Lessepsian migration and parasitism: richness, prevalence and intensity of parasites in the invasive fish *Sphyraena chrysotaenia* compared to its native congener *Sphyraena sphyraena* off Tunisia

Wiem Boussellaa [Corresp., 1, 2] , Lassad Neifar [1] , M. Anouk Goedknegt [2] , David W. Thieltges [2]

[1] Department of Life Sciences, Faculty of Sciences of Sfax, Sfax University, Sfax, Tunisia

[2] Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Utrecht University, Den Burg Texel, Netherlands

Corresponding Author: Wiem Boussellaa
Email address: wiem.boussellaa@hotmail.com

Background Parasites can play various roles in the invasion of non-native species, but these are still understudied in marine ecosystems. This also applies to invasions from the Red Sea to the Mediterranean Sea via the Suez Canal, the so-called Lessepsian migration. In this study, we investigated the role of parasites in the invasion of the Lessepsian migrant *Sphyraena chrysotaenia* in the Tunisian Mediterranean Sea. **Methods** We compared metazoan parasite richness, prevalence and intensity of *S. chrysotaenia* (Perciformes: Sphyraenidae) with infections in its native congener *S. sphyraena* by sampling these fish species at seven locations along the Tunisian coast. Additionally, we reviewed the literature to identify native and invasive parasite species recorded in these two hosts. **Results** Our results suggest the loss of at least two parasite species of the invasive fish species. At the same time, the Lessepsian migrant has co-introduced three parasite species, during the initial migration to the Mediterranean Sea, that are assumed to originate from the Red Sea of which only one parasite species has been reported during the spread to Tunisian waters. In addition, we found that the invasive fish has acquired six parasite species that are native in the Mediterranean Sea. However, parasite richness, prevalence and intensity were overall much lower in the invasive compared to the native fish host in the Mediterranean Sea. **Discussion** These results suggest that the Lessepsian migrant may affect native fish hosts by potentially altering the dynamics of native and invasive parasite-host interactions via parasite release, parasite co-introduction and parasite acquisition. They further suggest that the lower infection levels in the invasive fish may result in a competitive advantage over native fish hosts (enemy release hypothesis). This study demonstrates that cross-species comparisons of parasite infection levels are a valuable tool to identify the different roles of parasites in the course of Lessepsian migrations.

1   **Lessepsian migration and parasitism: richness, prevalence and intensity of parasites in the**

2   **invasive fish *Sphyraena chrysotaenia* compared to its native congener *Sphyraena sphyraena***

3   **off Tunisia**

4

5

6   **Wiem Boussellaa [1,2], Lassad Neifar [1], M. Anouk Goedknegt [2], David W. Thieltges [2]**

7

8

9   [1] Department of Life Sciences, Faculty of Sciences of Sfax, and Sfax University, Sfax, Tunisia

10

11   [2] Department of Coastal Systems, Royal Netherlands Institute for Sea Research, and Utrecht

12   University, Den Burg Texel, Netherlands

13

14

15

16   Corresponding author: Wiem Boussellaa

17   E-mail: wiem.boussellaa@hotmail.com

18   ORCID: 0000-0002-6728-9262

19

20

21

22

23

Abstract

Background Parasites can play various roles in the invasion of non-native species, but these are still understudied in marine ecosystems. This also applies to invasions from the Red Sea to the Mediterranean Sea via the Suez Canal, the so-called Lessepsian migration. In this study, we investigated the role of parasites in the invasion of the Lessepsian migrant *Sphyraena chrysotaenia* in the Tunisian Mediterranean Sea.

Methods We compared metazoan parasite richness, prevalence and intensity of *S. chrysotaenia* (Perciformes: Sphyraenidae) with infections in its native congener *S. sphyraena* by sampling these fish species at seven locations along the Tunisian coast. Additionally, we reviewed the literature to identify native and invasive parasite species recorded in these two hosts.

Results Our results suggest the loss of at least two parasite species of the invasive fish species. At the same time, the Lessepsian migrant has co-introduced three parasite species, during the initial migration to the Mediterranean Sea, that are assumed to originate from the Red Sea of which only one parasite species has been reported during the spread to Tunisian waters. In addition, we found that the invasive fish has acquired six parasite species that are native in the Mediterranean Sea. However, parasite richness, prevalence and intensity were overall much lower in the invasive compared to the native fish host in the Mediterranean Sea.

Discussion These results suggest that the Lessepsian migrant may affect native fish hosts by potentially altering the dynamics of native and invasive parasite-host interactions via parasite release, parasite co-introduction and parasite acquisition. They further suggest that the lower infection levels in the invasive fish may result in a competitive advantage over native fish hosts (enemy release hypothesis). This study demonstrates that cross-species comparisons of parasite

46   infection levels are a valuable tool to identify the different roles of parasites in the course of

47   Lessepsian migrations.

Introduction

49   One of the potential explanations for the establishment and subsequent spread of invasive

50   species in marine and other ecosystems is the enemy release hypothesis (Elton, 1958; Keane &

51   Crawley, 2002). This hypothesis states that invasive species may gain a competitive advantage

52   over native species by losing all or part of their natural enemies, such as predators and parasites,

53   during the invasion process. For parasites, such a release or reduction has been documented for a

54   wide range of host taxa including marine species (Torchin, Lafferty & Kuris, 2001; Keane &

55   Crawley, 2002; Torchin et al., 2003; Torchin & Mitchell, 2004; Blakeslee, Fowler & Keogh,

56   2013). However, invasive hosts do not necessarily lose all their native parasites during an

57   invasion, but can often co-introduce parasites to their non-indigenous range (Lymbery et al.,

58   2014). The likelihood of this co-introduction depends, among others, on the host specificity and

59   life cycle of the respective parasite species. Generalist parasites which infect a larger range of

60   host species and parasites with direct life cycles are more likely to be co-introduced than highly

61   specific parasites or parasites with complex life cycles (i.e., depending on several sequential

62   different host species; Torchin, Lafferty & Kuris, 2002; Poulin & Morand, 2004; Lymbery et al.,

63   2014). In the new range, co-introduced parasites may also infect native hosts (parasite spillover;

64   Prenter et al., 2004, Kelly et al., 2009), with potentially serious impacts on native species and

65   ecosystems (emerging diseases; Daszak, Cunningham & Hyatt, 2000). Finally, invasive species

66   can also acquire native parasites from native host species. This parasite acquisition may have

67   deleterious effects on naïve invasive host species ('increased susceptibility hypothesis' *sensu*

68   Colautti et al., 2004), but may also ultimately amplify native parasite population sizes, resulting

69   in increased parasite loads in native hosts, a phenomenon which is referred to as parasite

70   spillback (Kelly et al., 2009). While many of these mechanisms may result in a competitive

71   advantage for invasive over native species, the magnitude of this advantage will depend on the

72   actual difference in parasite infection levels between invasive and native hosts. Several studies

73   comparing infection levels in invasive and introduced hosts (community studies or cross-species

74   comparisons; *sensu* Colautti et al., 2004; Torchin & Mitchell, 2004) have shown that infection

75   levels are often lower in invasive host species (Georgiev et al., 2007; Dang et al., 2009; Roche et

76   al., 2010; Gendron, Marcogliese & Thomas, 2012). However, such cross-species comparisons of

77   infection levels in invasive and native competitors are surprisingly scarce (Goedknegt et al.,

78   2017). In addition, our knowledge on the role of parasites in biological invasions in general is

79   still limited, especially in the marine realm (Vignon & Sasal, 2010; Goedknegt et al., 2016).

80   This also applies to species invasions in the Mediterranean Sea, an ecosystem with an

81   extraordinarily high rate of species introductions, with more than 1000 alien species listed

82   (Bilecenoglu et al., 2013). Especially via the Suez Canal, which was opened in 1869, many

83   benthic invertebrates and fish species have migrated from the Indian Ocean over the Red Sea to

84   the Mediterranean Sea, a massive human-initiated invasion referred to as Lessepsian migration

85   (*sensu* Por, 1978). Despite this high migration rate and the resulting high number of species

86   introductions, parasitological investigations of invasive species have been surprisingly rare in

87   this region (Pérez-del-Olmo, Kostadinova & Gibson, 2016) and have only focused on a few host

88   species such as a portunid crab (Galil & Innocenti, 1999), the Lessepsian fishes *Siganus* spp.

89   (Diamant, 2010), *Fistularia commersonii* (Merella et al., 2016), *Etrumeus golanii* (Boussellaa et

90   al., 2016) and *Lagocephalus sceleratus* (Bakopoulos, Karoubali & Diakou, 2017). Initially, 18

91   species of parasites spread over four taxonomic groups (Monogenea, Crustacea, Protozoa and

92   Digenea) had been recognized as Lessepsian migrants which have been co-introduced with their

93   hosts to the Mediterranean Sea (Zenetos et al., 2008), and more recently this list has been

94   updated by the addition of many other parasite species (Diamant, 2010, Merella et al., 2016).

95   Given that there are many Lessepsian migrants that have never been under parasitological

96   investigation, the actual list of co-introduced parasite species is likely to be much longer. In

97   addition, invasive hosts may have acquired native parasite species but whether the resulting

98   parasite loads of hosts are actually lower, equal to or higher than the ones in native species in the

99   Mediterranean Sea has scarcely been studied to date.

100   In the present study, we investigated metazoan parasite infections in the Lessepsian

101 migrant fish *Sphyraena chrysotaenia* Klunzinger, 1884, along the Tunisian coast in the central

102 Mediterranean Sea. This fish species was first recorded in the eastern Mediterranean Sea in 1931

103 (Spicer, 1931) and has since then spread westwards, after which it was reported for the first time

104 at the Tunisian coast in 2002 (Bradai et al., 2002). It is now a relatively common piscivorous fish

105 of about 20-25 cm length, living in the pelagic and demersal zones to a depth of 50 m in inshore

106 waters where it is captured by local artisanal fisheries (Golani & Ben Tuvia, 1995; Wadie &

107 Riskhallah, 2001; Zouari-Ktari, Bradai & Bouain, 2009). A cross-species comparison of the

108 parasite communities was carried out considering the parasite richness and levels of infection in

109 the invasive fish and in the congeneric native one *Sphyraena sphyraena* Linnaeus, 1758. This

110 native fish species is usually larger than the invasive species (30-60 cm length) but has an

111 overlapping prey spectrum (Kalogirou et al., 2012), lives in the same habitats and is also used by

112 local fisheries (Relini & Orsi Relini, 1997; Allam, Faltas & Ragheb, 2005). By sampling

113 invasive (*S. chrysotaenia*) and native (*S. sphyraena*) fish hosts along the Tunisian coast and by

114 conducting an additional parasitological literature survey, we aimed to answer the following

115   specific research questions: 1) Is there evidence that *S. chrysotaenia* experienced a release from

116   its native parasites from the Red Sea?, 2) did *S. chrysotaenia* co-introduce parasites from the Red

117   Sea and/or did it acquire native parasites from the Mediterranean Sea? and 3) how do parasite

118   richness, prevalence and intensity in the invasive *S. chrysotaenia* compare with those in the

119   native *S. sphyraena*?

120   **Material and methods**

121   *Fish sampling*

122   Between October 2012 and July 2015, a total of 107 specimens of *Sphyraena sphyraena*

123   (native fish) and 148 specimens of *Sphyraena chrysotaenia* (invasive fish) were collected at

124   seven fishing localities along the Tunisian coast (off the cities of Sfax, Kerkennah, Skhira,

125   Chebba, Zarat, Zarzis and Sayeda; Fig. 1, Table 1). Fish were mostly bought from local

126   fishermen operating landing trawlers along the Tunisian coast at a depth of about 30 m. In

127   addition, some specimens were recovered from artisanal inshore fishery of Kerkennah and

128   Chebba. Only adult individuals were examined, with total lengths of 25.7-42.7 cm for *S.*

129   *sphyraena* and 18.5-26.2 cm for *S. chrysotaenia*. Samples were kept fresh or were deep-frozen in

130   individual plastic bags at -10°C, until examination in the laboratory. After defrosting, all fish

131   individuals were identified to species level using Whitehead et al. (1984) and Fisher et al. (1987)

132   and examined for parasites as described below. During our study, Faculty of Sciences of Sfax

133   provided full approval for this purely observational research.

134

135   *Parasite sampling*

136   We only checked for metazoans parasites, as this was the focus of our study. Fish skin, fins,

137   nasal pits, eyes and buccal cavities were thoroughly examined for the presence of ectoparasites

138 under a stereomicroscope with incident light. Gill arches were separated by incision, and then

139 placed in petri dishes filled with sea water and examined for the presence of ectoparasites.

140 Internal organs (stomach, pyloric caeca, intestines, heart, liver, spleen, gall bladder and gonads)

141 were separated and individually examined for the presence of endoparasites. Platyhelminthes

142 were fixed between a slide and coverslip with 70% ethanol. Fixed specimens were stained with

143 Semichon's acetic carmine, dehydrated using a graded ethanol series then cleared in clove oil

144 and mounted in Canada balsam. Other parasites (copepods, isopods, nematodes and annelids)

145 were directly fixed in 70% ethanol for later examination. Parasites were identified to the lowest

146 taxonomic level possible using Gibson et al. (2002) for Digenea, Neifar (1995) and Theisen et al.

147 (2017) for Monogenea, Euzet (1994) for Cestoda, Berland (1961) and Petter & Maillard (1988)

148 for Nematoda and the keys of Kabata (2003) for Copepoda.

149

150 *Literature review*

151 We searched literature databases (Host-Parasite database from the Natural History Museum in

152 London, Web of Science, Google Scholar) for published records of additional parasite species

153 from the Mediterranean Sea and the Red Sea. Search strings included the species names and the

154 different parasite taxa. In addition, we searched the reference sections of publications and our

155 own reference collections for potential further studies reporting parasite infections in the two

156 fish.

157

158 *Statistical analyses*

159 As sampling effort differed between native (n = 107) and invasive fish hosts (n = 148),

160 we produced rarefaction curves to identify the level of dependence of species accumulation on

161   sampling effort. Sample-based rarefaction curves were computed based on sample sizes at the

162   different locations (Gotelli & Colwell 2001) using Estimates S 9.1.0 (Colwell, 2013). Based

163   recommendations by Walther & Morand (1998) in regard to parasites, we used the

164   nonparametric species estimator Chao2 for our rarefaction analyses. This species estimator

165   algorithm uses the frequency of unique species in samples to estimate the number of missing

166   species in a population (Chao, 2005).

167   We used general linear models (GLMs) to test for statistical differences between the fish

168   species and among locations in parasite richness of individual fish (Poisson distribution; n =

169   255), infection status of individual fish (infected or uninfected; binomial distribution; n = 255)

170   and intensity of infected fish (negative binomial distribution; n = 127). In each model, we added

171   host species and location as fixed factors and an interaction term. As the parasite fauna of the

172   two host species was very different, we used the total infection status and intensity of parasite

173   species per host species to compare infection levels between hosts. Although this procedure may

174   obscure the potentially different effects on hosts exerted by different parasite species, this

175   lumping procedure still allows for an approximate comparison of overall infection levels. We did

176   not add fish size as a covariate in the models because preliminary analyses using GLMs did not

177   show an effect of fish size on any of the response variables. All statistical models were run using

178   the statistical software environment R v3.3.0. (R Development Core Team 2016).

179

180   **Results**

181   After the dissections of 107 individuals of the native *Sphyraena sphyraena* and 148 individuals

182   of the invasive *S. chrysotaenia* caught along the coast of Tunisia, ten different parasite species

183   infecting the two fish were found. Our additional literature survey added another ten parasite

184 species records from the Mediterranean or Red Sea to the total parasite species list of both fish

185 species (Table 2).

186

187 *Parasite release*

188 In total, five parasite species were collected from the Lessepsian migrant *Sphyraena*

189 *chrysotaenia* in Tunisian coastal waters (Table 2). In addition, the literature survey indicated that

190 four other parasite species have been found in this invasive host species elsewhere in the

191 Mediterranean Sea (Table 2). Hence, *S. chrysotaenia* is infected by at least nine parasite species in

192 its invaded range. In its native range, the Red Sea, two parasite species of *S. chrysotaenia* have been

193 reported in the literature (Table 2). In addition, three of the parasite species found in *S. chrysotaenia*

194 in the Mediterranean Sea most likely originate from Red Sea, although published records are not

195 available. This suggests that the Lessepsian migrant harbours at least five parasite species in its

196 native range, the Red Sea (Table 2).

197

198 *Parasite co-introduction and acquisition*

199 The examination and the literature survey revealed that the Lessepsian migrant *S. chrysotaenia* is

200 infected by three parasite species in the Mediterranean Sea that are assumed to originate from the

201 Red Sea (Table 2). Our results further revealed that the Lessepsian migrant *S. chrysotaenia* has

202 acquired six native parasite species in the Mediterranean Sea (Table 2). Five of those species

203 were found in our survey in Tunisian coastal waters and a fifth species had been noted in *S.*

204 *chrysotaenia* elsewhere in the Mediterranean Sea (Table 2).

205

206 *Comparison with the native congeneric species Sphyraena sphyraena*

207   The native congeneric species *Sphyraena.sphyraena* was infected with six parasite

208   species in Tunisian coastal waters and four additional species have been described in the

209   literature (Table 2). Of all these parasite species, only one was shared with the introduced fish

210   host *S. chrysotaenia*, the presumably native isopod *Gnathia* sp.. None of the parasites that were

211   co-introduced by the Lessepsian migrant have been found to infect the native congeneric host

212   species (Table 2).

213   In general, the rarefaction curves did not reach asymptotic levels in the two congeneric

214   host species, indicating that a higher sampling effort may reveal more (albeit rare) parasite

215   species in Tunisian coastal waters (Fig. 2). The species accumulation curves further indicate that

216   the total parasite species richness at a given sampling effort could be higher in the native than in

217   the invasive host species. This was also reflected in the mean parasite richness per individual fish

218   found at the seven locations, which was generally significantly higher in the native *S. sphyraena*

219   than in the invasive *S. chrysotaenia* (GLM: $\beta = 0.705$, SE $= 0.586$, $\Delta_{\text{Deviance}} = 110.655$, df $= 253$, p

220   < 0.001; Fig. 3). However, at some locations this pattern was reversed, resulting in a significant

221   interaction term ($\Delta_{\text{Deviance}} = 3.470$, df $= 241$, p < 0.01; Fig. 3).

222   Likewise, the infection status of fish hosts was generally significantly higher in the native

223   *S. sphyraena* than in the invasive *S. chrysotaenia* (GLM: $\beta = 1.966$, SE $= 1.201$, $\Delta_{\text{Deviance}} =$

224   162.599, df $= 247$, p < 0.001; Fig. 4a). This was consistent over all locations as there was no

225   significant difference in overall infection status between locations (p $= 0.294$; Fig.4a). However,

226   due to the absence of infections at two locations, there was a significant interaction term

227   ($\Delta_{\text{Deviance}} = 168.19$, df $= 241$, p < 0.05: Fig. 4a). Mean intensity of infections also differed

228   between host species, with the native fish being infected with higher numbers of parasites than

229   the invasive fish host (GLM: $\beta = 0.337$, SE $= 0.586$, $\Delta_{\text{Deviance}} = 35.420$, df $= 119$, p < 0.001; Fig.

230   4b). There was also a significant effect of location on overall infection intensities ($\Delta_{Deviance}=$

231   26.295, df = 120, p < 0.001), with location 1 showing much lower values than the other locations

232   (Fig. 4b). However, there was no significant interaction between location and host species (p =

233   0.249).

234

235   **Discussion**

236   Based on samples from the Tunisian coast and additional literature data, our analyses indicate that

237   the invasive Lessepsian migrant *S. chrysotaenia* lost two parasite species during its introduction to

238   the Mediterranean Sea, but that the invasive fish also co-introduced parasites from the Red Sea

239   and acquired one generalist parasite from native fish hosts in the Mediterranean Sea (Table 2).

240   However, parasite richness and infection levels were overall much lower in the invasive

241   compared to the native fish host, suggesting a potential competitive advantage for the Lessepsian

242   migrant.

243   *Parasite release*

244   In its native range (the Red Sea), the invasive *S. chrysotaenia* harbours at least five parasite

245   species (Table 2). Of these five parasite species, only three species have been recorded in the

246   Mediterranean Sea and only one in Tunisian coastal waters (Table 2). Hence, two parasite

247   species, the digenean *Bucephalus sphyraenae* and the monogenean *Pseudolamellodiscus*

248   *sphyraenae* have been lost in the process of the initial invasion to the Mediterranean Sea. Two

249   other species, the copepod *Nothobomolochus denticulatus* and the isopod *Cymothoa indica,* have

250   been observed elsewhere in the Mediterranean Sea, but not in Tunisian coastal waters (Table 2),

251   suggesting a loss of these parasite species in the course of the spread to the Tunisian coast. This

252   loss of several natural parasite species is consistent with the enemy release hypothesis (Torchin

253   et al., 2003; Blakeslee, Fowler & Keogh, 2013) and has previously been observed in other

254   Lessepsian migrant fish, the rabbitfish *Siganus rivulatus* (see Diamant, 1989) and partially

255   reported from the bluespotted cornet fish *Fistularia commersonii* (see Merella et al., 2016).

256

257   Several processes may be responsible for a loss of parasites in the course of passing the Suez

258   Canal "filter" or "bottleneck" (Por, 1978). First of all, parasites may not be able to cope with the

259   environmental conditions in the canal or in the Mediterranean Sea and do not survive to the

260   migration the new ecosystem. This negative impact of environmental conditions should be

261   particularly relevant for ectoparasites, which are more exposed to the external environment than

262   endoparasites, and may explain the loss of the monogenean *Pseudolamellodiscus sphyraenae.*

263   Second, parasites may survive the passage through the canal, but, in the case of parasites with

264   complex life cycles, they may be unable to find suitable intermediate hosts in the recipient

265   ecosystems. In general, parasite co-introductions seem to be more common in parasites with

266   simple life cycles as the necessity for all hosts being present for parasites with complex life

267   cycles makes invasions less likely (Lymbery et al., 2014; Goedknegt et al., 2016). Such a lack of

268   suitable hosts may explain the loss of the trematode *Bucephalus sphyraenae* as trematodes are

269   generally very host specific in respect to their first intermediate gastropod host (Poulin & Cribb,

270   2002; Galaktionov & Dobrovolskij, 2003). The respective gastropod host species that serves as

271   first intermediate host for *B. sphyraenae* is not known, but a (co-)introduction of snails is

272   unlikely because of their relatively reduced mobility. Finally, even in the case that all potential

273   hosts are present in the new environment, the number of introduced parasite individuals may be

274   too low to maintain a viable population. In general, propagule pressure is known to be a strong

275   determinant of invasion success in biological invasions in general (Wonham et al., 2000; Forsyth

276   & Duncan, 2001; Rouget & Richardson, 2003; Colautti et al., 2004). In the case of parasites,

277   propagule pressure may be low if infection levels are low in the native region, reducing both the

278   chances for a co-introduction and for developing viable populations after introduction to the

279   Mediterranean Sea. This could explain the loss of infections with the monogenean

280   *Pseudolamellodiscus sphyraenae* as this species may show only very low infection levels in its

281   native range. These different mechanisms are not only acting during the passage of Lessepsian

282   migrants through the Suez Canal, but also during the spread in the Mediterranean Sea after the

283   initial introduction. This is illustrated by the copepod *Nothobomolochus denticulatus* and the

284   isopod *Cymothoa indica* which have both been co-introduced into the Mediterranean Sea and

285   have been found on *S. chrysotaenia* in the eastern Mediterranean Sea (Trilles & Bariche, 2006;

286   El-Rashidy & Boxshall, 2012), but not in Tunisian waters (our study).

287

288   *Parasite co-introduction*

289   The present results and literature review revealed that the Lessepsian migrant *S.*

290   *chrysotaenia* is infected by three parasite species in the Mediterranean Sea that most likely

291   originate from the Red Sea (Table 2). One of these species, the monogenean parasite

292   *Pseudempleurosoma* sp., was recorded in our study in Tunisian waters. There are several reasons

293   why we believe that this parasite species has been co-introduced to the Mediterranean Sea

294   (although this still needs to be confirmed by records from its presumed native range).

295   First of all, the species has not been recorded in any native fish species in the Mediterranean Sea

296   in earlier studies, although fish parasites are relatively well studied in this coastal ecosystem

297   (Oliver, 1987; Neifar & Euzet, 2007; Pérez-del-Olmo, Kostadinova & Gibson, 2016; Chaabane

298   et al. 2016a; Chaabane et al. 2016b). Second, the genus *Pseudempleurosoma,* represented by four

299   species in the literature, seems to have a strict specificity to its host (Santos, Mourão &

300   Cárdenas, 2001), suggesting that it can only be co-introduced with its host. Finally, with their

301   direct life cycles, monogeneans are likely to be introduced and persist in a new environment.

302   Especially in gregarious fish such as the Sphyraenidae, the transmission of parasites with a direct

303   life cycle can easily take place so that the lifecycle can be maintained in the new environment

304   after an initial introduction.

305

306   The two other parasite species, the copepod *Nothobomolochus denticulatus* and the isopod

307   *Cymothoa indica* are less host specific and have also been found on other fish species from the

308   Red Sea (El-Shahawy & Desouky, 2010). These two species have not been recorded in our study

309   in Tunisian waters but have been reported elsewhere in the Mediterranean Sea (Trilles &

310   Bariche, 2006; El-Rashidy & Boxshall, 2012). Both species have not been recorded in any native

311   fish before their invasion but are considered to be co-introduced by the describing authors

312   (Trilles & Bariche, 2006; El-Rashidy & Boxshall, 2012). However, as there are no published

313   records of the two species available from the native range of the host, their invasive status still

314   has to be confirmed. Both species have not (yet) been co-introduced into Tunisian coastal waters

315   in the course of the spread of their hosts after the initial introduction in the Mediterranean Sea,

316   probably due some of the mechanisms discussed above.

317

318   *Parasite acquisition*

319   Besides being infected with co-introduced parasites, our study also revealed that the

320   Lessepsian migrant *S. chrysotaenia* has acquired six native parasite species in the Mediterranean

321   Sea. Four of those species were found in our survey in Tunisian coastal waters and a fifth species

322   had been noted in *S. chrysotaenia* elsewhere in the Mediterranean Sea (Table 2). We consider

323   these acquired parasite species to be native species from the Mediterranean Sea due to the

324   following reasons. The digenean *Lecithochirium* sp. has not been reported from the invasive *S.*

325   *chrysotaenia,* neither in the Mediterranean Sea nor in the Red Sea (Fischthal, 1982; Nahhas, Sey

326   & Nakahara, 2006). Given the complex life cycle of the Hemiuridae that need at least one

327   intermediate host species, and the fact that this genus now contains at least more than 100

328   species (Surekha & Lakshmi, 2005) which at least 10 are reported from Mediterranean Sea with

329   scarcely life cycles (Table 3) and that the genus *Lecithochirium* is very specific to its first

330   intermediate gastropod host (Gibson & Bray 1994), *Lecithochirium* sp. is most likely of

331   Mediterranean origin and has been acquired after the introduction of *S. chrysotaenia* to the

332   Mediterranean Sea. Specimens of the copepod *Caligus* sp. reported from *S. chrysotaenia* were in

333   poor condition and their identification to the species level was impossible. According to the

334   literature, no caligids were collected from *S. chrysotaenia* in the Red Sea but these parasitic

335   copepods have been recorded in native Mediterranean fish (Benmansour & Ben Hassine, 1998;

336   Raibaut, Combes & Benoit, 1998). Although many species are highly host specific there are also

337   many *Caligus* species with low host specificity (Yuniar, Palm & Walteret, 2007), making a host

338   switch to the invasive host likely. However, further studies will be needed to ascertain the native

339   status of *Caligus* individuals found on the invasive host. Annelids of the family Piscicolidae are

340   considered to be generalists with a broad host specificity and are regularly reported from many

341   native fish hosts from Tunisian coasts and the Mediterranean Sea in general (Châari & Neifar,

342   2015). According to the literature, no gnathiids were reported previously from *S. chrysoteania* in

343   the Red Sea. In contrast, this isopod genus is very common in the Mediterranean Sea and along

344   the Tunisian coasts, particularly on the skin of Sphyraenidae host species so that it is most likely

345   native to the area. However, the native status of gnathiids found on the invader. The native

346   Cymothoid *Anilocra physodes* has been reported from many native hosts of the Mediterranean

347   Sea (Innal et al., 2007) and was only observed from the invasive fish *S. chrysotaenia* off Turkish

348   (Innal et al., 2007). Finally, the trematode *Bucephalus labracis*, which was not found in the

349   Lessepsian migrant elsewhere in the Mediterranean Sea (Fischhal, 1982), is considered to be

350   native as it uses a native bivalve (*Ruditapes decussatus*) as first intermediate host, a native fish

351   (*Atherina boyeri*) as second intermediate host and a native fish (*Dicentrarchus labrax*) as

352   definitive host (Paggi & Orecchia (1965); Maillard (1976); Gargouri-Ben Abdallah & Maamouri

353   (2005); Dhrif et al., 2015). The acquisition of these native parasites may generally have

354   potentially adverse effects naïve invasive host species, but also on native species, as the invasive

355   additional hosts can potentially elevate infection levels in native species via parasite spill back.

356   However, whether significant parasite spillback occurs in Tunisian waters remains to be studied.

357

358   *Cross-species comparison*

359   Our comparison of parasite infections in the Lessepsian migrant with the native

360   congeneric *Sphyraena sphyraena* revealed considerable qualitative and quantitative differences

361   between the parasite communities of the two fish species. The native fish was infected with six

362   parasite species in Tunisian coastal waters and three additional species have been described

363   elsewhere in the Mediterranean Sea (Table 2). Of all these parasite species, only one was shared

364   with the invasive fish host, the presumably native isopod *Gnathia* sp.. As only larval stages of

365   gnathiid parasite can infect fish and all larvae are morphologically very similar, identification to

366   species level was not possible. Native *Gnathia* species have been reported from the study area

367   (Châari & Neifar, 2015) and we assume that the species found in our study is native but without

368   further genetic work the native-invasive status in the invader cannot be fully clarified.

369   Interestingly, none of the parasites that were co-introduced with the Lessepsian migrant has been

370   found to infect the native congeneric host species. While the total number of parasite species

371   found in the two fish hosts in the Mediterranean Sea was similar (nine in the invasive and ten in

372   the native fish), the mean number of parasite species found in an individual fish was significantly

373   higher in the native compared to the invasive fish. Although the rarefaction analyses suggested

374   that further sampling would likely reveal more rare parasite species for each fish host, this

375   general pattern of a lower richness of the more common parasite species in the invasive host

376   species would remain at higher sampling efforts. In general, the parasite fauna of the invasive

377   fish was mainly composed of generalist native parasites acquired in the new environment and

378   one co-introduced parasite species, while the parasite community in native fish included more

379   specialist parasites. This is consistent with the general idea that invasive hosts often lose specific

380   parasites (especially with complex life cycles) in the course of the introduction and acquire

381   mainly native generalist parasites in the new range (Blakeslee, Fowler & Keogh, 2013; Lymbery

382   et al., 2014).

383   In addition to parasite species richness, also total parasite prevalence (parasite infection

384   status in the models) and total infection intensity were generally higher in the native than in the

385   invasive fish. Hence, despite the acquisition of native parasites by the invasive host *S.*

386   *chrysotaenia*, the native *S. sphyraena* still showed higher total infection levels. This suggests that

387   the invasive host is experiencing lower parasite infection levels compared with the native host

388   species. Several factors may explain the lower infection levels of the invasive compared to the

389   native host species. First, the relatively small size of the invasive fish (20-25 cm length)

390   compared to the native fish (30-60 cm) may cause a space constraint and reduce exposure of the

391   invasive fish to native parasites. However, the lack of a significant effect of fish size on infection

392   levels in our analyses suggests that body size may only play a minor role. Second, differences in

393   the feeding behaviour of the two fish hosts might explain why their parasite infection levels are

394   different. While the invasive *S. chrysotaenia* narrows its food spectrum to pelagic fish species,

395   the native *S. sphyraena* extended their feeding to supra-benthic species (Kalogirou et al., 2012).

396   The broader food spectrum of the native fish may result in a relative higher exposure to parasites.

397   Third, host suitability of the two fish species may differ and in particular invasive hosts may be

398   less suitable for native parasites due to compatibility issues. Finally, phylogenetic niche

399   conservatism (Wiens & Graham, 2005; Mouillot et al., 2006) and a variety ecological factors

400   such as microhabitat use and life history strategies (Poulin, 2010) may play a role.

401   The presumably native isopod *Gnathia* sp. was the only parasite genus shared by the two

402   fish hosts in Tunisian coastal waters, with a higher prevalence and intensity in the native *S.*

403   *sphyraena* than in the invasive *S. chrysotaenia*. However, for both fish species there was only a

404   single record (at location 1 in the invasive host and at location 7 in the native host),

405   compromising a formal statistical comparison, rendering a solid discussion on the subsequent

406   host and parasite populations.

407

408

409   **Conclusion**

410   Our study found evidence for the loss of parasite species of the Lessepsian migrant in the course

411   of the introduction as well as for co-introduction of parasites and the acquisition of native

412   parasites. These results suggest that the Lessepsian migrant has the potential to affect native fish

413   hosts by altering the population dynamics of native parasite species via parasite release, parasite

414   co-introduction and acquisition of native parasites, resulting in increased infection levels in

415   native hosts. They further suggest that the lower infection levels in the invasive host may give

416   them a potential competitive advantage over native hosts. Further studies will be needed to

417   investigate the resulting effects on native parasite dynamics and well as on native fish stocks.

418   This study demonstrated that community studies or cross-species comparisons such as the one

419   presented here, are valuable tools to identify the role of metazoan parasite in Lessepsian

420   migration.

421

427

428

429

430

431

432   **References**

433 **Allam SM, Faltas SN, and Ragheb E. 2005.** Stock assessment of Barracudas, genus *Sphyraena*,

434   along the Egyptian Mediterranean Coast. *Egyptian Journal of Aquatic Research* **31**: 281-

435   292.

436 **Bakopoulos V, Karoubali I, and Diakou A. 2017.** Parasites of the Lessepsian invasive fish

437   *Lagocephalus sceleratus* (Gmelin 1789) in the eastern Mediterranean Sea. *Journal of*

438   *Natural History* **51**: 421-434. DOI: 10.1080/00222933.2017.1279690

439 **Benmansour B, and Ben Hassine OK. 1998.** Preliminary analysis of parasitic copepod species

440   richness among coastal fishes of Tunisia. *Monitore zoologico italiano*. **65:** 341-344 DOI

441   10.1080/11250009809386844

442 **Berland B.(1961).** Nematodes from some Norwegian marine fishes. *Sarsia* **2**: 1- 50.

443 **Bilecenoglu M, Alfaya JEF, Azzurro E, Baldacconi R, Boyaci YO, Circosta V, Compagno**

444   **LJV, Coppola F, Deidun A, Durgham H, Durucan F, Ergüden D, Fernández-**

445   **Álvarez FÁ, Gianguzza P, Giglio G, Gökoğlu M, Gürlek M, Ikhtiyar S, Kabasakal**

446   **H, Karachle PK, Katsanevakis S, Koutsogiannopoulos D, Lanfranco E, Micarelli P,**

447   **Özvarol Y, Peña-Rivas L, Poursanidis D, Saliba J, Sperone E, Tibullo D, Tiralongo**

448   **F, Tripepi S, Turan C, Vella P, Yokeş MB, Zava B. 2013.** New Mediterranean marine

449   biodiversity records (December, 2013). *Mediterranean Marine Science* **14**: 463-480 DOI

450   10.12681/mms.676

451 **Blakeslee AMH, Fowler AE, and Keogh CL. 2013.** Marine invasion and parasite escape:

452   updates and new perspectives. *Advances in Marine Biology*. **66:** 87-169 DOI

453   10.1016/B978-0-12-408096-6.00002-X

454 **Boussellaa W, Boudaya L, Derbel H, and Neifar L. 2016.** A new record of the Lessepsian fish

455 *Etrumeus golanii* (Teleostei: Clupeidae) in the Gulf of Gabes, Tunisia, with notes on its

456 parasites. *Cahier de Biologie Marine* **57:** 389-395 DOI 10.21411/CBM.A.843F287A

457 **Bradai MN, Saidi B, Ghorbel M, Bouain A, Guelorget O, and Capape C. 2002.** Observations

458 sur les requins du golfe de Gabès (Tunisie méridionale, Méditerranée centrale). *Mesogée*

459 **60:** 61-77.

460 **Chaabane A, Justine J-L, Gey D, Bakenhaster MD, and Neifar L. 2016a.**

461 *Pseudorhabdosynochus sulamericanus* (Monogenea, Diplectanidae), a parasite of deep-

462 sea groupers (Serranidae) occurs transatlantically on three congeneric hosts (*Hyporthodus*

463 spp.), one from the Mediterranean Sea and two from the western Atlantic. *PeerJ* 4:e2233.

464 DOI 10.7717/peerj.2233

465 **Chaabane A, Neifar L, Gey D, and Justine J-L. 2016b.** Species of *Pseudorhabdosynochus*

466 (Monogenea, Diplectanidae) from groupers (*Mycteroperca* spp., Epinephelidae) in the

467 Mediterranean and Eastern Atlantic Ocean, with special reference to the

468 "beverleyburtonae group" and description of two new species. *PLoS ONE* **11**: e0159886.

469 DOI 10.1371/journal.pone.0159886

470 **Châari M, and Neifar L. 2015.** Parasitic infections in the Mediterranean needle fish *Tylosurus*

471 *acus imperialis* (Teleostei: Belonidae) off Tunisian coast. *Journal of Coastal Life*

472 *Medicine* **3:** 673-676 DOI 10.12980/jclm.3.2015j5-78

473 **Chao A. 2005.** Species richness estimation. In: Balakrishnan N, Read CB, Vidakovic B, eds.

474 *Encyclopedia of statistical sciences*. Wiley: New York, 7909-7916.

475 **Colautti RI, Ricciardi A, Grigorovich IA, and MacIsaac HJ. 2004.** Is invasion success

476   explained by the enemy release hypothesis? *Ecology Letters* **7:**721-733 DOI

477   10.1111/j.1461-0248.2004.00616.x

478 **Colwell RK. 2013.** *EstimateS: Statistical estimation of species richness and shared species from*

479   *samples*. Version 9. User's Guide and application published at:

480   http://purl.oclc.org/estimates.

481 **Dang C, Montaudouin X, Bald J, Jude F, Raymond N, Lanceleur L, Paul-Pont I, and Caill-**

482   **Milly N. 2009.** Testing the enemy release hypothesis: trematode parasites in the non-

483   indigenous Manila clam *Ruditapes philippinarum*. *Hydrobiologia* **630:** 139-148 DOI

484   10.1007/s10750-009-9786-9

485 **Daszak P, Cunningham AA, and Hyatt AD. 2000.** Emerging infectious diseases of wildlife:

486   threats to biodiversity and human health. *Science* **287:** 443-449 DOI

487   10.1126/science.287.5452.443

488 **Dhrif E, Antar R, Abidli S, and Gargouri L. 2015.** Digenean larvae parasitizing *Ruditapes*

489   *decussatus* (Bivalvia) from Tunisian coasts. *Helminthologia* **52:** 104-112 DOI

490   10.1515/helmin-2015-0019

491 **Diamant A. 1989.** Lessepsian migrants as hosts: a parasitological assessment of rabbitfish

492   *Siganus luridus* and *S. rivulatus* (Siganidae) in their original and new zoogeographical

493   regions. In: Spanier E, Steinberger Y, Lurin M, eds. *Environmental quality and*

494   *ecosystem stability*: Environmental Quality ISEEQS Pub, Jerusalem, Israel. **4:** 187-194.

495 **Diamant A. 2010.** Red-Med immigration: a fish parasitology perspective, with special reference

496   to Mxyxosporea. In: Golani D, Appelbaum-Golani B, eds. *Fish Invasions of the*

497   *Mediterranean Sea*: *Change and Renewal*. Pensoft Publishers: Sofia-Moscow, 85-97.

498 **El-Rashidy HH, and Boxshall GA. 2012.** Bomolochid copepods (Crustacea: Copepoda:

499   Bomolochidae) parasitizing immigrant and native barracuda (Actinopterygii:

500   Sphyraenidae) caught off the Egyptian Mediterranean coast. *Zoosymposia* **8:** 20-28 DOI

501   10.11646/zoosymposia.8.1.5

502 **El-Shahawy IS, and Desouky ARY. 2010.** *Myripristis murdjan* (Beryciformes: Holocentridae)

503   a new host record for *Cymothoa indica* (Crustacea, Isopoda, Cymothoidae). *Acta*

504   *Adriatica* **51:** 103-110.

505 **Elton CS. 1958.** *The ecology of invasions*. Methuen: London, UK.

506 **Euzet L. 1994.** Order Tetraphyllidea Carus, 1863. In: Khalil LF, Jones A and Bray RA, ed. *Keys*

507   *to the cestode parasites of vertebrates*. CAB International, Wallingford, U.K., 149-194.

508 **Euzet L, and Trilles J-P. 1960.** Sur deux Monogènes nouveaux de *Sphyraena sphyraena* (L.)

509   (Teleostei Sphyraenidae). *Bulletin de la Société Zoologique de France*. **85:** 189-198.

510 **Fischthal JH. 1982.** Additional records of digenetic trematodes of marine fishes from Israel's

511   Mediterranean coast. *Proceedings of the Helminthological Society of Washington* **49:** 34-

512   44.

513 **Fisher W, Schneider M, and Bauchot ML. 1987.** Fiches FAO d'identification des espèces pour

514   les besoins de la pêche (Révision 1). *Méditerranée et Mer Noire*. Zone de pêche 37.

515   Vertébrés. Rome FAO **2**: 1-1045.

516 **Forsyth DM, and Duncan RP. 2001.** Propagule size and the relative success of exotic ungulate

517   and bird introductions to New Zealand. *The American Naturalist* **157:** 583-595 DOI

518   10.1086/320626

519   **Galaktionov K, and Dobrovolskij AA. 2003.** *The biology and evolution of trematodes*: An

520   essay on the biology, morphology, life cycles, transmissions, and evolution of digenetic

521   trematodes. Springer, Dordrecht, Netherlands.

522   **Galil BS, and Innocenti G. 1999.** Notes on the population structure of the portunid crab

523   *Charybdis longicollis* Leene, parasitized by the rhizocephalan *Heterosaccus dollfusi*

524   Boschma, off the Mediterranean coast of Israel. *Bulletin of Marine Science* **64:** 451-463.

525   **Gargouri M, and Maamouri F. 2005.** The life cycle of *Bucephalus labracis* Paggi and

526   Orecchia, 1965 (Digenea, Bucephalidae), a parasite of *Dicentrarchus labrax* in Tunisia.

527   *Bulletin of the European Association of Fish Pathologists* **25:** 297-302.

528   **Gendron AD, Marcogliese DJ, and Thomas M. 2012.** Invasive species are less parasitized than

529   native competitors, but for how long? The case of the round goby in the Great Lakes-St.

530   Lawrence Basin. *Biological Invasions* **14:** 367-384 DOI DOI 10.1007/s10530-011-0083-

531   y

532   **Georgiev BB, Sanchez MI, Vasileva GP, Nikolov, PN, and Green AJ. 2007.** Cestode

533   parasitism in invasive and native brine shrimps (*Artemia* spp.) as a possible factor

534   promoting the rapid invasion of *A. franciscana* in the Mediterranean region. *Parasitology*

535   *Research* **101:** 1647-1655 DOI 10.1007/s00436-007-0708-3

536   **Gibson DI, and Bray RA. 1994.** The evolutionary expansion and host-parasite relationships of

537   the Digenea. *International Journal for Parasitology* **24:** 1213-1226 DOI 10.1016/0020-

538   7519(94)90192-9

539   **Gibson DI, Jones A, and Bray RA. 2002.** *Keys to the Trematoda*, Vol. 1. CABI Publishing:

540   Wallingford, UK DOI 10.1016/S0035-9203(03)90052-6

541 **Goedknegt MA, Havermans J, Waser AM, Luttikhuizen PC, Perdomo EV, Camphuysen K**

542   **(CJ), van der Meer J, and Thieltges DW. 2016.** Parasites and marine invasions:

543   Ecological and evolutionary perspectives. *Journal of Sea Research* **113:** 11-27 DOI

544   10.1016/j.seares.2015.12.003

545 **Goedknegt MA, Havermans J, Waser AM, Luttikhuizen PC, Vellila E, Camphuysen K**

546   **(CJ), Van der Meer J, and Thieltges DW. 2017.** Cross-species comparison of parasite

547   richness, prevalence, and intensity in a native compared to two invasive brachyuran

548   crabs. *Aquatic Invasions* **12:** 201-212 DOI 10.3391/ai.2017.12.2.08

549 **Golani D, and Ben Tuvia A. 1995.** Lessepsian migration and the Mediterranean fisheries of

550   Palestine. In: Armantrout NB, ed. *Conditions of the world's aquatic habits. Proceedings*

551   *of the World Fishery Congress.* New Delhi, India. 279-289.

552 **Gotelli NJ, and Colwell RK. 2001.** Quantifying biodiversity: procedures and pitfalls in the

553   measurement and comparison of species richness. *Ecology Letters* **4:** 379-391 DOI

554   10.1046/j.1461-0248.2001.00230.x

555 **İnnal D, Kirkim F, and Erk'akan F. 2007.** The parasitic isopods, *Anilocra frontalis* and

556   *Anilocra physodes* (Crustacea; Isopoda) on some marine fish in Antalya Gulf, Turkey.

557   *Bulletin of the European Association of Fish Pathologists* **27:** 239-241.

558 **Kabata Z. 2003.** Copepods Parasitic on Fishes. In: Crothers JH, Hayward PJ, eds. *Synopsis of*

559   *British Fauna* (New Series), Vol. 47 (revised). The Linnean Society & The Estuarine &

560   Coastal Sciences Association, London, 274 pp.

561 **Kalogirou S, Mittermayer F, Pihl L, and Wennhage H. 2012.** Feeding ecology of indigenous

562   and non-indigenous fish species within the family Sphyraenidae. *Journal of Fish Biology*

563   **80:** 2528-2548 DOI 10.1111/j.1095-8649.2012.03306.x

564 **Keane RM, and Crawley MJ. 2002.** Exotic plant invasions and the enemy release hypothesis.

565   *Trends in Ecology & Evolution* **17:** 164-170 DOI 10.1016/S0169-5347(02)02499-0

566 **Kelly DW, Paterson RA, Townsend CR, Poulin R, and Tompkins DM. 2009.** Parasite

567   spillback: A neglected concept in invasion ecology? *Ecology* **90:** 2047-2056 DOI

568   10.1890/08-1085.1

569 **Kritsky DC, Jiménez-Ruiz FA, and Sey O. 2000.** Diplectanids (Monogenoidea:

570   Dactylogyridea) from the gills of marine fishes of the Persian Gulf off Kuwait.

571   *Comparative Parasitology* **67:** 145-164.

572 **Looss A. 1899.** Weitere Beiträge zur Kenntnis der Trematoden-Fauna Aegyptens, zugleich

573   versuch einer natürlichen Gliederung des Genus *Distomum* Retzius. *Zoologische*

574   *Jabrbucher* **12:** 521-784.

575 **Lymbery AJ., Morine M., Kanani HG., Beatty SJ., and Morgan DL. 2014.** Co-invaders: The

576   effects of alien parasites on native hosts. *International Journal for Parasitology:*

577   *Parasites and Wildlife* **3:** 171-177 DOI 10.1016/j.ijppaw.2014.04.002

578 **Maillard C. 1976.** Distomatoses de poissons en milieu lagunaire. Dr. Sci. Thesis. Montpellier:

579   Université des Sciences et Techniques du Languedoc.

580 **Merella P, Pais A, Follesa MC, Farjallah S, Mele S, Piras MC, and Garippa G. 2016.**

581   Parasites and Lessepsian migration of *Fistularia commersonii* (Osteichthyes,

582   Fistulariidae): shadows and light on the enemy release hypothesis. *Marine Biology* **163:**

583   97-97 DOI 10.1007/s00227-016-2865-3

584 **Mouillot D, Krasnov BR, Shenbrot GI, Gaston KJ, and Poulin R. 2006.** Conservatism of

585   host specificity in parasites. *Ecography* **29:** 596-602 DOI 10.1111/j.0906-

586   7590.2006.04507.x

587 **Nahhas FM, Sey O, and Nakahara G. 2006.** Digenetic trematodes of marine fishes from the

588 Arabian Gulf off the coast of Kuwait. Family Bucephalidae Poche, 1907, and the

589 description of a new species. *Helminthologia* **43:** 147-157 DOI 10.2478/s11687-006-

590 0028-7

591 **Neifar L. 1995.** Contribution à l'étude de la biodiversité des monogènes parasites de poissons du

592 secteur nord-est de la Tunisie. Mémoire de Diplôme d'Etudes Approfondies. Université

593 de Tunis II.

594 **Neifar L, and Euzet L 2007.** Five new species of *Pseudorhabdosynochus* (Monogenea:

595 Diplectanidae) from the gills of *Epinephelus costae* (Teleostei: Serranidae). *Folia

596 Parasitologica* **54:** 117-128 DOI 10.14411/fp.2007.017

597 **Oliver G. 1987.** Les Diplectanidae Bychowsky, 1957 (Monogenea, Monopisthocotylea,

598 Dactylogyridea). Systématique. Biologie. Ontogénie. Écologie. Essai de phylogenèse. Dr.

599 Sci. Thesis. Université de Montpellier. DOI: 10.6084/m9.figshare.1295274

600 **Paggi L, and Orecchia P. 1965.** Su un nuovo trematode parassita dell'intestino di Morone

601 *labrax: Bucephalus labracis* n. sp. *Parassitologia* 7: 69-74.

602 **Pérez-del-Olmo A, Kostadinova A, and Gibson DI. 2016.** The Mediterranean: high discovery

603 rates for a well-studied trematode fauna. *Systematic Parasitology* **93:** 249-256 DOI

604 10.1007/s11230-016-9626-z

605 **Petter AJ, and Maillard C. 1988.** Larves d'Ascarides parasites de poissons en Méditerranée

606 occidentale. *Bulletin du Muséum national d'histoire naturelle*. Section A, Zoologie,

607 biologie et écologie animales. Muséum national d'Histoire naturelle: 4e série, tôme **10**:

608 347-369.

609   **Por FD. 1978.** Lessepsian migration: the influx of Red Sea biota into the Mediterranean by way

610   of the Suez Canal. Ecological studies. Springer-Verlag, Berlin, Germany.

611   **Poulin R, and Cribb TH. 2002.** Trematode life cycles: short is sweet? *Trends in Parasitology*

612   **18:** 176-183.

613   **Poulin R, and Morand S. 2004.** *Parasite Biodiversity*. Smithsonian Books, Washington DC,

614   USA DOI 10.1017/S003118200521908X

615   **Poulin R. 2010.** Network analysis shining light on parasite ecology and diversity. *Trends in*

616   *Parasitology* **26:** 492-498 DOI 10.1016/j.pt.2010.05.008

617   **Prenter J, MacNeil C, Dick JTA, and Dunn AM. 2004.** Roles of parasites in animal invasions.

618   *Trends in Ecology & Evolution* **19:** 385-390 DOI 10.1016/j.tree.2004.05.002

619   **Raibaut A, Combes C, and Benoit F. 1998.** Analysis of the parasitic copepod species richness

620   among Mediterranean fish. *Journal of Marine Systems* **15:** 185-206 DOI 10.1016/S0924-

621   7963(97)00079-1

622   **Ramdane Z, Bensouilah MA, and Trilles J-P 2009.** Étude comparative des crustacés isopodes

623   et copépodes ectoparasites de poissons marins algériens et marocains. *Cybium* **33:** 123-

624   131.

625   **R Development Core Team 2016.** R: A language and environment for statistical computing. R

626   Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-

627   project.org/

628   **Relini M, and Orsi Relini L. 1997.** The two species of barracuda (Sphyraenidae) in the western

629   mediterranean. *Cybium* **21:** 216-222.

630   **Roche DG, Leung B, Franco EFM, and Torchin ME 2010.** Higher parasite richness,

631   abundance, and impact in native versus introduced cichlid fishes. *International Journal*

632   *for Parasitology* **40:** 1525-1530 DOI 10.1016/j.ijpara.2010.05.007

633   **Rouget M, and Richardson DM. 2003.** Inferring process from pattern in plant invasions: a semi

634   mechanistic model incorporating propagule pressure and environmental variables. *The*

635   *American Naturalist* **162:** 713-724.

636   **Santos CP, Mourão ED, and Cárdenas MQ. 2001.** *Pseudempleurosoma gibsoni* n. sp., a new

637   ancyrocephalid monogenean from *Paralonchurus brasiliensis* (Sciaenidae) from off the

638   southeastern coast of Brazil. *Memórias do Instituto Oswaldo Cruz* **96:** 215-219 DOI

639   10.1590/S0074-02762001000200013.

640   **Spicer IJ. 1931.** Report of the Department of Agriculture and Forests for the years 1927-30.

641   Jerusalem: Printing Office, Russian Building, 159-160.

642   **Surekha P, and Lakshmi C.V. 2005.** *Lecithochirium testelobatus* n. sp. (Digenea: Hemiuridae)

643   from the Lizard fish, *Saurida undosquamis* from Andhrapradesh Coast. *Journal of*

644   *Parasitic Diseases* **29:** 143-146

645   **Theisen S, Palm HW, Al-Jufaili SH, and Kleinertz S. 2017.** *Pseudempleurosoma haywardi* sp.

646   nov. (Monogenea: Ancyrocephalidae (sensu lato) Bychowsky & Nagibina, 1968): An

647   endoparasite of croakers (Teleostei: Sciaenidae) from Indonesia. PLoS ONE **12:**

648   e0184376. DOI 10.1371/journal.pone.0184376

649   **Torchin ME, Lafferty KD, and Kuris AM. 2001.** Release from parasites as natural enemies:

650   increased performance of a globally introduced marine crab. *Biological Invasions* **3:** 333-

651   345 DOI 10.1023/A:1015855019360

652   **Torchin ME, Lafferty KD, and Kuris AM. 2002.** Parasites and marine invasions. *Parasitology*

653   **124:** 137-151 10.1017/S0031182002001506

654   **Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, and Kuris AM. 2003.** Introduced

655   species and their missing parasites. *Nature* **421:** 628-630 DOI 10.1038/nature01346

656   **Torchin ME, and Mitchell CE. 2004.** Parasites, pathogens, and invasions by plants and

657   animals. *Frontiers in Ecology and the Environment* **2:** 183-190 DOI 10.1890/1540-

658   9295(2004)002[0183:PPAIBP]2.0.CO;2

659   **Townsend S. 2009.** Incorporating sustainable practices for zoos and aquariums: a Triple Bottom

660   Line approach. *International Zoo Yearbook* **43:** 53-63 DOI 10.1111/j.1748-

661   1090.2008.00065.x

662   **Trilles JP, and Bariche M 2006.** First record of the Indo-Pacific *Cymothoa indica* (Crustacea,

663   Isopoda, Cymothoidae), a Lessepsian species in the Mediterranean Sea. *Acta*

664   *Parasitologica* **51:** 223-230 DOI 10.2478/s11686-006-0035-3

665   **Vignon M, and Sasal, P. 2010.** The use of geometric morphometrics in understanding shape

666   variability of sclerotized haptoral structures of monogeneans (Platyhelminthes) with

667   insights into biogeographic variability. *Parasitology International* **59:** 183-191 DOI

668   10.1016/j.parint.2010.01.006

669   **Wadie WF, and Riskallah SI 2001.** Fisheries for the genus *Sphyraena* (Perciformes,

670   sphyraenidae) in the southeastern part of the Mediterranean Sea. *Pakistan Journal of*

671   *Science* **10**: 21-34.

672   **Walther BA, and Morand S. 1998.** Comparative performance of species richness estimation

673   methods. *Parasitology* **116:** 395-405.

674 **Whitehead PJP, Bauchot ML, Hureau JC, Nielsen J, and Tortonese E, eds. 1984.** *Fishes of*

675   *the North-eastern Atlantic and the Mediterranean.* UNESCO, Paris, France.

676 **Wiens JJ, and Graham CH. 2005.** Niche conservatism: integrating evolution, ecology, and

677   conservation biology. *Annual Review of Ecology, Evolution, and Systematics* **36:** 519-

678   539. DOI 10.1146/annurev.ecolsys.36.102803.095431

679 **Wonham MJ, Carlton JT, Ruiz GM, and Smith LD. 2000.** Fish and ships: relating dispersal

680   frequency to success in biological invasions. *Marine Biology* **136:** 1111-1121.

681 **Yamaguti S. 1953.** Parasitic worms mainly from Celebes. Part. 2. Monogenetic Trematodes of

682   fishes. *Acta Medica Okayama* **8:** 204-256.

683 **Yuniar AT, Palm HW, and Walter T. 2007.** Crustacean fish parasites from Segara Anakan

684   Lagoon, Java, Indonesia. *Parasitology Research* **100:** 1193-1204

685   DOI 10.1007/s00436-006-0391-9

686 **Zenetos A, Meriç E, Verlaque M, Galli P, and Boudouresque CF. 2008.** Additions to the

687   annotated list of marine alien biota in the Mediterranean with special emphasis on

688   Foraminifera and Parasites. *Mediterranean Marine Science* **9:** 119-166 DOI

689   10.12681/mms.146

690 **Zouari-Ktari R, Bradai MN, and Bouain A. 2009.** Reproduction and growth of the

691   Yellowstripe Barracuda *Sphyraena chrysotaenia* Klunzinger 1884, in Central

692   Mediterranean. *Reviews in Fisheries Science* **17:** 485-493

693   DOI 10.1080/10641260903082471

Table 1(on next page)

Information on the sampling design of fish hosts collected for this study in Tunisian coastal waters.

Given are the location numbers used in Figure 1, location name, geographic coordinates, sampling dates and sample sizes (per sex) for the two fish host species (*Sphyraena sphyraena* and *Sphyraena chrysotaenia*).

1

2

Location number	Location name	Geographic coordinates	Sampling dates	*Sphyraena sphyraena* (native)		*Sphyraena chrysotaenia* (invasive)	
				Females	Males	Females	Males
1	Sfax	34° 44′ 26″ N 10° 45′ 37″ E	22/10/2012 08/03/2013	3	3	9	9
2	Kerkennah	34° 39′ 29″ N 11° 04′ 07″ E	10/02/2013 10/03/2013 10/09/2013	20	11	18	15
3	Skhira	34° 17′ 57″ N 10° 04′ 11″ E	06/11/2014 04/07/2015	10	8	7	10
4	Chebba	35° 14' 14" N 11° 6' 54" E	05/11/2012	8	1	5	14
5	Zarat	33° 39' 59" N 10° 20' 59" E	07/02/2014	6	1	15	6
6	Zarzis	33° 30′ 14″ N 11° 06′ 43″ E	11/05/2015 19/06/2015	11	6	9	7
7	Sayada	35° 40' 7" N 10° 53' 32" E	07/02/2014 03/06/2014	15	4	7	17
	Total			73	34	70	78

Table 2(on next page)

Parasite species of *Sphyraena sphyraena* and *Sphyraena chrysoteania* found in this study and recorded in the literature.

Information on the life cycle and the invasive/native status in the Mediterranean Sea and occurrence in the two host species and regions (Mediterranean Sea and Red Sea). If quantitative data were available, mean prevalence and intensity (± SE) in a host species and region are given. + denotes published records of specific parasite species in a host species in a region; (+) denotes an assumed occurrence in a host species and region without published records.

Parasite taxa	Parasite species	Life cycle	Host specificity	Status Med Sea	*Sphyraena sphyraena* (native range- Med Sea)	*Sphyraena chrysotaenia* (invasive range - Med Sea)	*Sphyraena chrysotaenia* (native range - Red Sea)	Reference
Annelida	*Piscicolid* sp.	complex	generalist	native		0.7% (1 ± 0)		This study
Cestoda	Tetraphyllidea	complex	generalist	native	3.7% (16 ± 0.4)			This study
Copepoda	*Caligus* sp.	direct	Specialist/generalist?	native		3.8% (1± 0)		This study
	Bomolochus unicirrus	direct	specialist	native	29% (2 ± 0.1)			This study
	Nothobomolochus denticulatus	direct	specialist	invasive		+	(+)	El-Rashidy and Boxshall, 2012
	Pennella filosa	complex	generalist	native	+			Ramdane et al. 2009
Digenea	*Lecithochirium* sp.	complex	generalist	native		12.2% (1.4 ± 0)		This study
	Didymozoon sphyraenae	complex	specialist	native	85% (5.5 ± 0.4)			This study
	Bucephalus sphyraenae	complex	specialist	not present			+	Nahhas et al. 2006
	Bucephalus labracis	complex	specialist	native		+		Fischthal, 1982
	Plerurus digitatus	complex	generalist	native	+			Looss, 1899
Isopoda	*Gnathia* sp.	complex	generalist	native	0.9% (13 ± 0.1)	0.7% (2± 0)		This study
	Cymothoa indica	complex	generalist	invasive		+	(+)	Trilles and Bariche, 2006
	Anilocra physodes	complex	generalist	native		+		İnnal et al. 2007
Monogenea	*Pseudempleurosoma* sp.	direct	specialist	invasive		4 % (1± 0)	(+)	This study
	Chauhanea mediterranea	direct	specialist	native	5.6% (1.4 ± 0.1)			This study
	Pseudolamellodiscus sphyraenae	direct	specialist	not present			+	Yamaguti, 1953; Kritsky et al. 2000
	Cotyloatlantica mediterranea	direct	specialist	native	+			Euzet and Trilles, 1960
	Rhinecotyle crepitacula	direct	specialist	native	+			Euzet and Trilles, 1960
Nematoda	*Anisakis* sp.	complex	generalist	native	1.9% (3 ± 0)			This study
Total species richness					**10**	**9**	**5**	

1

2

3

4

Table 3(on next page)

Parasite species of the genus *Lecithochirium* recorded in the literature, with information on the life cycle (Intermediate host and Definitive host) in the Mediterranean Sea.

1

Parasites	Intermediate host	Definitive host
Lecithochirium fusiforme Luhe, 1901	*Gibbula cineraria*	*Conger conger* *Lophius piscatorius*
Lecithochirium musculus (Looss, 1907)	*Conger myriaster* *Conger japonicus*	*Anguilla anguilla* *Trachurus trachurus* *Serranus hepatus* *Crenilabrus cinereus* *Conger conger* *Atherina Hepsetus* Serranus scriba
Lecithochirium physcon Luhe, 1901	-	*Lophius piscatorius*
Lecithochirium rufoviride (Rudolphi, 1819)	*Gibbula cineraria* *Blennius pholis*	*Anguilla anguilla*
Lecithochirium texanum (Chandler, 1941)	-	*Euthynnus alleteratus*
Lecithochirium jaffense Fischthal, 1982	*Seriola dumerili*	*Trachinotus ovatus* *Epinephelus* sp. *Echeneis naucrates* *Pomatomus saltatrix* *Gobius cobitus* *Etrumeus golanii*
Lecithochirium haifense Fischthal, 1980	-	*Atule djeddaba*
Lecithochirium magnicaudatus (Fischthal & Kuntz, 1963)	-	Saurida undosquamis *Labeo forskalii*
Lecithochirium microstomum Chandler, 1935	-	*Trichiurus lepturus*
Lecithochirium grandiporum (Rudolphi,1819)	-	*Muraena helena* *Lophius piscatorius* *Conger conger* *Saurida tumbil*

Figure 1

Sampling locations (1-7) of the native *Sphyraena sphyraena* and the invasive Lessepsian migrant *Sphyraena chrysotaenia* in the central Mediterranean Sea (a) along the Tunisian coast (b) .

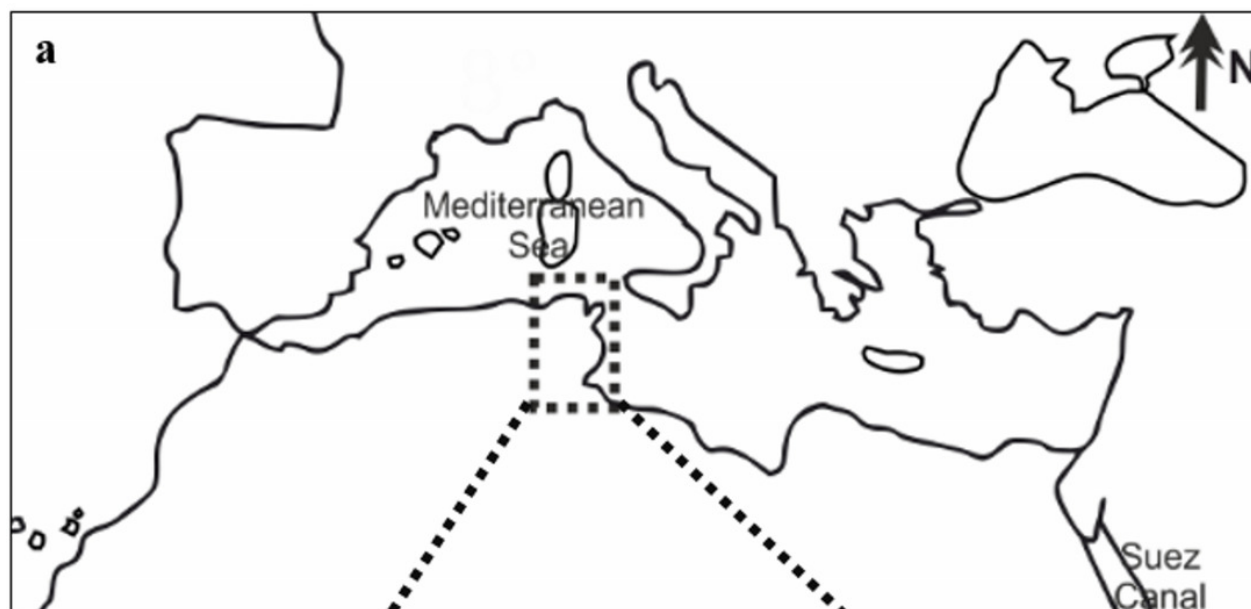For location names, coordinates, sampling dates and sampling effort per species see Table 1.

PeerJ

Figure 2

Rarefraction curves for parasite richness for a) the native fish Sph*yraena sphyraena* and b) the invasive Lessepsian migrant *Sphyraena chrysotaenia*.

Shown are the observed species richness accumulation curves (S_{obs}) which is the mean number of species among runs and the predicted number of species (± SE) based on the Chao2 estimator algorithm.
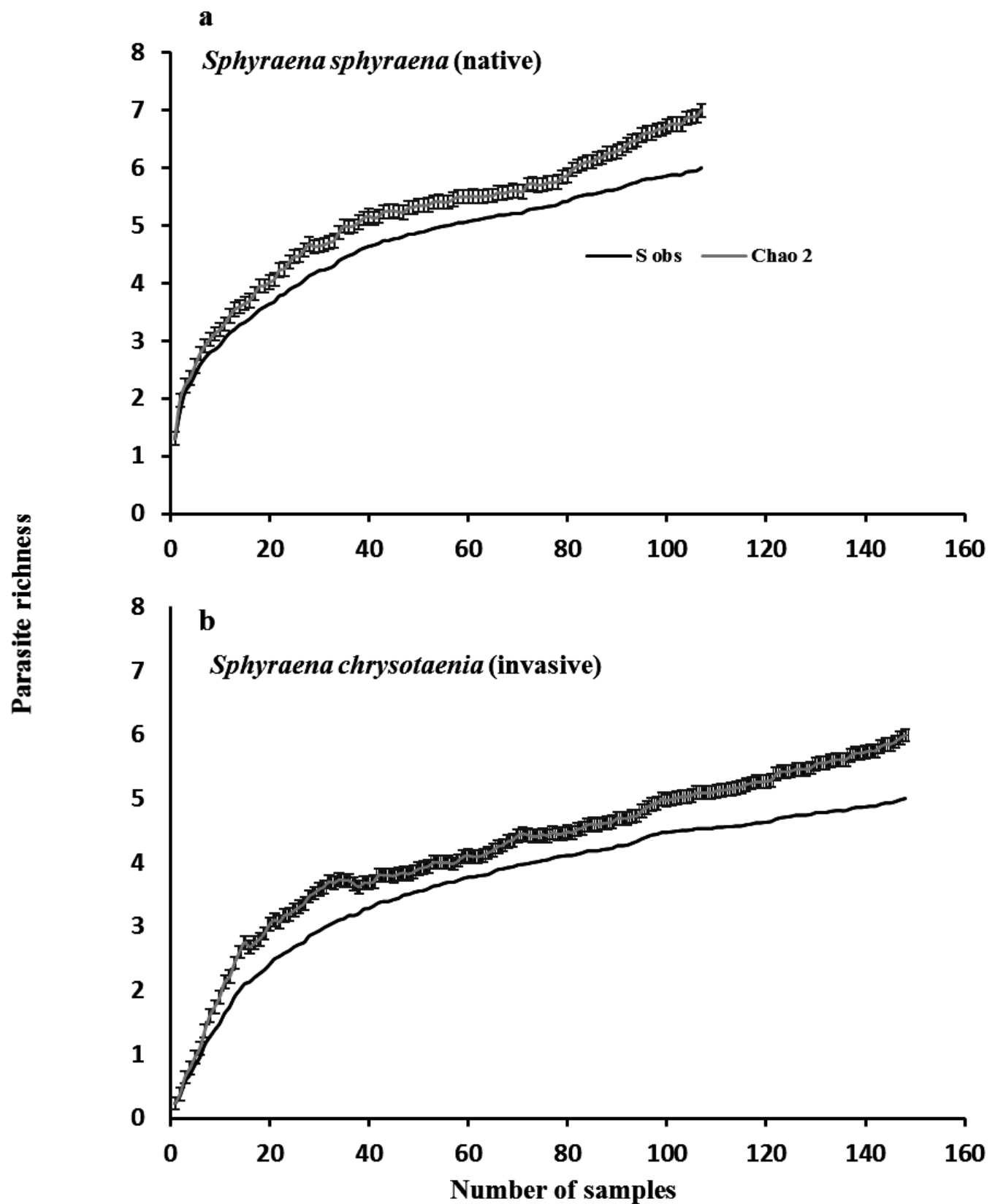
Figure 3

Mean parasite species richness per individual fish.

(including non-infected hosts; ± SE) at the seven locations in the native fish *Sphyraena sphyraena* (n = 107) and the invasive congeneric *Sphyraena chrysotaenia* (n = 148).
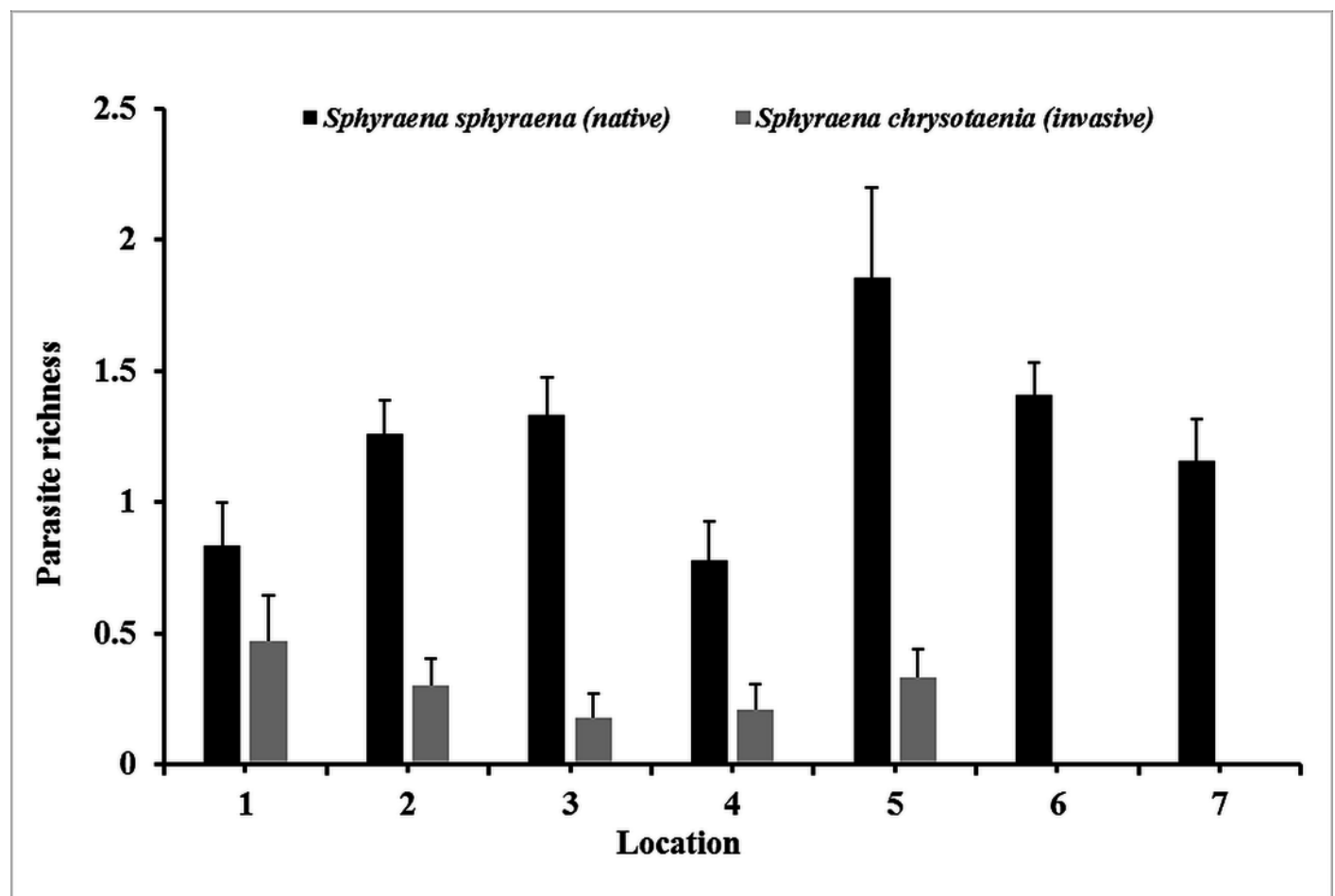
Figure 4

a) Mean total prevalence of all parasites in hosts and b) mean intensity of total parasite loads in native *Sphyraena sphyraena* and invasive *Sphyraena chrysotaenia* at the seven sampling locations.

Mean total prevalence (i.e. hosts infected by 1 or more parasite species); and mean intensity loads (i.e. sum of all parasite individuals found in a host) For sample size (n) per host species and location, see Table 1.