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Drivers of parasite community structure in fishes of the continental shelf of the Western Mediterranean: the importance of host phylogeny and autecological traits

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ABSTRACT

We explored the relationships between features of host species and their environment, and the diversity, composition and structure of parasite faunas and communities using a large taxonomically consistent dataset of host-parasite associations and host-prey associations, and original environmental and host trait data (diet, trophic level, population density and habitat depth vagility) for the most abundant demersal fish species off the Catalonian coast of the Western Mediterranean. Altogether 98 species/taxa belonging to seven major parasite groups were recovered in 683 fish belonging to 10 species from seven families and four orders. Our analyses revealed that (i) the parasite fauna of the region is rich and dominated by digeneans; (ii) the host parasite faunas and communities exhibited wide variations in richness, abundance and similarity due to a strong phylogenetic component; (iii) the levels of host sharing were low and involved host generalists and larval parasites; (iv) the multivariate similarity pattern of prey samples showed significant associations with hosts and host trophic guilds; (v) prey compositional similarity was not associated with the similarity of trophically transmitted parasite assemblages; and (vi) phylogeny and fish autecological traits were the best predictors of parasite community metrics in the host-parasite system studied.

1. Introduction

Parasites have emerged during recent decades as an important tool for elucidating traits related to host biology and ecology, and for assessing environmental health based on their response to host-related and environmental factors (Williams et al., 1992; MacKenzie, 1999; Vidal-Martínez et al., 2010). The simultaneous interaction of host-related evolutionary, physiological, ecological, geographical and stochastic factors, at different scales and with diverse intensities, structures parasite communities and yields the particular parasite fauna observed for each host species. In addition, extrinsic factors, e.g. temperature, can have an effect on parasite biology and distribution by a direct impact on parasite survival or by affecting hosts' distribution patterns.

Considering parasites in host assemblages rather than in a single host species can provide a better understanding of the factors driving the structure and composition of parasite communities, and broaden the possibilities associated with their use as biological and environmental indicators. A number of studies have been devoted to exploring parasite community patterns in marine and freshwater fish assemblages (e.g. Takemoto et al., 2005; Luque and Poulin, 2008; Valtonen et al., 2010; Vignon and Sasal, 2010; Bellay et al., 2011; Poulin and Leung, 2011; Lima et al., 2016; Baia et al., 2018; Calhoun et al., 2018). These studies have highlighted the prominent role of host phylogeny and/or ecological convergence, in terms of similar habitat use or trophic level, in explaining the resemblance among fish parasite communities (Marcogliese, 2002; Luque and Poulin, 2008). Habitat use, which mostly results from the dietary preferences of the local fauna, is

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directly related to factors such as the distributional patterns of resident organisms or resource partitioning which may have a direct impact on the characteristics of parasite communities of these animals (Marcogliese, 2002). For example, benthic fishes are known to host more abundant and diverse parasite communities than their pelagic counterparts due to the higher diversity and density of invertebrates, which promote parasite transmission, near the sea floor than in the water column (Campbell et al., 1980; Marcogliese, 2002; Klimpel et al., 2006). These biotic factors are in turn influenced by abiotic conditions such as depth, substrate texture (in the case of benthic species), temperature, etc. (Marcogliese, 2002; Luque and Poulin, 2008; Calhoun et al., 2018).

Similarly to habitat use, host distribution (i.e. biogeographical factors) directly affects parasite geographical ranges and has an influence in the diversification of parasite assemblages (Luque and Poulin, 2008). Indeed, similarity among parasite communities is expected to decay exponentially with geographical distance as a result of ecological or evolutionary events (Pérez-del-Olmo et al., 2009; Timi et al., 2010; Locke et al., 2013). Similarly, the similarity in the composition of host parasite faunas and communities was found to decrease with increasing phylogenetic distance between hosts so that phylogenetically close host species tend to share many parasite species (Poulin, 2010; Locke et al., 2013).

The importance of trophic interactions in determining parasite communities has been repeatedly emphasised (Marcogliese, 2002; Luque and Poulin, 2008, Culurgioni et al., 2015; Münster et al., 2015). Marine fishes tend to be large, vagile, gregarious and to have fairly generalist diets, and these factors allow for prey switching and dietary overlap, which eventually favour a highly diversified diet in comparison with hosts in terrestrial environments (Marcogliese, 2002). Because many trophically-transmitted parasites have complex life-cycles involving more than one host, a given parasite community is largely shaped by the structure of the local food web and can provide valuable information on the position that the host occupied within it at a certain time (Marcogliese, 2002; Valtonen et al., 2010; Culurgioni et al., 2015). Host diet shifts, for example, which involve the consumption of different intermediate hosts, are rapidly reflected in changes in parasite community composition and structure (Münster et al., 2015; Dallarés et al., 2017a).

Recently, considerable efforts have been devoted to the characterization of parasite communities in fish species of the continental shelf and slope of the continental coast of the Western Mediterranean off Spain (e.g. Pérez-del-Olmo et al., 2008, 2009, 2011; Grau et al., 1999; Carreras-Aubets et al., 2011, 2012; Mateu et al., 2014; Dallarés et al., 2014, 2016, 2017a, 2017b; Constenla et al., 2015; Pérez-i-García et al., 2015, 2017). Most of these studies have addressed in detail the influence of host biology and ecology, and of environmental variables, on the composition and structure of parasite communities in a range of fish species. Thus, the knowledge of the regional parasite fauna is based on taxonomically consistent data, a prerequisite for the application of comparative approaches aiming to better understand the determinants to the patterns of parasite community diversity and structure.

Hosts with divergent phylogenetic affinities sharing habitats in a narrow geographical range with a well-studied parasite fauna represent an excellent system to address the role of phylogenetic and ecological factors in shaping parasite community composition and structure. Here, the relationships between features of host species and their environment, and the diversity, composition and structure of parasite faunas and communities, are explored in a large original dataset of host-parasite associations, host-prey associations, host traits (diet, trophic level, population density and habitat depth vagility) and environmental data for the 10 most abundant demersal fish species inhabiting the continental shelf of the Western Mediterranean region off Barcelona (Spain).

2. Materials and methods

2.1. Study area

Fishes were collected in the Western Mediterranean off Barcelona (region of Catalonia, Spain). The continental shelf off the Catalonian coast is characterised by particularly rich invertebrate and fish communities, associated with the existence of a variety of substrates and feeding resources (Demestre et al., 2000; Abelló et al., 2002; Domènech et al., 2006; Ramírez-Amaro et al., 2016; DeLaHoz et al., 2018). About 100 decapod crustacean species, up to 25 chondrichthyans and more than 120 species of teleosts have been reported in the area (Demestre et al., 2000; Abelló et al., 2002; Ramírez-Amaro et al., 2016). Marked seasonal variations in the composition of animal communities, with higher diversity and biomass in summer, have been reported in shallower waters and linked to changes in inputs of organic material throughout the year, in turn associated with blooms of primary production, river discharges and temperature variations (Demestre et al., 2000; Rumolo et al., 2015; DeLaHoz et al., 2018). The high richness of commercial species, mainly decapods and fishes, makes the study area an important fishing ground heavily exposed to trawling activity, which represents a threat to the structural complexity of the habitats and their biodiversity (De Juan et al., 2007; Cartes et al., 2009).

2.2. Fish sampling

A total of 683 fishes representing 10 species were collected seasonally in 2007 during an extensive survey of macroparasites from off the coasts of Barcelona in the Western Mediterranean (41°08.42′N, 01°40.50′E – 41°25.50′N, 02°22.76′E) (Table 1) within the framework of the project "Identification of biomarkers of the anthropogenic impact on marine communities: an ecosystemic approach" (BIOMARE, Spain). Fishes were sampled on board of research (*García del Cid*) and commercial (*Stella Maris III*) trawling vessels at shelf depths of 53–68 m. The 10 fish species, selected out of a total of 64 species identified in the BIOMARE samplings at these depths, represented 53% of the total number of fishes collected and 61% of total fish biomass (BIOMARE, our unpublished data). One seasonal sample per fish species was aimed for during sampling as follows: winter (25th February and 14th March 2007); spring (28th April and 9th May 2007); summer (6th, 18th and 20th July 2007); and autumn (2nd and 13th October 2007). However, species assemblages exhibited strong seasonal variation, and only six species were well represented during the four seasons (see sample sizes in Table 1): the teleosts *Merluccius merluccius* (L.), *Mullus barbatus* L., *Spicara maena* (L.), *Trachinus draco* L. and *Pagellus erythrinus* (L.), and the shark *Scyliorhinus canicula* (L.). Two additional species were represented during three seasons (*Boops boops* (L.) and *Citharus linguatula* (L.)), whereas *Trisopterus minutus* (L.) and *Pagellus acarne* (Risso) were abundant (and sampled) only in winter (Table 1).

Immediately upon capture, each fish was measured (total length (TL) in mm), weighed (total weight (TW) in g) and frozen at −20 °C in an individual plastic bag (to prevent the loss of ectoparasites) for parasitological and dietary studies.

2.3. Parasites

In the laboratory, fish were thawed, and external surfaces, gills and the oral cavity were carefully inspected macroscopically and under a stereomicroscope for the presence of ectoparasites. All organs and musculature were dissected out and checked for endoparasites under a stereomicroscope. All parasites were

Table 1
Data for the fish species and samples examined in the present study and the autecological variables are fish density, habitat depth vagility and diet richness.

Species	Season	*n*	Sample code	Total length (cm) (Mean ± S.D.)	Fish density (ind./ha)	Habitat depth vagility	Diet range[a]
Order Carcharhiniformes							
Scyliorhinus canicula (Scyliorhinidae)	W	20	ScW	41.5 ± 3.0	0.11	16.10	3 (4)
	S	9	ScS	42.9 ± 1.1	0.14		6 (3)
	Su	13	ScSu	42.2 ± 4.8	0.19		6 (4)
	A	12	ScA	43.6 ± 2.3	0.19		8 (10)
Order Gadiformes							
Trisopterus minutus (Gadidae)	W	16	TmW	17.3 ± 1.6	1.60	0.20	17 (22)
Merluccius merluccius (Merlucciidae)	W	22	MmW	26.8 ± 11.4	1.18	3.36	9 (24)
	S	15	MmS	28.9 ± 7.1	1.16		3 (9)
	Su	42	MmSu	23.3 ± 4.3	15.47		11 (39)
	A	15	MmA	19.6 ± 8.4	2.13		5 (4)
Order Perciformes							
Pagellus acarne (Sparidae)	W	12	PaW	22.1 ± 3.3	3.91	0.80	9 (10)
Pagellus erythrinus (Sparidae)	W	16	PeW	14.3 ± 3.9	0.88	3.20	7 (11)
	S	13	PeS	18.9 ± 4.3	0.59		6 (9)
	Su	23	PeSu	18.7 ± 2.7	0.62		6 (12)
	A	20	PeA	18.6 ± 4.1	0.64		16 (19)
Boops boops (Sparidae)	S	20	BbS	13.0 ± 2.1	0.92	3.31	13 (17)
	Su	18	BbSu	16.8 ± 3.1	2.83		11 (8)
	A	11	BbA	16.9 ± 3.8	0.30		–
Spicara maena (Sparidae)	W	20	SmW	10.6 ± 2.6	2.15	8.05	6 (4)
	S	20	SmS	12.5 ± 2.9	4.09		10 (17)
	Su	60	SmSu	16.2 ± 3.9	16.07		19 (70)
	A	23	SmA	13.8 ± 3.8	2.11		7 (26)
Mullus barbatus (Mullidae)	W	20	MbW	16.4 ± 3.7	7.35	1.91	20 (68)
	S	20	MbS	13.0 ± 1.3	9.20		8 (8)
	Su	59	MbSu	17.5 ± 3.7	11.90		15 (37)
	A	20	MbA	17.9 ± 3.6	8.18		24 (101)
Trachinus draco (Trachinidae)	W	19	TdW	24.0 ± 4.1	0.28	1.69	10 (13)
	S	10	TdS	22.6 ± 2.1	0.17		–
	Su	38	TdSu	20.6 ± 4.4	0.65		7 (11)
	A	20	TdA	22.6 ± 3.1	0.37		9 (10)
Order Pleuronectiformes							
Citharus linguatula (Citharidae)	W	26	ClW	15.9 ± 3.0	1.03	0.40	6 (14)
	Su	21	ClSu	18.9 ± 2.3	4.18		15 (69)
	A	10	ClA	12.7 ± 3.1	2.53		9 (12)

W, winter; S, spring; Su, summer; A, autumn; *n*, number of specimens examined for parasites.

[a] Number of prey taxa identified (number of specimens examined for diet content).

preserved in 70% ethanol. Digeneans, monogeneans, cestodes and acanthocephalans were stained with iron acetocarmine, dehydrated through a graded ethanol series, cleared in dimethyl phthalate and examined as permanent mounts in Canada balsam. Nematodes and crustaceans were examined as temporary mounts in saline solution or glycerine. All parasites were identified to the lowest possible taxonomic level and counted.

2.4. Fish diet contents

After the parasitological study, stomachs of 665 fishes belonging to the 10 target species were further used for the fish diet study. Stomachs were dissected and the food items were identified under a stereomicroscope (at magnifications of 10–40×). Prey were identified to the lowest possible taxonomic level (crustaceans usually to the species level) and counted. The diet range (number of prey taxa) of each fish species was determined for each seasonal sample. The food items identified in individual fish were ascribed to one of the following four ecological (related to habitats in the water column-sediment) categories (as defined for deep-sea fishes by Carrassón et al., 1997): (i) planktonic (pla): copepods, euphausiids, siphonophores, salps and chaetognaths; (ii) suprabenthic (sub): peracarids (mysids, gammaridean amphipods), decapods and swimming teleosts; (iii) epibenthic (epi): brachyurans (crabs) and non-swimming teleosts; and (iv) endobenthic (end): polychaetes and bivalves.

2.5. Host autecological data

To account for the possible influence of autecological variables on parasite abundance patterns, the trophic level, habitat depth vagility (also referred to as vagility for simplicity) and density of each fish species were assessed for the four sampling periods.

The trophic level was estimated for each species/season combination. This variable was based on 50 original stable isotope analyses for $\delta^{15}N$ performed on eight of the 10 target species. For *P. erythrinus* and *P. acarne*, $\delta^{15}N$ values were (fully or partially) adopted from Fanelli et al. (2011), recalculating the trophic level based on the baseline of particulate organic matter (POM) of the present study. Stable isotope analyses for $\delta^{15}N$ were performed on samples of fish white muscle. Dried samples (to constant weight at 60 °C) were grounded to a fine powder, encapsulated (*c.*1 mg of dry weight) in tin cups and analysed using a Thermo Electron Delta Plus XP isotope ratio mass spectrometer (IRMS) at the Geochemistry Laboratory of the Institute for Coastal Marine Environment-Consiglio Nazionale delle Recherche (IAMC-CNR) at Naples (Italy) (see Papiol et al., 2013 for details).

Fish density was calculated by dividing the total number of individuals of a given species by the swept area per haul or season.

Fish habitat depth vagility was estimated as a relative indicator of where each species typically inhabits (its relative distance from the seabed, see Solé et al., 2010), by comparing the density of a given species (individuals/ha) in hauls performed at the same grounds (depths) and period with two different trawls (a commercial trawl, CT, and an OSTB-14 trawl) with two different opening heights (3 m and 1.1 m, respectively). An index (habitat depth vagility index) comprising the relation between catches obtained with both trawls (CT/OTSB-14) was calculated for each fish species.

2.6. Environmental data

Environmental data were recorded at 5 m above the sea bottom by deployment of a CTD device almost simultaneously (same data, same depth) for hauls performed to sample fish specimens. Five environmental variables were considered: temperature (T in °C); salinity (S in ‰); oxygen concentration (O_2 in mg/l); chlorophyll *a* (Chl *a* in mg/m^3); and turbidity (Tu, voltage) representing a proxy measure for organic and inorganic suspended material.

2.7. Study scales and statistical analyses

Ecological terms used follow Bush et al. (1997). Three hierarchical spatial scales were considered in the comparisons of parasite diversity, composition and structure: (i) local parasite fauna (all parasites of all species exploiting a given host species in a local ecosystem); (ii) component community (all parasites of all species in a host population sample in a given locality at one point in time); and (iii) infracommunity (all parasites of all species within an individual host) (Bush et al., 1997; Pérez-del-Olmo et al., 2009). Brillouin's diversity index was calculated from infracommunity data using PRIMER v6.1.13. Parasite species with a prevalence higher than 10% in any of the host samples will further be referred to as common. Parasite prevalence and abundance data and infracommunity richness and diversity were analysed by generalised linear models (GZM) using individual fish as replicate samples. Correlations were estimated using Spearman's rank correlation coefficient.

Relationships between parasite abundance in the seasonal component community samples and environmental data (T, S, O_2, Chl *a* and Tu) or autecological variables (fish trophic level, density and habitat depth vagility) were explored using multivariate canonical correspondence analysis (CCA) (ter Braak, 1986).

Community composition/structure analyses were carried out with PRIMER v6.1.13 & PERMANOVA+ software which provides a range of routines for describing and modelling multivariate community data using Monte Carlo permutation hypothesis testing (Clarke and Gorley, 2006; Anderson et al., 2008). Non-metric multi-dimensional scaling (MDS) ordinations based on the Bray–Curtis similarity matrix were derived from the log $(x + 1)$ transformed abundance data to visualise low-dimensional relationships among parasite component community data or prey samples reflecting the relative similarity in composition and abundance. Mean similarity/dissimilarity for parasite communities and prey samples were calculated using the SIMPER routine. The permutational ANOVA (PERMANOVA) routine performing randomization tests (unrestricted model, 9999 permutations) on similarity matrices was used to test the null hypothesis of no differences in parasite community structure/prey composition among the hosts and among the fish trophic guilds (prey samples only).

Further, the effect of host phylogeny on multivariate patterns of parasite faunas and component communities was assessed using the RELATE routine. A permutation test (9999 permutations) for correlation between the multivariate patterns of matching faunal dissimilarity (Jaccard dissimilarity index based on presence-absence data) or component community similarity (Bray–Curtis index), and host genetic distance (p-distance) matrices was carried out. Genetic distances among fish hosts were calculated in MEGA-X (Kumar et al., 2018) using a 1779 bp alignment of concatenated partial sequences of the mitochondrial genes cytochrome *b* (*cytb*) and cytochrome *c* oxidase subunit 1 (*cox*1) retrieved from GenBank as follows: (i) complete mitochondrial genomes (Y16067: *S. canicula*; FR751402: *M. merluccius*; MG736083: *P. acarne*; MG653592: *P. erythrinus*; and NC_009854: *S. maena*); (ii) *cytb* (DQ174084: *T. minutus*; EU224049: *B. boops*; EU036452: *M. barbatus*; EU492284: *T. draco*; and EF439511: *C. linguatula*; and (iii) *cox*1 (KJ205321: *T. minutus*; JQ774987: *B. boops*; KJ709568: *M. barbatus*; KJ205435: *T. draco*; and EU513622: *C. linguatula*).

Finally, the relative importance of host phylogeny and the autecological and environmental variables considered in the present study was assessed in several boosted regression tree (BRT) models. Boosted regression trees combine the strengths of two algorithms (regression trees and boosting) and can handle different types of predictor variables, and model outcomes are unaffected by differing scales of measurement among predictors (Elith et al., 2008). BRTs also provide a means of estimating the importance of individual variables in regression. The relative contribution (influence, importance) measure is based on the number of times a variable is selected for the recursive binary splits, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Friedman and Meulman, 2003). The variables with the most explanatory power were identified in a series of models built with three categorical variables associated with three levels of phylogenetic relationships of the fish hosts ("order", "family" and "host").

3. Results

3.1. General characteristics of parasite faunas

A total of 683 fish belonging to 10 species from seven families and four orders were examined for metazoan parasites: six perciform species, two gadiform species, one carcharhiniform and one pleuronectiform species (Table 1). Altogether 98 species/taxa (9706 parasite individuals) belonging to seven major parasite groups (Table 2) were recovered. The clearly predominant group of parasites with respect to species diversity was the Digenea (47 species) followed by Nematoda (19 species) and Monogenea (13 species). The other groups were represented by fewer species: Copepoda (nine species); Cestoda (six species); Isopoda and Acanthocephala (two species each). Another characteristic feature of the local parasite fauna was the high representation (21 species, 21%) of larval parasite stages (12 digeneans, 26%; five nematodes, 26%; three cestodes, 50%; and one isopod, 50%).

The mean abundance and prevalence of the parasites comprising the local parasite faunas of the fish hosts studied are provided in Supplementary Tables S1 and S2. These differed in several aspects. Parasite richness varied from very low (faunas of *Scylorhinus canicula*: six species; *Citharus linguatula*: eight species; and *Trisopterus minutus*: nine species) to very high (*Spicara maena*: 28 species and *Pagellus erythrinus*: 29 species) and the overall local diversity of the parasite faunas of the remaining fish species was generally high (*Merluccius merluccius*: 24 species; *Mullus barbatus*: 21 species; *Trachinus draco*: 20 species; *Boops boops*: 19 species; and *Pagellus acarne*: 16 species) (Supplementary Tables S1 and S2). Digeneans predominated in faunas with high species richness (9–17 species) whereas nematodes predominated in species-poor faunas (*P. acarne*: six species; *T. minutus*: five species; *S. canicula*: three species; and *C. linguatula*: three species).

Of the 98 species, 58 were considered common (marked in Table 2). Of these, 32 (57%) are trophically transmitted parasites. The distribution of host sharing was highly aggregated with nearly half of the common species (28 species, 48%) found in a single host species, 13 species sharing two hosts, eight species sharing three hosts, two species sharing four hosts and three species sharing five hosts. A total of 13 parasites utilised three to five host species: seven

Table 2
Parasite species identified in the present study and the number of host species infected.

Species	Tax[a]	Code[b]	No. of hosts	Species	Tax[a]	Code[b]	No. of hosts
Echinorhynchus gadi	A	ecga	1	*Phyllodistomum* sp.[c]	D	phsp	1
Neoechinorhynchus agilis	A	neag	1	*Poracanthium furcatum*	D	pofu	1
Bothriocephalus sp.[c]	C	bosc	1	*Proctoeces maculatus*	D	prma	1
Clestobothrium crassiceps[c]	C	clcr	1	*Proctotrema bacilliovatum*[c]	D	prba	1
Grillotia sp. (l.)	C	grsp	1	*Prosorhynchus crucibulum* (m.)[c]	D	prcr	3
Nybelinia lingualis	C	nyli	1	*Prosorhynchus squamatus* (m.)	D	prsq	1
Tetraphyllidea fam. gen. sp. (l.)[c]	C	scpl	5	*Pycnadenoides* sp.	D	pysp	1
Trypanorhyncha fam. gen. sp. (l.)	C	tryp	2	Renicollidae gen. sp. (m.)	D	resp	1
Alella pagelli[c]	Co	alpa	1	Aporocotylidae gen. sp. (juv.)	D	sasp	1
Caligus sp.[c]	Co	cgsp	1	*Stephanostomum cesticillus* (m.)[c]	D	shce	2
Clavellotis sp.[c]	Co	clsp	1	*Stephanostomum euzeti* (m.)[c]	D	sheu	3
Hatschekia mulli[c]	Co	hamu	1	*Stephanostomum lophii* (m.)	D	shlo	1
Lernaeocera lusci[c]	Co	lelu	1	*Steringotrema pagelli*[c]	D	stpa	2
Lernaeopoda galei	Co	lega	1	*Tetrochetus coryphaenae*	D	teco	1
Naobranchia cygniformis	Co	nacy	2	*Tormopsolus* sp. (m.)[c]	D	tosp	3
Neobrachiella exigua	Co	neex	1	*Ceratothoa oestroides*[c]	I	ceoe	2
Neobrachiella merlucii	Co	neme	1	*Gnathia* spp. praniza larva (l.)[c]	I	gnsp	5
Allopodocotyle jaffensis[c]	D	alja	2	*Aspinatrium* sp.[c]	M	aisp	1
Aphallus tubarium (m.)[c]	D	aptu	3	*Anthocotyle merluccii*[c]	M	anme	1
Aphanurus stossichii[c]	D	apst	2	*Atrispinum acarne*[c]	M	atac	1
Aphanurus virgula	D	apvi	1	*Axine* sp.	M	axsp	1
Aponurus laguncula	D	apla	2	*Bivagina* sp.[c]	M	bisp	1
Aponurus mulli[c]	D	apmu	1	*Choricotyle chrysophryi*[c]	M	chch	2
Aporocotyle spinosicanalis[c]	D	apsp	1	*Cyclocotyla bellones*[c]	M	cybe	1
Arnola microcirrus	D	armi	1	*Diclidophora luscae*[c]	M	dilu	1
Bacciger bacciger	D	baba	2	*Encotyllabe pagelli*[c]	M	enpa	2
Bacciger israelensis[c]	D	bais	1	*Hexabothrium appendiculatum*[c]	M	heap	1
Brachyphallus crenatus[c]	D	brcr	3	*Lamellodiscus* spp.[c]	M	lasp	3
Cardiocephaloides longicollis (m.)[c]	D	calo	4	*Microcotyle erythrini*[c]	M	mier	2
Derogenes latus[c]	D	dela	1	*Pseudaxine trachuri*	M	pstr	1
Derogenes varicus	D	deva	2	*Anisakis physeteris* (l.)[c]	N	anph	2
Didymozoidae gen. sp. (m.)	D	disp	1	*Anisakis simplex* (l.)	N	ansi	1
Ectenurus lepidus[c]	D	ecle	1	*Ascarophis capelanus*[c]	N	asca	1
Galactosomum timondavidi (m.)[c]	D	gati	1	*Ascarophis mullus*[c]	N	asmu	1
Helicometra fasciata[c]	D	hefa	2	*Ascarophis* sp.[c]	N	assp	4
Hemiurus communis[c]	D	heco	3	*Capillaria gracilis*[c]	N	cagr	2
Holorchis sp.	D	hosp	1	*Capillaria* sp.	N	casp	2
Juvenile lepocreadiids[c]	D	lepo	2	*Collarinema collaris*	N	coco	1
Lasiotocus mulli	D	lamu	1	*Contracaecum* sp. (l.)[c]	N	cosp	8
Lecithaster gibbosus	D	legi	1	*Cucullanus longicollis*	N	culo	1
Lecithochirium musculus[c]	D	lemu	5	*Cucullanus* sp.[c]	N	cusp	3
Lecithocladium excisum[c]	D	leex	6	*Dichelyne* sp.	N	dysp	1
Lepocreadium album	D	lpal	1	*Goezia* sp.	N	gzsp	1
Macvicaria crassigula[c]	D	macr	2	*Hysterothylacium aduncum* (l.)[c]	N	hyad	10
Monascus filiformis	D	mofi	1	*Hysterothylacium fabri* (l.)[c]	N	hyfa	9
Monilicaecum sp. (m.)	D	moni	1	*Paracapillaria* sp.[c]	N	pcsp	1
Monorchis monorchis	D	momo	1	*Philometra filiformis*	N	phfi	1
Opecoelidae gen. sp.	D	opec	1	*Philometra globiceps*[c]	N	phgl	1
Opecoeloides furcatus[c]	D	opfu	1	*Proleptus obtusus*[c]	N	prob	1

l, larva; m, metacercaria.

[a] Codes for higher level taxa (Tax): A, Acanthocephala; C, Cestoda; Co, Copepoda; D, Digenea; I, Isopoda; M, Monogenea; N, Nematoda.

[b] Species codes used in multivariate analyses.

[c] Parasite species considered common (i.e. with a prevalence of ≥10% in at least one component community) and used in the analyses testing relationships between parasite load and host species or environmental/host-related data.

larval forms (metacercariae of *Aphallus tubarium*, *Prosorhynchus crucibulum*, *Stephanostomum euzeti*, *Cardiocephaloides longicollis* and *Tormopsolus* sp.; larval tetraphyllideans usually reported as "Scolex pleuronectis"; and praniza larvae of *Gnathia* spp.) and six adult forms (the digeneans *Brachyphallus crenatus*, *Lecithochirium musculus* and *Hemiurus communis*, the nematodes *Ascarophis* sp. and *Cucullanus* sp., and the monogeneans *Lamellodiscus* spp.). Notably, only four parasite species (all generalists) were found in 6–10 fish hosts: the digenean *Lecithocladium excisum* (six host species) and the larval nematodes *Contracaecum* sp. (eight host species), *Hysterothylacium fabri* (nine host species) and *Hysterothylacium aduncum* (10 host species) (Supplementary Tables S1 and S2).

The pattern of host sharing by the common species was similar within the family Sparidae, represented by four fish hosts. Only three parasites (all at the larval stage) were shared by all four sparid hosts (*Cardiocephalloides longicollis*, *H. aduncum* and *H. fabri*). *Pagellus acarne*, *P. erythrinus* and *S. maena* had three additional species in common (larval *Contracaecum* sp., *Ascarophis* sp. and *Lamellodiscus* spp.) and *B. boops* and *S. maena* had six additional species in common (*A. stossichii*, *H. communis*, *L. excisum*, *Tormopsolus* sp., Tetraphyllidea fam. gen. sp. and juvenile lepocreadiids) (Supplementary Tables S1 and S2).

Five levels of host sharing associated with host taxonomy were identified among the generalist parasite species in the present dataset: (i) a single species, the larval nematode *H. aduncum*, was shared by all hosts belonging to four orders and can thus be considered to be an unrestricted generalist; (ii) five species, the digeneans *B. crenatus*, *L. excisum* and *L. musculus*, and the larval nematodes *H. fabri* and *Contracaecum* sp., were shared by hosts of three orders (excluding Carcharhiniformes); (iii) five species, the adult (*H. communis*) and larval (*P. crucibulum* and *Tormopsolus* sp.) digeneans, the larval tertaphyllideans and larval isopods

Gnathia spp., were shared by hosts of two orders (Gadiformes and Perciformes); (iv) four species, the larval digeneans *A. tubarium* and *S. euzeti* and the nematodes *Cucullanus* sp. and *Ascarophis* sp. were shared by hosts of the order Perciformes; and (v) two taxa, the larval digenean *C. longicollis* and the monogeneans *Lamellodiscus* spp., were shared by hosts of the Sparidae and can be considered sparid generalists.

Regarding infection parameters of the common species, significant differences between host species were detected for mean abundance and prevalence (19 and 16 species, respectively, out of 58; GZM, $P < 0.05$) (detailed in Supplementary Tables S1 and S2). The differences in parasite faunal richness between hosts, coupled with the unequal distribution of the common species shared between hosts and significant differences in infection parameters, indicated a possible strong effect of host phylogeny. This hypothesis was tested using the RELATE routine in PRIMER. A permutation test for correlation between the multivariate patterns of matching faunal dissimilarity (based on the Jaccard dissimilarity index) and host genetic distance (p-distance) matrices revealed a significant agreement (Spearman's $\rho = 0.607$, $P = 0.0084$) between the multivariate patterns of parasite faunal dissimilarity and genetic distance between hosts.

3.2. Parasite communities

3.2.1. Component communities

The overall parasite prevalence ranged between 75% and 100% across the component communities of the 10 fish species analysed (Table 3). A species richness pattern similar to that of the parasite faunas was observed in component communities. There was considerable variation overall (3–27 species) but hosts with most depauperate parasite faunas fell within the lower range for component community richness (CCR): *S. canicula* (3–6 species); *C. linguatula* (4–7 species) and *T. minutus* (nine species). The two sparid hosts with the most species-rich faunas also had rich component communities (*S. maena*: 8–27 species and *P. erythrinus*: 13–26 species).

Fig. 1A shows a two-dimensional non-metric MDS plot of the 32 component communities with superimposed clusters resulting from group average clustering, at similarity levels of 50% and 70%. There was a clear separation between communities in *S. canicula* and those in the remaining hosts along the *X*-axis and a further differentiation of communities in three sparid hosts (*P. acarne*, *P. erythrinus* and *B. boops*), plus those in the gadid *T. minutus* along the *Y*-axis. The subset MDS plot (28 communities with those in the only shark species excluded) revealed a clear pattern of host-related separation albeit at a very low similarity threshold (50%) for communities in *P. erythrinus* and *B. boops* (Fig. 1B).

Overall levels of within-host similarity between component communities typically ranged from 69% to 78% except for the rather divergent community samples of *P. erythrinus* (similarity of 49.4%; see Fig. 1A, B) and the extremely homogenous community samples of *S. canicula* (similarity of 90.7%; Fig. 1A). Overall levels of between-host component community dissimilarity were high, with the majority exceeding 80% (34/45 pairwise comparisons). Communities in *S. canicula* were the most distinct (dissim-

Table 3

Overall parasite prevalence (P), component community richness (CCR), infracommunity abundance (ICA), infracommunity richness (ICR) and Brillouin's diversity index for parasite communities broken down by host species and season. Equal superscript letters in a column indicate the lack of significant differences in mean infracommunity abundance among hosts within a given season.

Season and host	P (%)	CCR	ICA Mean ± S.D.	ICR Mean ± S.D.	Brillouin's index Mean ± S.D.
Winter					
Scyliorhinus canicula	100	6	34.40 ± 23.1^{a}	1.30 ± 0.5	0.04 ± 0.08
Trisopterus minutus	75	9	8.75 ± 12.8^{de}	1.88 ± 1.7	0.37 ± 0.31
Merluccius merluccius	86	13	4.73 ± 4.3^{ef}	2.09 ± 1.4	0.44 ± 0.33
Pagellus acarne	100	16	23.58 ± 18.7^{abc}	4.50 ± 1.9	0.84 ± 0.34
Pagellus erythrinus	75	13	1.81 ± 1.6^{g}	1.25 ± 1.1	0.21 ± 0.26
Spicara maena	95	8	11.05 ± 9.6^{cd}	3.00 ± 1.3	0.72 ± 0.27
Mullus barbatus	100	16	12.45 ± 11.7^{bcd}	3.20 ± 1.5	0.60 ± 0.31
Trachinus draco	100	13	25.42 ± 27.4^{ab}	3.58 ± 1.6	0.71 ± 0.29
Citharus linguatula	85	7	2.65 ± 2.0^{fg}	1.35 ± 0.9	0.21 ± 0.24
Spring					
Scyliorhinus canicula	100	4	80.56 ± 59.9^{a}	1.44 ± 1.0	0.03 ± 0.05
Merluccius merluccius	93	10	3.93 ± 4.4^{cd}	1.87 ± 1.1	0.39 ± 0.33
Pagellus erythrinus	85	15	2.54 ± 1.9^{d}	1.92 ± 1.3	0.40 ± 0.29
Boops boops	100	12	8.40 ± 6.3^{bc}	2.80 ± 1.6	0.47 ± 0.39
Spicara maena	95	13	6.85 ± 6.1^{bc}	2.55 ± 1.4	0.55 ± 0.34
Mullus barbatus	100	13	9.10 ± 8.6^{b}	2.85 ± 1.5	0.50 ± 0.32
Trachinus draco	100	9	18.90 ± 12.7^{b}	3.80 ± 1.4	0.73 ± 0.23
Summer					
Scyliorhinus canicula	100	3	48.00 ± 29.4^{a}	1.38 ± 0.6	0.07 ± 0.11
Merluccius merluccius	86	16	3.62 ± 2.8^{cd}	2.00 ± 1.4	0.39 ± 0.33
Pagellus erythrinus	96	26	6.52 ± 9.6^{c}	2.39 ± 1.5	0.39 ± 0.36
Boops boops	100	15	5.83 ± 4.2^{c}	2.83 ± 1.2	0.51 ± 0.31
Spicara maena	98	27	17.38 ± 15.5^{b}	4.15 ± 2.0	0.81 ± 0.33
Mullus barbatus	100	19	20.39 ± 19.7^{b}	3.59 ± 1.6	0.71 ± 0.33
Trachinus draco	97	16	22.21 ± 21.5^{ab}	3.37 ± 1.5	0.68 ± 0.36
Citharus linguatula	91	5	2.05 ± 1.5^{d}	1.52 ± 0.8	0.23 ± 0.22
Autumn					
Scyliorhinus canicula	100	3	41.50 ± 18.5^{a}	1.17 ± 0.4	0.04 ± 0.11
Merluccius merluccius	87	8	5.07 ± 4.7^{cd}	2.00 ± 1.4	0.45 ± 0.36
Pagellus erythrinus	75	15	2.20 ± 2.0^{d}	1.45 ± 1.1	0.29 ± 0.26
Boops boops	91	11	6.18 ± 5.3^{cd}	2.55 ± 1.7	0.52 ± 0.41
Spicara maena	96	11	9.09 ± 6.2^{bc}	2.74 ± 1.3	0.62 ± 0.31
Mullus barbatus	100	15	16.80 ± 9.2^{ab}	4.05 ± 1.5	0.73 ± 0.30
Trachinus draco	100	12	26.05 ± 14.7^{a}	4.00 ± 1.3	0.80 ± 0.19
Citharus linguatula	80	4	3.20 ± 2.9^{d}	1.20 ± 0.9	0.18 ± 0.27

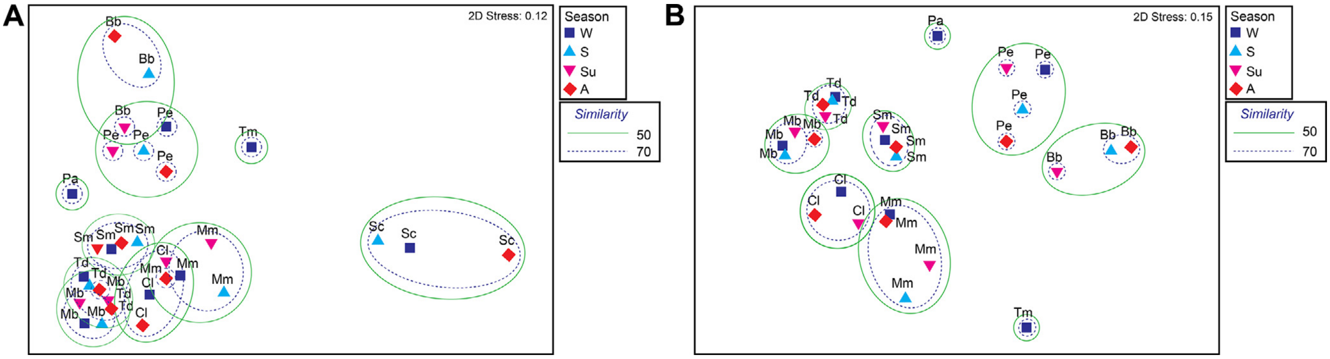

Fig. 1. Two-dimensional non-metric multi-dimensional scaling plots of the 32 parasite component communities with superimposed clusters resulting from group average clustering, at similarity levels of 50% (continuous line) and 70% (dashed line). (A) Communities in all host species. (B) A subset of the configuration shown in A with *Scyliorhinus canicula* excluded. Seasons: W, winter; S, spring; Su, summer; A, autumn. Hosts: Bb, *Boops boops*; Cl, *Citharus linguatula*; Mb, *Mullus barbatus*; Mm, *Merluccius merluccius*; Pa, *Pagellus acarne*; Pe, *Pagellus erythrinus*; Sc, *Scyliorhinus canicula*; Sm, *Spicara maena*; Td, *Trachinus draco*; Tm, *Trisopterus minutus*.

ilarity with any other host exceeding 98%) whereas the most "similar" communities were found in just three pairwise comparisons: *T. draco* versus *M. barbatus* (dissimilarity of 64.4%); *T. draco* versus *S. maena* (dissimilarity of 66.3%), and *S. maena* versus *P. acarne* (dissimilarity of 67.3%) (see detailed results of the SIMPER routine of PRIMER in Supplementary Table S3).

Host species had a significant effect on the observed multivariate pattern of similarity in both sets of communities shown in Fig. 1 explaining 58.5% of the variation in the full dataset (PERMANOVA, Pseudo-$F_{(9,22)} = 23.674$, $P = 0.0001$; Fig. 1A) and 55.0% of the variation in the subset (PERMANOVA, Pseudo-$F_{(8,19)} = 18.048$, $P = 0.0001$; Fig. 1B). The multivariate pattern of community similarity (Bray–Curtis index; 496 pairwise comparisons) was significantly correlated with the pattern of host genetic distance (Spearman's $\rho = 0.623$, $P = 0.001$).

3.2.2. Infracommunities

Infracommunity richness and diversity exhibited patterns very similar to that of the component community richness and there was a significant correlation between CCR and ICR (Spearman's $\rho = 0.618$, $P < 0.05$). The mean number of species per host individual ranged between 1.17 and 4.50 but exceeded 3.00 only in less than one-third of community samples (10 out of 32, see Table 3 for details). Brillouin's diversity was typically low with means ranging between 0.03 and 0.84 and exhibiting significant association with both CCR (Spearman's $\rho = 0.566$, $P < 0.05$) and ICR (Spearman's $\rho = 0.964$, $P < 0.05$).

There were significant differences in infracommunity richness (GZM, $\chi^2 = 65.104$, $P < 0.001$ and diversity ($\chi^2 = 320.045$, $P < 0.001$) (Table 4) among hosts but not among seasons (GZM, $P > 0.05$). The maximum values for both measures were detected in communities of *P. acarne* (examined only in winter) followed by *S. maena* (summer sample), *M. barbatus* and *T. draco* (autumn samples for both) (Table 3). Consistent with the pattern observed at the component community level, infracommunities in *S. canicula* exhibited the lowest richness and diversity values, joined by communities in *C. linguatula* and *P. erythrinus* (winter sample) (Tables 3 and 4).

Infracommunity abundance (ICA) varied greatly (means ranging between 1.81 and 80.56 parasites per infracommunity; see Table 3). Infracommunities in the shark *S. canicula* exhibited the greatest levels of parasite abundance with means ranging between 34.4 and 80.6, followed by those in *P. acarne* and *T. draco*. The lowest abundance levels were recorded in *P. erythrinus* (winter, spring and autumn samples) and *C. linguatula* (winter and summer samples). There were significant differences in infracommunity abundance among hosts (GZM, $\chi^2 = 429.592$, $P < 0.001$) (Table 4) but a significant interaction was detected between the factors "host" and "season" (GZM, $\chi^2 = 44.493$, $P = 0.003$). Therefore, contrasts between hosts were conducted for each season; these revealed significant differences in infracommunity abundance between hosts in all four seasons: winter (GZM, $\chi^2 = 128.810$, $P < 0.001$); spring ($\chi^2 = 72.442$, $P < 0.001$); summer ($\chi^2 = 168.620$, $P < 0.001$); and autumn ($\chi^2 = 96.052$, $P < 0.001$) (Table 3).

3.3. Host-related variables

3.3.1. Host diet

A total of 41 prey taxa were identified and counted in stomach contents of representative samples of the 10 fish species examined ($n = 665$ individual fish). Diet range (the number of prey taxa consumed) varied widely across hosts and seasonal samples (3–24

Table 4
Infracommunity descriptors of metazoan parasites of the 10 fish hosts studied in the Western Mediterranean off Catalonia, Spain. Different superscript letters indicate significant differences among hosts.

	Overall P	ICA	ICR	B
Scyliorhinus canicula	100^{a}	46.94^{a}	1.31^{a}	0.05^{a}
Trisopterus minutus	75^{c}	8.75^{de}	1.87^{abc}	0.38^{bcd}
Merluccius merluccius	87^{c}	4.16^{fg}	2.00^{bc}	0.39^{cd}
Pagellus acarne	100^{a}	23.58^{bc}	4.50^{d}	0.85^{e}
Pagellus erythrinus	83^{c}	3.56^{fg}	1.79^{abc}	0.33^{c}
Boops boops	98^{ab}	6.96^{e}	2.76^{cd}	0.50^{de}
Spicara maena	97^{b}	13.21^{cd}	3.46^{d}	0.69^{e}
Mullus barbatus	100^{a}	16.55^{c}	3.48^{d}	0.63^{e}
Trachinus draco	99^{ab}	23.41^{b}	3.61^{d}	0.70^{e}
Citharus linguatula	86^{c}	2.53^{g}	1.39^{ab}	0.21^{b}

P, prevalence (%); ICA, mean infracommunity abundance; ICR, mean infracommunity richness; B, mean Brillouin's diversity.

taxa) with the lowest values in *S. canicula* in winter (three taxa) and the highest values in *M. barbatus* in autumn (24 taxa) (see Table 1 for details). Overall, the diet range was relatively poor, with less than 10 taxa found in nearly 60% of host seasonal samples examined. Diet range was moderately but significantly correlated with two autecological variables, fish density ($r_s = 0.565$, $P < 0.05$) and habitat depth vagility (Spearman's $\rho = -0.380$, $P < 0.05$) and with parasite community richness (CCR, Spearman's $\rho = 0.442$, $P < 0.05$: ICR, Spearman's $\rho = 0.432$, $P < 0.05$).

Fig. 2A shows a two-dimensional non-metric MDS plot of the prey composition in 30 fish seasonal samples with superimposed clusters resulting from group average clustering, at similarity levels of 45% and 60%. Overall levels of within-fish species similarity between prey samples were very low, ranging between 27% and 56% except for the two samples of *B. boops* exhibiting a relatively high compositional similarity (69.1%) (Fig. 2A; see detailed results of the SIMPER routine of PRIMER in Supplementary Table S4). Overall levels of between-fish species prey dissimilarity were high (>60%), with samples of *B. boops* and *S. maena* exhibiting the highest dissimilarity values (>90%) in almost all pairwise comparisons (Supplementary Table S4); prey samples in these two species were also less dissimilar (62%).

No clear separation in relation to season was evident (PERMANOVA, Pseudo-$F_{(3,26)} = 0.814$, $P = 0.7639$) but a significant effect of the factor "host" on prey compositional similarities was detected (PERMANOVA, Pseudo-$F_{(9,22)} = 23.674$, $P = 0.0001$). However, this variable explained only 39.5% of the variation in the dataset.

Fig. 2B illustrates the two-dimensional relationships between prey samples with host feeding habits superimposed. Based on the diet composition, fish species were classified as feeding on planktonic, suprabenthic, epibenthic and endobenthic prey. A much clearer pattern emerged albeit at a relatively high stress value. PERMANOVA revealed a significant effect of host trophic guild on the multivariate similarity pattern of prey samples (Pseudo-$F_{(3,26)} = 5.141$, $P = 0.0001$).

Prey samples of the two plankton feeders (*B. boops* and *S. maena*) were clearly separated from the remaining samples. A large proportion of the diet of *B. boops* (85.6%) was represented by copepods from a range of taxa (*Temora stylifera*, *Candacia* spp., *Pleuromamma abdominalis*, *Centropages typicus* and harpacticoids) and, to a lesser extent (6.4%), by jellyfish (siphonophores, salps). The main prey (89.9%) of *S. maena* were also copepods (33.3%, mainly Calanidae, *Temora stylifera* and harpacticoids), together with chaetognaths (34.7%) and mysids (*Leptomysis gracilis*, 21.9%).

There was no clear-cut separation between prey samples of supra-, endo- and epibenthos-feeders. Among these, four fish species preyed on suprabenthic but also on some planktonic prey (euphausiids), so their diets were more diverse than those of plankton feeders. The predominant prey of *M. merluccius* (mainly small specimens examined) (84.6%) were gammaridean amphipods (*Ampelisca* spp., *Westwoodilla rectirostris*, 41.0%), mysids (*L. gracilis*, 14.1%), decapods (*Processa* sp., 11.5%), teleosts (*Deltentosteus quadrimaculatus*, 9.9%) and euphausiids (*Nyctiphanes couchi*, 8.1%). The flatfish *C. linguatula* preyed on the same groups but showing a different order: 86.3% its diet comprised mysids (*L. gracilis*, 48.0%), euphausiids (*N. couchi*, 22.2%), decapods (Crangonidae, 9.8%) and teleosts (*Lesuerigobius* sp., 6.3%). The diet of *P. acarne* (only analysed in winter) comprised predominantly (64.2%) teleosts (42.8%), and amphipods (*Ampelisca* spp., Phoxocephalidae, 21.4%). Prey composition in the single sample of the suprabenthos feeder *T. minutus* (only examined in winter) appeared most similar to those in *M. barbatus* (Fig. 2B). The predominant components of the diet of *T. minutus* (92.1%) were decapods (*Processa* sp., *Alpheus glaber*, 68.9%), brachyurans (*G. rhomboides*, 12.9%) and teleosts (*Lesuerigobius* sp., 10.3%).

Prey samples of *M. barbatus*, the only representative of endobenthos feeders, formed a tight cluster. This species had a diverse diet, comprising predominantly (82.5%) amphipods (*W. rectirostris*, *Ampelisca* spp., 26.8%), brachyurans (*G. rhomboides*, 25.5%), polychaetes (mainly Eunicida and Glyceridae, 15.8%) and decapods (*A. glaber*, 14.4%). The similarity between prey samples of *T. minutus* and *M. barbatus* was largely due to sharing *A. glaber* and *G. rhomboides*.

Prey samples of the three species feeding on epibenthos formed a relatively well-defined group except for one spring sample each of *P. erythrinus* and *S. canicula,* and the summer sample of *T. draco*. *Trachinus draco* had a more epibenthic diet, mainly based on non-swimming benthos. The predominant prey (81.2%) comprised fish (*Lesuerigobius* sp., 33.3%), brachyurans (crabs) (*Goneplax rhomboides*, *Macropipus* spp., 27.7%) together with mysids (*L. gracilis*, 11.0%) and decapods (*A. glaber*, 9.2%). The remaining two fish species in this group (*P. erythrinus* and *S. canicula*) included infauna, especially polychaetes, as an important part of their diets. The predominant diet (71.6%) of *P. erythinus* comprised polychaetes (Aphroditomorpha and Eunicida among the identified, 41.1%), brachyurans (*G. rhomboides* and Paguridae, 22.2%) and decapods (*A. glaber*, 8.3%). The predominant preys of the shark *S. canicula* (86.0%) were decapods (*A. glaber*, 32.3%), polychaetes (27.6%, Aphroditomorpha and Glyceridae), bivalves (17.9%) and teleosts (8.2%).

The availability of original data for diet composition of the seasonal samples of the 10 fish species studied provided an opportunity to test for association with the composition of component parasite communities. Only the assemblages of trophically

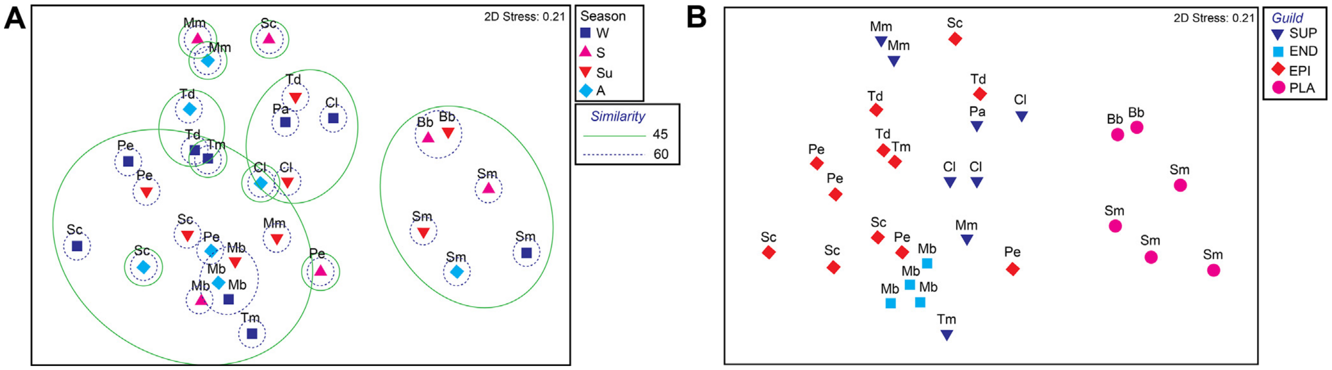

Fig. 2. Two-dimensional non-metric multi-dimensional scaling plots of the 30 host-prey samples. (A) Seasonal variation (note superimposed clusters resulting from group average clustering) at similarity levels of 45% (continuous line) and 60% (dashed line). (B) The configuration in A with an indication of host trophic guilds (sup, suprabenthos-feeder; end, endobenthos-feeder, epi, epibenthos-feeder; pla, plankton-feeder). Bb, *Boops boops*; Cl, *Citharus linguatula*; Mb, *Mullus barbatus*; Mm, *Merluccius merluccius*; Pa, *Pagellus acarne*; Pe, *Pagellus erythrinus*; Sc, *Scyliorhinus canicula*; Sm, *Spicara maena*; Td, *Trachinus draco*; Tm, *Trisopterus minutus*.

transmitted parasites (32 species) were considered in this analysis. However, the permutation test (RELATE routine in PRIMER) for correlation revealed a lack of agreement (Spearman's $\rho = 0.059$, $P = 0.191$) between the multivariate patterns of matching assemblage community similarity and diet compositional similarity matrices (both based on Bray–Curtis similarity).

3.3.2. Host autecological variables

The effect of fish traits known to affect, at least in part, infection parameters in fish was tested considering three autecological variables based on original data: trophic level, habitat depth vagility and density. Values of $\delta^{15}N$ for the 10 fish target species ranged from 5.78‰ for *B. boops* (summer sample) to 11.40‰ for *P. erythrinus* (spring sample) (Table 5). There was some seasonal variation in $\delta^{15}N$ levels with most species (50%) showing highest (more enriched) $\delta^{15}N$ in winter (end of February), coinciding with the peak of primary production (February–March) in the study area.

Values for trophic level ranged between 1.65 (*B. boops*, summer sample) and 3.76 (*P. erythrinus*, winter sample). Benthos feeders *P. erythrinus* and *M. barbatus* exhibited among the highest trophic level values whereas those in plankton feeders *B. boops* and *S. maena* were among the lowest. Two trophic levels (accepting a trophic enrichment of 3‰ per trophic level) can be identified in the fish assemblage analysed.

The habitat depth vagility index of the 10 hosts studied ranged between 0.2 (*T. minutus*) and 16.1 (*S. canicula*) (Table 1). Two other species exhibited very low vagility (*P. acarne* and *C. linguatula*) whereas *S. maena* showed the second highest vagility. The remaining species exhibited low (*M. barbatus* and *T. draco*) to intermediate vagility levels (*B. boops*, M. *merluccius* and P. *erythrinus*).

Fish density ranged widely between 0.11 (*S. canicula*) and 16.07 (*S. maena*) with only two species' samples (both collected in summer) exhibiting values close to the upper range, *M. merluccius* (15.47) and *M. barbatus* (11.9) (Table 1).

Overall, there was a significant negative correlation between fish habitat depth vagility and trophic level (Spearman's $\rho = -0.434$). Of the three autecological variables, only fish density was correlated with fish total length (Spearman's $\rho = -0.531$); this was largely influenced by the features of the only shark species characterised by maximum values for total length and minimum values for density. Parasite community richness (CCR Spearman's $\rho = 0.470$; ICR, Spearman's $\rho = 0.375$) and diversity (Spearman's $\rho = 0.380$) were moderately but significantly positively correlated with fish density whereas parasite abundance was negatively correlated with fish trophic level (Spearman's $\rho = -0.398$) (all $P < 0.05$).

The two-dimensional CCA plot relating parasite abundance in the component community samples and autecological variables (Fig. 3) explained 84.95% of the total variance. Variation along the first axis, associated with fish habitat depth vagility and, to a lesser extent, trophic level, revealed a clear separation of parasite communities in two species with high vagility (*S. canicula* and *S. maena*) from the remaining whereas the second axis influenced by fish density further differentiated communities in the summer samples of *S. maena* and *M. merluccius,* and all samples of *M. barbatus* for which high fish density levels were recorded. A similar pattern was observed when the only shark species was excluded from the analysis (data not shown).

3.4. Environmental variables

Environmental variables varied within narrow ranges, with minima for near-bottom temperature (13.6 °C) and oxygen concentration (4.88 mg/l) and maxima for salinity (38.22‰) and Chl *a* concentration (1.02 mg/m^3) in winter and a minimum salinity (38.03‰), associated with maxima in temperature (17.0 °C), turbidity (0.83 V) and oxygen concentration (7.67 mg/l) in autumn. Most of the environmental variables were correlated; of note, there were significant (all $P < 0.05$) negative correlations between salinity and temperature (Spearman's $\rho = -0.803$), oxygen concentration (Spearman's $\rho = -0.836$) and turbidity (Spearman's $\rho = -0.573$), and between oxygen concentration and Chl *a* concentration (Spearman's $\rho = -0.460$), reflecting concerted seasonal variation in the fish habitats studied. None of the parasite community metrics was correlated with environmental factors.

Fig. 4 provides a two-dimensional CCA plot relating parasite abundance in the component community samples and environmental variables and explaining a large proportion of the total variance (86.14%). All communities sampled in winter were strongly separated along the second axis influenced by four of the environmental variables, whereas turbidity contributed to the differentiation along the first axis of communities sampled in spring and summer (associated with minimum turbidity levels, 0.7 and 0.2 V, respectively) from those sampled in autumn (associated with maximum turbidity 0.83 V). However, there was a high variation in communities sampled in summer, forming two groups at the extremes (plus one extreme outlier, *C. linguatula*).

3.5. Variable importance

The relative importance (or influence, contribution) of the variables considered in the present study was assessed in three BRT

Table 5
$\delta^{15}N$ and trophic level (TrL) estimated for the seasonal samples of the 10 fish species examined.

Species/Season	Winter		Spring		Summer		Autumn	
	$\delta^{15}N$	TrL	$\delta^{15}N$	TrL	$\delta^{15}N$	TrL	$\delta^{15}N$	TrL
Scyliorhinus canicula		2.52[a]	7.11	2.11	9.57	2.91	8.79	2.94
Trisopterus minutus		3.76[b]						
Merluccius merluccius	9.77	3.17	9.47	2.90	9.71	2.96		3.07[a]
Pagellus acarne	10.40[c]	3.47[c]						
Pagellus erythrinus	11.00[c]	3.67[c]	11.40[c]	3.54[c]		3.59[a]	10.90[c]	3.64[c]
Boops boops			8.92	2.72	5.78	1.65	8.46	2.83
Spicara maena	7.03	2.26	8.78	2.67	7.95	2.37	9.25	3.09
Mullus barbatus	10.79	3.51	10.25	3.16	9.65	2.94	10.41	3.48
Trachinus draco	10.01	3.25	8.26	2.49	7.83	2.33	8.39	2.80
Citharus linguatula		3.10[a]			9.63	2.93	9.84	3.29
Sediment POM	3.25	1	4.3	1	3.37	1	2.59	1

[a] Calculated as the average of the autumn and spring values.

[b] Data from Stergiou and Karpouzi (2002).

[c] Recalculated from Fanelli et al. (2011) considering the present baseline on Particulate Organic Matter (POM).

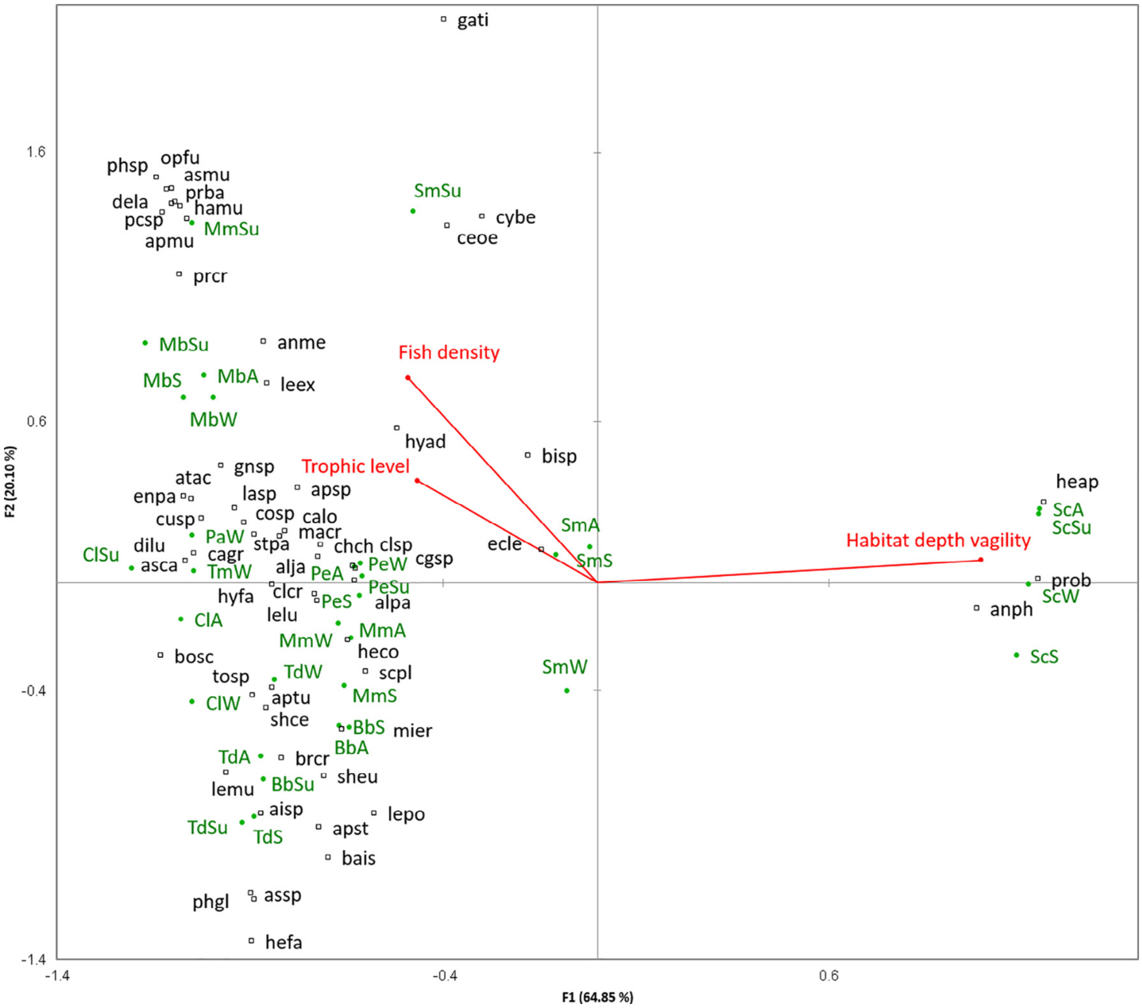

Fig. 3. Two-dimensional canonical correspondence analysis plot relating parasite abundance in the component community samples and host autecological variables. Seasons: W, winter; S, spring; Su, summer; A, autumn. Host names: Bb, *Boops boops*; Cl, *Citharus linguatula*; Mb, *Mullus barbatus*; Mm, *Merluccius merluccius*; Pa, *Pagellus acarne*; Pe, *Pagellus erythrinus*; Sc, *Scyliorhinus canicula*; Sm, *Spicara maena*; Td, *Trachinus draco*; Tm, *Trisopterus minutus*. Abbreviations for parasite names are provided in Table 2.

models (i.e. using order, family and host as predictor variables) developed for each of the four community parameters for richness, abundance and diversity. These helped identify variables with the most explanatory power (see the list of the top three predictor variables in the models in Table 6). Notably, the variables associated with fish phylogeny (order, family and host), were invariably depicted as most important in explaining the variation in community parameters. Fish total length, density, habitat depth vagility and trophic level were identified among the top two contributing variables. Of these, fish total length and density were important predictors of all parasite community metrics (Table 6). The variable season was ranked 5–7th in importance, followed by all environmental variables which contributed little to explaining the variation in the dataset.

4. Discussion

To the best of our knowledge, this is the first comparative study of possible determinants of the diversity, composition and structure of parasite communities in a marine fish assemblage from a geographically narrow region and the first to utilise simultaneously collected original data for host-related traits and environmental variables. This study also provides, to our knowledge, the first data for communities in *T. minutus*, *P. acarne* and *T. draco* and adds to the knowledge of the geographical variation in parasite communities in *P. erythrinus*, *S. maena* and *B. boops*. Overall, the abundant host-parasite data gathered indicate that the local parasite fauna (98 species) is comprehensively defined because the fish hosts studied represent a large portion of fish diversity and biomass collected in an exhaustive sampling.

Our analyses show that (i) the parasite fauna of the region is rich and dominated by digeneans; (ii) the host parasite faunas and communities exhibited wide variations in richness, abundance and similarity due to a strong phylogenetic component; (iii) the levels of host sharing were low and involved host generalists and larval parasites; (iv) the multivariate similarity pattern of prey samples showed significant associations with hosts and host trophic guilds; (v) prey compositional similarity was not associated with the similarity of trophically transmitted parasite assemblages; and (vi) phylogeny and fish autecological traits were best predictors of parasite community metrics in the host-parasite system studied.

Perhaps the most important result of our study based on taxonomically consistent identification of the parasites is the substantial phylogenetic component to the composition and structure of parasite faunas and communities in the host assemblage studied. Parasite communities exploiting a given host species are assem-

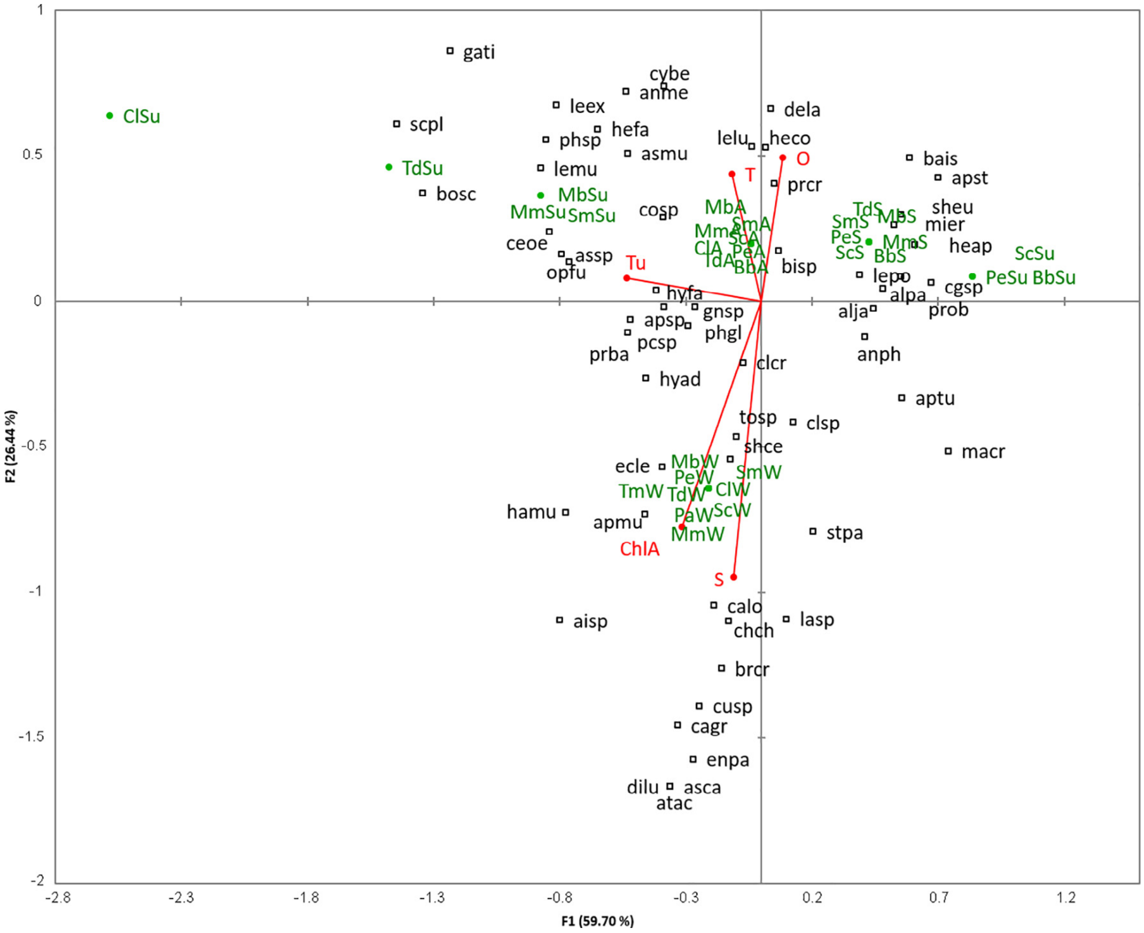

Fig. 4. Two-dimensional canonical correspondence analysis plot relating parasite abundance in the component community samples and environmental variables. Seasons: W, winter; S, spring; Su, summer; A, autumn. Host names: Bb, *Boops boops*; Cl, *Citharus linguatula*; Mb, *Mullus barbatus*; Mm, *Merluccius merluccius*; Pa, *Pagellus acarne*; Pe, *Pagellus erythrinus*; Sc, *Scyliorhinus canicula*; Sm, *Spicara maena*; Td, *Trachinus draco*; Tm, *Trisopterus minutus*. Environmental variables: Chl *a*, chlorophyll *a*; O, oxygen concentration; S, salinity; T, temperature; Tu, turbidity. Abbreviations for parasite names are provided in Table 2.

Table 6
Summary of the ranking of predictor variables for boosted regression tree (BRT) models developed in runs with three categorical variables associated with three levels of phylogenetic relationships of the fish hosts: "order" (O), "family" (F) and "host" (H) models.

Dependent variable	Top three predictor variables	Variable rank[a]
CCR	Order, family, host	100
	Density	66 (O); 51 (F); 55 (H)
	Depth habitat vagility	47 (O)
	Trophic level	50 (H)
	Total length	43 (F)
ICR	Order, family, host	100
	Density	76 (O); 46 (H)
	Total length	53 (F)
	Trophic level	51 (F); 46 (H)
Brillouin's diversity	Order, family, host	100
	Density	92 (O); 72 (H)
	Depth habitat vagility	65 (F and H)
	Total length	83 (O); 62 (F)
ICA	Order, family, host	100
	Total length	98 (O); 61 (F); 64 (H)
	Depth habitat vagility	98 (O)
	Density	60 (F); 63 (H)

CCR, component community richness; ICA, infracommunity abundance; ICR, infracommunity richness.

[a] The specific model is indicated in parentheses.

bled over evolutionary time and the importance of host specificity to shaping parasite communities has long been recognised (see Poulin et al., 2011 for a review). Our data collected within a well-defined, narrow geographical scale support the idea that, for the fish taxa concerned, host switches are not frequent enough to allow a substantial homogenisation of community composition.

In contrast to our initial expectations, we observed low levels of host sharing in the area of study and this was reflected in the very low levels of similarity of parasite communities between hosts. A total of 18 common species were found in more than three fish hosts. Most of these species are host generalists shared between sympatric species (see Pérez-del-Olmo et al., 2008; Benhamou et al., 2017) and most (10 species) are larval forms. In a study of host-parasite networks, Bellay et al. (2011) observed similar patterns using a much larger and phylogenetically broader dataset (170 parasite species in 39 species of marine fish representing 21 families of 10 orders) collected in coastal waters off the state of Rio de Janeiro, Brazil. These authors found that less than one-third of the parasite species in the regional fauna infect more than one host; of these only three occurred in more than 10 host species. This high degree of specialisation of the host-parasite interactions was reflected in a low degree of network connectance; our data indicate that this may be a typical feature of marine fish-parasite networks.

A hierarchy of generalist parasites related to host ordinal and familial taxonomic levels was identified with a single unrestricted generalist shared by all hosts (belonging to the four orders represented in the dataset), 10 wide generalist species shared by hosts of three (Gadiformes, Perciformes and Pleuronectiformes; five species) and two (Gadiformes and Perciformes, five species) orders, four perciform generalists and two sparid generalists. Additionally, host sharing in the system studied can be categorised into two categories: habitat-driven (seven species, the larval stages of *Gnathia* spp. and five digeneans which are linked to snail distributions in the benthic habitats) and diet-driven (the remaining species, all trophically transmitted except for the monogeneans *Lamellodiscus* spp. which may be affected by host density and vagility). However, it is possible that the levels of similarity between parasite faunas and communities in the hosts studied are even lower due to the relatively low level of taxonomic resolution for the dataset of shared species. Thus, eight taxa were not identified to the species level and may well represent different host-specific forms and five taxa represent species complexes (*Gnathia* spp. and *Lamellodiscus* spp.) or putative species complexes (*L. musculus*, *L. excisum* and *H. communis*) rather than single species with extremely low host specificity. For example, summary data for the Mediterranean include 30 hosts of 18 families for *L. musculus*, 14 hosts of eight families for *L. excisum* and 14 hosts of four families for *H. communis* (see Pérez-del-Olmo et al., 2016). Future molecular studies may reveal the real patterns of host specificity of these digeneans; currently, there is morphological evidence that *L. musculus* (sensu stricto) parasitises *T. draco* and *C. linguatula* in the present dataset (Carreras-Aubets et al., 2012).

There was a significant effect of host species on the abundance, prevalence and similarity of parasite faunas and communities. As shown in Fig. 1A, parasite communities formed heterospecific host clusters only at very low similarity levels (50%) even in the presence of the only chondichthyan species, *S. canicula*, which strongly affected the multivariate pattern. Removing the effect of shark parasite communities resulted in a clear host-related pattern of parasite composition and structure albeit at very low similarity levels for some host species (*B. boops*, *P. erythrinus* and *M. barbatus*) exhibiting greater seasonal variation (Fig. 1B).

Furthermore, the multivariate patterns of both faunal and component community dissimilarity were significantly associated with those of genetic divergence between fish hosts. The latter analysis is similar to approaches combining data on host phylogenetic relatedness and data on relative abundances, i.e. combining structural specificity and phylogenetic specificity sensu Poulin et al. (2011). Although the dataset is small, the availability of quantitative data from seasonal samples in a narrow region with well-sampled local parasite fauna offered the advantage of a pilot assessment of the two aspects of host specificity in marine fishes. Further parasite community data from the region will be essential for testing the hypothesis of a strong phylogenetic component to parasite community structure.

The apparent divergence of the parasite fauna and community structure and composition of the only chondichthyan species in the dataset, *S. canicula*, was not unexpected. An analysis including Neotropical representatives of 18 marine chondichthyan families revealed that parasite richness in this group is significantly lower compared with both marine and freshwater actinopterygians (Luque and Poulin, 2008); these authors treated the group in separate analyses based on the habitat and phylogenetic gaps between chondrichthyans and actinopterygians. The present data confirm this notion as the only shark species examined, *S. canicula*, differed substantially from the actinopterygian hosts studied with respect to total length, diet composition, density and habitat depth vagility (Table 1). This species had a poor parasite fauna (six species), characterised by the prominent lack of digeneans and with only two species (the generalist larval nematodes *A. physeteris* and *H. aduncum*) shared with other fish species in the dataset.

Both the diversified diet of *S. canicula* (see Valls et al., 2011) and its great vagility suggest high habitat overlap and, consequently, accessibility to different prey with distinct parasite loads, which would presumably enhance parasite richness, diversity and abundance (Campbell et al., 1980; Sasal et al., 1997; Marcogliese, 2002). However, and contrary to these expectations, parasite fauna of *S. canicula* exhibited the lowest richness; this translated into impoverished component and infracommunities (Table 4) with a composition and structure highly divergent from parasite communities in the actinopterygian hosts studied (Fig. 1A).

Elasmobranchs display a rather characteristic metazoan parasite fauna, dominated by platyhelminths and crustaceans, with cestodes (with *c.*1000 species reported and a diversity exceeding that of all other metazoan parasite groups together) and copepods being the most represented taxa within each of those two groups (Caira and Healy, 2004). The finding of a single cestode species is an apparent deviation from the expectations. However, impoverished parasite communities have been repeatedly reported for small-sized shark species and can be considered a typical feature for this group of fishes (Isbert et al., 2015). Parasite community richness in the present study of *S. canicula* varied within the known range for six small-sized shark species (CCR: 3–6 versus 4–10 species; ICR: 1.17–1.44 versus 0.6–2.5 species per individual fish) but infracommunity abundance exceeded many-fold the maximum of the known range (34.4–80.56 versus 1.2–9.5) (see estimates in Isbert et al., 2015) and was also significantly much greater than the abundance recorded in the actinopterygian hosts studied here. It is possible that selective feeding on specific highly infected prey species in the area has led to the abundant communities in *S. canicula* being strongly dominated by a single parasite species, the shark generalist nematode *Proleptus obtusus*.

The only representative of the order Pleuronectiformes, *C. linguatula*, was the second species in the dataset with species-poor fauna (eight species) and communities (4–7 species) dominated by the larval nematode *H. fabri*. This host exhibited low habitat depth vagility and some prey compositional overlap with *T. draco* and *P. acarne* (Fig. 2) but had a distinct community composition and structure (Fig. 1).

The parasite fauna and communities of the gadiform *T. minutus*, was also impoverished and markedly dominated by the nematodes *Ascarophis capelanus* (Cystidicolidae) and *Capillaria gracilis* (Capillariidae) (Supplementary Table S2) although, in contrast to *S. canicula*, community abundance was low. *Trisopterus minutus* was characterised by a very high trophic position, which is expected for a strict benthos-feeder (Papiol et al., 2013). Fishes with high trophic levels (i.e. high positions in the local food web) are exposed to a wider array of larval forms of different parasites through their diet than those with lower trophic levels, and thus tend to display higher parasite diversity (e.g. Luque and Poulin, 2008; Valtonen et al., 2010; Poulin and Leung, 2011; Baia et al., 2018). However, this is not the case for *T. minutus*, suggesting that other factors such as resource partitioning in terms of dietary preferences may have a stronger influence on the characteristics of the parasite community independently of host trophic level (Luque and Poulin, 2008). Indeed, the strictly benthic and specialised diet of *T. minutus*, essentially based on decapod crustaceans and a few teleost fishes, may play against the effects that its high trophic position may have in increasing parasite diversity. An alternative explanation may be the fact that the trophic level used here was estimated for populations in the Eastern Mediterranean (see Stergiou and Karpouzi, 2002) and that only one (collected in winter) sample of *T. minutus* was examined.

The presence of four hosts of the family Sparidae provided two striking examples depicting the complex interaction of host-related factors in structuring parasite communities that defines the pattern of high host specificity in the system studied. Two closely-related congeners (*P. acarne* and *P. erythrinus*) had a similar diet range and trophic position. However, in contrast to our expectations, their parasite faunas and communities exhibited sharp differences with respect to faunal richness (16 versus 29 species), component community richness (16 versus 13–26 species), infracommunity richness (4.50 versus a mean of 1.79) and abundance (23.58 versus a mean of 3.56), and a largely dissimilar parasite community composition with communities in *P. acarne* being more similar to communities in *S. maena* rather than those in *P. erythrinus* (Supplementary Table S3). The two species differed with respect to fish density (distinctly greater in *P. acarne*), vagility (much lower in *P. acarne*) and prey composition (Fig. 2). The suprabenthos-feeder *Pagellus acarne* was found to feed predominantly on teleosts, whose consumption has been associated with more diverse and abundant parasite faunas (Marcogliese, 2002; Dallarés et al., 2017a) whereas the epibenthos feeder *P. erythrinus* mainly preyed on infaunal invertebrates and decapods.

Two other sparid fishes, *B. boops* and *S. maena*, were the only plankton feeders in the dataset and exhibited the greatest similarity in prey composition, resulting in their differentiation from the remaining species (Fig. 2). Overall, the two species had similar diet ranges and trophic positions, but the latter was lower in summer and autumn samples of *B. boops*. The high vagility of *S. maena* may have contributed to the high richness of its parasite fauna (28 versus 19 species in *B. boops*) but community richness and abundance varied within similar ranges except for the very high levels detected in *S. maena* in summer (CCR: 27 versus 15 species; ICR: 4.15 versus 2.83; ICA: 17.38 versus 5.83; see Table 3). Notably, the maximum levels of fish density among all fish populations sampled were registered in the summer samples of *S. maena*. Again, in contrast to our expectations based on phylogenetic relatedness and trophic similarity of the two sparid hosts, their parasite communities were markedly differentiated with respect to composition and structure (Fig. 1). The hypothesis 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, would contribute to a homogenisation of their parasite community composition, and structure has recently been tested by Benhamou et al. (2017). There are some differences between the host-parasite systems studied here and off the coasts of Algeria examined by Benhamou et al. (2017). Thus, in spite of the similar total number of parasite species found in the two fish hosts (36 species off Algeria versus 38 species in the present study) and the equal richness of the fauna of *S. maena* (28 species), *B. boops* had a much impoverished fauna off Barcelona (Spain) (19 species versus 28 species off Algeria) and the number of shared species differed between the two locations: 20 species (56% of the total number of species found in the two hosts) off Algeria and 10 species (26%) off Barcelona. In spite of these differences reflecting regional variation in parasite distribution in the north-western and south-western Mediterranean, both studies depict a substantial differentiation in parasite community composition and structure, indicating a significant phylogenetic component in this sparid host-parasite system.

There was notable seasonal variation in the composition and structure of prey taxa in most hosts (except those in *B. boops* and *M. barbatus*, see Fig. 2A) resulting in very low mean similarity levels per host species. Importantly, the multivariate similarity pattern of prey samples showed significant associations with hosts and host trophic guilds but prey compositional similarity was not associated with the similarity of trophically transmitted parasite assemblages. Furthermore, in spite of the large number of parasites available in the local food web (61 species, including 34 digeneans and all nematodes, cestodes and acanthocephalans) the strength of the relationship between parasite community richness and host diet range was moderate and a significant variability was detected. Generally, large numbers of trophically transmitted parasites were found in fish samples in which a broad diet range was identified. It is worth noting that the four generalist parasites shared by 6–10 fish hosts (i.e. *L. excisum*, *Contracaecum* sp., *H. fabri* and *H. aduncum*) all use harpacticoid copepods as intermediate hosts; of these, at least two species utilise additional alternative routes of transmission, i.e. via ctenophores (*L. excisum* and *H. aduncum*) and all three larval nematodes use fishes as second intermediate or paratenic hosts in which the larvae accumulate in time. Additionally, the transmission of *H. aduncum* involves amphipods, mysids, isopods, decapods, chaetognaths and echinoderms (Marcogliese, 1996; Pérez-del-Olmo et al., 2008); this use of a diversity of alternative transmission routes and paratenic hosts makes it one of the most widespread parasites in the marine environment worldwide. Overall, the above considerations and the lack of association between the composition and structure of parasite communities and prey samples suggest that host specificity may have contributed to the pattern in which only broad generalist parasites with multiple transmission routes (i.e. a wide open encounter filter sensu Combes, 1995) can overcome the apparently narrow compatibility (specificity) filter in the system studied.

This study provides a range of novel data on the seasonal variation of trophic levels in the fish populations studied in the Western Mediterranean. The values estimated for *M. barbatus*, *P. erythrinus* and *B. boops* (except for the summer sample) varied within the known species ranges but those for the remaining species were below the lower limits of the known ranges (Stergiou and Karpouzi, 2002; FishBase, https://www.fishbase.se). Host trophic level and vagility were moderately but significantly correlated due to species populations with a high trophic position (*T. minutus*, *P. acarne* and *C. linguatula*) exhibiting very low vagility whereas the populations with very high vagility (*S. canicula* and *S. maena*) all had relatively low trophic level values. The opposing influence of these two host-related factors on parasite community composition and structure is depicted in Fig. 3 which also shows a gradient of communities associated with increasing fish density even within a species (e.g. communities in *M. merluccius* and *S. maena* sampled in summer versus those sampled in winter, spring and autumn).

Fish density appeared to affect both community composition and diversity since of the three autecological variables, only density was significantly associated with CCR, ICR and Brillouin's diversity. Epidemiological models predict that host population density is the key factor determining whether a parasite species can infect and persist in a host population (Roberts et al., 2002) and the importance of host density in maintaining parasite species richness has been highlighted in mammalian hosts (Morand and Poulin, 1998; Arneberg, 2002) and freshwater fish hosts (Takemoto et al., 2005). Aggregation of potential hosts is likely to facilitate transmission of parasites with direct life-cycles, leading to more abundant and diverse ectoparasite assemblages (Caro et al., 1997; Raibaut et al., 1998). Regarding endoparasites, Morand et al. (2000) highlighted that if host density is related to habitat productivity, increased host density then implies higher abundance of intermediate hosts on one hand, which enhances parasite transmission, and larger population sizes of definitive hosts on the other hand, which facilitate parasite reproduction. Therefore, hosts with denser populations will be able to sustain several parasite populations, leading to higher ectoparasite and endoparasite richness. The fact that density was also estimated based on original data linked to the community samples studied here, strengthens the importance of this finding.

Environmental variables varied in narrow ranges and most were correlated, thus reflecting concerted seasonal variation in fish habitats studied. Concordant seasonal patterns were detected in parasite communities of most fish hosts, notably resulting in low predictability of component communities in *P. erythrinus*, *B. boops* and *M. barbatus* (Fig. 1B). This may be partly explained by seasonal variations of local animal communities involved in the life-cycles of trophically transmitted parasites. Thus, the maxima for infracommunity abundance, richness and diversity recorded during the spring-summer period for *B. boops*, *M. barbatus*, *P. erythrinus*, *S. canicula* and *S. maena*, are in agreement with reports of the highest meiofaunal abundance at a depth of 60 m on the continental shelf off Barcelona during spring and summer, followed by a sharp decrease in autumn (Rumolo et al., 2015), and a sharp increase in macrofaunal biomass from winter to spring-summer (0.79 to 325–145 gww/m^2) (authors' unpublished data). It is worth noting that rivers flowing close to the sampling area (e.g. River Besós) contribute to seasonal inputs of terrestrial organic matter and show maximum discharge rates in spring, and a delay of 2 months between these peaks and increases in food consumption of benthic crustaceans has been suggested in nearby areas (Cartes et al., 2010; Papiol et al., 2013). Similarly, the increase in macrofauna and meiofauna in spring and summer on the Catalan slope follows the input of new production from the surface, which peaks in winter-spring (Mamouridis et al., 2011; Rumolo et al., 2015).

In summary, applying a broad comparative approach to parasite communities in a range of sympatric host populations, we identified that host specificity is a key determinant of community similarity. Indirect ordination methods were useful in portraying the complex association between community structure and host-related and environmental variables, but permutation-based tests including both coding host taxonomy and genetic divergence based on two mitochondrial genes provided strong evidence supporting this conclusion. Furthermore, the application of both GZM and BRT approaches in modelling the relationship between parasite community richness, diversity and abundance revealed a strong effect of host taxonomy. BRT models also allowed identification of the variables with the most explanatory power. Consistently, the variables indicating the phylogenetic relationships of the fish hosts were revealed to be most important in explaining the patterns of parasite diversity and abundance in the dataset, followed by the host-related factors total length, density, habitat depth vagility and trophic level whereas the environmental variables tested were found to be poor predictors. Ecological factors are also important in structuring fish parasite communities, but strong effects have been reported over broad geographical scales (see e.g. Luque and Poulin, 2008). The relative environmental stability in the small-scale area of study may provide an explanation for the overall poor explanatory power of the environmental variables considered here, in predicting parasite community richness, abundance and diversity.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2019.04.004.

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