Community structure of digenean parasites of sparid and labrid fishes of the Mediterranean sea: a new approach

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SUMMARY

The aim of this work was to study the structure of the parasite communities of Digeneans of 2 families of Teleost fishes (Sparidae and Labridae) of the Mediterranean sea. We tried to quantify the importance of both the microhabitat requirements of the parasite species and the effect of host biological factors on the parasite communities. We applied, for the first time in parasite community studies, the Canonical Correspondence Analysis (CCA) to analyse (i) the spatial distribution of parasite species within the digestive tract of the hosts; (ii) the host's biological factors (such as diet, host length, gregariousness and abundance) that may influence this spatial distribution of parasite species. Our results showed that potential microhabitats were vacant in the 2 host families studied revealing a lack of niche saturation because either there was little inter- and/or intraspecific competition or there were enough available space and resources within the host. Our results also indicated that the position of the parasite in the digestive tract is much more important than host biological factors for the structure of parasite community. Finally, we highlight the potential use of the CCA method for controlling for phylogenetic constraints in multi-species analyses.

Key words: Canonical Correspondence Analysis, parasite community, fish, specificity, digeneans.

INTRODUCTION

Macroparasite communities have usually been considered as unstructured, stochastic assemblages where potential niches are vacant (Kennedy, 1990, 1993; Rohde, Hayward & Heap, 1995). However, some other studies have revealed structuring processes that could indicate some inter- or intraspecific competition on a more restricted geographical scale (Chappell, 1969; Price & Clancy, 1983; Bates & Kennedy, 1990; Holmes, 1990; Holmes & Bartoli, 1993; Kennedy & Guégan, 1994). Species niches are influenced by many variables including the physical environment, the quality and abundance of food resources but also the competition with sympatric individuals for limiting resources (food and/or space) (May, 1981). Interspecific competition is one of the most invoked biotic mechanisms thought to be responsible for niche restriction (MacArthur, 1972; Holmes, 1973; Pianka, 1974). Moreover, intraspecific factors, such as increasing the chance of finding a mate (Rohde, 1979), are supposed to favour the restriction of the niche for the parasite. Niche limitation for parasites can be studied at 2 levels. First, in terms of host range reduction, i.e. host specificity. Second, in terms of microhabitat limitation, the niche (or microhabitat) specialization. Such spatial partitions are usually considered as essential factors controlling the species dynamics of communities (Tilman, 1994). However, only rare studies have attempted to quantify the factors influencing parasite community structure (Holmes & Price, 1986).

The analyses used in this study are based on Canonical Correspondence Analysis (CCA), a constrained multivariate analysis created by Ter Braak (1986). The first aim of such an analysis was to look, in a species–site table, for a structure that could be explained by the environmental variables of each site. Applications of this numerical method remain mostly limited to ecological studies even if it has been widened with different kinds of variables since its origin. The application of CCA to host–parasite studies is an extension of its use treating hosts as ecosystems for their parasite species (Holmes, 1987; Price, 1987). We found only 1 study using both CCA for a parasitological question, though the study has no ecological aim (Fraile, Escoufier & Raibaut, 1993). In our case, the species–site table corresponds

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to the parasite–host table for each individual fish dissected, at each site in the digestive tract. The explicative variables are the microhabitat used by the parasite within each host and some of the life-traits of the host. This method gives us the opportunity to analyse the structure of the parasite community and to quantify the importance of each factor tested. Finally, because biochemistry, body morphology and size of hosts are factors determining their colonization by parasites (Freeland, 1983), phylogenetically closely related host species are likely to harbour closely related parasite communities. Consequently, CCA is applied with a control for phylogenetic relationships among hosts that could induce some confounding effects (Harvey & Pagel, 1991; Morand, 1997).

Beside the descriptive role of this method in ecology of parasite communities, we intended to find if the spatial distribution of digenean species was caused by the physical environment of the parasite, by host biotic factors or by species interactions. Therefore, we proposed to test 3 hypotheses. (i) Conditions vary among the potential niches in the digestive tract and will prevent parasite species from occupying many different niches; thereafter we should find a very strong impact of the niche choice in community structure. (ii) Host biological factors, known to influence parasite species richness (e.g. Guégan & Morand, 1996; Poulin & Rohde, 1997; Sasal, Morand & Guégan, 1997) were considered, in regard to their possible alteration of interspecific relationships. For example, host size should influence parasite communities, as larger hosts offer more space for the parasite to install and larger fish are also supposed to eat more (i.e. ingest more intermediate hosts); host diet should be an important biotic factor as digeneans are transmitted via the intermediate hosts serving as prey items; host schooling behaviour and host abundance may also influence parasite community structure by favouring parasite transmission at a local scale. (iii) Parasite life-history may also play a role in structuring the community by influencing the selection of the microhabitat by the parasite species (Holmes, 1973).

MATERIALS AND METHODS

The data base

Geographical differences between the host species may induce bias in the study of the parasite community structure (Kennedy & Guégan, 1994). Therefore, all the fish used in this study were sampled in the same locality, off the Western coast of Corsica in the Mediterranean Sea. Moreover, in order to avoid seasonal variations of the parasites (MacKenzie & Gibson, 1970), fish were sampled during 1 summer month.

A total of 243 sparids representing 11 species and harbouring 23 digenean species and 224 labrids representing 7 species and harbouring 11 digenean species were studied separately in order to compare the results in the 2 host families.

For each parasite encountered in one host, we determined its position in the digestive tract, i.e. stomach, pyloric caeca, duodenum, anterior, medium or posterior part of the intestine, and rectum. The gall-bladder was omitted because of its very special position in the digestive tract and the specificity of parasite species found in it.

For each fish, the following variables were recorded: (a) body size, taken as the standard length (in cm); (b) schooling behaviour classified as isolated, small groups and large groups, according to Whitehead *et al*. (1986) and scoring respectively 0, 1 and 2; (c) diet behaviour classified as planktivorous, omnivorous and carnivorous, according to Whitehead *et al*. (1986) and scoring respectively 1, 2 and 3 (this variable is only taken into account for sparids as the labrid species studied all have the same diet); (d) abundance in the Mediterranean sea classified from rare to very common according to Whitehead *et al*. (1986) and scoring from 1 to 5.

Data analysis

The technique applied to date was the Canonical Correspondence Analysis (CCA, Ter Braak, 1986). People are invited to refer to the original paper for more details concerning the method. This method was developed in order to look for environmental influences (the explicative variables) on a distribution of species abundance (the explained variables). Each application of a CCA was submitted to a Monte Carlo permutation test of the sum of the canonical eigenvalues (100 permutations, $\alpha = 0{\cdot}05$).

In the following procedure, each site was a place in the digestive tract, in an individual and in a species of host. The first step was then to look for an influence of the position in the digestive tract on the distribution of the parasites. Therefore, we applied CCA with a disjunctive table of the digestive tract position as the explicative table. A second application of the CCA was carried out using the biotic factors characterizing the host individual as explicative variables.

For both analyses, a phylogenetic correction was applied by working on the residual effect of the position in the tract or of the host biological factors when the effect of the fish phylogeny (previously tested as significant) was removed. To remove this effect of the phylogeny, several methods have been proposed (see review by Miles & Dunham (1993) or Morand (1997)). In the absence of a robust phylogeny of fishes, we reduced the bias induced by multi-species analysis at 2 levels: first in restraining our study at the within-family level and second in using the disjunctive table of the genus as a covariable in the CCA analysis. The use of the

Table 1. Number of known hosts (inverse of host specificity), number of niches occupied (microhabitat specialization) and mean aggregation (±S.D.) of the 30 digenean species studied

Parasite species	Number of known hosts in the Mediterranean Sea	Number of occupied niches in the studied fish species	Mean aggregation $\mathcal{J}$ ± S.D.
Allopodocotyle jaffensis (ALJA)	4	3	−0·9 ± 0·2
A. pedicellata (ALPE)	3	2	3·9
Aphallus rubalo (APRU)	2	1	1·0
A. tubarium (APTU)	7	4	25·0
Cainocreadium labracis (CALA)	7	3	240·7
Diphtherostomum brusinae (DIBR)	20	2	25·1 ± 25·4
Gaevskajatrema perezi (GAPE)	5	4	17·8 ± 26·5
Genitocotyle mediterranea (GEME)	2	3	11·0
Helicometra fasciata (HEFA)	46	4	6·6 ± 12·2
Holorchis micracanthum (HOMI)	2	2	0·3 ± 1·8
H. pycnoporus (HOPY)	6	4	6·1 ± 4·7
Lecithaster stellatus (LECSL)	2	2	−0·1
Lepidauchen stenostoma (LEPIST)	6	1	0·3 ± 1·0
Lepocreadium album (LEPOAL)	6	3	1·1 ± 1·1
Macvicaria alacris (MAAL)	7	4	6·0 ± 7·6
M. crassigula (MACR)	7	5	2·3 ± 1·2
M. dubia (MADU)	1	3	−0·3 ± 1·1
M. maillardi (MAMA)	1	3	1·1
M. mormyri (MAMO)	1	2	−0·5
M. obovata (MAOB)	1	4	2·2
Metadena depressa (METDE)	1	4	5·4
Monorchis monorchis (MOMO)	12	4	16·0 ± 20·1
Pachycreadium carnosum (PACCA)	3	3	0·8 ± 2·0
Peracreadium characis (PECH)	1	1	6·8
Peracreadium genu (PEGE)	3	4	13·4 ± 4·6
Proctoeces maculatus (PRSMA)	23	3	0·3 ± 2·6
Pseudopycnadena fischthali (PSFI)	3	2	−0·6 ± 0·4
Pycnadenoides senegalensis (PYSE)	3	3	1·9 ± 3·2
Wardula sarguicola (WASA)	2	1	−0·3
Zoogonus rubellus (ZORU)	12	1	30·4 ± 29·6

genus, in order to correct for phylogenetic relationships between species has previously been done by Fisher & Chapman (1993).

The canonical factorial map spreads the parasite species according to their favourite position in the digestive tract (or to their lack of preference) or to the influence of the biotic factors. The position of the head of the arrow for the explicative variables (microhabitats or biotic factors) depends on the importance of the variable in the canonical factorial map represented.

For each parasite species, we calculated the intraspecific aggregation $\mathcal{J}$ (Ives, 1988), taking into account the 5 different potential microhabitats within a host (among microhabitats). Mean intraspecific aggregation was then calculated for each parasite species (among hosts).

RESULTS

Basic analysis of the epidemiological data

Considering only the known host species in the Mediterranean Sea, the 30 parasite species we studied can be divided into 4 main groups (Table 1). (1) Species with no strict host specificity and no strict niche specialization: *Allopodocotyle jaffensis*, *Aphallus tubarium*, *Cainocreadium labracis*, *Diphtherostomum brusinae*, *Gaevskajatrema perezi*, *Genitocotyle mediterranea*, *Helicometra fasciata*, *Holorchis micracanthum*, *H. pycnoporus*, *Lecithaster stellatus*, *Lepocreadium album*, *Macvicaria alacris*, *M. crassigula*, *Monorchis monorchis*, *Pachycreadium carnosum*, *Proctoeces maculatus*, *Pseudopycnadena fischthaldi* and *Pycnadenoides senegalensis*. (2) Species with no strict host specificity and a niche specialization: *Aphallus rubalo*, *Lepidauchen stenostoma*, *Wardula sarguicola* and *Zoogonus rubellus*. (3) Species with a host specificity and no strict niche specialization: *Allopodocotyle pedicellata*, *Macvicaria dubia*, *M. maillardi*, *M. mormyri*, *M. obovata* and *Metadena depressa*. (4) Species with a host specificity and a niche specialization: *Peracreadium characis*.

Epidemiological results are shown in Table 2 for sparids and in Table 3 for labrids. The first pattern in these tables is the absence of parasite species in potential host niches: stomach and anterior intestine for the sparid species and pyloric caeca, stomach and anterior intestine for the labrid species. Moreover, parasite species that were able to colonize a niche in some host species, were found in other niches in

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Table 2. Host biological factors (Greg., gregariousness; Abund., abundance; Mean L., mean standard length) and epidemiological data (abundance (Ab. ± S.D.), prevalence (P %) and microhabitat occupied (Microh.: a, pyloric caecum; b, duodenum; c, medium intestine; d, posterior intestine and e, rectum)) for each parasite species (abbreviations are the same as in Table 1) studied for each sparid species (DeDe, *Dentex dentex*; DiAn, *Diplodus annularis*; DiPu, *Diplodus puntazzo*; DiSa, *Diplodus sargus*; DiVu, *Diplodus vulgaris*; LiMo, *Lithognathus mormyrus*; ObMe, *Oblada melanura*; PaEr, *Pagellus erythrinus*; PaPa, *Pagrus pagrus*; SpaAu, *Sparus aurata*; SpoCa, *Spondyliosoma cantharus*)

Host	DeDe	DiAn	DiPu	DiSa	DiVu	LiMo	ObMe	PaEr	PaPa	SpaAu	SpoCa
N	9	50	8	39	26	34	5	32	19	13	7
Diet	3	2	1	3	3	3	1	3	3	3	1
Greg.	0	1	1	2	1	2	2	2	0	1	2
Abund.	3	4	3	4	3	3	4	4	2	4	4
Mean L.	39·6	11·5	20·9	21·7	19·1	22·3	21·5	21·1	22·3	46·5	19·9
ALJA											
Ab. ± S.D.	0·1 ± 0·3							0·1 ± 0·2	0·5 ± 0·8		
P %	11	—	—	—	—	—	—	6	37	—	—
Microh.	d							d	c, d, e		
ALPE											
Ab. ± S.D.										4·9 ± 3·7	
P %	—	—	—	—	—	—	—	—	—	85	—
Microh.										d, e	
APRU											
Ab. ± S.D.									0·2 ± 0·7		
P %	—	—	—	—	—	—	—	—	5	—	—
Microh.									d		
APTU											
Ab. ± S.D.	23·8 ± 22·5										
P %	100	—	—	—	—	—	—	—	—	—	—
Microh.	b, c, d, e										
CALA											
Ab. ± S.D.	95·3 ± 258·3										
P %	89	—	—	—	—	—	—	—	—	—	—
Microh.	a, b, c										
DIBR											
Ab. ± S.D.		2·1 ± 3·1		9·8 ± 18·8	14·9 ± 26·1	0·1 ± 0·4				9·4 ± 21·9	
P %	—	58	—	46	54	6	—	—	—	31	—
Microh.		e		e	e	e				d, e	
HOMI											
Ab. ± S.D.								0·2 ± 0·9	0·1 ± 0·2		
P %	—	—	—	—	—	—	—	6	5	—	—
Microh.								b, c	c		
HOPY											
Ab. ± S.D.				1·9 ± 4·9	2·2 ± 5·2	3·5 ± 4·3		1·9 ± 4·8	1·1 ± 2·7		
P %	—	—	—	33	27	76	—	44	37	—	—
Microh.				b, c, d, e	b, c, d, e	b, c, d, e		b, c, d	c, d, e		
LEPIST											
Ab. ± S.D.								0·1 ± 0·5			
P %	—	—	—	—	—	—	—	3	—	—	—
Microh.								c			
LEPOAL											
Ab. ± S.D.				0·1 ± 0·6	0·1 ± 0·6	0·1 ± 0·3	1·0 ± 2·2	0·3 ± 1·0			1·3 ± 2·0
P %	—	—	—	3	4	3	20	9	—	—	43
Microh.				b, c	a	a	a	a			a, b
MACR											
Ab. ± S.D.		1·1 ± 1·8		1·0 ± 2·5	1·9 ± 3·0			0·3 ± 1·3	1·2 ± 1·8		
P %	—	52	—	36	38	—	—	16	58	—	—
Microh.		b, c, d, e		a, b, c, d	a, b, c, d			b, c, d	b, c, d		

MADU											
Ab. ± S.D.							2·4 ± 2·1				0·4 ± 0·5
P %	—	—	—	—	—	—	80	—	—	—	43
Microh.							b, c, d				c, d
MAMA											
Ab. ± S.D.										2·2 ± 2·5	
P %	—	—	—	—	—	—	—	—	—	69	—
Microh.										b, c, d	
MAMO											
Ab. ± S.D.						0·6 ± 0·8					
P %	—	—	—	—	—	38	—	—	—	—	—
Microh.						b, c					
MAOB											
Ab. ± S.D.										4·2 ± 3·5	
P %	—	—	—	—	—	—	—	—	—	77	—
Microh.										b, c, d, e	
METDE											
Ab. ± S.D.	3·2 ± 6·7										
P %	33	—	—	—	—	—	—	—	—	—	—
Microh.	a, b, c, d										
MOMO											
Ab. ± S.D.		17·1 ± 25·9	0·3 ± 0·5		2·6 ± 9·0						0·1 ± 0·4
P %	—	78	25	—	19	—	—	—	—	—	14
Microh.		a, b, c, d	a		a, b						a
PACCA											
Ab. ± S.D.	0·2 ± 0·7							0·5 ± 0·7	1·1 ± 2·1		
P %	11	—	—	—	—	—	—	44	42	—	—
Microh.	b							b, c, d	b, c, d		
PECH											
Ab. ± S.D.			6·1 ± 6·6								
P %	—	—	88	—	—	—	—	—	—	—	—
Microh.			a, b, c								
PRSMA											
Ab. ± S.D.				0·4 ± 1·6	0·1 ± 0·2						
P %	—	—	—	13	4	—	—	—	—	—	—
Microh.				c, d, e	e						
PSFI											
Ab. ± S.D.		0·1 ± 0·6		0·1 ± 0·4	0·2 ± 0·4						
P %	—	4	—	8	15	—	—	—	—	—	—
Microh.		c, d		c, d	c, d						
PYSE											
Ab. ± S.D.					0·1 ± 0·2	0·2 ± 1·0				3·4 ± 5·9	
P %	—	—	—	—	4	6	—	—	—	38	—
Microh.					d	b, c				b, c, d	
WASA											
Ab. ± S.D.				0·2 ± 0·5							
P %	—	—	—	10	—	—	—	—	—	—	—
Microh.				e							
ZORU											
Ab. ± S.D.				4·7 ± 19·8	1·3 ± 5·0				0·2 ± 0·5	1·5 ± 5·0	
P %	—	—	—	23	12	—	—	—	11	15	—
Microh.				e	e				e	e	

Table 3. Host biological factors (Greg., gregariousness; Abund., abundance; Mean L., mean standard length) and epidemiological data (abundance (Ab. ± S.D.), prevalence (P%) and microhabitat occupied (Microh.: a, pyloric caecum; b, duodenum; c, medium intestine; d, posterior intestine and e, rectum)) for each parasite species (abbreviations are the same as in Table 1) studied for each labrid species (LaMe, *Labrus merula*; LaVi, *Labrus viridis*; SyCin, *Symphodus cynereus*; SyOce, *Symphodus ocellatus*; SyRoi, *Symphodus roissali*; SyRos, *Symphodus rostratus*; SyTin, *Symphodus tinca*)

Host	LaMe	LaVi	SyCin	SyOce	SyRoi	SyRos	SyTin
N	38	7	5	72	56	16	30
Greg.	1	0	0	0	0	0	2
Abund.	3	4	5	4	5	4	5
Max. L.	45	50	15	12	17	17	35
Mean L.	26·0	22·5	8·5	8·2	9·3	9·4	18·8
DIBR							
Ab. ± S.D.	0·1 ± 0·8						
P%	3						
Microh.	e						
GAPE							
Ab. ± S.D			0·2 ± 0·4		11·3 ± 22·0		
P%	—		20		88		
Microh			c		b, c, d, e		
GEME							
Ab. ± S.D.				2·7 ± 5·6			
P%				42			
Microh.				b, c, d			
HEFA							
Ab. ± S.D.	2·4 ± 3·5	7·0 ± 14·6		0·2 ± 0·7	0·1 ± 0·3	2·8 ± 3·4	0·9 ± 1·3
P%	61	71		8	12	81	47
Microh.	b, c, d, e	b, d, e		b, e	c, d, e	b, c, d, e	b, c, d, e
HOPY							
Ab. ± S.D.					0·3 ± 0·7		
P%					18		
Microh.					b, c, d, e		
LECSL							
Ab. ± S.D.				0·6 ± 0·9			
P%				38			
Microh.				d, e			
LEPIST							
Ab. ± S.D.	0·2 ± 0·6						
P%	11						
Microh.	b, c						
MAAL							
Ab. ± S.D.			1·2 ± 1·1	0·6 ± 1·3		2·9 ± 10·2	2·2 ± 4·1
P%			80	36		38	71
Microh.			b, c	b, c, d		b, c, d	b, c, d, e
PRSMA							
Ab. ± S.D.	0·1 ± 0·2						0·1 ± 0·3
P%	5						13
Microh.	e						e
PEGE							
Ab. ± S.D.	4·6 ± 9·6	7·4 ± 17·1					
P%	47	43					
Microh.	b, c, d, e	b, c, d, e					
ZORU							
Ab. ± S.D.	1·7 ± 8·3						3·8 ± 9·7
P%	8						64
Microh.	e						e

different host species. This occurred several times in our results but the most notable case was for *Lepocreadium album* (LepoAl) in sparids. This parasite species was encountered only in the pyloric caeca of 4 host species, *Diplodus vulgaris* (DiVu), *Lithognathus mormyrus* (LiMo), *Oblada melanura* (ObMe) and *Pagellus erythrinus* (PaEr) and in 2 different microhabitats (duodenum and mid-intestine) in *Diplodus sargus* (DiSa).

Importance of the microhabitat on the parasite community structure

The results of the CCA using the parasite micro-

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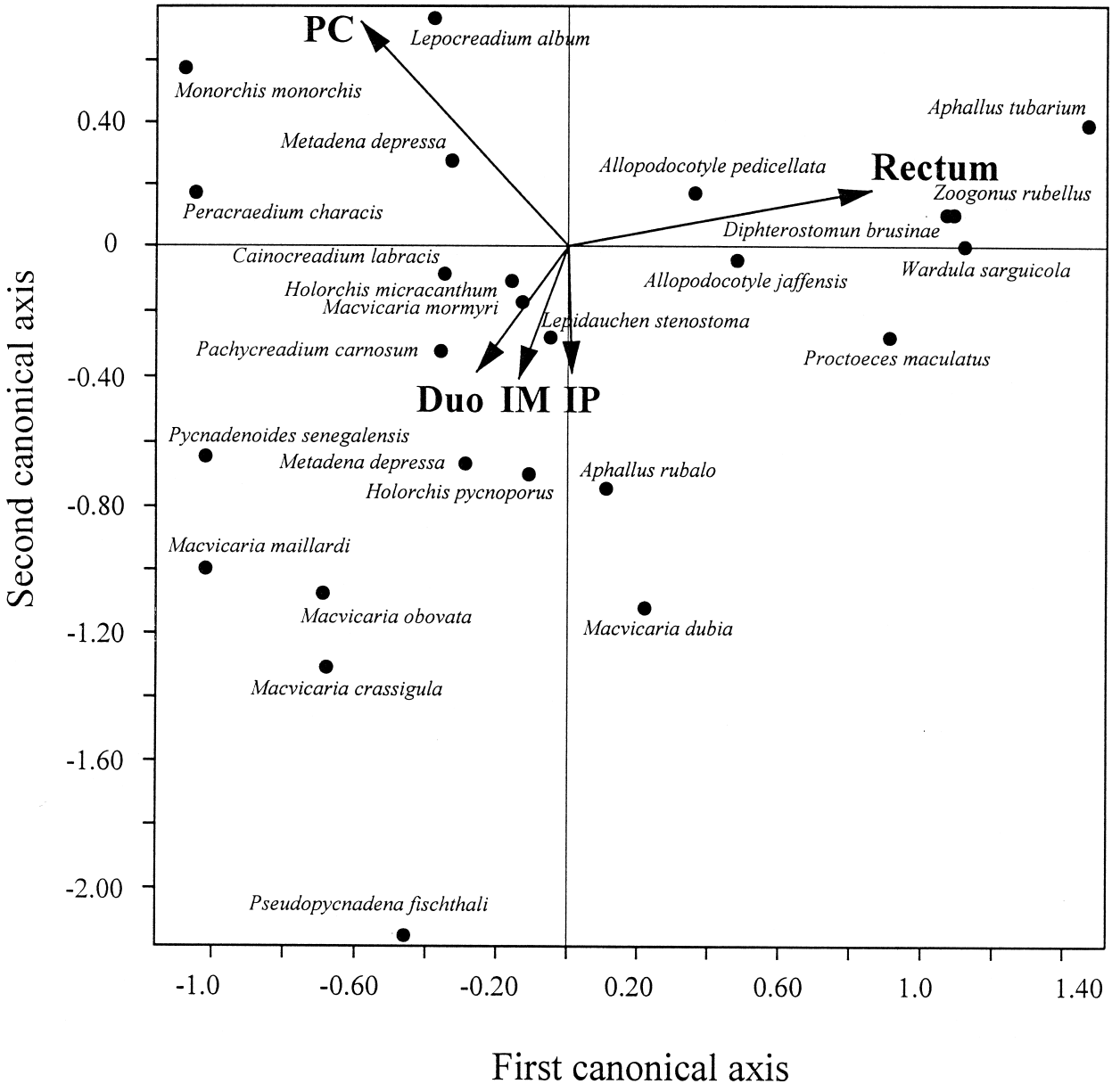

Fig. 1. Canonical factorial map representing the distribution of the digenean endoparasites of Sparids within the digestive tract, depending on their affinity with the microhabitats (PC, pyloric caeca; Duo, duodenum; IM, mid-intestine; IP, posterior intestine).

habitat as the explicative variable for the structure of the parasite community were significant ($P \leqslant 0{\cdot}01$) both for sparids and labrids. These results remain significant ($P \leqslant 0{\cdot}01$) when host genus was used as a covariable which previously tested as significant ($P \leqslant 0{\cdot}01$). Thereafter, in order to avoid repetition, data are only presented when host genus is used as a covariable (Figs 1 and 2). This application of the CCA is similar to a multivariable analysis of variance, as it tests the effect of the niche on the parasite community structure.

In the case of the parasite species of sparids, the canonical factorial map (Fig. 1) reflects 2 gradients in the position of the different microhabitats in the digestive tract: one from the duodenum to mid-intestine, posterior intestine and the rectum, and the other from the duodenum to the caeca (percentage of explained inertia = 7·57 %). The disposition of the arrows indicated that 2 microhabitats, the rectum and the caeca, were the best factors for structuring the parasite community. The duodenum, the mid-intestine and the posterior intestine were clustered in the same group of preference for the parasites. This pattern gave us 4 different groups of parasite species with different microhabitat specialization: (i) species without a strong niche specialization (*Allopodocotyle jaffensis*, *A. pedicellata*, *Cainocreadium labracis*, *Holorchis micracanthum*, *Lepidauchen stenostoma*, *Macvicaria mormyri* and *Metadena depressa*); (ii) species living preferentially in the duodenum and the intestine (*Aphallus rubalo*, *Holorchis pycnoporus*, *Macvicaria dubia*, *M. crassigula*, *M. maillardi*, *M.*

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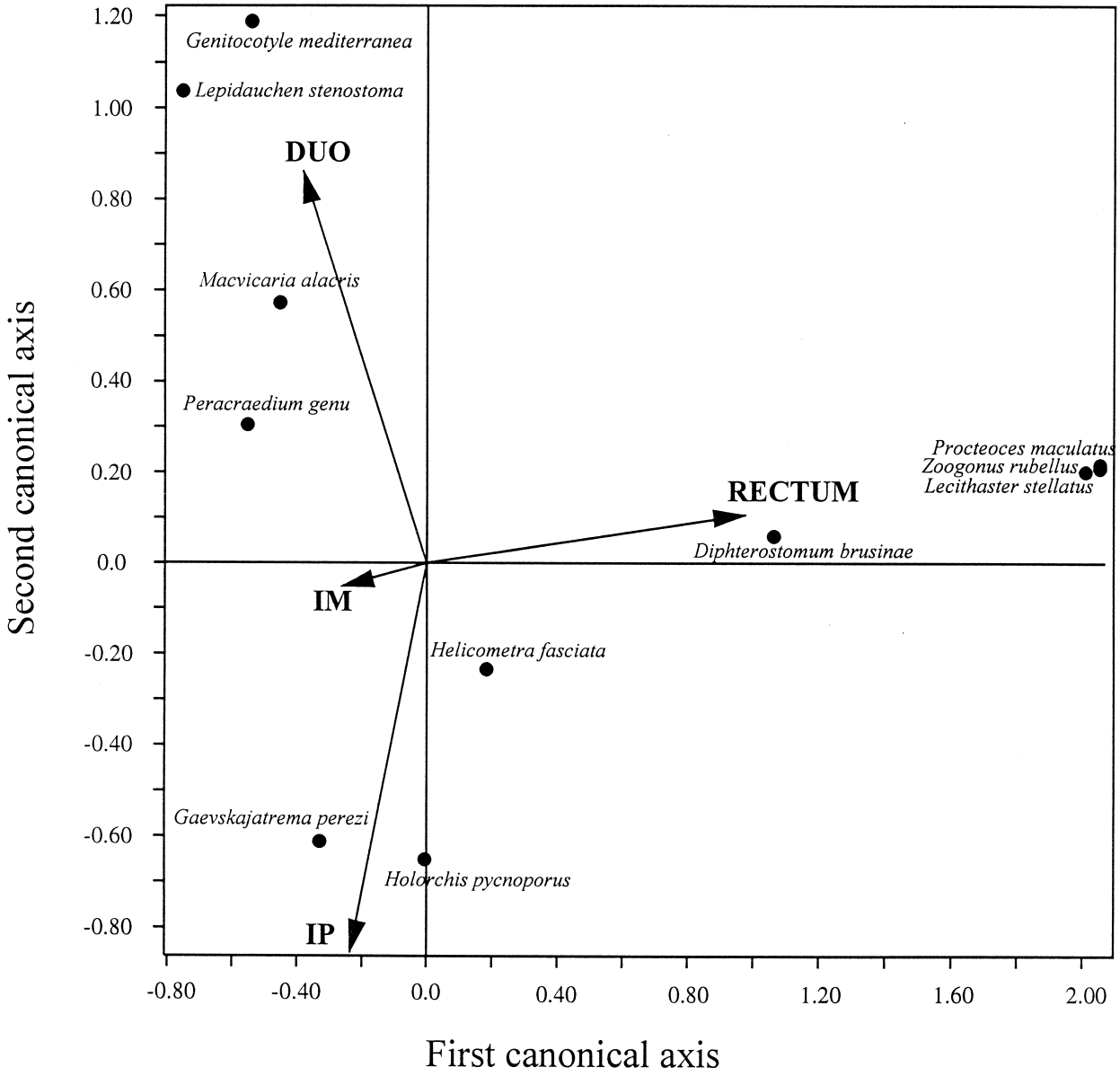

Fig. 2. Canonical factorial map representing the distribution of the digenean endoparasites of Labrids within the digestive tract, depending on their affinity with the microhabitats (DUO, duodenum; IM, mid-intestine; IP, posterior intestine).

obovata, *Pachycreadium carnosum*, *Pseudopycnadena fischthali* and *Pycnadenoides senegalensis*); (iii) species with a niche specialization in the pyloric caeca (*Lepocreadium album*, *Monorchis monorchis* and *Peracreadium characis*); (iv) species with a niche specialization, living more precisely in the rectum (*Aphallus tubarium*, *Diphtherostomum brusinae*, *Proctoeces maculatus*, *Wardula sarguicola* and *Zoogonus rubellus*).

When considering the parasite species of labrids, the specialization between duodenum, mid-intestine and posterior intestine seems stronger, each microhabitat being spread over each side of the factorial map (Fig. 2) determining 5 groups of parasite species (percentage of explained inertia = 12·02 %). One group of species has a marked preference for the duodenum (*Genitocotyle mediterranea* and *Lepidauchen stenostoma*). The second group with 2 species lives preferentially in the anterior part of the digestive tract (*Macvicaria alacris* and *Peracreadium genu*). The third group with 2 species (*Gaevskajatrema perezi* and *Holorchis pycnoporus*) uses preferentially the posterior part of the intestine as habitat. One group shows a significant propensity for the rectum (*Diphtherostomum brusinae*, *Lecithaster stellatus*, *Proctoeces maculatus* and *Zoogonus rubellus*). Finally, the last species, *Helicometra fasciata*, situated near the middle of the figure, shows an opportunistic behaviour in terms of microhabitat.

Importance of the host biological factors for parasite community structure

The CCA revealed that host biological factors, used as explicative factors influencing the parasite com-

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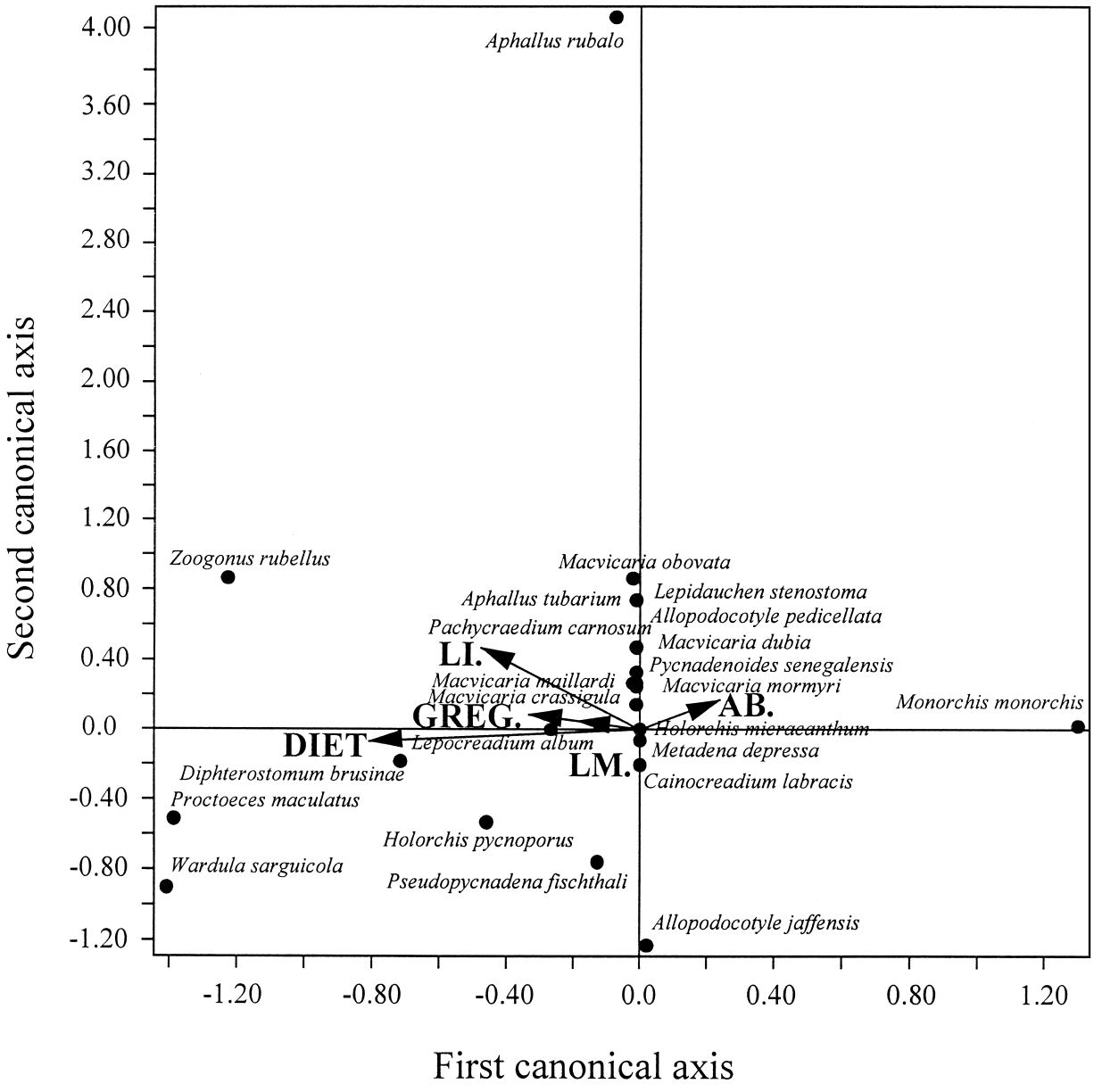

Fig. 3. Canonical factorial map representing the distribution of the digenean endoparasites of Sparids, depending on their affinity with host biological factors (AB, abundance; LI, individual standard length; LM, mean standard length; GREG, gregariousness).

munity structure, were significant ($P \leqslant 0{\cdot}01$) both for sparids and labrids. Moreover, these results remain significant when host genus was used as covariable ($P \leqslant 0{\cdot}01$). For the same reasons as in the previous section, data are only presented when host genus is used as a covariable (Figs 3 and 4).

In the parasite community of sparids the percentage of explained inertia was 4·87 % (Fig. 3). Diet and host abundance were the main factors affecting this structure. Moreover, these 2 factors influenced the parasite community structure in 2 opposite ways, i.e. species influenced positively by a high trophic position (diet) were negatively influenced by the host abundance. The other factors were less important in the structure of the community and influenced the community in the same direction as the diet. Finally, even if diet remains the most important structuring factor, only few species were influenced: *Diphtherostomum brusinae*, *Holorchis pycnoporus*, *Lepocreadium album*, *Monorchis monorchis* (in the opposite direction of the other species), *Proctoeces maculatus*, *Pseudopycnadena fischthali*, *Wardula sarguicola*, *Zoogonus rubellus*. Host length was the main factor influencing the other species. The position of *Aphallus rubalo* may be explained by its presence in this study on only the host species, *Pagrus pagrus*, which have

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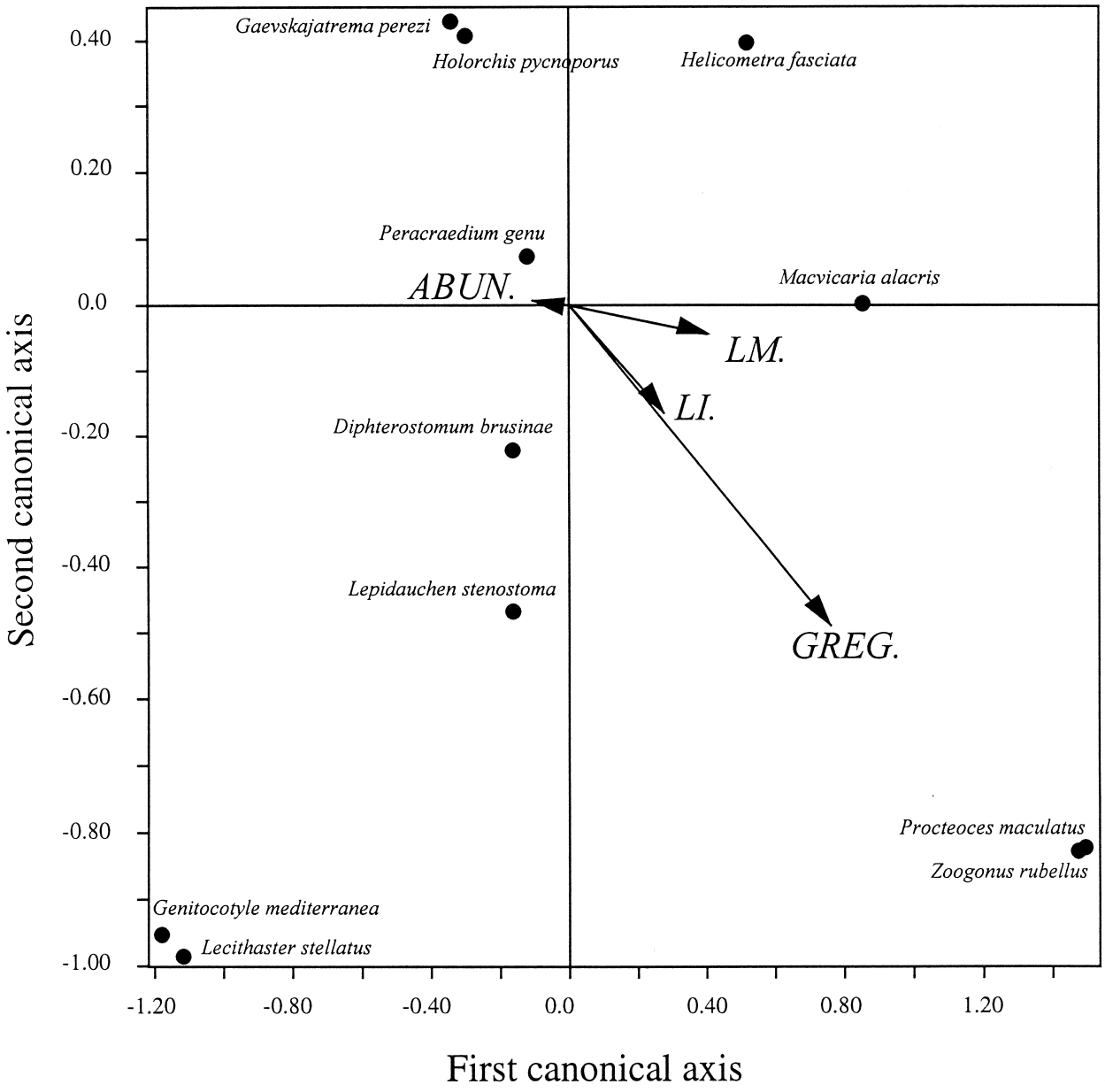

Fig. 4. Canonical factorial map representing the distribution of the digenean endoparasites of Labrids, depending on their affinity with host biological factors (AB, abundance; LI, individual standard length; LM, mean standard length; GREG, gregariousness).

particular biological factor scores (solitary and relatively rare species).

In the case of the parasites of labrids (Fig. 4), host biological factors have a much more important structuring effect than for the parasites of sparids (percentage of explained inertia = 12·40 %). In this analysis, diet was not taken into account as all the fish species studied had the same diet. Schooling behaviour of the host was the main factor influencing the parasite community structure. Gregariousness, maximal length and individual length performed positively on *Genitocotyle mediterranea*, *Lecithaster stellatus*, *Lepidauchen stenostoma*, *Proctoeces maculatus* and *Zoogonus rubellus* and negatively on *Gaevskajatrema perezi*, *Holorchis pycnoporus*, whereas host abundance exerted an opposite effect on the same species.

Parasite community structure and intraspecific aggregation in host

For each parasite species aggregation (γ) depended upon the host species infected. We found a positive significant relationship between the number of microhabitats used by the parasite and the aggregation within each host species (in log: $R = 0{\cdot}24$; $N = 81$; $P = 0{\cdot}03$). This relationship was no more significant when mean values of aggregation in the different parasitized host species were used (in log:

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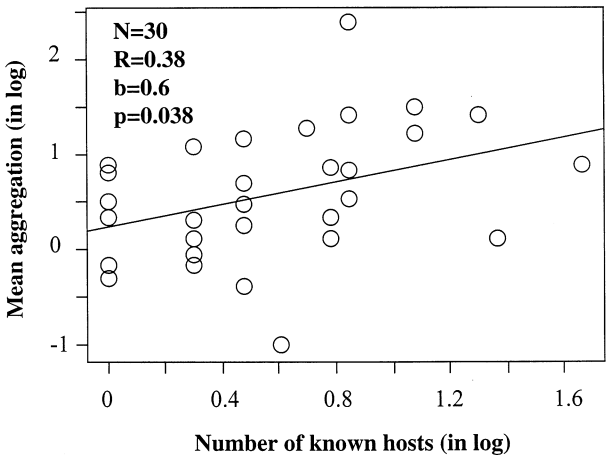

Fig. 5. Relationship between the number of known hosts in log (inverse of hosts specificity) and the mean aggregation within the parasitized host species.

$N = 30$; $P = 0{\cdot}26$). There was no significant relationship between the number of known hosts in the Mediterranean Sea and the parasite aggregation within each host species studied (in log: $N = 81$; $P = 0{\cdot}07$). However, this relationship was significant when mean values of aggregation were used (in log: $R = 0{\cdot}38$; $N = 30$; $P = 0{\cdot}04$) (Fig. 5).

DISCUSSION

Basic analysis of the epidemiological data

As has been shown for ectoparasites (Rohde *et al*. 1995), our results for endohelminths revealed that some potential niches for parasites were vacant (stomach and anterior intestine for the sparid species and pyloric caeca, stomach and anterior intestine for the labrid species). This result can be interpreted in 2 complementary ways. First, environmental conditions in those niches are so extreme that parasite species were not able to live there properly (this should be especially true for the stomach because of the mechanical grinding and the chemical conditions (Crompton, 1973)). Nonetheless, parasite species are commonly found in the stomach of fishes. Most of the species found in fish stomachs belong, however, to the families of Hemiuroidea, with a thick tegument (Yamaguti, 1971). The second interpretation is linked to a lack of niche saturation. This may reveal either little inter and/or intraspecific competition or enough available space and resources for all the parasites in the host species studied. The presence of parasite species in those vacant niches in other host species may be the result of a longer-term association between the host and the parasite and/or the consequence of greater competition (because of a richer parasite community or because of less available space). However, even if the present study did not give any answer to these questions, we may expect lower interspecific competition, in the absence of a niche saturation (Stock & Holmes, 1988). We used only the Digenean community in this study, but this may be also true if other groups of parasites inducing interspecific competition are considered (Colwell & Fuentes, 1975).

Importance of the microhabitat for parasite community structure

Our results showed that the microhabitat was an important factor in determining the structure of the parasite community. Pyloric caeca and rectum appeared to favour habitat specialization. We assume that because of their strategic position in the digestive tract, these environments show more stable and predictable conditions than those in the intestine or the duodenum which are supposed to fluctuate more (Crompton, 1973). Thereafter, more stable and predictable environments, with less disturbance and variation in time, will allow a narrow niche and promote high species specificity of parasite species (Sasal *et al*. 1999). In contrast, instability will favour the presence of more generalist species, which have, by definition, a broader tolerance and flexibility in their microhabitat requirements.

Niche specialization should not only reflect the selective pressure to which the parasite is or was subjected, but also the existence of a physical or chemical barrier due to the environmental conditions of each microhabitat. When considering sessile taxa, barriers are difficult to cross and the position of suitable habitat will determine the community structure at a larger scale (Ricklefs & Schluter, 1993). In the case of parasite species, unsuitable habitats may be crossed. This may explain 2 results of the analysis of community structure. First, it may be possible to find specialist parasite species in several microhabitats. This may be especially true for individuals found in the intestine being on their way to the rectum. The CCA is a quantitative method taking into account these 'uninstalled' individuals and the factorial map highlights the strong inclination of the parasite to its preferred microhabitat. The second result, a consequence of the first, is that it should be easier for parasite species to colonize new habitats while they are crossing them, even for niche specialist species. In the case of the pyloric caeca, the 'dead end' status of this organ may result in the presence of niche specialist parasite species in it. Finally, the structuring effect of the microhabitat within the host may also be explained by the large morphological variations of the teleost alimentary tract (Crompton, 1973).

Importance of host biological factors for parasite community structure

Our results show that host biological factors were not as important as niche specialization in parasite community structure. This result is especially true for parasite species of sparids as the percentage of

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explained variance (7·57 %) was higher than the one for biological factors (4·87 %). The diet of the host species was the main factor affecting the community structure. Digenean trematodes are transmitted to their final host through a predator–prey relationship between the final host and the intermediate host. It seems therefore quite normal that diet of the final host has an influential role in the parasite community. However, the role of the diet in parasite richness seems to be more evident, as hosts with a more diversified diet should encounter more intermediate hosts species and thereafter harbour more parasite species (Bell & Burt, 1991; Aho & Bush, 1993). The effect of the diet on the structure of the parasite community seems to be an indirect consequence of the species richness differences as interspecific competition for space should be more important in species rich communities.

In the case of parasite species of labrids, the sums of eigenvalues were very similar when we used microhabitats (12·02 %) or biological factors (12·40 %) as explicative variables. Three hypotheses may be proposed to explain this absence of difference between biological factors and microhabitats for Labrids: (i) because of the absence of parasite species in the pyloric caeca in Labrid species, this microhabitat has a strong effect on the community structure in the case of Sparids; (ii) the uniformity of the diet of Labrids which prevents this biological factor influencing the community structure and finally (iii) because of the stronger effect of host schooling behaviour on the community structure of Labrids.

Our work could be related to the work of Dobson & Roberts (1995) suggesting that interactions between parasites and their hosts were much more important in determining community structure than interactions between parasite species. This may be directly related to the absence of the niche saturation.

Parasite community structure and intraspecific aggregation in host

We found a significant relationship between the mean aggregation and the number of known hosts (inverse of host specificity) suggesting that when individuals of one parasite species are in more fragmented habitat (different host species), they will tend to be more aggregated. This has already been demonstrated in other groups of animals (Shorrocks & Rosewell, 1986; Jaenike & James, 1991). Moreover, there was a significant relationship between the number of niches used by a parasite species and the intraspecific aggregation of parasite species. This means parasite species found in a lower number of niches were the least aggregated. Interactions between individuals of the same species may lead to individual exclusion via intraspecific competition. For parasite species with a low microhabitat specialization (i.e. found in a large number of niches), resources will be more fragmented and they should be more prone to allopatric speciation than microhabitat generalist species, because of their more fragmented distribution (Futuyma & Moreno, 1988). Thereafter, to limit their niche fragmentation, specialist species may aggregate within their host species (if they are host specific) or increase their host range through a host capture (Bush & Kennedy, 1994). An increase of the host range or of the microhabitat may be a way to reduce inter- or intraspecific competition. However, because both the host specificity and the microhabitat specialization require special adaptation for the parasite, it has been supposed that specialization will be a consequence of a long-term association between host and parasite (Futuyma & Moreno, 1988). It is then commonly presumed that parasites with a strict host specificity have evolved from more generalist species (Ward, 1992). Our results did not provide any evidence for such a hypothesis and a comparison of phylogenetic trees and parasite host specificity or microhabitat specialization should be a way to test this hypothesis.

Finally, the most important application of the CCA in this study is the use of the phylogenetic information as a covariable. In our case, the absence of a really well-known phylogeny and the lack of a large divergence between the studied host species did not highlight the real importance of correcting for phylogenetic influences. The use of completed matrices of distances between species should increase the usefulness of this method in comparative analysis. Such an application should be possible in groups where phylogenetic relationships of both hosts and parasites are known. In such cases, it would be possible to determine if the parasite community structure is determined by the interactions with other species (in the past or in the present) or by the degree of niche specialization.

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