Endoparasite communities of five fish species (Labridae: Cheilininae) from Lizard Island: how important is the ecology and phylogeny of the hosts?

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SUMMARY

The parasite community of animals is generally influenced by host physiology, ecology, and phylogeny. Therefore, sympatric and phylogenetically related hosts with similar ecologies should have similar parasite communities. To test this hypothesis we surveyed the endoparasites of 5 closely related cheilinine fishes (Labridae) from the Great Barrier Reef. They were *Cheilinus chlorourus*, *C. trilobatus*, *C. fasciatus*, *Epibulus insidiator* and *Oxycheilinus diagramma*. We examined the relationship between parasitological variables (richness, abundance and diversity) and host characteristics (body weight, diet and phylogeny). The 5 fishes had 31 parasite species with 9–18 parasite species per fish species. Cestode larvae (mostly Tetraphyllidea) were the most abundant and prevalent parasites followed by nematodes and digeneans. Parasites, body size and diet of hosts differed between fish species. In general, body weight, diet and host phylogeny each explained some of the variation in richness and composition of parasites among the fishes. The 2 most closely related species, *Cheilinus chlorourus* and *C. trilobatus*, had broadly similar parasites but the other fish species differed significantly in all variables. However, there was no all-encompassing pattern. This may be because different lineages of parasites may react differently to ecological variables. We also argue that adult parasites may respond principally to host diet. In contrast, larval parasite composition may respond both to host diet and predator-prey interactions because this is the path by which many parasites complete their life-cycles. Finally, variation in parasite phylogeny and parasite life-cycles among hosts likely increase the complexity of the system making it difficult to find all-encompassing patterns between host characteristics and parasites, particularly when all the species in rich parasite communities are considered.

Key words: parasite communities, wrasses, Labridae, host body weight, host diet, host phylogeny, coral reefs, ecology.

INTRODUCTION

The composition of the community of parasites of animals is considered to be a product of their present-day ecology, their physiological traits, and the phylogenetic history of the hosts (Vickery and Poulin, 1998). For fishes, numerous studies have examined the role of host body size (mostly body length) as a predictor of infra- and component communities of parasites (e.g. Poulin and Rohde, 1997; Grutter and Poulin, 1998). Several other studies have examined the role of host diet (e.g. Muñoz, Valdebenito and George-Nascimento, 2002), habitat, locality (e.g. Grutter, 1994, 1998; Aldana *et al.* 2002), and host distribution (e.g. Kennedy and Bush, 1994; Cribb *et al.* 2002) in explaining the parasite community structure of fishes. Although many studies have mentioned the importance of host phylogeny, few studies have considered it in analyses of parasite communities (e.g. Poulin, 1995; Morand *et al.* 2000).

Host ecology and phylogeny can greatly influence parasite communities, but more importantly, they usually do so in different ways (see Morand *et al.* 2002). For example, Janovy, Clopton and Percival (1992) suggested that ecological variables should influence the overall parasite population structure (i.e. prevalence and abundance), whereas the evolution of host species, and thus phylogeny, should only affect the species of parasites.

Parasite communities are often complex because several hosts may be involved in the parasite's life-cycle, the transmission rates between hosts can vary, and because host specificity varies among parasites. Parasite communities can be described quantitatively using a wide range of so-called descriptors including the abundance, intensity, richness, prevalence, incidence, and diversity of parasites. All of these provide different information about the structure of the parasite community (Bush *et al.* 1997). Many parasitological studies that have used different databases, however, have found varied patterns in

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the relationships between descriptors and ecological variables of hosts, especially when phylogeny is included or not (e.g. Poulin, 1995; Poulin and Rohde, 1997; Sasal, Niquil and Bartoli, 1999; Morand *et al.* 2000). Studies of parasite communities involving many species of hosts, for example, have generally used only the presence/absence of a parasite (e.g. Bush, Aho and Kennedy, 1990; Poulin, 1995; Choudhury and Dick, 2000; Dove, 2000). Although this is a relatively simple way to analyse a large database, much useful numerical information is lost. By using other numerical descriptors, rather than only the presence/absence of a parasite species, a more complete view of the structure of a parasite community can be obtained.

Despite the increasing evidence that coral reef fishes support highly diverse parasite assemblages, few quantitative studies have been done on their parasite community structure. Coral reef fishes, however, are useful for examining the effects of ecology and phylogeny on parasite community structure as they are abundant and have closely phylogenetically related fishes found living sympatrically. Only one previous study has attempted to identify the relative importance of host phylogeny and ecology traits in coral reef fishes (Morand *et al.* 2000).

Labrid fishes are one of the most speciose and ecologically diverse groups of coral reef fishes (Randall, Allen and Steene, 1997) and are often found living sympatrically (Bellwood and Wainwright, 2001). They are therefore useful for examining the role of ecology and phylogeny on coral reef fish parasite communities. Few studies have been performed on ectoparasites of labrid fishes (Grutter, 1994, 1998) and only one based on the endoparasite communities of a labrid species from the GBR has been done (Muñoz and Cribb, 2005).

To determine whether sympatric and phylogenetically related coral reef fishes have similar parasite communities, we surveyed the endoparasites of 5 closely related fishes (Labridae: Cheilininae) from Lizard Island (Great Barrier Reef) and examined the relationship between parasitological descriptors (richness, abundance and diversity) and host characteristics (body weight, diet and phylogeny). We analysed and compared the endoparasite communities in 2 ways. This involved analysing the species composition and the numerical distribution of parasites per host individual. We also used univariate and multivariate statistical methods to develop a comprehensive understanding of the parasite community structure.

We used 3 congeneric labrid fishes from the subfamily Cheilininae: *Cheilinus chlororus* (Bloch, 1791), *C. trilobatus* Lacepède, 1801, and *C. fasciatus* (Bloch, 1791), and 2 other related species, *Oxycheilinus diagramma* Lacepède, 1801 and *Epibulus insidiator* (Pallas, 1770). These 5 fishes are each other's closest relatives available on Lizard Island (Randall *et al.* 1997; Westneat, 1993), except for *Cheilinus undulatus* which is considered endangered and excluded from scientific research. Although these fishes are closely related phylogenetically and are broadly sympatric in reef habitats (Bellwood and Wainwright, 2001), they have different diets. For example, *Cheilinus* spp. feed primarily on molluscs and crustaceans whereas *O. diagramma* and *E. insidiator* prey mainly on crustaceans and fishes (Westneat, 1995). Thus, we predict that the congeneric species (i.e. *Cheilinus* spp.) are more likely to be similar in their parasite communities than the other fishes of Cheilininae.

MATERIALS AND METHODS

Ninety-two specimens from 5 fish species from the subfamily Cheilininae: *Cheilinus chlorourus* $n=23$, *C. trilobatus* $n=18$, *C. fasciatus* $n=18$, *Oxycheilinus diagramma* $n=14$, *Epibulus insidiator* $n=19$ were collected from Lizard Island, Australia (14°40′S, 154°28′E). Fishes were sampled from August 2002 to May 2004, corresponding to 3 seasons (summer, autumn and late winter). As similar as possible sample sizes of fish species were caught in different seasons (3–8 individuals/species/season), to reduce possible bias on parasite community structure. When the influence of season and sex (separately) of fish on parasite communities has been considered in other studies, generally few species of the whole community have been affected in terms of numbers of parasites and this has not been strong enough to change significantly the community structure of parasites (e.g. Rodríguez and George-Nascimento, 1996; Fiorillo and Font, 1999; Hemmingsen, Halvorsen and MacKenzie, 2000). Furthermore, parasitological descriptors are typically correlated with the host body size rather than sex (see Bartoli *et al.* 2000). Therefore, season and the sex of fishes were not considered further as the sample for each was often relatively small.

Fish were caught by snorkellers using spear guns or with a barrier net and hand net by scuba divers. Most fish were kept alive in a 10 litre bucket with aeration until they were dissected. The fishes were weighed and body length was measured. The sex of each fish was determined by direct observation of the gonads; juveniles had undeveloped or immature gonads, males and females were identified in mature stages, and undetermined sex was when the gonads had both female and male characteristics (perhaps during sex reversal (De Loach, 1999)). The digestive tract, body cavity, gallbladder, muscles and flesh of the fishes were examined for endoparasites. Trematodes and most cestodes were heat-fixed in near boiling saline solution (0·85%) and preserved in 5% formalin for later identification.

Table 1. Mean (X) and standard deviation (S.D.) for body length, body weight and 3 infracommunity descriptors: richness, abundance and diversity of parasites for 5 fish species

(C. chlo, *C. chlorourus*; C. trilo, *C. trilobatus*; C. fasc, *C. fasciatus*, O. diag, *O. diagramma*, E. insi, *E. insidiator*.)

	C. chlo	C. trilo	C. fasc	E. insi	O. diag
	X (S.D.)	X (S.D.).	X (S.D.)	X (S.D.)	X (S.D).
Body length (cm)	19·5 (4·0)	20·9 (4·9)	22·9 (5·1)	19·9 (4·5)	18·9 (3·7)
Body weight (g)	148·6 (76·9)	208·5 (137·0)	306·3 (217·6)	211·3 (147·3)	116·4 (61·9)
Richness	5·4 (1·7)	6·1 (1·9)	2·3 (1·2)	1·0 (1·5)	7·3 (2·1)
Abundance	1467·4 (118·4)	174·5 (134·8)	32·6 (42·3)	4·68 (13·3)	755·1 (370·1)
Simpson's Diversity index	0·32 (0·14)	0·37 (0·15)	0·33 (0·25)	0·32 (0·43)	0·26 (0·18)

Trematodes and cestodes were stained in Mayer's haematoxylin and mounted in Canada balsam, whereas nematodes were cleared with chlorolactophenol. All these specimens were examined by light microscopy. Larval stages of tetraphyllidean cestodes were identified only as morphotypes according to Chambers, Cribb and Jones (2000); however, for convenience, each type is referred to as a species. Trypanorhynch cestodes were identified using Campbell and Beveridge (1994); acanthocephalans were identified using Pichelin and Cribb (2001); digeneans were identified by consulting Bray and Cribb (1989) and Cribb, Bray and Barker (1994); nematodes were identified by consulting Chabaud (1975), Olsen (1952) and Cannon (1977). Richness, abundance and prevalence of parasites were calculated according to Bush *et al.* (1997). Simpson's diversity index was calculated as given by Magurran (1988).

The digestive tract of wrasses is composed of an undifferentiated tube (intestine) and rectum, so that dietary items were collected from the entire gut and then identified to family, where possible (hereafter prey categories), according to Wilson (1993) and Abbott and Dance (1998) for gastropods, Lamprell and Whitehead (1992) and Lamprell and Healy (1998) for bivalves, and Jones and Morgan (2002) for crustaceans. The frequency of occurrence for each prey category was expressed as a percentage of the total number of fish that had food items in the gut.

Statistical analysis to compare parasite communities

All statistical analyses were performed using STATISTICA software. Logarithm transformation was used for some variables to satisfy the assumptions of normality and homogeneity of variances (Zar, 1996). We used $\log_{10}(x+1)$ for species richness and abundance of parasites (per fish individual) and $\log_{10}(x)$ for fish body weight. To determine whether there were significant correlations between parasitological descriptors and host body weight, Pearson correlations were performed for each descriptor and fish species (Zar, 1996). The significant level was 0·05 for all statistical analyses.

Separate principal component analyses (PCA) were used to compare the abundance-parasite composition and diet composition among the fishes (for details of the PCA see Clarke and Warwick, 1994). For the analysis using parasites, the $\log_{10}$ (abundance + 1) was used, whereas for dietary categories the presence-absence of each was used. In the PCA, variance maximizing rotation (Clarke and Warwick, 1994) was the method used to obtain the ordination axes. Each PC axis represents the position of all variables in the new dimension space. When variables are in positions distant relative to other variables, then those variables contribute significantly to the variance of the PC axis (Clarke and Warwick, 1994). There may be one to several PC axes, but generally the first 2 axes were the most important in explaining the total variance of the data.

The relatedness of hosts based on parasite composition was made using cluster analysis. We used prevalence of parasite and frequency of occurrence of diet categories because these are more informative than only presence-absence data. This was performed for all parasite species and diet categories for host species. Cluster analyses were applied for parasites and diet separately. Euclidean distances for parasite composition and diet between host species were used, and Ward's methods were considered for the agglomerative procedure (Everitt, 1993). The relatedness of host species based on their parasites was compared with the phylogeny of the Cheilininae proposed by Westneat (1993).

The 3 host descriptors used in this study, body weight, diet and phylogeny of hosts, were categorized to use them as factors in ANOVAs. Body weight was classified into 3 groups according to significant differences obtained statistically (ANOVA and a post hoc analysis), diet was categorized into 3 groups according to the results of a cluster analysis, and phylogeny was categorized by genus into 3 groups, *Cheilinus*, *Epibulus* and *Oxycheilinus*. The latter assumed that congeneric species belong to one phylogenetic clade (categorized as one group) and that the other species belong each to different clades (each genus considered as a different group).

Table 2. Prevalence (P%) and abundance (ABU) with its standard deviation (s.d.) of each parasite species of 5 fish species of Cheilininae from Lizard Island (MS = maturity stage of parasites (l = larva, a = adult).)

		C. chlo		C. trilo		C. fasc		E. insi		O. diag	
Parasite species	MS	P%	ABU (s.d.)	P%	ABU (s.d.)	P%	ABU (s.d.)	P%	ABU (s.d.)	P%	ABU (s.d.)
CESTODA											
Tetraphyllidea type 1	l	73·9	5·4 (1·1)	66·7	2·8 (4·10)					100	45·4 (38·0)
Tetraphyllidea type 4	l	95·7	119·4 (98·7)	100	141·8 (121·0)	77·8	9·6 (16·6)	21·1	0·4 (0·9)	100	646·7 (351·0)
Tetraphyllidea type 6	l	87	7·4 (8·3)	72·2	5·6 (7·1)	5·6	0·1 (0·2)	15·8	2·9 (9·2)	92·9	13·2 (12·2)
Tetraphyllidea type 8	l	34·8	2·0 (4·6)	27·8	1·3 (2·2)	5·6	0·1 (0·2)	10·5	0·9 (2·7)	85·7	23·4 (47·6)
Tetraphyllidea type 10	l	47·8	1·8 (2·4)	61·1	1·1 (1·3)					85·7	5·1 (4·7)
Tetraphyllidea type 18	l	4·3	<0·1 (0·2)								
Tetraphyllidea type 19	l			5·6	0·1 (0·3)						
Tetraphyllidea type 21	l	4·3	<0·1 (0·2)								
Tetraphyllidea type 22	l	4·3	0·2 (0·8)	38·9	5·7 (12·8)			5·3	0·5 (1·9)		
Tetraphyllidea type 23	l									35·7	3·1 (5·9)
Tetraphyllidea type 26	l							5·3	0·1 (0·2)	50	7·3 (16·6)
Tetraphyllidea type 29	l	4·3	0·9 (0·4)								
Tetraphyllidea type 30	l	13	1·6 (4·9)	16·7	0·4 (1·0)					21·4	3·9 (11·3)
Pterobothrium sp.	l	13	0·3 (0·9)	50·04	1·1 (1·2)					64·3	5·4 (7·4)
Dollfusiella sp.	l					11·1	0·1 (0·3)				
TREMATODA											
Helicometra fasciata	a	73·9	2·8 (3·9)	50·0	3·1 (4·6)	22·2	0·3 (0·8)			28·6	0·7 (1·4)
Bivesicula sp.	a	13	1·3 (4·8)								
Proctoeces sp.	a	4·3	<0·1 (0·2)	11·1	0·2 (0·4)	5·6	0·1 (0·5)				
Macvicaria (2 spp.)	a					22·2	2·8 (3·5)				
Megacreadium sp.	a					5·6	0·1 (0·2)				
NEMATODA											
Spirocamallanus spp.*	a	21·7	0·6 (1·7)	11·1	0·2 (0·8)						
Camallanus sp.	l							5·3	0·1 (0·2)		
Hysterothylacium sp.	l	34·8	3·5 (6·5)	94·4	20·5 (30·2)	77·8	21·6 (36·3)	26·3	0·3 (0·5)	21·4	0·4 (1·1)
Pseudoterranova sp.	l							5·3	0·1 (0·2)		
Philometra sp.	a									28·6	0·3 (0·5)
Cucullanus sp.	l							5·3	0·1 (0·2)	7·1	0·1 (0·3)
Heliconema sp.										7·1	0·1 (0·3)
Ascaroidea gen sp	l	4·3	<0·1 (0·3)								
Spiruridae gen sp.	l	13	0·2 (0·6)	16·7	0·2 (0·6)						
ACANTHOCEPHALA											
Transvena annulospinosa	a					5·6	0·1 (0·5)				
Component community richness**			18		14		11		9		14

* Two morphotypes that may be 2 species. ** No. of parasite species in a host sample.

Table 3. Pearson correlations between abundance, richness and Simpson's index diversity of parasites in the infra- and component communities and the host body weight

(r = correlation coefficient, *P* = probability.)

	C. chorourus		*C. trilobatus*		*C. fasciatus**		*E. insidiator*†		*O. diagramma*		Component communities (*n* = 5)	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Abundance	0·58	0·003	0·71	0·001	0·43	0·082	0·36	0·307	−0·01	0·989	−0·71	0·188
Richness	0·55	0·007	0·47	0·046	0·23	0·375	0·55	0·101	0·63	0·015	−0·70	0·178
Diversity	0·01	0·97	−0·11	0·676	0·09	0·975	0·54	0·110	0·49	0·080	0·57	0·317

* 18 and † 10 individuals for calculation of diversity.

Multiple regressions with backward elimination procedures were applied to determine if each factor (body weight, diet and phylogeny of hosts) can be a predictor of parasite communities in a linear regression model. Species richness of parasites (as $\log_{10}(x+1)$) and PC ordination axes, as representative of parasite composition based on abundances, were used as dependent variables. The significance level was 0·01 for the multiple regression tests using the backward elimination procedure according to Bonferroni *P*-value corrections (García, 2004).

RESULTS

General description of hosts and parasites

Fish body lengths were similar between species although the body weight differed among fish species (Table 1). *Oxycheilinus diagramma* had the smallest body weight and *Cheilinus fasciatus* had the largest (Table 1). Even though we did not analyse the body weight of fish species relative to sex, because of the small sample size in some groups, there were relatively similar patterns among species; the smallest were juveniles, females tended to be smaller than males, and those of undetermined sex generally had a body length in between those of males and females.

All individuals of the 5 species, except for 1 *C. fasciatus*, were infected with parasites. We collected 17,939 parasite individuals belonging to 31 taxa. Tetraphyllidea types 4, 6 and 8, and *Hysterothylacium* sp. were found in all 5 fishes; Tetraphyllidea type 4 had the highest abundance and prevalence (Table 2). Most parasite species were larvae (cestodes and nematodes); only 9 were adults (Table 2). The adult parasite species had a low prevalence and abundance, except for *Helicometra fasciata* in *C. chlorourus* (Table 2).

Comparison of parasite species among host species

The 31 parasite species (or types) identified were distributed between the 5 host species in 4 conceptually distinct ways. Ten species were found in only a single infection in 1 host species (Tetraphyllidea: Types 18, 19, 21, 29; Trematoda: *Megacreadium* sp.; Nematoda: *Pseudoterranova* sp., *Camallanus* sp., *Heliconema* sp. Ascaroidea gen. sp.; Acanthocephala: *Transvena annulospinosa*). These are not considered informative because they were found in only 1 host species and thus give no indication of the similarity between host species and because they are so rare it is not possible to convincingly infer that they are host specific. Confirmation of this comes from the fact that *Transvena annulospinosa* is known to be common in some other species of labrids (e.g. *Anampses* spp.) (Pichelin and Cribb, 2001) and *Megacreadium* is almost certainly a stray as this genus has been reported previously only from tetraodontiforms (Hafeezullah, 1981). Four species were found more than once in a single host although with low abundances (Trypanorhyncha: *Dollfusiella* in *C. fasciatus*; *Bivesicula* sp. in *C. chlorourus* and *Macvicaria* spp. in *C. fasciatus*; *Philometra* sp. in *Oxycheilinus diagramma*). Eleven species occurred in at least 2, but not all 5 species (Table 2) and thus may be considered as relatively common species. Four species were found in all 5 fish species (Tetraphyllidea: Tetraphyllidea type 4, 6 and 8; Nematoda: *Hysterothylacium* sp.) and differ only if the abundances are considered.

Comparisons of parasitological descriptors

The component community richness of parasites (i.e. all species in the sample of a fish species) in the 5 fish species ranged from 9 to 18 endoparasite species (Table 2). *Oxycheilinus diagramma* had the highest mean infracommunity richness and abundance and *E. insidiator* and *C. fasciatus* had the lowest (Table 1). Simpson's Diversity indices of parasites had similar values between the 5 fish species (Table 1).

The relationships between parasitological descriptors of infracommunities and host body weight varied between fish species (Table 3). Abundance and richness of parasites increased with host body weight for only some host species, although the Simpson's Diversity index was not correlated to host

Table 4. Summary of the Principal Component Analysis for parasites and diet of 5 cheilinine fish species

(The first and second principal component axes are indicated by PC1 and PC2, respectively. Parasites and diet categories that contribute to the variance of the analysis are in bold. Eigenvalues, percentage of variance and accumulative variance are shown for each analysis (parasites and diet).)

	Parasites			Diet	
	PC1	PC2		PC1	PC2
Tetraphyllidea type 1	**0·903**	0·014	Echinodermata	0·181	−0·349
Tetraphyllidea type 4	**0·773**	0·454	Gastropoda	**0·732**	0·074
Tetraphyllidea type 6	**0·711**	0·193	Bivalvia	0·617	0·109
Tetraphyllidea type 8	**0·807**	−0·215	Polyplacophora	0·059	0·170
Tetraphyllidea type 10	**0·827**	0·136	Brachyura	0·176	−**0·763**
Tetraphyllidea type 22	−0·007	0·467	Anomura	−0·101	0·549
Tetraphyllidea type 30	0·410	−0·040	Isopoda	0·430	0·509
Helicometra fasciata	0·192	**0·625**	Ostracoda	−0·067	0·025
Spirocamallaunus spp.	0·092	0·280	Insecta	−0·047	0·206
Hysterothylacium spp.	−0·259	**0·681**	Porifera	0·288	0·437
Spirurida gen sp.	−0·010	0·455	Tunicata	0·130	0·066
Pterobothrium sp.	**0·706**	0·005	Polychaeta	−0·033	−0·158
			Fishes	−0·631	0·137
			Algae	−0·440	0·278
			Coral	0·459	0·015
Eigenvalue	4·035	1·669		2·09	1·67
% total variance	34·14	13·38		13·93	11·11
Accumulative variance	34·14	47·52		13·93	25·04

body weight (Table 1). No descriptor was correlated with body weight for *C. fasciatus* and *E. insidiator* (Table 3). In component communities of parasites, richness and abundance tended to decrease with host body weight, however, these correlations were not significant (Table 3).

There were 2 important axes of PCA based on abundances of 12 parasite species. The variation of the first axis was due to 6 cestode species (5 types of Tetraphyllidea and *Pterobothrium* sp.), whereas 2 parasite species (nematodes *Hysterothylacium* and the digenean *Helicometra fasciata*) were responsible for the variation in the second PC axis (Table 4). The cumulative variance explained by the variables used (i.e. parasite species) was 47% for both axes (Table 4, Fig. 1). In the first PC axis, tetraphyllideans as well as *Pterobothrium* sp. characterized *O. diagramma*, whereas the *Hysterothylacium* spp. and *Helicometra fasciata* characterized *Cheilinus* spp. (Fig. 1).

Dietary categories

Most fish specimens (89·1%) had food in their gut. Forty-seven distinct dietary items were identified; 31 Mollusca, 9 Crustacea, 2 Echinodermata and 5 other categories (Tunicata, Porifera, Cnidaria, Polychaeta, Pisces). The diet was organized in 15 categories in a high hierarchical taxonomy (order, class or phylum), because the diet was different at this level. Molluscs were frequent prey categories of the 3 species of *Cheilinus*. Decapod crustaceans (Brachyura and Anomura) were present in all 5 fish species, although Brachyura were more frequent in *C. chlorourus*, *C. trilobatus* and *E. insidiator* than in the other 2 fish species. *Cheilinus fasciatus* had a higher frequency of occurrence of molluscs and a lower frequency of crustaceans than its congeners (Table 5). Fish were only present in the diet of *E. insidiator* and *O. diagramma* (Table 5).

The fifteen diet categories were used in the PCA. Two axes were important in describing the diet although they explained a low percentage of the variance, with a 25% cumulative variance for both axes (Table 4). Only 2 diet categories were responsible for the variation in the two axes, Gastropoda on the first PC axis and Brachyura on the second axis (Table 4). Gastropoda were mostly in *Cheilinus* spp. and Brachyura were characteristic of *Cheilinus chlorourus* and *E. insidiator*. Because of the low variance found in the first and second axes, the representation of PC axes is not shown in a figure. Differences in diet between fish species can be observed in Table 5.

Cluster analysis of parasites and diet categories

In the cluster analysis based on the prevalence of all parasite species, 2 groups were distinguished: one composed of *C. chlorourus*, *C. trilobatus* and *O. diagramma* and other composed of *C. fasciatus* and *E. insidiator* (Fig. 2A).

The cluster analysis based on fish diet showed that 2 main groups can be distinguished: one composed

Table 5. Frequency of occurrence of 15 food categories found in 5 cheilinine fishes

(n = number of fish with food contents in the gut. Fish name abbreviations as in Table 1.)

	C. chlo $n = 23$	C. trilo $n = 18$	C. fasc $n = 18$	E. insi $n = 14$	O. diag $n = 9$
ECHINODERMATA	8·70	11·11	—	7·14	—
MOLLUSCA					
Bivalvia	69·57	55·56	77·78	—	—
Gastropoda	82·61	88·89	94·44	14·29	—
Polyplacophora	8·70	—	11·11	—	—
ARTHROPODA					
Brachyura	69·57	61·11	22·22	64·29	33·33
Anomura	39·13	50·00	38·89	35·71	44·44
Isopoda	4·35	11·11	5·56	—	—
Ostracoda	—	—	5·56	—	—
Insecta	—	—	5·56	—	—
TUNICATA	—	—	11·11	—	—
ANNELIDA					
Polychaeta	—	—	5·56	7·14	—
PISCES	—	—	—	21·43	44·44
ALGAE	—	—	—	7·14	—
CNIDARIA (corals)	8·70	27·78	5·56	—	—
PORIFERA (sponges)	—	—	5·56	—	—

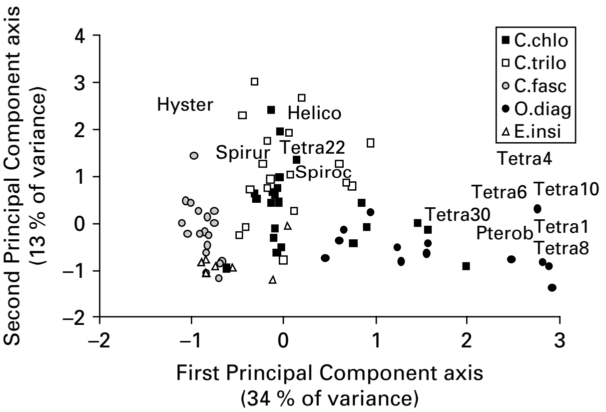

Fig. 1. Two-dimensional PCA ordination (first and second axes) of 12 endoparasite species from 5 cheilinine fish species. Abbreviations: host names as in Table 1, Hyste, *Hyterothylacium* sp.; Spiru, Spirurida; Helico, *Helicometra fasciata*; Spiro, *Spirocamallanus* spp.; Ptero, *Pterobothrium* sp.; Tetra, Tetraphyllidea. The numbers correspond to the type as in Table 2.

of *Cheilinus* spp., and the other by *E. insidiator* and *O. diagramma*. However, *Cheilinus fasciatus* preyed more frequently on molluscs and less frequently on crustacean than its congeners (Table 5, Fig. 2B). This difference is important since crustaceans are the main intermediate hosts for parasites. Therefore, *C. fasciatus* was considered as a distinct group in the next section (Table 6).

The dendrogram that represents groups of hosts based on parasites differed from the phylogeny of the hosts in the positions of *O. diagramma* and *C. fasciatus* (Fig. 2B, C). Thus, *O. diagramma* was closer to *C. chlorourus* and *C. trilobatus* in parasite composition because of the cestodes (Table 2), whereas *C. fasciatus* was placed in another group, close to *E. insidiator* (Fig. 2). In the diet of fishes, the categorization of fish group based on prey categories was associated with the host phylogeny as suggested in a previous study by Westneat (1995). This will be considered in analyses of the next section.

Effect of the host descriptors on parasite communities

Body weight, diet and phylogeny of hosts influenced parasite communities. Parasite richness, PC1 and PC2 showed significant differences when tested against each categorized variable (Table 6). It was not possible to implement the combined effect of variables because there were not appropriate numbers of combinations between variables.

Partial regression analysis showed that regression coefficients (b) were significant when considering each variable: body weight, diet and phylogeny. All variables together significantly contributed to parasite richness and parasite composition represented by PC1 and PC2 (Table 7A). In a multiple regression analysis, variables should not be correlated because it affects the interpretation of the results. In this study, phylogeny and diet of host were associated thus 2 multiple regression analyses were performed for: diet *vs* body weight and host phylogeny *vs* body weight. The partial regressions were significant for some variables. Diet was correlated with richness and composition of parasites (PC2) when phylogeny was removed from the

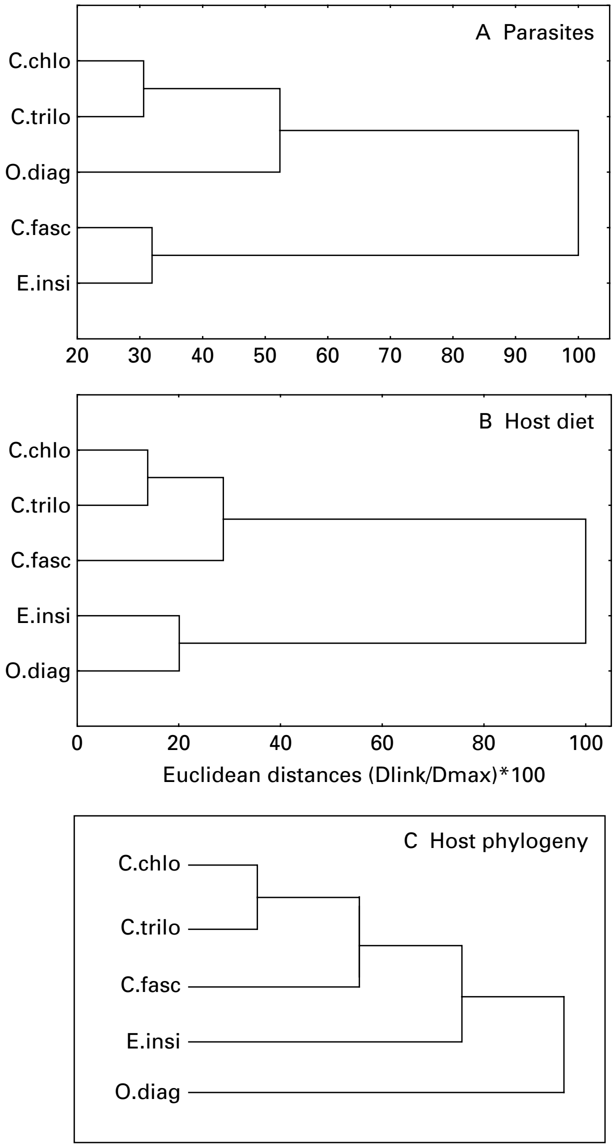

Fig. 2. (A) Cluster analysis based on the presence/absence of all parasite species, (B) cluster analysis for diet categories, and (C) phylogeny of 5 cheilinine fishes according to Westneat (1993) considering only the species here studied.

Table 6. Categorization of host descriptors and the results of the comparison between variable categorized through ANOVA

(Only probability (*P*) is shown.)

Fish spp.	Phylogeny	Diet	Body weight
C. chlo	1	1	1
C. trilo	1	1	1
C. fasc	1	2	3
E. insi	2	3	1
O. diag	3	3	2
Variable and ANOVA result	*P*	*P*	*P*
Richness	0·001	0·037	0·001
PC1	0·001	0·037	0·001
PC2	0·001	0·001	0·038

analysis (Table 7B), whereas phylogeny was important for PC1 and PC2 when diet was removed. Body weight was a significant variable in the composition of parasites when phylogeny was removed, however, body weight was not important for any variable when diet was removed (Table 7B).

DISCUSSION

The data presented here allow us to explore the interaction and potential importance of phylogenetic relatedness, host size, host diet, parasite richness, parasite life-cycle and parasite abundance. Host phylogeny is the principle 'yardstick' against which we compared the variation in our data. 'All things being equal', we would predict that the most phylogenetically closely related fish species would have the most similar parasite communities. Overall, we found no pattern that was completely consistent except that the two most closely phylogenetically related species (Westneat, 1993), *Cheilinus chlorourus* and *C. trilobatus*, had the most similar diets and body size, and had the most similar parasite communities. For a comprehensive analysis of the associations between the hosts and parasites of this study we analysed the data from 2 perspectives: that of the parasite species and that of the host species.

Perspectives from parasite species: transmission

As predicted on the basis of their phylogenetic relatedness and co-occurrence, the cheilinine species studied here had broadly similar endoparasites that were generally dominated by larval cestodes together with smaller numbers of trematodes and nematodes. While *Epibulus insidiator* had no adult parasites at all, *C. chlorourus*, *C. triolobatus* and *O. diagramma* each had more than 3 times as many larval species as adults and only *C. fasciatus* had equal numbers of adult and larval species.

The most lightly infected species overall was *Epibulus insidiator*. This species had by far the lowest helminth abundance, about 1/7th that of the next most lightly infected species. Because this species had the second highest weight it is clear that this factor is not responsible for this depauperate fauna. The general rarity of parasites may reflect the diet of this species. *Epibulus insidiator* has, uniquely for the Labridae, a remarkably protrusible mouth, indeed it is reported by Westneat (1991) as being proportionally the most protrusible mouth known for any fish species. This structure is presumably associated with feeding habits different from those of other cheilinines. The diet of this species was

Table 7. Multiple regression using backward elimination procedure for parasite richness and first and second axes of principal component analysis (PC1, PC2) for 5 cheilinine fish species considering 3 host variables, host body weight, host phylogeny and diet category. (A) Multiple regression analysis applied for 3 host characteristics; (B) analysis for pair of host characteristics

(*b* coeff., standardized regression coefficient; R^2, determinant regression coefficient for multiple regression model and P=probability.)

	Richness		PC1		PC2	
	b coeff.	*P*	*b* coeff.	*P*	*b* coeff.	*P*
(A) All variables						
Dietary category	−1·57	0·0001	−1·31	0·0001	−0·99	0·0001
Host phylogeny	1·36	0·0001	1·63	0·0001	0·401	0·0063
$\log_{10}$ body weight	0·28	0·0001	0·18	0·0001	0·274	0·0001
Regression results	R^2=0·66	0·0001	R^2=0·69	0·0001	R^2=0·50	0·001
(B) Pair of variables						
Dietary category (3)	−0·44	0·001	0·04	0·724	−0·66	0·0001
$\log_{10}$ body weight	N.S.	N.S.	−0·16	0·120	0·19	0·0016
Regression results	R^2=0·18	0·0001	R^2=0·01	0·275	R^2=0·46	0·001
Host phylogeny (3)	0·03	0·815	−0·47	0·0001	−0·48	0·0001
$\log_{10}$ body weight	−0·06	0·955	N.S.	N.S.	N.S.	N.S.
Regression results	R^2<0·01	0·973	R^2=0·22	0·0001	R^2=0·23	0·0001

No variables eliminated in procedure (A). One variable was eliminated in some cases (B) and they are indicated as N.S., meaning the partial regression was not significant. In these cases R^2 and probability are given for variables that are significant in the analysis.

composed of decapods and fishes, and was apparently similar to that of *O. diagramma*. Most likely, *E. insidiator* prey on specific prey items because of their particular mouth structure. However, probably because of the broad level of diet categorization that we used we did not observe this.

Apart from the 4 parasite species found in all 5 fish species, *C. trilobatus* shares only 2 species with any other cheilinine. These are *Helicometra fasciata* that is shared with *C. chlorourus*, *C. trilobatus* and *Oxycheilinus diagramma* and *Proctoeces* sp. that is shared with the other 2 species of *Cheilinus*. The sharing of *H. fasciata* by these 4 species serves to emphasize the distinction between the 4 other fishes and *Epibulus insidiator*. *Proctoeces* sp. uses molluscs as second intermediate hosts (Hua, 1989). This is strongly consistent with the dietary patterns that we found; only the 3 *Cheilinus* species eat bivalves and gastropods regularly. In contrast, *C. chlorourus*, *C. trilobatus* and *Oxycheilinus diagramma* share 3 larval cestode species, usually at high prevalences, to the exclusion of *C. fasciatus*. These parasites are all likely to be transmitted via crustaceans. All 3 fish species eat substantial numbers of crustaceans but it is notable that the frequencies for *C. fasciatus* are lower than those for *C. chlorourus* and *C. trilobatus*. In addition, *C. fasciatus* is evidently more of a generalist than the other species. We found 12 dietary categories for *C. fasciatus* as compared with just 8 and 7 for *C. chlorourus* and *C. trilobatus* respectively. Conceivably, this generalization in diet by *C. fasciatus* may result in a failure to eat the specific hosts of the 3 missing cestode larvae.

Perspective from host species: body weight, diet and phylogeny of hosts

A positive correlation between the richness and abundance of parasites and host body size is commonly found in studies of component communities (e.g. Poulin, 1995; Grutter and Poulin, 1998; Poulin, 1999; George-Nascimento *et al*. 2004). However, in this study, *Oxycheilinus diagramma* had the smallest body weight but harbored the highest load of parasites. This is in contrast to *C. fasciatus*, which was the largest fish, but had the fewest parasite individuals and species. Thus, the general tendency (although not significant) was that large hosts had lower richness and abundance of parasites than smaller hosts.

Most of the nematodes (Anderson, 1992), cestodes (e.g. Sakanari and Moser, 1989) and digeneans (e.g. Meenakshi, Madhavi and Swarnakumari, 1993) reported here use crustaceans or fishes as intermediate hosts, which are eaten by the labrid fishes. Therefore, the difference in parasites may be due to the differences in the crustacean and fish diet categories. Accordingly, *C. fasciatus* had the lowest frequency of occurrence of crustacean decapods and also harbored less richness and abundance of parasites than the other *Cheilinus* spp. However, the differences in parasites are not associated completely with differences in diets. For example, *E. insidiator* and *O. diagramma* had similar diets (mainly fish and crustacean decapods), but there was a great difference in the richness and abundance of endoparasites; and *E. insidiator* had few parasites whereas *O. diagramma* had many. Generally, no relationship between diet and parasites has been found in studies that have related diet with parasite infracommunities (Aldana *et al.* 2002; Muñoz *et al.* 2002). This is because it is difficult to obtain an association between parasites and the current diet as the current parasites would have been introduced to the host via prey eaten before the hosts were sampled (Aldana *et al.* 2002; Muñoz *et al.* 2002). Also, diet may vary with season, between years or during the host's ontogeny. Thus, studies that have considered several individual hosts with the diet categorized into broad groups have found a relationship between diet and parasites (Price and Clancy, 1983; Houston and Haedrich, 1986; Morand *et al.* 2000). Indeed, in this study parasite richness and composition (represented by PC1 and PC2, Tables 4, 6) were only related with diet when the diet was separated into just 3 groups.

The relatedness of the hosts based on the composition of parasite community of each fish species differed from the relatedness based on host phylogeny. The greatest difference was that the parasite composition of *C. fasciatus* differed from its congeners. *Oxycheilinus diagramma*, which is the sister taxon to the remaining 4 species of Cheilininae (Westneat, 1993), had a parasite composition similar to those of *C. chlorourus* and *C. trilobatus*. The parasite community of *Epibulus insidiator* differed greatly from that of the other fishes.

We determined that body weight, diet and phylogeny contributed significantly to the differences of parasite communities of the cheilinine fishes. Diet was correlated with host phylogeny, however, when one of these variables was removed from the multiple regression analysis, diet and phylogeny of hosts affected parasite communities differently (richness and composition) and also influenced the importance of host body weight. This may indicate that there are combined effects of the 3 host descriptors on parasite communities, but we were unable to test this because there were not enough combinations between the variables. Multicausality of variables on parasite communities can produce variable results. Consequently, the patterns and the processes that structure communities may become less detectable at the infracommunity level or for parasite communities from few host species (Poulin, 1997). Some 'small patterns' were detected at the component community level of parasites that at the infracommunity level (e.g. similarity of parasites in *C. chlorourus* and *C. trilobatus*), for these species we suggest only that host descriptors (body weight, diet and phylogeny) influence the structure of parasite communities. However, with only 5 fish species and 3 host characteristics, combined with the especially rich communities of parasites found in these fishes, determining an all-encompassing pattern for component parasite communities is almost impossible.

Lineages of parasites evolve in different ways depending on host distribution and the relationship of other species in the ecosystem (prey, competitors and predators) (e.g. Hoberg, 1997; Pulkkinen *et al.* 1999). Adult parasites, such as digeneans and some nematodes, seemed to be more associated with diet, as was observed in *Cheilinus* spp. However, larval parasite composition may depend on other processes linked to predators because such parasites need to be in a predator-prey system in which they can complete their life-cycles. This hypothesis may explain why some species, such as *E. insidiator* and *C. fasciatus*, were not characterized by cestode larvae. Many (perhaps all) of the types of cestodes found in this study mature in elasmobranchs (Khalil, Jones and Bray, 1994). Thus, if these species, *E. insidiator* and *C. fasciatus* are not eaten by elasmobranchs then one would not expect to find many cestodes in such fish, as these fishes would not be serving as intermediate host for these parasites. Even though our first conclusion was that the most consistent pattern was the high similarity of parasite community structure between *C. chlorourus* and *C. trilobatus*, the other 3 fish species showed conflicting results when all host characteristics were considered. This may be a consequence of different biological processes act in different parasite groups. Thus, the same variable may not affect different groups of parasites in a similar way.

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