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Parasite communities in two sparid fishes from the western Mediterranean: a comparative analysis based on samples from three localities off the Algerian coast

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Article info	Summary
Received October 19, 2016 Accepted January 9, 2017	We provide the first known comparative assessment of metazoan parasite communities in two tax- onomically and ecologically related sparids, <i>Boops boops</i> and <i>Spicara maena</i> , that are common in the coastal infralittoral habitats in the Mediterranean. Using abundant data for infracommunities in three localities off the Algerian coasts of the Mediterranean, we tested the general prediction that the phylogenetic proximity of the two hosts, their overlapping geographical distribution and habitat occupation, as well as the similar feeding habits and diet would contribute to a homogenization of their parasite community composition and structure. The regional fauna of parasites of <i>B. boops</i> and <i>S. maena</i> along the Algerian coasts of the western Mediterranean was species-rich (36 species) and dominated by heteroxenous species (27 spp; of these 20 digenean spp.). The phylogenetic related- ness between the two hosts resulted in a large number of shared parasites (56 %, 20 spp.). However, the significant overlap in the parasite faunas of the two sparid hosts and their similar feeding habits and diet did not translate into homogeneous parasite community pattern; a significant differentiation in terms of both, composition and structure, was observed. Keywords: <i>Spicara maena; Boops boops</i> ; parasite communities; western Mediterranean; Algeria

Introduction

Parasite ecologists have long been interested in the extent to which phylogenetic and ecological factors shape parasite community composition and structure (e.g. Holmes & Price, 1980; Holmes, 1990; Hoberg & Adams, 2000). The ideal system to address this question would comprise hosts with divergent phylogenetic affinities but sharing ecological niches and habitats in a narrow geographical range. Fishes of the family Sparidae are widely distributed in the Mediterranean coastal waters and exhibit a diverse range of feeding habits and diets, with representation in all functional trophic groups (Stergiou & Karpouzi, 2002). Some of these species coexist in overlapping habitats (Corbera *et al.*, 1998). However, despite this diversity of potential sparid hosts,

faunistic and taxonomic data allowing reliable identification of all metazoan parasite groups exist for just one species, *Boops boops* (L.) (see Renaud *et al.*, 1980; Pérez-del-Olmo *et al.*, 2006, 2007a, 2008); this species is also considered as one of the most abundant species in the Mediterranean (Valle *et al.*, 2003; Boyra *et al.*, 2004). The patterns of composition and structure of parasite communities in *B. boops* have been studied in detail in relation to ontogenetic community development, geographical variability and anthropogenic effects such as pollution accidents and overfishing (Pérez-del-Olmo *et al.*, 2007b, 2008, 2009a, b, 2010; Marzoug *et al.*, 2012). *Boops boops* therefore, represents an excellent sparid candidate host for comparative parasite community studies.

Until recently, Spicara maena (L.) has been classified within the family Centracanthidae (see Tortinese, 1986) and even used as

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the outgroup in molecular phylogenetic analyses of the Sparidae (see Hanel & Sturmbauer, 2000). However, subsequent studies supported a monophyletic Sparidae with the inclusion of the centracanthid genus *Spicara* Rafinesque (see Orrell *et al.*, 2002; Orrell & Carpenter, 2004; Chiba *et al.*, 2009). These authors also suggested that the feeding types traditionally used for definition of subfamilies within the Sparidae, were independently derived multiple times; multiple transitions from a durophagous to a non-durophagous diet were also suggested by Santini *et al.* (2014). These data indicate that *S. maena* appears a good candidate for comparative parasite community analyses within the Sparidae.

In this study we report on the metazoan parasite faunas and examine communities in the two taxonomically and ecologically related sparids, *B. boops* and *S. maena*, that are common in the coastal infralittoral habitats in the Mediterranean. These two species are demersal, found over seaweed beds, on sand or muddy bottoms and their geographical distribution is overlapped (Froese & Pauly, 2015). Both species are omnivorous, feeding mainly on crustaceans and showing an overlap in their trophic levels: *S. maena* 3.00 - 3.30; *B. boops* 2.53 - 3.30 (Stergiou & Karpouzi, 2002). *Boops boops* and *S. maena* also exhibit similarities in mouth morphology; both have protruded jaws that contribute to the suction feeding habits when they feed on planktonic organisms (Linde *et al.*, 2004). Although both species have a similar mouth shape, *S. maena* has a relatively larger mouth area than *B. boops* (Karpouzi & Stergiou, 2003).

We test the general prediction that the phylogenetic proximity of *B. boops* and *S. maena*, their overlapping geographical distribution and habitat occupation, as well as the similar feeding habits and diet contribute to a homogenization of their parasite community composition and structure. No detailed faunistic or taxonomic data on parasites of *S. maena* are yet available but we expect that the two hosts would share a large number of species, especially sparid generalist parasites.

Further, the two hosts exhibit intermediate trophic levels, well below the highest value (4.5) reported for top predator fishes in the Mediterranean (Stergiou & Karpouzi, 2002). We, therefore hypothesise that this would be reflected in similar patterns of richness and abundance of larval parasite stages reflecting hosts' position within local food webs and trophic interactions in fish communities. Finally, we addressed the possible spatial variability and seasonal effects on community parameters by examination of seasonal samples collected at three localities off the Algerian coast of the Mediterranean.

Materials and Methods

A total of 475 fish [238 *B. boops* (total length 17.5 - 24.0 cm) and 237 *S. maena* (total length 12.5 - 18.5 cm); all adult] was collected by local fishermen during spring and autumn of 2013 - 2014 at three localities [off Bouzedjar ($35^{\circ}34'57.83''N$, $1^{\circ}09'04.97''W$), Alger ($36^{\circ}45'04.02''N$, $3^{\circ}06'31.72''E$) and Skikda ($36^{\circ}54'21.23''N$,

 $6^{\circ}53'36.00''E)$] along the Mediterranean coast of Algeria. Sixteen distinct samples (eight per host species; n = 27 – 32) were examined. Fish transferred on ice to laboratory were measured, labelled individually and examined for both ecto- and endoparasites according to a standardized protocol. All metazoan parasites were collected and fixed in 70 % ethanol. Monogeneans, cestodes and digeneans were stained with iron acetocarmine and identified as permanent mounts in Canada balsam. Nematode larvae and crustaceans were identified on temporary mounts in saline solution. All parasites were identified to the lowest taxonomic level possible and counted. Voucher specimens are deposited in the Helminthological Collection of the Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Ecological terms used for parasite populations and communities follow Bush *et al.* (1997): prevalence (P in %) was calculated as the proportion of the hosts infected with a given parasite species in the sample and mean abundance was calculated as the total number of individuals of a given parasite species in a sample divided by the number of hosts examined. Only adult fish were used in the analyses. Analyses were performed at two hierarchical community levels: infracommunity (i.e. all parasite populations within an individual host) and component community (infracommunities in a host population sample in a given locality at a particular time). Species with prevalence higher than 10 % in at least one of the samples will further be referred to as common. Analyses were performed for spring and autumn separately because a seasonal change in the diet of both fish species has been reported (Derbal & Kara 2008; Karachle & Stergiou, 2014).

The following infracommunity parameters were assessed: overall richness (mean no. of species per fish), overall abundance (mean no. of worms per fish), Brillouin's diversity index and Berger-Parker dominance index. All parasite taxa were split into two main groups with respect to the mode of transmission reproduction: (i) monoxenous (single-host life-cycle); and (ii) heteroxenous (multiple-host life-cycle); the latter group contained parasites utilising the two fish hosts as definitive, intermediate or paratenic hosts. The richness and abundance of the monoxenous species and of the larval and adult stages of the heteroxenous species, were also calculated. Generalized linear model (GLM) analyses were carried out using Statistica 9.0 (StatSoft, Inc.; www.statsoft.com) and on In (x+1)-transformed data to assess the effects of locality (three levels, Bouzedjar, Alger and Skikda) and host species (two levels, B. boops and S. maena) and their interaction, on the variation of community parameters; a separate analysis was carried out for the abundance of the species contributing to the dissimilarity between communities in the two hosts.

Community similarity analyses were carried out with PRIMER v6 software (Clarke & Gorley, 2006) on a subset of 16 generalist parasites with a prevalence > 10 % in any of the host samples (common species, see above) that were recovered in both host species; these will further be referred to as shared common species. Both

 Table 1. Overall prevalence (P%) and mean abundance (± standard deviation) of parasites of Boops boops and Spicara maena sampled in Algeria.

 The shared common species are marked in bold.

Species	Status		Boops	boops	Spicara	maena
			(n = 23	8)	(n = 23	7)
	Specificity	Life- cycle	P%	MA ± SD	(// 20 P%	MA ± SD
Monogenea						
Bivagina alcedinis ^b	SS	Μ	-	-	2.1	0.08 ± 0.63
Cyclocotyla bellones ^{a,b}	G	Μ	2.5	0.03 ± 0.22	5.9	0.08 ± 0.38
Encotyllabe sp.	_	Μ	0.4	0.004 ± 0.06	0.4	0.004 ± 0.06
Lamellodiscus knoepffleri ^b	SG	Μ	-	-	9.7	0.53 ± 2.88
Microcotyle erythrini ^a	SG	Μ	27.7	0.53 ± 1.07	-	_
Digenea						
Aponurus laguncula	G	HA	-	-	1.3	0.01 ± 0.11
Aphanurus stossichii ^{a,b}	G	HA	47.1	2.05 ± 6.22	5.1	0.05 ± 0.22
Bacciger israelensis ^a	BS	HA	52.9	1.92 ± 3.08	-	_
Derogenes sp.	_	HA	0.4	0.004 ± 0.06	-	-
Ectenurus lepidus	G	HA	0.4	0.004 ± 0.06	3.4	0.04 ± 0.21
Hemiurus communis ^{a,b}	G	HA	9.2	0.11 ± 0.40	3.8	0.05 0.31
Lepocreadium album ^ь	SG	HA	1.3	0.03 ± 0.28	21.1	0.74 2.47
Lecithocladium excisumª	G	HA	4.6	0.05 ± 0.24	3.8	0.04 0.19
Lecithaster sp. juv.	-	HA	0.4	0.004 ± 0.06	0.4	0.004 ± 0.06
Lepidauchen sp. juv.	-	HA	-	-	0.8	0.01 ± 0.09
Lepocreadiidae gen. sp. juv. ^{a,b}	-	HA	8.8	0.18 ± 0.69	13.5	0.26 0.79
Magnibursatus bartoliiª	BS	HA	4.2	0.07 ± 0.41	0.4	0.004 0.06
Opecoelidae gen. sp. juv. ^b	-	HA	-	_	2.1	0.03 ± 0.18
Robphildollfusium martinezgomezi ^a	BS	HA	2.1	0.05 ± 0.50	-	_
Renicolidae gen. sp. met.	-	HL	0.4	0.004 ± 0.06	-	-
Prosorhynchus crucibulum met. ^{a,b}	G	HL	58.4	5.28 ± 7.63	3.8	0.05 0.25
Stephanostomum sp. met.ª	G	HL	11.3	0.18 ± 0.71	0.4	0.004 ± 0.06
Steringotrema sp. juv.	-	HA	_	-	0.4	0.004 ± 0.06
Tormopsolus sp. met. ^{a,b}	G	HL	47.1	1.18 ± 1.79	47.3	1.08 ± 1.64
Wardula bartolii	BS	HA	0.8	0.01 ± 0.09	_	-
Cestoda						
Tetraphyllidea fam. gen. <i>incertae sedis^{a,b}</i>	G	HL	34.9	1.28 ± 3.05	53.6	1.61 ± 2.19
Nematoda						
Anisakis type I (sensu Berland, 1961)	G	HL	2.5	0.03 ± 0.22	_	-
Anisakis type II (sensu Berland, 1961)	G	HL	0.8	0.01 ± 0.09	0.4	0.01 ± 0.19
Capillariidae gen. sp.	_	HA	_	-	0.4	0.004 ± 0.06
Contracaecum sp. ^b	G	HL	2.5	0.03 ± 0.22	5.5	0.08 ± 0.34
Hysterothylacium aduncum ^{a,b}	G	HL	1.7	0.05 ± 0.48	9.7	0.12 ± 0.38
Hysterothylacium fabri ^{a,b}	G	HL	12.6	0.18 ± 0.61	85.7	4.79 ± 4.91
Crustacea						
Ceratothoa oestroides⁵	G	М	0.8	0.01 ± 0.09	5.1	0.07 ± 0.33
Gnathia sp.	G	М	_	_	1.3	0.01 ± 0.11
Caligus sp.	G	М	0.4	0.004 ± 0.06	_	_
Naobranchia cvgniformisª	SG	М	8.0	0.11 ± 0.45	0.8	0.01 ± 0.09

^aSpecies considered common (prevalence >10% in at least one sample) in *Boops boops* ^bSpecies considered common (prevalence >10% in at least one sample) in *Spicara maena*

Abbreviations: M, monoxenous species; HL, larval stages of heteroxenous species; HA, adult stages of heteroxenous species; SS, Spicara spp. specialist; BS, B. boops specialist; SG, sparid generalist; G, generalist

component communities and infracommunities were used as replicate samples in the analyses and Bray-Curtis similarity matrices were calculated based on squared root-transformed data. Principal Coordinates Analysis (PCO) of parasite abundance data at the component community level was carried out in order to examine the multivariate relationships between the samples in relation to the three factors (i.e. locality, season and host species). Additionally, multidimensional scaling (MDS) plots based on Bray-Curtis similarities were performed to obtain an ordination of infracommunities based on relative similarity in composition and abundance of the shared common species. The ANOSIM (2-way crossed layout) procedure that performs randomization tests on similarity matrices was used in order to separate the effect of geographical variation from any changes associated with the host species (Clarke & Gorley, 2006). Thereafter, the SIMPER procedure was used to identify 'key discriminating' parasite species (i.e. species with overall per cent contribution to the average dissimilarity between host species of > 10 %).

Results

The two host species had a rich parasite fauna (36 species) in the area studied [20 digeneans, 6 nematodes (5 larval), 5 monogeneans, four crustaceans (1 larval) and 1 larval cestode] with heteroxenous species (27 spp; 17 spp. represented by adults and 10 spp. represented by larval stages) clearly predominating over monoxenous species (9 spp.) (Table 1). Most of the species were classified as generalists (i.e. parasitising in a large number of fish hosts; 18 spp.) and there were few species in the other specificity categories (4 sparid generalists, 4 *B. boops* specialists and 1 *Spicara* spp. specialist; 9 species identified to the generic level only were not assigned to a specificity category) (Table 1).

A total of 3,249 specimens belonging to 28 species was recovered in *B. boops* (3 monogeneans, 16 digeneans, 1 larval cestode, 5 larval nematodes, 1 isopod and 2 copepods). Of these, six were monoxenous species (3 monogeneans, 1 isopod and 2 copepods), 10 were larval stages of heteroxenous species (4 dige-



Fig. 1. Plots showing differences in infracommunity richness (mean number of species), abundance (mean number of individuals), diversity (mean Brillouin's index) and dominance (mean Berger-Parker's dominance index) between *B. boops* (triangles) and *S. maena* (squares) sampled in spring at three localities in the western Mediterranean off Algeria: Bouzedjar (Bo), Alger (AI) and Skikda (Sk). Vertical bars represent 95 % confidence intervals.

	Spring						Autumn					
	Global model		Factor "host"		Factor "locality"		Global model		Factor "host"		Factor "locality"	
	$F_{(5.171)}$	д.	$F_{_{(1,171)}}$	д.	$F_{(2, 171)}$	д.	$F_{(1,174)}$	٩	$F_{_{(1,171)}}$	٩	F _(2.171)	д.
Overall richness	12.51	< 0.0001	25.42	< 0.0001	6.70	0.002	I	ns	I	1	I	I
Overall abundance	4.90	0.0003	I	ns	I	ns	9.90	< 0.0001	34.89	< 0.0001	I	ns
Brillouin's diversity index	18.98	< 0.0001	40.10	< 0.0001	15.76	< 0.0001	I	ns	I	I	I	I
Berger-Parker's dominance index	20.24	< 0.0001	51.94	< 0.0001	15.10	< 0.0001	3.05	0.011	I	ns	3.044	ns
Monoxenous species richness	3.45	0.005	I	ns	I	ns	2.66	0.023	7.33	0.007	I	ns
Monoxenous species abundance	4.58	0.0006	I	ns	4.20	0.017	I	ns	I	I	I	I
Heteroxenous species richness (larval)	3.32	0.006	I	ns	3.63	0.029	7.75	< 0.0001	12.50	0.0004	6.131	0.002
Heteroxenous species abundance (larval)	3.06	0.011	11.38	0.001	I	ns	3.38	0.006	I	ns	I	ns
Heteroxenous species richness (adult)	17.79	< 0.0001	82.29	< 0.0001	I	ns	17.83	< 0.0001	47.10	< 0.0001	12.40	< 0.0001
Heteroxenous species abundance (adult)	24.45	< 0.0001	107.23	< 0.0001	3.34	0.038	19.52	< 0.0001	51.24	< 0.0001	12.80	< 0.0001
Species			Percent c	ontribution	GLM		Boc	sdooq sd	Sr	vicara maena		
					ш	٩	MA:	ESD	Ŵ	A±SD		
Aphanurus stossichii												
Spring			9.56		37.03	< 0.0001	0.82	土 1.10	0	13 ± 0.33		
Autumn			11.24		70.05	< 0.0001	2.80	i ±7.76	0.(01 ± 0.08		
Prosorhynchus crucibulum m	et.											
Spring			14.75		61.83	< 0.0001	2.57	± 3.74	0.0	01 ± 0.11		
Autumn			24.09		197.07	< 0.0001	6.93	±8.84	0.0	07 ± 0.30		
Tormopsolus sp. met.												
Spring			13.35		10.79	0.001	1.33	: 土 1.55	0.(57 ± 1.07		
Autumn			10.88		I	su	1.05	1±1.92	1.:	33 ± 1.86		
Tetraphyllidea fam. gen. <i>ince</i> ,	rtae sedis											
Spring			16.05		I	su	1.47	· ± 3.71	1.	55 2.00		
Autumn			12.00		9.46	0.002	1.17	. <u>+</u> 2.58	1.(54 ± 2.30		
Hysterothylacium fabri												
Spring			31.37		229.71	< 0.0001	90.06	1 ± 0.27	5	72 ± 6.22		
Autumn			20.92		345.19	< 0.0001	0.25	±0.74	4.	25 ± 3.88		

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Fig. 2. Plots showing differences in infracommunity richness (mean number of species), abundance (mean number of individuals), diversity (mean Brillouin's index) and dominance (mean Berger-Parker's dominance index) between *B. boops* (triangles) and *S. maena* (squares) sampled in autumn at three localities in the western Mediterranean off Algeria: Bouzedjar (Bo), Alger (AI) and Skikda (Sk). Vertical bars represent 95 % confidence intervals.

neans, 1 cestode and 5 nematodes) and 12 were adult stages of heteroxenous species (12 digeneans). *Boops boops* is a new host record for two species, *Encotyllabe* sp. and *Ectenurus lepidus* and one species, *Wardula bartolii*, was recorded for the first time in the Mediterranean. Sixteen species were considered as common in parasite communities in *B. boops*.

A total of 3,481 individuals of 28 species was recovered in *S. maena* (4 monogeneans, 15 digeneans, 1 larval cestode, 5 nematodes, 2 isopods and 1 copepod). Of these, seven were monoxenous species (4 monogeneans, 2 isopods and 1 copepod), eight were larval stages of heteroxenous species (3 digeneans, 1 cestode and 4 nematodes) and 13 were adult stages of heteroxenous species (12 digeneans and 1 nematode). *Spicara maena* is a new host record for five species (*Magnibursatus bartolii, Prosorhynchus crucibulum, Encotyllabe* sp., *Lepidauchen* sp., *Anisakis* type II (*sensu* Berland, 1961) and *Gnathia* sp.). Fifteen species were considered as common in parasite communities in *S. maena*. The two host species shared 20 species of parasite (i.e. 56 % of the species found); of these, 16 species were common in parasite communities of at least one of the fish hosts (indicated in bold in Table 1).

The GLMs constructed for each season separately for the measures of infracommunity structure and diversity revealed a significant effect of both factors ("host" and "locality") with interactions between the two factors being more conspicuous in spring (Table 2, Figs. 1, 2). In spring, there was a significant effect of the host species on infracommunity richness, diversity and dominance (see Table 2, Fig. 1). Communities in *B. boops* exhibited a significantly higher infracommunity richness and diversity associated with a higher richness of heteroxenous species (adult stages) (all P < 0.0001). Communities in Spicara maena showed significantly higher dominance, with 69 % of the infracommunities dominated by the larvae of Hysterothylacium fabri and 22 % dominated by larval tetraphyllideans; these contributed to the significantly higher abundance of the larval stages of heteroxenous species in this host. There was a significant effect of locality on infracommunity richness, diversity and dominance with generally overlapping confidence intervals for samples of the two hosts off Bouzedjar and Skikda, whereas communities in *S. maena* sampled off Alger exhibited much lower richness and diversity and higher dominance (Fig. 1).

In autumn, the only significant host effect on total communities was associated with infracommunity abundance and dominance with higher levels in *B. boops* (especially off Alger and Skikda; see Table 2 and Fig. 2). Furthermore, significantly higher richness and abundance of adult stages of heteroxenous species as well as significantly higher richness of monoxenous species and adult stages of heteroxenous species and adult stages of heteroxenous species as opposed to the higher richness of larval stages of heteroxenous species in *S. maena* (all P < 0.007).

The PCO run on Bray-Curtis similarity matrix derived from the square root transformed abundance data for the shared common species in component communities of *B. boops* and *S. maena* showed that the first two principal components accounted for 75 % of the variation on the dataset (Fig 3). The PCO depicted a clear separation along the first principal component of the samples of *B. boops* and *S. maena*, this axis being highly positively correlated with the abundance of *Aphanurus stossichii* (Spearman's rho =

0.85), Stephanostomum sp. (Spearman's rho =0.85) and Prosorhynchus crucibulum (Spearman's rho =0.79) and highly negatively correlated with *H. fabri* (Spearman's rho = -0.86). The second principal component was highly negatively correlated with the abundance of juvenile lepocreadiids (-0.92) and revealed some separation between spring and autumn samples of *S. maena* but not between those of *B. boops*.

The MDS plots performed on infracommunity data for shared common species in the spring and autumn samples separately, showed an intermediate stress (0.15 in spring and 0.17 in autumn) with an overlap but also a generally good separation of the infracommunities in the two host species (Figs. 4, 5). ANOSIM analyses showed an effect of both factors, "host" and "locality", on infracommunity composition of the shared common species with lower R-values for "locality" in both spring and autumn analyses (spring, R = 0.51 vs 0.11; autumn, R = 0.61 vs 0.08, respectively; all P < 0.0001). The SIMPER procedure indicated that five species contributed to 85 % of the average dissimilarity (82.70 %) between infracommunities in the two host species in spring and to 79 % of the average



Fig. 3. Principal coordinates analysis (PCO) plot of component communities in *Boops boops* (triangles and circles) and *Spicara maena* (inverted triangles and squares) based on Bray-Curtis similarity matrix with a vector overlay showing species with vectors (Spearman's correlations of variables with the PCO axes) longer than 0.5. Autumn and spring samples are indicated by 1 and 2, respectively.



Fig. 4. Non-metric multidimensional scaling ordination of infracommunities in *Boops boops* (triangles) and *Spicara maena* (squares) sampled in spring at three localities in the western Mediterranean off Algeria.

dissimilarity (84 %) in autumn: the digeneans *A. stossichii, P. crucibulum* and *Tormopsolus* sp., and larval tetraphyllideans and *H. fabri* (Table 3). The GLMs constructed for the abundance of these species showed that factor "host" significantly explained the abundances of all but larval tetraphyllideans in spring and *Tormopsolus* sp. in autumn (Table 3). In both spring and autumn samples *A. stossichii* and *P. crucibulum* had higher abundance in infracommunities in *B. boops*. In contrast, *H. fabri* had higher abundance in infracommunities of *S. maena*. The abundance of *Tormopsolus* sp. was significantly higher in *B. boops* in spring only and the abundance of the larval tetraphyllideans was significantly higher in *S. maena* in autumn only (Table 3).

Discussion

To the best of our knowledge, this is the first comparative parasite community analysis for sparid fish hosts based on examination of community parameters from abundant data at the infracommunity level. The present study is also the first to provide comprehensive faunistic and community data for metazoan parasites in *S. maena*. The regional fauna of parasites of *B. boops* and *S. maena* along the Algerian coasts of the western Mediterranean was species-rich (36 species) and dominated by digeneans (20 species). A quarter of these (4 digeneans and 5 nematodes) were represented by larval forms thus reflecting the intermediate position within local food webs of the two hosts studied. As expected from the well-known fauna of *B. boops*, generalist parasites transmitted to the two sparids from other sympatric species accounted for a signifi-

cant portion of faunal diversity (61 %, 22 species; of these, only 4 are considered to be sparid generalists). This is in contrast with the rather low number of host-specific parasites indicating a weak phylogenetic element of the parasite fauna of the two sparid fishes studied: *Bivagina alcedinis* in *S. maena* and *Bacciger israelensis*, *Robphildollfusium martinezgomezi*, *Wardula bartolii* and *Magnibursatus bartolii* in *B. boops*. Although we listed the last species as *Boops* specialist, its recovery in *S. maena* in the present study indicates that this parasite may have a wider host range and is probably a sparid generalist species; data from other hosts and localities are required to confirm this suggestion.

Species parasite faunas were also species rich (28 spp. each) and, as expected, the phylogenetic relatedness between the two hosts resulted in a large number of shared parasites (56 %, 20 spp.). Notably, no host specialist was shared except for *M. bartolii* and only two of the four species considered to be sparid generalists were found in both hosts: the digenean Lepocreadium album and the copepod Naobranchia cygniformis. It is worth noting that the species-rich list (28 spp.) of parasites in B. boops is a result from a distinctly wider regional sampling in our study (compared with just 9 species reported in the Gulf of Oran by Marzoug et al., 2012) suggesting compositional differences between local parasite faunas. However, total infracommunity richness and abundance in the three localities sampled by us exhibited comparable levels to those reported for *B. boops* sampled in the Gulf of Oran. The main finding of our study is that the significant overlap in the parasite faunas of the two sparid hosts and their similar feeding habits and diet did not translate into homogeneous structure and



Fig. 5. Non-metric multidimensional scaling ordination of infracommunities in *Boops boops* (triangles) and *Spicara maena* (squares) sampled in autumn at three localities in the western Mediterranean off Algeria

composition of their parasite communities indicating an influence of phylogenetic distinction of the two hosts might have been detected. Overall, the host-associated differences in community parameters were most pronounced in spring when communities in *B. boops* exhibited consistently higher richness and diversity and lower dominance primarily associated with adult stages of heteroxenous parasites infecting fish *via* food ingestion. This was unexpected as we assumed that if suction feeding is utilised by both species, no differential exploitation of the available food resources would occur, but the larger mouth area in *S. maena* may contribute to higher feeding rates that would lead to higher infection rates in this host.

In terms of composition, we observed clear patterns of significant differentiation of both component and infracommunities in the two sparids. Generalist species not only dominated the faunas of both species but also contributed substantially to this differentiation. Notably, four of the five key discriminating species were larval forms. This is in contrast with our prediction for similar patterns of richness and abundance of larval parasites; instead significant host-related differences in the overall abundance (spring) and richness (autumn) of larval parasites and the abundance of the four key discriminating species were detected. Another differentiating feature is the mode of transmission of these larval parasites. Overall, species infecting the fish hosts directly (the trematodes P. crucibulum and Tormopsolus sp.) were more abundant in communities in B. boops whereas those infecting via the ingestion of food (H. fabri and tetraphyllidean larvae) were more abundant in S. maena. These data may indicate differential habitat utilisation (benthic vs pelagic, respectively) rather than a variation of the interactions between *B. boops* and *S. maena* and their predators. Finally, the wider geographical sampling conducted in our study revealed some spatial effects on the host-associated variability in parasite community structure as evidenced by the significant interactions between the factors "host" and "locality" thus emphasising the influence of local conditions.

In conclusion, our comparative study revealed that parasite communities in the two phylogenetically related sparid hosts are characterised by a significant differentiation in terms of both, composition and structure, in the coastal habitats of the western Mediterranean.

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