caecum and intestine; *Nybelinia africana* in the stomach wall; and *Pseudogrillotia* sp. in the body cavity. Among nematodes, four taxa were identified: third and fourth stage larvae of

**Table 3** List of the parasites of *Fistularia commersonii* from the two areas of the Mediterranean Sea

Parasite	Location	Sardinia			North Africa		
		P %	mI	(range)	P %	mI	(range)
<b>Class Trematoda</b>							
<i>Allolepidapedon fistulariae</i> <sup>a</sup>	Digestive tract	73.5	11.6	(1–37)	66.7	7.5	(2–12)
<i>Neoallopepidapedon hawaiiense</i> <sup>a</sup>	Stomach				16.7	1.0	(1–1)
<i>Lecithocladium</i> sp. (juvenile)	Stomach	2.9	1.0	(1–1)			
Lepocreadiidae (juvenile)	Intestine	2.9	7.0	(7–7)			
<i>Stephanostomum</i> (juvenile)	Intestine	2.9	1.0	(1–1)			
Bucephalidae (juvenile)	Intestine	2.9	3.0	(3–3)			
Hemiuridae (juvenile)	Stomach	2.9	1.0	(1–1)			
Trematoda (juvenile)	Stomach	2.9	1.0	(1–1)			
Trematoda (metacercaria)	Stomach	8.8	1.3	(1–2)			
<b>Class Cestoda</b>							
<i>Nybelinia africana</i> (plerocercoid) <sup>a</sup>	Stomach wall	82.4	49.7*	(4–200)	100	18.5*	(3–53)
<i>Pseudogrillotia</i> sp. (plerocercoid) <sup>a</sup>	Body cavity	23.5	1.9	(1–6)			
Phyllobothriidae (plerocercoid) <sup>a</sup>	Caecum/intestine	20.6	20.7	(1–68)			
<b>Phylum Nematoda</b>							
<i>Hysterothylacium aduncum</i> (L <sub>3</sub> –L <sub>4</sub> ) <sup>a</sup>	Body cavity/digestive tract	8.8*	2.3	(1–4)	50.0*	8.0	(1–20)
<i>Hysterothylacium fabri</i> (L <sub>3</sub> –L <sub>4</sub> ) <sup>a</sup>	Body cavity/digestive tract	41.2	5.1	(1–15)	16.7	2.0	(2–2)
<i>Spinitectus</i> sp. (L <sub>3</sub> )	Intestine	8.8	1.3	(1–2)			
Cystidicolidae (L <sub>4</sub> )	Stomach	2.9	1.0	(1–1)			
Philometridae (male)	Stomach	2.9	1.0	(1–1)			
<b>Phylum Acanthocephala</b>							
<i>Breizacanthus ligur</i> <sup>a</sup>	Intestine	17.6	1.5	(1–2)			
<b>Class Hirudinea</b>							
<i>Trachelobdella lubrica</i> <sup>a</sup>	Mouth/gills	8.8*	1.0	(1–1)	50.0*	1.0	(1–1)
<b>Subphylum Crustacea</b>							
<i>Caligus elongatus</i> (chalimus)	Mouth/gills	5.9	1.0	(1–1)			
<i>Caligus minimus</i> (female)	Mouth	2.9	1.0	(1–1)			
Gnathiidae (praniza) <sup>a</sup>	Mouth/gills	35.3	5.2	(1–34)	33.3	15.0	(10–20)

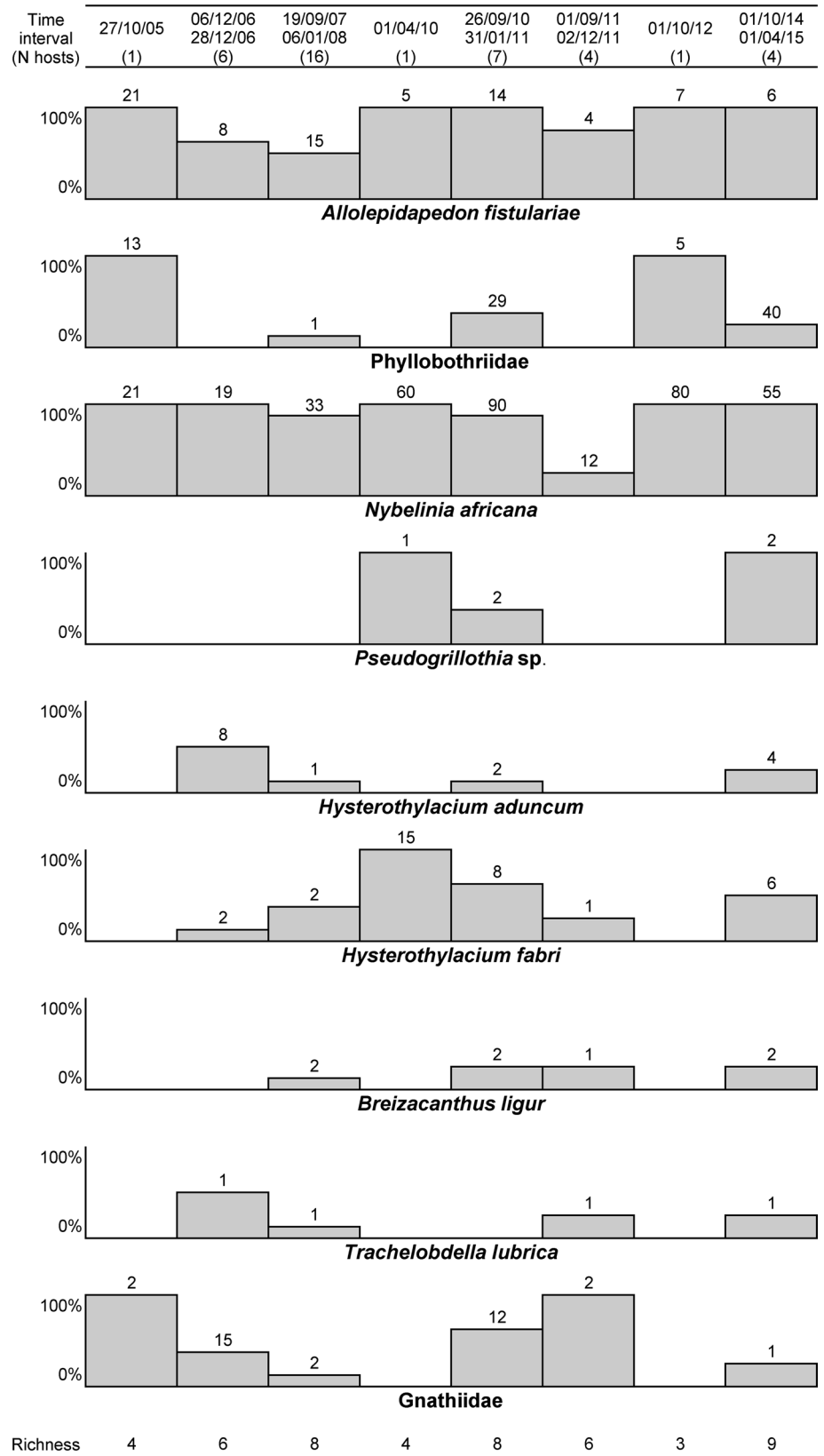
P % prevalence, mI mean intensity (range in brackets). \* Significant differences between localities. Supposed specific and/or frequently occurring parasites are mentioned with superscript a

*Hysterothylacium aduncum* (Rudolphi 1802) and *Hysterothylacium fabri* (Rudolphi 1819) in the digestive tract and body cavity; a fourth stage larva of an unidentified cystidicolid in the stomach; and a third stage larva of *Spinitectus* sp. in the intestine. Finally, regarding crustaceans, chalimi of *Caligus elongatus* von Nordmann 1832 and praniza larvae of Gnathiidae were found on the gills and in the mouth.

Table 3 shows the quantitative data of the parasites of *F. commersonii* found in the two Mediterranean localities (Sardinia and North Africa). Due to the opportunistic sampling strategy, the levels of infection (particularly the intensity of infection) may have been partially underestimated; therefore, the quantitative data should be intended as minimal possible values. Regarding the component community, nine species/taxa can be considered as common, with a prevalence greater than 15 % in one of the two localities,

whereas the rare and/or accidental ones had a prevalence ranging between 2.9 and 8.8 % (1–3 hosts infected) and intensities of infection between 1 and 3, apart from the juvenile lepecreadiids with seven specimens in one single host. The parasite assemblages were mainly characterised by two species, *N. africana* plerocercoids (prevalence 82.4–100 %, mean intensity 18.5–49.7, the dominant species in both localities) and *A. fistulariae* adults (66.7–73.5 %, 7.5–11.6). Among the other seven common species, most of them were larval stages (Phyllobothriidae, *Pseudogrillotia* sp., *H. aduncum*, *H. fabri*, Gnathiidae), but also two adult stages were found, *T. lubrica* and *B. ligur*. The few significant differences found between localities were the higher mean intensity of *N. africana* in Sardinia, and the higher prevalence of *H. aduncum* and *T. lubrica* in North Africa (Table 3).

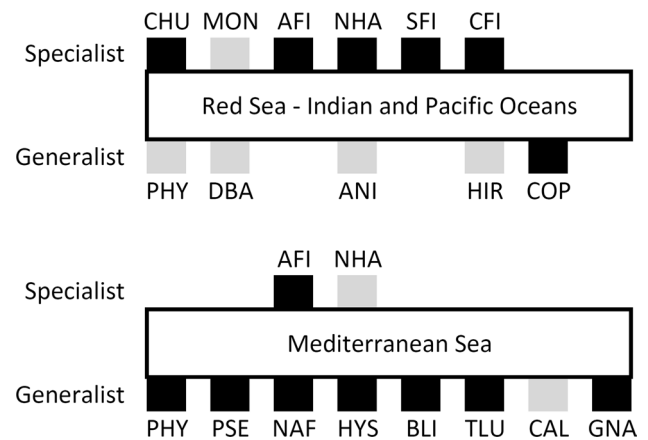
**Fig. 1** Number of hosts examined (in brackets), prevalence (bars), mean intensity (on top of the bars), and richness (at the bottom) of the specific and/or frequently occurring parasites of *Fistularia commersonii* in the Mediterranean Sea according to the sampling year



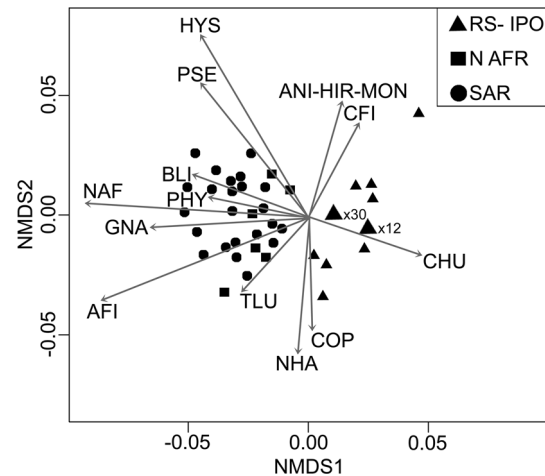


Considering that the hosts were mainly present during the cold seasons (autumn and winter), temporal data were grouped across the end of a year and the beginning of the next one. There was no a clear trend/pattern of the levels of infection according to time (Fig. 1), with the two most important species (*N. africana* and *A. fistulariae*) almost always recorded with prevalence close to 100 % and high mean intensity. The other species oscillated with no evident pattern, apart from a slight apparent increase in *Pseudogrillotia* sp., confirmed by a significant relationship of the mean abundance with the time (Spearman rank correlation index,  $R_s = 0.55$ ,  $P = 0.0001$ ). The correlation analysis of the levels of infection with host length did not show any significant trend, apart from a positive relationship of the abundance of *H. aduncum* with the host total length ( $R_s = 0.40$ ,  $P = 0.01$ ).

It is not easy to compare the Mediterranean parasite assemblage (Table 3) with the Red Sea/Indo-Pacific one (Table 1), particularly because of the few data on the parasites of *F. commersonii* in its original habitat. The Mediterranean invaders most likely came from the Red Sea/Indian Ocean, or ultimately from the nearby areas of the Pacific Ocean, whereas the parasites from the eastern Pacific Ocean are probably irrelevant to the comparison. Taking into account the biological and ecological features of the parasites, it is possible to identify seven specific and/or frequently occurring parasites of *F. commersonii* in the Red Sea, Indian Ocean and nearby areas of the Pacific Ocean. These are *Ceratomyxa hurghadensis*, Monogenea, *A. fistulariae*, *N. hawaiiense*, *Stephanostomum fijiensis* Nahas, Nasser & Tam 2004, and *Caligus fistulariae* Yamaguti 1936, because some of them have been described in *F. commersonii* with high levels of infection, and/or are common parasites of other *Fistularia* spp., and/or are considered specialist parasites. A comparison between the parasite assemblages of the Mediterranean Sea and the Indo-Pacific area, considering the specific and/or frequently occurring species of one or another locality (including the equivalent one in the other area also if rare), is shown in Fig. 2. The total species richness in the Mediterranean Sea is about the same as in the Red Sea/Indo-Pacific area (10 vs. 11), with a reduction in the specialist parasites and an increase in the generalist ones. From this comparison some analogies and differences can be highlighted: (i) only the two specific trematodes *A. fistulariae* and *N. hawaiiense* match exactly in the two lists, although the two species have a significantly different importance in the Mediterranean Sea; (ii) a group of generalist parasites with analogous systematic position/life cycle are shared between the two lists, in a relationship of vicariance (Phyllobothriidae; *Dasyrhynchus basipunctatus* (Carvajal, Campbell & Cornford 1976) versus *Pseudogrillotia* sp.; Anisakidae vs. *Hysterothylacium* spp.; Hirudinea vs. *T. lubrica*; Copepoda vs. *Caligus* spp.);



**Fig. 2** Change of the structure of the parasite assemblage of *Fistularia commersonii* after the Lessepsian migration. The same position indicates analogous systematic position/life cycle. *Pale cases* indicate rare/accidental species. AFI *Allolepidapedon fistulariae*; ANI Anisakidae; BLI *Breizacanthus ligur*; CAL *Caligus* spp.; CFI *Caligus fistulariae*; CHU *Ceratomyxa hurghadensis*; COP Copepoda; DBA *Dasyrhynchus basipunctatus*; GNA Gnathiidae; HIR Hirudinea; HYS *Hysterothylacium* spp.; MON Monogenea; NAF *Nybelinia africana*; NHA *Neoalolepidapedon hawaiiense*; PHY Phyllobothriidae; PSE *Pseudogrillotia* sp.; SFI *Stephanostomum fijiensis*; TLU *Trachelobdella lubrica*



**Fig. 3** Non-metric multidimensional scaling plots based on the Bray–Curtis distance of the infracommunity richness of *Fistularia commersonii*. RS-IPO, Red Sea and Indian and Pacific Oceans; N AFR, North Africa; Sar, Sardinia. For species abbreviations see Fig. 2. *Larger symbols* represent several data points at the same position, whose number is given by a multiplication factor (e.g.,  $\times 12$ )

(iii) a number of specialist parasites have been described only in the natural habitat (*C. hurghadensis*, Monogenea, *S. fijiensis*, *C. fistulariae*); and (iv) three generalist parasites with high levels of infection appear only in the Mediterranean Sea (*N. africana*, *B. ligur*, Gnathiidae).

The NMDS of the Bray–Curtis dissimilarity of the infracommunity richness of *F. commersonii* from the native and new habitat is driven by the presence/absence of 15 species (Fig. 3). Stress value for the NMDS analysis was lower than 0.10 (p-value < 0.03), indicating a sufficient resolution for reliable interpretation (Clarke 1993). According to the NMDS1 axis, the infracommunities grouped into two clusters: one with the hosts of the native range, and one with those of the invaded Mediterranean Sea (Sardinia and North Africa). Dissimilarity was higher within the native range than within the Mediterranean regions. The infracommunities of the native range were discriminated by two specialist parasites *C. hurghadensis* ( $r^2 = 0.2096$ ) and *C. fistulariae* ( $r^2 = 0.1788$ ), whereas those of the invaded Mediterranean area were characterised by a number of generalist parasites, i.e. *N. africana* ( $r^2 = 0.7603$ ), *Pseudogrillotia* sp. ( $r^2 = 0.4561$ ), Gnathiidae ( $r^2 = 0.3834$ ), and *B. ligur* ( $r^2 = 0.2406$ ), but also by the specific *A. fistulariae* ( $r^2 = 0.7547$ ). According to the NMDS2 axis, no separation between the infracommunities was found.

## Discussion

There are very few data on the parasites of *Fistularia commersonii* in its original habitat and, so far, 19 species/taxa of metazoan parasites have been reported in ten scientific papers, with limited quantitative information. In addition, the parasite assemblage of this migrant fish in the recently invaded Mediterranean Sea includes 22 species/taxa, and it is mainly a combination of generalist juvenile/larval species (probably acquired in the new habitat) with some of its adult natural parasites (probably co-introduced during migration). The overall result of the evolution of structure and composition of the parasite assemblage of *F. commersonii* after the Lessepsian migration is a reduction in the natural specialist parasites and the acquisition of native generalist ones, with no evident decrease of the richness and levels of infection in the Mediterranean Sea. Studies on the parasites of other Lessepsian fish have shown evidence of similar situations, with hosts infected with both natural and native parasites, without a clear reduction in the parasite assemblage in the new habitat (Diamant 1989, 1998). Analogous results have also been reported for other migrant fish worldwide (Poulin and Mouillot 2003; Kvach and Skóra 2007; Roche et al. 2010; Lacerda et al. 2013), but other authors showed a dramatic decrease of the parasite species after migration (Vignon et al. 2009; Gendron et al. 2012), showing a high variability of the patterns of parasitic infection in migrant fish.

The reduction/loss of natural parasites could be due to several reasons (Torchin et al. 2002; Vignon et al. 2009): heteroxenous parasites as *Ceratomyxa hurghadensis*, *Neoalolepidapedon hawaiiense* and *Stephanostomum fijiensis* require at least two hosts to accomplish their life cycle

(Cribb 2005; Lom 2005), and these hosts may not be found in the new habitat. On the other hand, holoxenous Monogenea and Copepoda are ectoparasites, hence more subject to the influence of the environmental conditions (Hayward 2005; Taraschewski 2005; Whittington 2005); thus, they could be lost during host migration. *Allolepidapedon fistulariae*, in spite of its heteroxenous life cycle, seems to be co-introduced in the Mediterranean Sea; a first hypothesis relevant to this finding was that it had found suitable hosts and environmental conditions to complete the life cycle in the new habitat (Pais et al. 2007; Merella et al. 2010), as formerly suggested for other trematode parasites of Lessepsian fish (Fischthal 1980; Diamant 1989, 1998). However, some data, such as its prevalence in the Mediterranean hosts regardless of size, year and locality, and the fact that all the specimens of this parasite were retrieved at the adult stage, could also suggest a residual infection that took place before of the host migration. Very little is known about the longevity of adult trematodes, and although many species show a seasonality which suggests lifespan of less than a year, larger marine trematodes probably live longer, and some of them could live for years (Cribb 2005).

Regarding the generalist parasites recorded in the Mediterranean Sea, this group is richer and with higher levels of infection than in the Red Sea/Indo-Pacific area, with some taxa replaced by others closely related, in a relationship of vicariance. New parasites also emerged with high levels of infection, for example the dominant species *Nybelinia africana*, *Breizacanthus ligur*, and gnathiid isopods. Among these generalist parasites, *B. ligur* has been previously recorded only in the Mediterranean Sea and *C. minimus* in the Mediterranean Sea and the Atlantic Ocean. Thus, these native species must have switched to *F. commersonii* after its migration. The others have been described both in the Mediterranean Sea and the natural range of *F. commersonii*, but their short lifespan would suggest they have been acquired in the new invaded habitat. Exceptions are the two trypanorhynch *N. africana* and *Pseudogrillotia* sp., which because of their long lifespan (permanent parasites, sensu MacKenzie and Abaunza 2014) co-introduction or new acquisition, or even both, would be possible.

A further element to consider is if host switching by native parasites could be more harmful to non-indigenous species (NIS) than natives. The long coevolutionary history of a host and its natural parasites contributes to shape the phylogenesis of both of them (Hoberg 2005). On the other hand, NIS are naïve hosts to native parasites, which can cause novel and sometimes profound instances of pathology (Colautti et al. 2004). Therefore, native parasites could represent an important source of selection against migrants (MacColl and Chapman 2010). This was shown by Scharfack et al. (2007), who exposed river-adapted specimens of *Gasterosteus aculeatus* Linnaeus 1758 (Osteichthyes,



Gasterosteidae) to parasite-dense lake conditions, finding that although these fish had an elevated activation of the immune system (respiratory burst, granulocyte counts, head kidney lymphocyte proliferation), they had significantly higher parasite loads compared to the native fish.

Moreover, invasion bottlenecks may reduce the genetic diversity of polymorphic defences, which are important in avoiding disease outbreak; thus, enemies could have negative effects on populations of NIS if compared with more genetically diverse native species (Colautti et al. 2004). According to the so-called “increased susceptibility hypothesis”, the loss of defences due to invasion bottlenecks may interact with the *naïveté* to native parasites leading to an increase in susceptibility of introduced populations, leaving NIS more subject to enemy effects than the source population (Colautti et al. 2004).

Although population bottlenecks are a common feature of biological invasions, almost all the Lessepsian migrant fish populations display a high genetic similarity with the Red Sea/Indo-Pacific ones, with no evidence of genetic bottlenecks (Bernardi et al. 2010). Conversely, *F. commersonii*, in spite of the extraordinary speed of its colonisation which has no equals among the Mediterranean NIS (Azzurro et al. 2013), is the only Lessepsian fish that shows a severe bottleneck, and for this reason Sanna et al. (2015) nicknamed it “Lessepsian paradox”.

The above results suggest that the “enemy release hypothesis” (ERH) cannot be considered as a general principle; in fact, the success of *F. commersonii* in the Mediterranean Sea does not seem related with the liberation from its parasites but, on the contrary, this fish may have found in the new habitat a rich parasite assemblage that potentially would threaten it more than in its native range. Therefore, caution is suggested against the uncritical acceptance of the ERH, as recommended in other studies (see Colautti et al. 2004, MacColl and Chapman 2010, Lacerda et al. 2013, among others). Indeed, according to Jackson et al. (2015) a combination of ecological, physiological and behavioural factors would influence different phases of the invasion process. In this regard, Arndt and Schembri (2015) have recently observed that the establishment success of Lessepsian fish is significantly linked to size and spawning type and that benthic spawners and species with a tendency to form schools are successful colonisers.

The parasitological results also offer new elements to evaluate the establishment of a self sustaining population of *F. commersonii* in the western Mediterranean Sea. The hypothetical presence of a residual infection of *A. fistulariae* in all the examined hosts suggests that all fish arrived as adult/juvenile from the Red Sea (only these stages can be infected with these parasites by preying on the intermediate host), and none were born in the new invaded habitat. Thus, this seems to be still a pioneer phase in the spread of the invader, as already

stated by Garibaldi and Orsi Relini (2008); actually, the evidence of reproduction and/or the presence of small juveniles refers only to the eastern basin or the Adriatic Sea (Deidun and Germanà 2011; Bariche et al. 2013; Dulčić et al. 2013).

Besides, the significant infection of adult males and females of *Breizacanthus ligur*, a species described by Paggi et al. (1975) in *Chlorophthalmus agassizi* Bonaparte 1840 and other fish caught at 400–650 m depth, gives new hints on the life history of *F. commersonii* in the Mediterranean Sea. The presence of this parasite suggests that this fish may spend part of its life in a relatively deep-water habitat, undergoing periodical migrations to the shallow waters. Actually, this fish is considered a deep-water species in some studies from the southwestern Pacific Ocean (Anderson et al. 2011; Zintzen et al. 2011), and also Azzurro et al. (2013) suggested a periodical migration of *F. commersonii*, which will lead to an increase in records at the beginning of the cold season. This hypothesis could help to explain how this presumed littoral fish (Fritzsche 1976; Froese and Pauly 2011) has been able to cover the distance from Suez to Gibraltar in just seven years, regardless of the water circulation, at speeds up to 1000–1500 km per year (Azzurro et al. 2013). Indeed, assuming such periodical migration, it would be possible to explain the rapid spread by the use of the open-water/deep-sea habitat as a shortcut, rather than making a circumnavigation along the perimeter of the Mediterranean Basin.

In conclusion, the study of the parasites of *F. commersonii* in the Mediterranean Sea sheds both shadows and light onto the role of ERH in the success of a NIS, but also contributes to the understanding of some of the biological and ecological traits of this Lessepsian fish. Future studies should help to fill the gaps in the knowledge, and to this end it is necessary to gather more data on the parasites of *F. commersonii* in the Red Sea/Indo-Pacific area, to search for and examine juvenile fish from the Mediterranean Sea, and to look for possible intermediate hosts of the natural Indo-Pacific parasites found in the Mediterranean Sea.

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## References

- Abdel-Ghaffar F, Ali MA, Al Quraishy S, Al Rasheid K, Al Farraj S, Abdel-Baki AS, Bashtar AR (2008) Four new species of *Ceratomyxa* Thelohan 1892 (Myxozoa: Myxosporae: Ceratomyxidae) infecting the gallbladder of some Red Sea fishes. *Parasitol Res* 103(3):559–565

- Anderson RM, May RM (1978) Regulation of host-parasite population interactions: I. Regulatory processes. *J Anim Ecol* 47(1):219–247
- Anderson TJ, Nichol SL, Syms C, Przeslawski R, Harris PT (2011) Deep-sea bio-physical variables as surrogates for biological assemblages, an example from the Lord Howe Rise. *Deep Sea Res Part II: Top Stud Oceanogr* 58(7):979–991
- Arndt E, Schembri PJ (2015) Common traits associated with establishment and spread of Lessepsian fishes in the Mediterranean Sea. *Mar Biol* 162(10):2141–2153
- Aznar FJ, Hernández-Orts J, Suárez AA, García-Varela M, Raga JA, Cappozzo HL (2012) Assessing host-parasite specificity through coprological analysis: a case study with species of *Corynosoma* (Acanthocephala: Polymorphidae) from marine mammals. *J Helminthol* 86(2):156–164
- Azzurro E, Pizzicori P, Andaloro F (2004) First record of *Fistularia commersonii* from the central Mediterranean. *Cybio* 28(1):72–74
- Azzurro E, Soto S, Garofalo G, Maynou F (2013) *Fistularia commersonii* in the Mediterranean Sea: invasion history and distribution modeling based on presence-only records. *Biol Invasions* 15(5):977–990
- Bariche M, Kajajian A, Azzurro E (2013) Reproduction of the invasive bluespotted cornetfish *Fistularia commersonii* (Teleostei, Fistulariidae) in the Mediterranean Sea. *Mar Biol Res* 9(2):169–180
- Ben-Souissi J, Zaouali J, Bradai MN, Quignard JP (2004) Lessepsian migrant fishes off the coasts of Tunisia. First record of *Fistularia commersonii* (Osteichthyes, Fistulariidae) and *Parexocoetemento* (Osteichthyes, Exocoetidae). *Vie et Milieu* 54(4):247–248
- Berland B (1984) Basic techniques involved in helminth preservation. *Syst Parasitol* 6(4):242–245
- Bernardi G, Golani D, Azzurro E (2010) The genetics of Lessepsian bioinvasions. In: Golani D, Appelbaum-Golani B (eds) *Fish invasions of the Mediterranean Sea: change and renewal*. Pensoft Publishers, Sofia and Moscow, pp 71–84
- Beveridge I, Bray RA, Cribb TH, Justine JL (2014) Diversity of trypanorhynch metacystodes in teleost fishes from coral reefs off eastern Australia and New Caledonia. *Parasite* 21(60):1–19
- Bilecenoglu M, Taskavak E, Kunt KB (2002) Range extension of three Lessepsian migrant fish (*Fistularia commersonii*, *Sphyræna flavicauda*, *Lagocephalus suezensis*) in the Mediterranean Sea. *J Mar Biol Assoc UK* 82(3):525–526
- Bray RA (2005) Family Lepocreadiidae Odhner, 1905. In: Jones A, Bray RA, Gibson DI (eds) *Keys to the Trematoda*, vol 2. CABI Publishing and the Natural History Museum, Wallingford, pp 545–602
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *J Parasitol* 83(4):575–583
- CIESM (2009) CIESM Atlas of exotic species in the Mediterranean Sea. <http://www.ciesm.org/online/atlas/index.htm>. Accessed 10 Nov 2015
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18(1):117–143
- Colautti R, Ricciardi A, Grigorovitch IA (2004) Is invasion success explained by the enemy release hypothesis? *Ecol Lett* 7(8):721–733
- Corsini M, Kondilatos G, Economidis PS (2002) Lessepsian migrant *Fistularia commersonii* from the Rhodes marine area. *J Fish Biol* 61(4):1061–1062
- Cribb TH (2005) Digenea (endoparasitic flukes). In: Rohde K (ed) *Marine parasitology*. CABI Publishing, Wallingford, pp 76–87
- DAISIE (2008) European invasive alien species gateway. <http://www.europe-alien.org>. Accessed 10 Nov 2015
- Darwin C (1859) *The origin of species*. John Murray, London
- Deidun A, Germanà A (2011) On the increasing occurrence of the bluespotted cornetfish *Fistularia commersonii* (Rüppel, 1838) in the central Mediterranean (Osteichthyes, Fistulariidae). *Biodivers J* 2(1):19–26
- Diamant A (1989) Lessepsian migrant as hosts: a parasitological assessment of rabbitfish *Siganus luridus* and *Siganus rivulatus* (Siganidae) in their original and new biogeographical regions. In: Spanier E, Steinberger Y, Luria M (eds) *Environmental quality and ecosystem stability: Vol IV-B, environmental quality*. ISEEQS Publication, Jerusalem, pp 187–194
- Diamant A (1998) Parasitological aspects in Red-Med fish migration. *Actes du Colloque scientifique OCEANOS*, Montpellier (France), April 11–12, 1996, pp 175–178
- Dulčić J, Antolović N, Kožul V, Dragičević B, Lipej L (2013) First records of juveniles of two Lessepsian migrants, *Fistularia commersonii* Rüppell, 1838 and *Siganus luridus* (Rüppell, 1829), in the Adriatic Sea. *J Appl Ichthyol* 29(3):661–662
- Elton CS (1958) *The ecology of invasion by animals and plants*. Methuen, London
- Fernández J, Villalba C (1986) Contribución al conocimiento del género *Caligus* Müller, 1785 (Copepoda: Siphonostomatoida) en Chile. *Gayana Zool* 50(1–4):37–62
- Fischthal JH (1980) Some digenetic trematodes of marine fishes from Israel's Mediterranean coast and their zoogeography, especially those from Red Sea immigrant fishes. *Zool Scr* 9(1–4):11–23
- Fritzsche RA (1976) A review of the cornetfishes, genus *Fistularia* (Fistulariidae), with a discussion of intrageneric relationship and zoogeography. *Bull Mar Sci* 26(2):196–204
- Froese T, Pauly D (eds) (2011) *Fishbase*, world wide web electronic publication. <http://www.fishbase.org>. Accessed 10 Nov 2015
- Galil BS (2007) Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Mar Pollut Bull* 55(7):314–322
- Garibaldi F, Orsi Relini L (2008) Record of the bluespotted cornetfish *Fistularia commersonii* Rüppell, 1838 in the Ligurian Sea (NW Mediterranean). *Aquat Invasions* 3(4):471–474
- Gendron AD, Marcogliese DJ, Thomas M (2012) Invasive species are less parasitized than native competitors, but for how long? The case of the round goby in the Great Lakes-St. Lawrence Basin. *Biol Invasions* 14(2):367–384
- Golani D (1998) Distribution of Lessepsian migrant fish in the Mediterranean. *Ital J Zool* 65(1):95–99
- Golani D (2000) First record of the bluespotted cornetfish from the Mediterranean Sea. *J Fish Biol* 56(6):1545–1547
- Golani D, Appelbaum-Golani B (eds) (2010) *Fish invasions of the Mediterranean Sea: change and renewal*. Pensoft, Sofia-Moscow
- Golani D, Azzurro E, Corsini-Foka M, Falautano M, Andaloro F, Bernardi G (2007) Genetic bottlenecks and successful biological invasions: the case of a recent Lessepsian migrant. *Biol Lett* 3(5):541–545
- Hänfling B (2007) Understanding the establishment success of non-indigenous fishes: lessons from population genetics. *J Fish Biol* 71(Suppl D):115–135
- Hayward C (2005) Monogenea Polyopisthocotylea (ectoparasitic flukes). In: Rohde K (ed) *Marine parasitology*. CABI Publishing, Wallingford, pp 55–63
- Ho J-S, Cheng S-H, Chang W-C, Lin C-L (2008) Two species of siphonostomatoid copepods parasitic on marine fishes of Taiwan. *J Fish Soc Taiwan* 35(1):87–99
- Hoberg EP (2005) Coevolution in marine systems. In: Rohde K (ed) *Marine parasitology*. CABI Publishing, Wallingford, pp 327–339
- Jackson AM, Tenggardjaja K, Perez G, Azzurro E, Golani D, Bernardi G (2015) Phylogeography of the bluespotted cornetfish, *Fistularia commersonii*: a predictor of bioinvasion success? *Mar Ecol* 36(4):887–896
- Kara MH, Oudjane F (2008) First observations of the Indo-Pacific bluespotted cornetfish *Fistularia commersonii* (Fistulariidae) from Algerian coasts. *Mar Biodivers Rec* 2:e83
- Karachle PK, Triantaphyllidis C, Stergiou KI (2004) Bluespotted cornetfish, *Fistularia commersonii* Rüppell, 1838: a Lessepsian sprinter. *Acta Ich Piscat* 34(1):103–108

- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol Evol* 17(4):164–170
- Kennedy MJ (1979) Basic methods of specimen preparation in parasitology. International Development Research Centre, Ottawa
- Kvach Y, Skóra KE (2007) Metazoa parasites of the invasive round goby *Apollonia melanostoma* (*Neogobius melanostomus*) (Pallas) (Gobiidae: Osteichthyes) in the Gulf of Gdańsk, Baltic Sea, Poland: a comparison with the Black Sea. *Parasitol Res* 100(4):767–774
- Lacerda AC, Takemoto RM, Poulin R, Pavanelli GC (2013) Parasites of the fish *Cichla piquiti* (Cichlidae) in native and invaded Brazilian basins: release not from the enemy, but from its effects. *Parasitol Res* 112(1):279–288
- Lom J (2005) Myxozoa (myxozoans). In: Rohde K (ed) *Marine parasitology*. CABI Publishing, Wallingford, pp 41–46
- MacColl AD, Chapman SM (2010) Parasites can cause selection against migrants following dispersal between environments. *Funct Ecol* 24(4):847–856
- MacKenzie K, Abaunza P (2014) Parasites as biological tags. In: Cadrin SX, Kerr LA, Mariani S (eds) *Stock identification methods, Applications in Fisheries Science*, 2nd edn. Elsevier Academic Press, New York, pp 185–203
- May RM, Anderson RM (1978) Regulation and stability of host-parasite population interactions: II. Destabilizing processes. *J Anim Ecol* 47(1):249–267
- Mele S, Pennino MG, Piras MC, Bellido JM, Garippa G, Merella P (2014) Parasite of the head of *Scomber colias* (Osteichthyes: Scombridae) from the western Mediterranean Sea. *Acta Parasitol* 59(1):173–183
- Merella P, Farjallah S, Pais A, Follesa MC, Garippa G (2007) *Fistularia commersonii* Rüppell, 1835: a Lessepsian host carrier of Indo-Pacific parasites into the Mediterranean Sea. VII International Symposium on Fish Parasites, Viterbo (Italy), September 24–28 2007. *Parassitologia* 49(Suppl. 2):249
- Merella P, Pais A, Follesa MC, Farjallah S, Gagliardi F, Mele S, Piras MC, Garippa G (2015) Parasites of the Lessepsian sprinter *Fistularia commersonii* (Osteichthyes: Fistulariidae): an update after 15 years since its arrival in the Mediterranean Sea. IX International Symposium on Fish Parasites, Valencia (Spain), August 31 2015–September 05 2015, p 87
- Møller AP (2005) Parasitism and the regulation of host populations. In: Thomas F, Renaud F, Guégan J-F (eds) *Parasitism and ecosystems*. Oxford University Press, Oxford, pp 43–53
- Moon SY, Kim IH (2012) Sea lice (Copepoda, Siphonostomatoida, Caligidae) new to Korea, including three new species. *J Species Res* 1(2):175–217
- Moravec F, Justine JL (2010) Some trichinelloid nematodes from marine fishes off New Caledonia, including description of *Pseudocapillaria novaecaledoniensis* sp. nov. (Capillariidae). *Acta Parasitol* 55(1):71–80
- Nahas FM, Nasser H, Tam J (2004) Digenetic trematodes of marine fishes from Suva, Fiji: families: Acanthocolpidae, Lepocreadiidae, Bivesiculidae, Zoogonidae, Monorchiiidae and description of a new species. *Riv Parassitol* 21(1):33–48
- Oksanen J (2015) Multivariate analysis of ecological communities in R: Vegan tutorial. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>. Accessed 04 Dec 2015
- Paggi L, Orecchia P, Della Seta G (1975) A new Acanthocephala *Breizacanthus ligur* sp. n. (Palaeacanthocephala: Arhythmacanthidae Yamaguti, 1935) parasite of some species of benthic fishes from the Ligurian Sea. *Parassitologia* 17(1–3):83–94
- Pais A, Merella P, Follesa MC, Garippa G (2007) Westward range expansion of the Lessepsian migrant *Fistularia commersonii* (Fistulariidae) in the Mediterranean Sea, with notes on its parasites. *J Fish Biol* 70(1):269–277
- Pérez-Ponce de León G, León-Règagnon V, Monks S (1998) *Theletrum lamothei* sp. nov. (Digenea), parasite of *Echidna nocturna* from Cuajiniquil, Guanacaste, and other digenes of marine fishes from Costa Rica. *Rev Biol Trop* 46(2):345–354
- Por FD (1971) One hundred years of Suez Canal: a century of Lessepsian migration: retrospect and viewpoints. *Syst Zool* 20(2):138–159
- Por FD (1978) Lessepsian migration. The influx of Red Sea biota into the Mediterranean by way of the Suez Canal. *Ecological Studies* 23. Springer, Berlin
- Poulin R, Mouillot D (2003) Host introductions and the geography of parasite taxonomic diversity. *J Biogeogr* 30:837–845
- Quignard JP, Tomasini JA (2000) Mediterranean fish biodiversity. *Biol Mar Medit* 7(3):1–66
- R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Reiczigel J, Rózsa L, Reiczigel A (2013) Quantitative Parasitology (QPweb). <http://www2.univet.hu/qpweb>
- Rigby MC, Lo CM, Cribb TH, Euzet L, Faliex E, Galzin R, Holmes JC, Morand S (1999) Checklist of the parasites of coral reef fishes from French Polynesia, with considerations on their potential role in these fish communities. *Cybiurn* 23(3):273–284
- Roche DG, Leung B, Mendoza EF, Torchin ME (2010) Higher parasite richness, abundance and impact in native versus introduced cichlid fishes. *Int J Parasitol* 40(13):1525–1530
- Sanchez-Tocino L, Hidalgo Puertas F, Pontes M (2007) First record of *Fistularia commersonii* Rüppell, 1838 (Osteichthyes: Fistulariidae) in Mediterranean waters of the Iberian Peninsula. *Zool Baetica* 18:79–84
- Sanna D, Scarpa F, Lai T, Cossu P, Falautano M, Castriota L, Andaloro F, Follesa MC, Francalacci P, Curini-Galletti M, Casu M (2015) *Fistularia commersonii* (Teleostea: Fistulariidae): walking through the Lessepsian paradox of mitochondrial DNA. *Ital J Zool* 82(4):499–512
- Santoro M, Badillo FJ, Mattiucci S, Nascetti G, Bentivegna F, Insacco G, Travaglini A, Paoletti M, Kinsella JM, Tomás J, Raga JA, Aznar FJ (2010) Helminth communities of loggerhead turtles (*Caretta caretta*) from Central and Western Mediterranean Sea: the importance of host's ontogeny. *Parasitol Int* 59(3):367–375
- Scharsack JP, Kalbe M, Harrod C, Rauch G (2007) Habitat-specific adaptation of immune responses of stickleback (*Gasterosteus aculeatus*) lake and river ecotypes. *Proc R Soc B* 274(1617):1523–1532
- Streftaris N, Zenetos A (2006) Alien marine species in the Mediterranean: the 100 “worst invasives” and their impact. *Medit Mar Sci* 7(1):87–118
- Taraschewski H (2005) Copepoda (copepods). In: Rohde K (ed) *Marine parasitology*. CABI Publishing, Wallingford, pp 123–138
- Tillier J-B (1902) Le Canal de Suez et sa faune ichthyologique. *Mém Soc Zool Fr* 15(3):279–318
- Torchin ME, Lafferty KD, Kuris AM (2002) Parasites and marine invasions. *Parasitology* 124:137–151
- Vignon M, Sasal P (2010) Fish introduction and parasites in marine ecosystems: a need for information. *Environ Biol Fish* 87(1):1–8
- Vignon M, Sasal P, Galzin R (2009) Host introduction and parasites: a case study on the parasite community of the peacock grouper *Cephalopholis argus* (Serranidae) in the Hawaiian Islands. *Parasitol Res* 104(4):775–782
- Whittington D (2005) Monogenea Monopisthocotylea (ectoparasitic flukes). In: Rohde K (ed) *Marine parasitology*. CABI Publishing, Wallingford, pp 63–72
- Zintzen V, Roberts CD, Clark MR, Williams A, Althaus F, Last PR (2011) Composition, distribution and regional affinities of the deepwater ichthyofauna of the Lord Howe Rise and Norfolk Ridge, south-west Pacific Ocean. *Deep Sea Res Part II: Topical Stud Oceanogr* 58(7):933–947