

## STRUCTURE OF THE PARASITE COMMUNITIES OF A CORAL REEF FISH ASSEMBLAGE (LABRIDAE): TESTING ECOLOGICAL AND PHYLOGENETIC HOST FACTORS

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**ABSTRACT:** The role of ecological and phylogenetic processes is fundamental to understanding how parasite communities are structured. However, for coral reef fishes, such information is almost nonexistent. In this study, we analyzed the structure of the parasite communities based on composition, richness, abundance, and biovolume of ecto- and endoparasites of 14 wrasse species (Labridae) from Lizard Island, Great Barrier Reef, Australia. We determine whether the structure of the parasite communities from these fishes was related to ecological characteristics (body size, abundance, swimming ability, and diet) and/or the phylogenetic relatedness of the hosts. We examined 264 fishes from which almost 37,000 individual parasites and 98 parasite categories (types and species) were recorded. Gnathiid and cestode larvae were the most prevalent and abundant parasites in most fishes. Mean richness, abundance, and biovolume of ectoparasites per fish species were positively correlated with host body size only after controlling for the host phylogeny, whereas no such correlation was found for endoparasites with any host variable. Because most ectoparasites have direct transmission, one possible explanation for this pattern is that increased space (host body size) may increase the colonization and recruitment of ectoparasites. However, endoparasites generally have indirect transmission that can be affected by many other variables, such as number of prey infected and rate of parasite transmission.

The compositions of parasite communities (the species that comprise these communities) are generally similar when hosts are closely related phylogenetically. This is considered to be a consequence of shared inheritance (Paterson and Gray, 1997). Cospeciation events between host and parasites may produce congruent phylogenies, but events such as extinction of parasites and host switching may create incongruent phylogenies between the 2 groups of organisms (Paterson and Gray, 1997). Moreover, parasite communities usually differ in their numerical descriptors, i.e., richness or abundance, even if the hosts are closely related (e.g., Fontenot and Font, 1996; Lile, 1998) because host species diverge ecologically, for example in habitat, geographic distribution, diet, and body size. Ecological factors act as filters for parasites, and each factor can affect each parasite species differently, modifying their infracommunities and component communities (Holmes, 1987). Thus, the structure of parasite communities is the consequence of the phylogenetic and ecological processes that have affected each parasite and host species over evolutionary time (Hoberg and Adams, 2000).

How parasite communities can be affected by ecological characteristics or phylogenetic relatedness of hosts depends on the nature of the parasites, i.e., if they are ecto- or endoparasites, which differ biologically. Ectoparasites usually have direct life cycles, and their transmissions are often influenced by external factors (Rohde and Heap, 1998). In contrast, endoparasites generally have indirect life cycles (Roberts and Janovy, 2000), and transmission is not directly influenced by environmental factors. For example, temperature can strongly affect ectoparasite communities, but has less effect on endoparasites (Rohde and Heap, 1998). Endoparasites can be transmitted actively (larval recruitment) or passively (via ingestion) thus producing variable transmission dynamics. Consequently, the patterns of coevolution between hosts and parasites may differ for ecto- and endoparasites. Therefore, the relationship between

parasite richness and abundance and host characteristics has been different for ecto- and endoparasite communities (e.g., Rohde and Heap, 1998).

The main objective of this study is to evaluate the influence of host characteristics such as body size, diet, abundance, swimming behavior, and host phylogeny on the structure of ecto- and endoparasite communities of a fish assemblage (Labridae). This family of host was selected because many of the species live sympatrically and they vary greatly in body size (Randall et al., 1997), diet (Sano et al., 1984), abundance (Green, 1996; Fulton et al., 2001), and swimming behavior (Bellwood and Wainwright, 2001; Fulton et al., 2001; Fulton and Bellwood, 2002a, 2002b). These host characteristics have the potential to affect parasite communities in different ways. For example, large-bodied fish may have more resources and varied niches for parasites than small ones and so may support more parasite species and a higher parasite abundance and biovolume (e.g., Poulin, 1998a; Sasal et al., 1999). Diet can affect the composition of endoparasite communities because most endoparasites are transmitted through infected prey (see Price and Clancy, 1983; Morand et al., 2000). Wrasses that move along the water column may have fewer ectoparasites than those that are close to the substratum, because parasite larvae may have restricted mobility or distribution; no study has evaluated the effect of swimming behavior on the structure of parasite communities. A high density of hosts may increase the transmission rate of parasites (Morand et al., 2000), so that abundant wrasses may have more parasites than rare wrasses.

### MATERIALS AND METHODS

#### Host and parasite collections

Two hundred and ninety-five fishes were collected between August 2002 and May 2004 off Lizard Island, Great Barrier Reef, Australia (14°40'S, 145°28'E). Fish were caught using a spear gun while snorkeling or a net while diving. They were then individually placed into a plastic bag to minimize loss of ectoparasites during handling (Grutter, 1995). Thirty fish species were collected, representing 37% of the 81 wrasse species recorded in the area (Russell, 1983). However, several species were not abundant, so that the collecting effort was concentrated on 14 species (17.3% of the total wrasse species at Lizard Island). In total, 264 individuals and sample sizes of 14–32 were recovered for

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these species. Five fish species belonged to the Cheiliniinae and 9 to the Corinae (Table I).

Each fish was dissected to collect all metazoan parasites except metacercariae. This was because metacercariae are small and can be found in almost any tissue and require an impracticable amount of search time. Moreover, because metacercariae are immature, taxonomic identification is difficult. Ectoparasites were sought from the body surface, eyes, and gills, and endoparasites were sought from the gut, heart, spleen, liver, brain, gall bladder, body cavity, gonads, muscles, and flesh. All parasites were preserved in 5% buffered formalin for later identification.

Trematodes, acanthocephalans, and cestodes were stained in Mayer's hematoxylin and mounted in Canada balsam, whereas copepods, isopods, and 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 et al. (2000) and Muñoz and Cribb (2006). Gnathiids were also classified into 5 types according to pigmentation patterns (unpublished descriptions, type 1: small spots on thorax, abdomen, and in front or posterior parts of the head; type 2: small and large spots on the head and anterior portion of the thorax; type 3: large spots on the whole body; type 4; no pigmentation; type 5: tiny spots on the whole body). Monogeneans were identified following Hayward (1996) and Whittington et al. (2001); corallanid isopods were identified consulting Bruce (1982). Additional literature for the identification of the parasites is summarized in Muñoz and Cribb (2005, 2006) and Muñoz, Gutter, and Cribb (2006).

The infracommunity abundance and richness of parasites was considered for each fish individual (Bush et al., 1997). For each host species sample, the average of each descriptor (richness and abundance) was calculated (Bush et al., 1997). The component community richness was considered as all the parasite species from the sample of each fish species even though the collections of fishes were performed at different times (see concepts in Bush et al., 1997). The biovolume of parasites was also considered according to the suggestion given by George-Nascimento et al. (2002) that biovolume may be more informative than number of parasites because parasite body sizes differ greatly between species. Therefore, length and width of each parasite species, for each host species, was measured to estimate body size using a geometric formula according to parasite body shape (see Muñoz and Cribb, 2005). The biovolume of parasites was calculated by multiplying the mean abundance of each parasite species by its mean parasite body volume and this was expressed as mm<sup>3</sup> of parasites (George-Nascimento et al., 2002; Poulin et al., 2003).

A prediction of the parasite richness was calculated using the statistical program EstimateS (Colwell, 2004) based on the data for infracommunities of ecto- and endoparasites separately and together for each host species.

#### Host characteristics

Four host characteristics (variables) were considered to test their influence on parasite communities: body weight, diet, swimming ability, and abundance of hosts. Body weight and diet of hosts were recorded directly from the fish samples used in this study. The dietary items were collected from the entire gut and then identified to family when possible, following 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. The total number of food items (identified as family, genus, or species) found in each host species was used in the correlation analyses.

The relative abundances of labrid species were obtained from the study of Fulton et al. (2001) as the percentage of all fish individuals of all species counted in the survey. Swimming ability was defined as the capacity of fishes to move along the column water. Thus, swimming ability was considered as the average distance that a fish is known to rise from the substratum (Fulton et al., 2001; Fulton and Bellwood, 2002a).

Pearson correlations were used to correlate the parasitological descriptors, e.g., component community richness, average of infracommunity richness, abundance and biovolume of parasites per fish species, and host characteristics, e.g., body weight, relative abundance, swimming ability, and diet. These variables, parasitological descriptors and

host characteristics, were previously transformed to log<sub>10</sub>. The potential effect of host phylogeny was controlled for, in correlation analyses between variables, to remove the effect of the host relatedness. The phylogeny of the 14 fish species was constructed from the literature (Westneat, 1993; Bernardi et al., 2004; Westneat and Alfaro, 2005). Contrasts, which are the data controlled for host phylogeny, were computed for each parasite descriptor and host characteristic using the CAIC 2.0 software (Purvis and Rambaut, 1994). The contrasts of the component community richness, mean infracommunity richness, abundance, and biovolume were related to host characteristics using correlation following Garland et al. (1992). Bonferroni's *P*-value adjustments were applied (Aickin and Gensler, 1996) considering 4 parasitological descriptors performing 4 tests per descriptor (*P*/number of tests run), so that the significant level was 0.05/4 = *P* < 0.0125.

To determine if the 4 host variables (body weight, abundance, swimming ability, and diet) were correlated with one another, Pearson correlations were used for data with or without host phylogenetic correction.

#### Host relatedness based on ecto- and endoparasite composition

The relatedness of hosts based on their parasite composition was calculated using the methodology in Cribb et al. (2002). The data matrix consisted of the presence or absence of each parasite species for each host species. Because some parasite species were infrequent in the typical parasite communities of a fish species, we included only species with prevalences >10%. This, therefore, omitted potential "accidental parasites" (parasite species that are common in other host species, Roberts and Janovy, 2000). We analyzed the data using the heuristic search parsimony algorithm in PAUP\* (Swofford, 1998). The usefulness of the relatedness of hosts based on parasites is that the distributions of hosts (tree arrangement) can be associated with host phylogeny (if the relatedness is similar to the host phylogeny) or with some ecological host characteristics (if some branches of fish exhibit some particular ecological characteristic). Thus, we can infer if the host phylogeny or ecological variables are associated with the parasite species composition.

## RESULTS

### Ectoparasite communities

A total of 4,883 ectoparasite individuals were collected from the 264 fish examined. Parasites were mainly found on the body surface, fins, and gills. Twenty-seven parasite species including 5 isopod morphotypes (Gnathiidae) were identified (Appendix 1). The component community richness of ectoparasites varied from 1 to 17 species. Isopoda, mostly gnathiids, were the most frequent ectoparasites for all fishes (Table I), although Copepoda had a high number of species. Cheilinine fishes harbored more copepod species than did corine fishes (Table I). Average richness, abundance, and biovolume of ectoparasite infracommunities varied greatly between fish species (Figs. 1A, B, C). These descriptors were higher for cheilinine fishes and *Hemigymnus melapterus* than for the other fish species (Fig. 1).

### Endoparasite communities

We collected 32,405 individual parasites in the total sample. Most endoparasites were collected from the gut and body cavity, and a few individuals were from the gall bladder, gonads, and muscles. Seventy-one endoparasite species, including 25 tetraphyllidean morphotypes, were identified (Fig. 2, Appendix 1). The total abundance of endoparasites was more than 6 times higher than that of ectoparasites and the total richness was more than twice that of ectoparasites (see in Muñoz, Muoillot, and Poulin, 2006). Cestodes were the most common endoparasites in all wrasses (Table I, Appendix 1). The component community richness of endoparasites varied from 9 to 27 species (Table

TABLE I. Summary of parasite composition in 14 wrasse species. Number of parasite species per major taxonomic group, species richness (ectoparasites, endoparasites, and all parasites) and estimated richness of the all parasite species per fish species.

Fish species	Isopoda	Copepoda	Turbellaria	Mono-genea	Trematoda (ectoparasite site)	Trematoda (endoparasite site)	Cestoda (larvae)	Nematoda	Acanthocephala	Richness of ectoparasites	Richness of endoparasites	Richness of all parasites	Estimated richness Bootstrap	Estimated richness Jackknife 1
<b>Cheiliniinae</b>														
<i>Cheilinus fasciatus</i> (Bloch, 1791)	5	10	1	1	5	4	4	1	1	17	11	28	33	38
<i>Cheilinus trilobatus</i> La-cepède, 1801	5	6			2	9	9	3		11	14	25	26	27
<i>Cheilinus chlorourus</i> (Bloch, 1791)	3	5	1	1	3	11	11	4		9	18	27	30	35
<i>Epibulbus insidiator</i> Pal-las, 1770	5	5				5	5	4		10	9	19	13	13
<i>Oxycheilinus diagramma</i> (Lacepède, 1801)	4	5	1	1	1	9	9	4		11	14	25	27	28
<b>Corinae</b>														
<i>Hemigymnus melapterus</i> (Bloch, 1791)	3	2	2	2	1	20	20	4	1	7	26	33	38	45
<i>Gomphosus varius</i> La-cepède, 1801	2	1			1	15	15	3		4	22	26	30	34
<i>Thalassoma lunare</i> (Linnaeus, 1758)	2	1			6	15	15	5	1	3	27	30	38	44
<i>Thalassoma janssenii</i> (Bleeker, 1856)	1	1			8	12	12	4	1	3	25	28	33	38
<i>Thalassoma hardwicke</i> (Bennett, 1830)	2	1	1	1	7	10	10	4		5	21	26	31	36
<i>Coris batuensis</i> (Bleeker, 1856)	3	2		1	4	10	10	2		6	16	22	25	26
<i>Stethojulis bandanensis</i> (Bleeker, 1851)	1	1			3	11	11	1	1	2	16	18	20	24
<i>Stethojulis strijgiverter</i> (Bennett, 1932)	1				3	11	11	1	1	1	16	17	19	23
<i>Halicoreas melanurus</i> (Bleeker, 1851)	1				2	6	6	2		1	10	11	12	14

I). Tetrphyllidean types 1, 4, 6, 8, and 10 were abundant and frequent parasites in most wrasse species. Cheiliniinae and Coriinae differed in some digeneans, nematodes, and cestodes. *Helicometra fasciata* was in several host species, whereas other digeneans were more specific; for example, the 2 species of *Diplobulbus* and *Deretrema nahaense* were only in species of *Thalassoma* and *Gomphosus varius*; *Proctoeces* sp. were only in species of *Cheilinus*; whereas *Lecithaster* species were only in corine species (Appendix 1). The most abundant nematode, *Hysterothylacium* spp. 1, was found only in Cheiliniinae. *Heliconema* sp. and *Pseudoterranova* sp. were frequent in several corine fishes (Appendix 1).

The averages of parasitological descriptors varied greatly between fish species (Figs. 1A, B, C). *Epibulus insidiator*, *Halichoeres melanurus*, and *Cheilinus fasciatus* harbored the lowest richness and abundance of endoparasites, whereas *Oxycheilinus diagramma* showed the highest average abundance (Fig. 1B). The average biovolumes of endoparasites showed that the corine fishes, except for *H. melapterus*, had low and similar loads, whereas the cheilinine fishes except for *E. insidiator* had high biovolumes of endoparasites (Fig. 1C).

The estimated richness tended to exceed the observed richness significantly (Table I), especially in fishes with several infrequent species, e.g., *H. melapterus* and *Thalassoma* spp. Probably, different methods can be used for different data characteristics (see Poulin, 1998b; Walter and Morand, 1998). However, estimated richness using bootstrap and Jackknife 1 were significantly correlated with the observed richness for ecto- and endo-, and all parasites ( $r > 0.73$ ;  $P < 0.0001$  in all cases). Thus, in the following analyses we used the observed data, although either estimated or observed richness could have been used in this analysis.

### Relationship of host descriptors to parasite communities

Fish body weight varied greatly among species mainly in that cheilinine fishes were far larger than most of the corine fishes (Table II); only *H. melapterus* had a body weight comparable to that of the cheiliniines. *Cheilinus fasciatus* was the largest fish. *Halichoeres melanurus* was the smallest fish and was similar in size only to *Stethojulis* spp. (Table II). The component community richness of ectoparasites ( $n = 14$ ,  $r = 0.24$ ;  $P = 0.817$ ) and endoparasites ( $n = 14$ ,  $r = 0.07$ ;  $P = 0.877$ ) were not correlated with host sample size. Thus, corrections for host sample size were not necessary.

The average fish swimming ability measured as mean swimming distance from the substratum ranged between 10 and 70 cm from the substratum (information from Fulton et al., 2001). Relative abundance of fishes ranged from 0.2 to 19% in relation to 43 labrid species examined by Fulton et al. (2001) (Table II). The fish species examined had a varied carnivorous diet which frequently included crustaceans such as copepods, amphipods, tanaidaceans, ostracods, crabs, and shrimps; molluscs were present in all fish species. The number of food items varied greatly between fishes; *O. diagramma* was the least diverse with only 3 items and *Cheilinus trilobatus* was the most diverse with 37 (Table II). The 4 fish variables considered here (body weight, abundance, swimming ability, and diet) were correlated with one another (except for swimming ability [vs.] host body

weight,  $P = 0.21$ ). However, after controlling for host phylogeny, none of them was correlated (for all cases  $P > 0.14$ ).

The average values of infracommunity richness, abundance, and biovolume of ectoparasites increased with body weight of host species (Table III). In contrast, a negative correlation was found between component community richness and biovolume of ectoparasites and relative abundance of hosts. For endoparasites, only biovolume was significantly correlated with host body weight. Only the component community richness was significantly correlated with diet and swimming ability of hosts (Table III). After controlling for host phylogeny, host body weight was correlated with all of the parasitological descriptors (average of richness, abundance, and biovolume) for ectoparasites only (Table III).

### Host relatedness based on parasite composition

Twenty-three equal-length trees were obtained for host relatedness based on 24 ectoparasite species. The consensus tree is shown in Figure 3A. Cheilinine fishes tended to be closer than corine fishes, but most relationships were not resolved. There was also generally poor resolution for endoparasites. Six equal-length trees were obtained for the host relatedness based on 40 endoparasite species (Fig. 3B). Resolution was slightly better than for the ectoparasites. One branch contained all the cheiliniines, plus 2 corines, *H. melapterus* and *Thalassoma janssenii*. Only *Cheilinus chlorourus* and *C. trilobatus* and *Thalassoma lunare* and *T. janssenii* formed strong groupings because these pairs of species were consistently close in all the 6 trees obtained (Fig. 3B).

## DISCUSSION

Ecological characteristics and phylogeny of wrasses had little detectable influence on the parasite community structure. The relatedness of fishes based on parasite species had little resolution, indicating that there is no strong pattern to the distribution of parasite species in the labrid assemblage studied here. Generally, the relatedness of fishes based on their parasite species has been explored for adult parasites (e.g., Morand et al., 2000; Cribb et al., 2002), which tend to have a higher specificity than larval parasites (George-Nascimento, 1987). However, wrasses harbored such a high proportion of larval parasites that comparisons between larval and adult parasites were not possible because the number of species and the frequency of adult parasites were small. Also, the parasites that have multiple hosts were generally distributed inconsistently. The lack of distribution patterns of endoparasites makes it impossible to associate parasite composition with host phylogeny and most ecological characteristics of hosts. The association between parasite and host species may be explained by stochastic events that allow the association between some species, but not between others.

There are few studies of the parasite component communities of coral reef fish and none about complete parasite communities. Morand et al. (2000) found that abundance and richness of endoparasites of butterfly fishes (Chetodontidae) were associated with diet and host density, and that host phylogeny was important for the analysis between variables. Grutter and Poulin (1998) found that the abundance of isopods from different coral reef fish species increases significantly with the host body size after controlling for the host phylogeny. In general, ecological

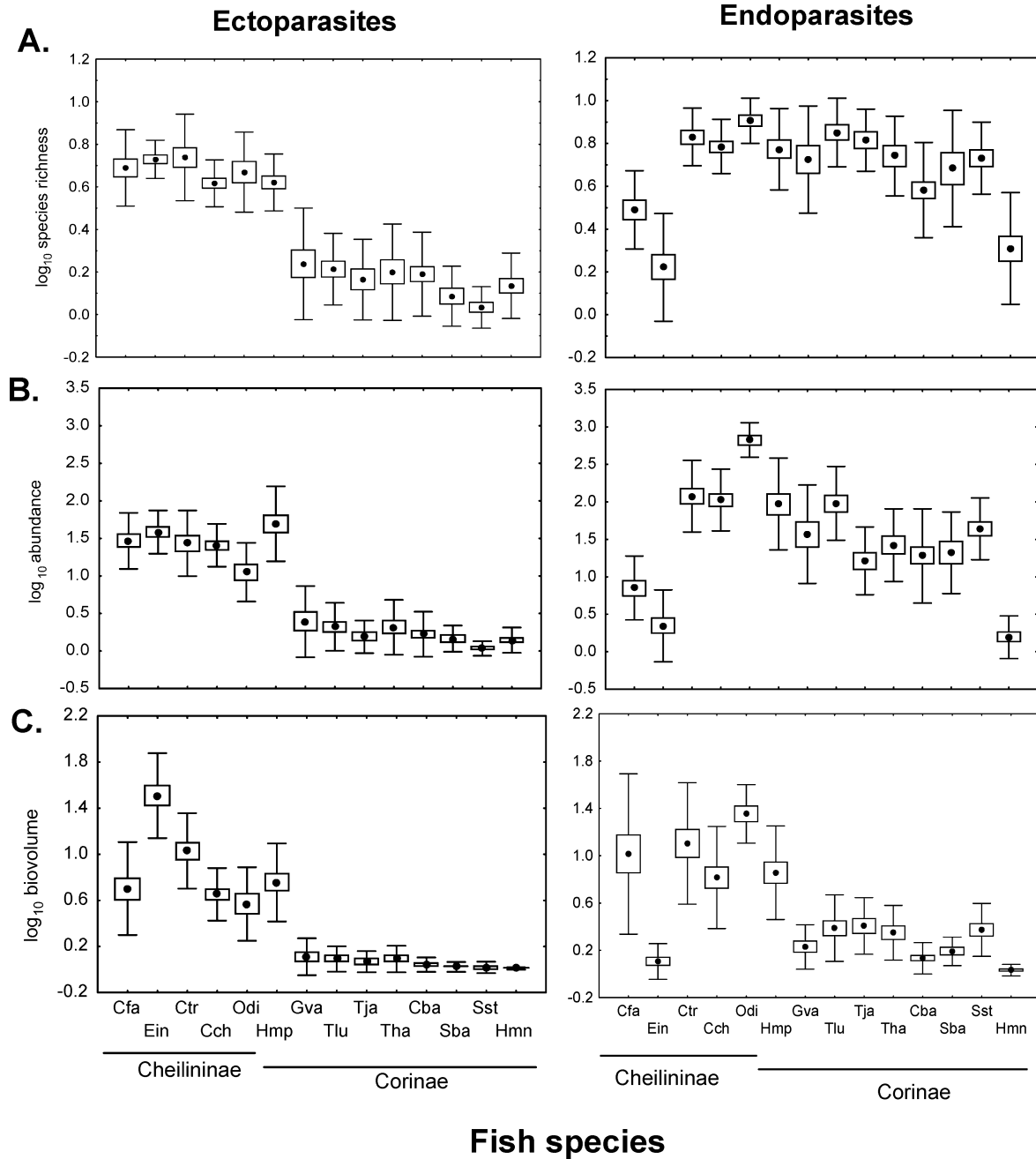


FIGURE 1. Box plots of average (black circle), standard error (square), and standard deviation (lines) of (A) species richness, (B) abundance, and (C) biovolume of the infracommunities of ectoparasites and endoparasites per fish species. Fish ordered by subfamily and then by descending mean body weight from left to right (see Table II). Abbreviations of fish names are shown in Table I.

variables influence parasite community structure, although they usually are associated with the host phylogeny. For example, Corinae and Cheiliniinae are subfamilies within Labridae which are largely diverged ecologically in body size, abundance, diet, and swimming behavior (Table II). *Hemigymnus melapterus* was the only corine fish that had a body size similar to that of the Cheiliniinae. Consequently, there was some influence from host phylogeny in the analyses of numerical descriptors of parasites because there were positive correlations between parasitological descriptors and host characteristics for the original data, but some of them vanished after controlling for the host

phylogeny (Table III). After this analysis, the host body weight was positively correlated with species richness, abundance, and biovolume of ectoparasite communities, but not for endoparasites. This indicates that host body size was genuinely important for ectoparasites and that it was not an artifact of the host phylogeny. Direct recruitment of ectoparasites to the hosts may depend mainly on the area available in the host body to be occupied (Price, 1990). This may explain the positive relationship between richness, abundance, and biovolume of ectoparasites and host body weight because larger hosts offer a larger area to be colonized by parasites.

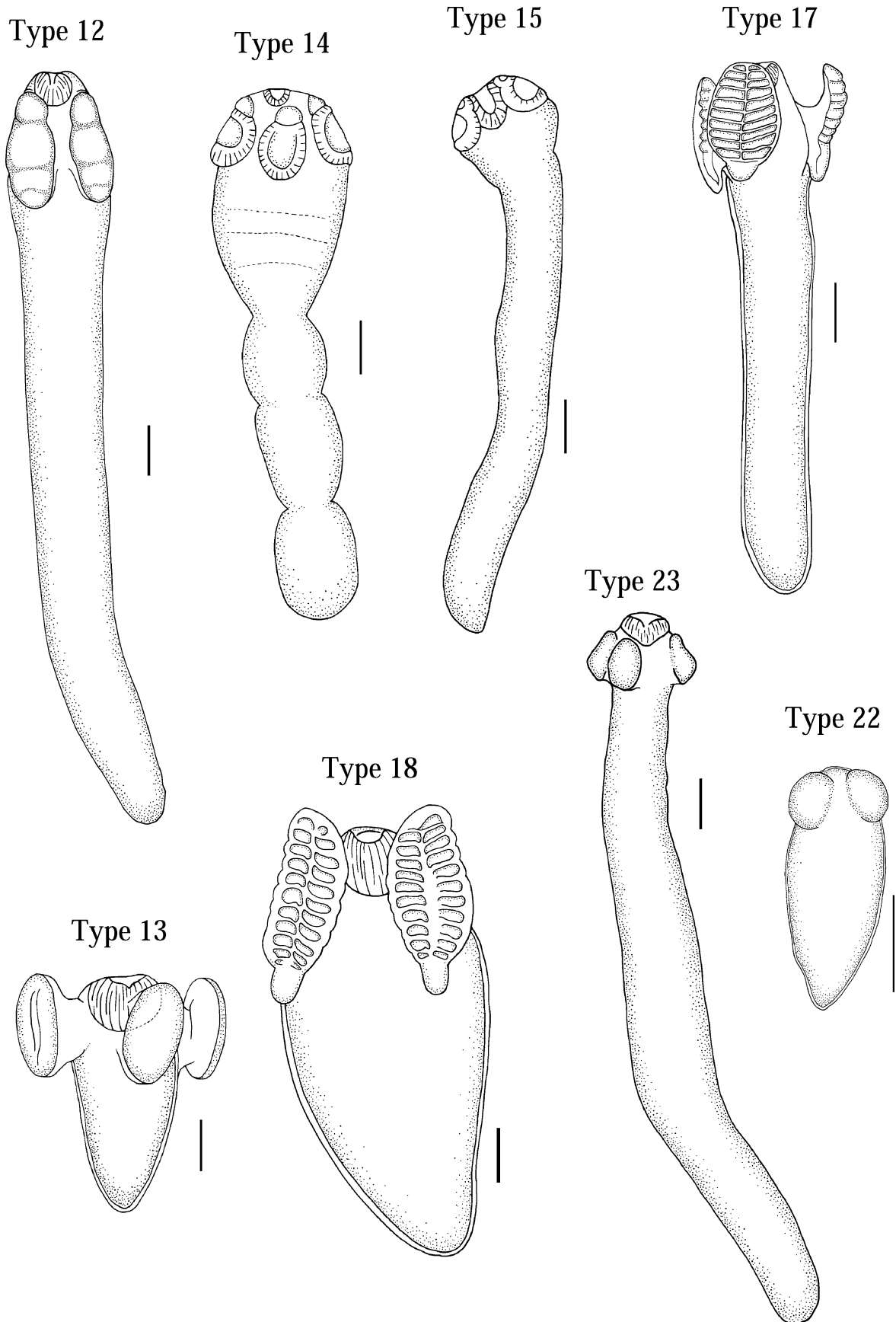


FIGURE 2. Sixteen new morphotypes of tetraphyllideans found in wrasses from Lizard Island. Tetraphyllideans types 1, 4, 6, 8, and 10 were shown in Chambers et al. (2000), and tetraphyllideans types 16, 19, 20, and 21 were shown in Muñoz and Cribb (2006) as types H, F, E, and G, respectively. Scale bars = 0.1 mm unless otherwise stated.

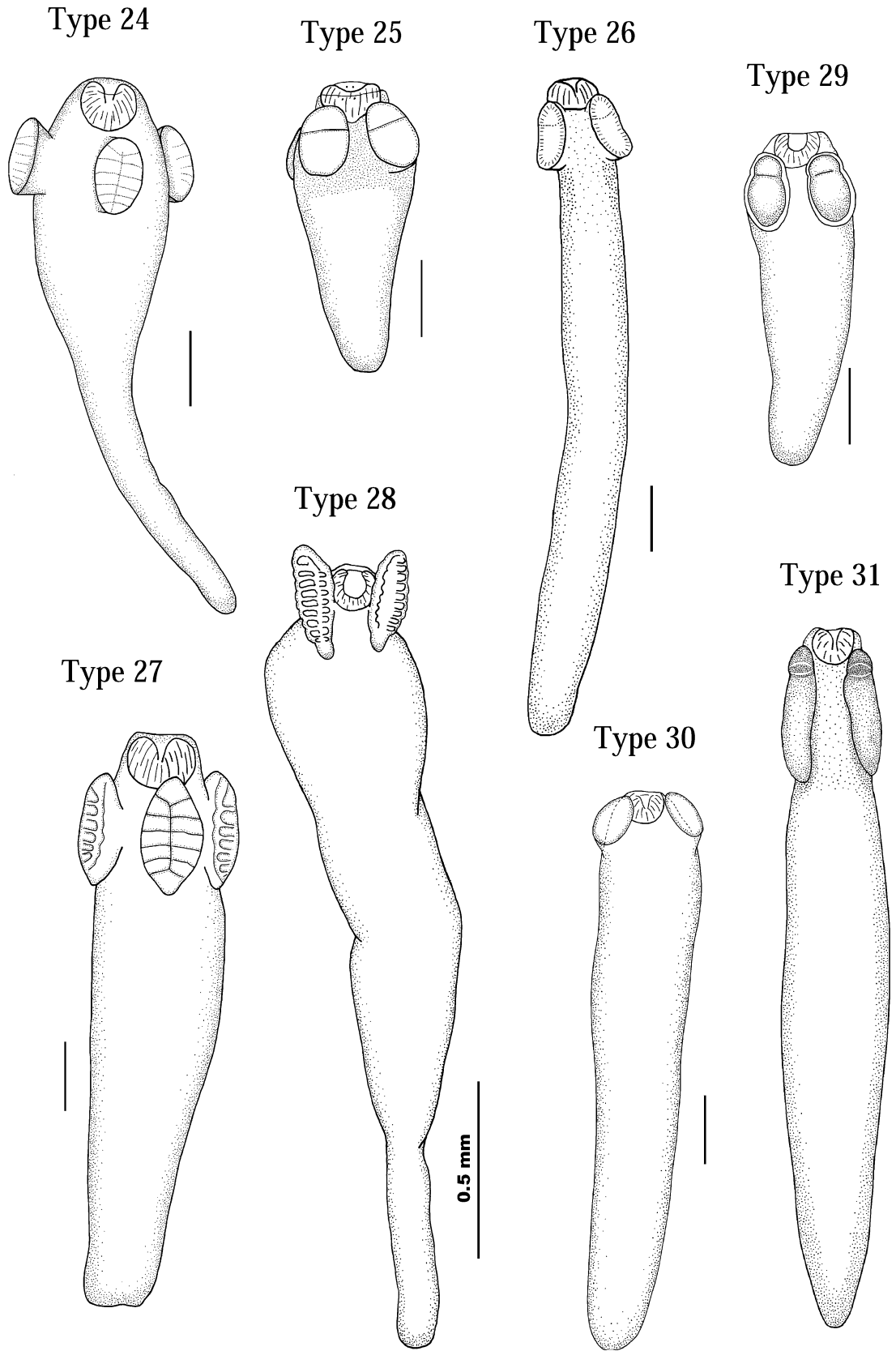


FIGURE 2. Continued.

TABLE II. Five host characteristics: average of fish weight (SD, standard deviation), swimming ability, relative abundance, and number of diet items (number of taxa) of 14 wrasse species from Lizard Island.

Fish species	Fish weight X (SD)	Swimming ability (cm)*	Relative abundance†	Diet (No. prey items)
<b>Cheilinae</b>				
<i>Cheilinus fasciatus</i>	306.3 (217.7)	10‡	0.2	26
<i>Cheilinus trilobatus</i>	198.0 (149.3)	10	0.7	37
<i>Cheilinus chlorourus</i>	148.7 (73.9)	11.5§	0.9	27
<i>Epibulus insidiator</i>	211.3 (147.3)	10‡	0.6	9
<i>Oxycheilinus diagramma</i>	116.4 (61.9)	12.4§	1.9	3
<b>Corinae</b>				
<i>Hemigymnus melapterus</i>	260.1 (253.9)	18	1.9	36
<i>Gomphosus varius</i>	56.7 (36.6)	20‡	3.7	8
<i>Thalassoma lunare</i>	48.0 (30.6)	40§	5.9	21
<i>Thalassoma janseni</i>	42.4 (19.8)	40	17.7	21
<i>Thalassoma hardwicke</i>	39.4 (22.2)	70	18.5	18
<i>Coris batuensis</i>	18.9 (11.6)	15‡	5.2	25
<i>Stethojulis bandanensis</i>	16.2 (5.2)	15	4.8	14
<i>Stethojulis strigiventer</i>	11.3 (4.2)	12‡	0.6	14
<i>Halichoeres melanurus</i>	9.1 (3.3)	18	11.8	25

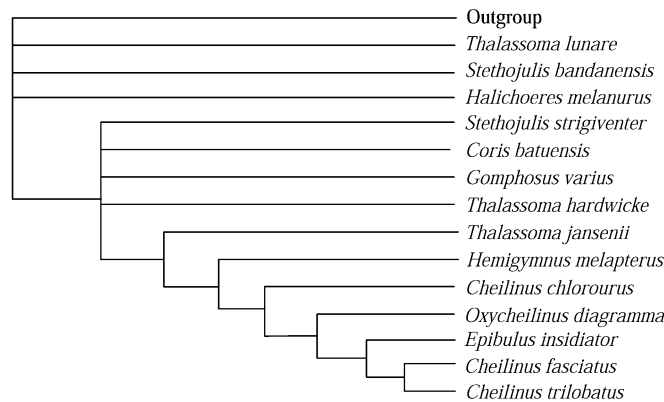
\* Data for swimming ability are from Fulton et al. (2001) and Fulton and Bellwood (2002a).

† Data for relative abundance are from Fulton et al. (2001).

‡ Information not available for these species; however, the data were taken from species that are closely related phylogenetically.

§ Information provided by personal communication with Chris Fulton.

**A) Ectoparasites**



**B) Endoparasites**

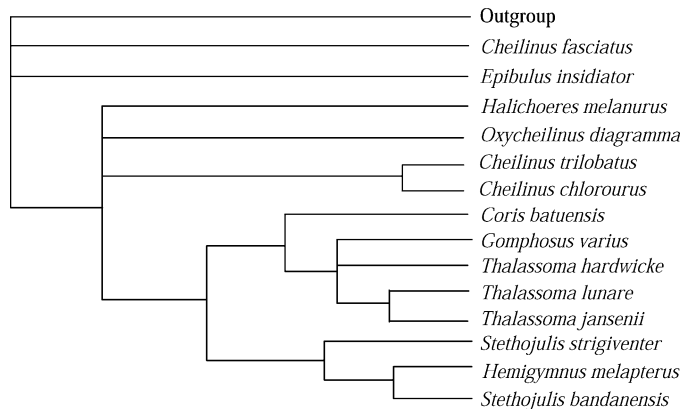


FIGURE 3. Host relatedness based on the presence or absence of parasite species in each fish species. (A) ectoparasites, and (B) endoparasites.



TABLE III. Pearson correlations for all descriptors, considering 14 fish species with 4 host descriptors and parasite body volume for data without host phylogenetic correction (only logarithmic transformation, see text) and for contrasts (data controlled for host phylogeny).

	Data without correction (n = 14)		Contrasts (n = 13)	
	Ectoparasites	Endoparasites	Ectoparasites	Endoparasites
Total community richness				
Host body weight	<b>0.89*</b>	0.01	<b>0.69*</b>	0.42
Relative abundance	<b>-0.70*</b>	0.44	-0.45	0.04
Swimming ability	-0.52	<b>0.66*</b>	-0.10	0.23
Diet (total food items)	—	0.23	—	0.27
Infracommunity richness				
Host body weight	<b>0.93*</b>	0.06	<b>0.92*</b>	0.18
Relative abundance	-0.65	0.20	-0.27	0.07
Swimming ability	-0.54	0.20	-0.10	0.08
Diet (total food items)	—	-0.08	—	-0.15
Abundance				
Host body weight	<b>0.94*</b>	0.36	<b>0.93*</b>	0.34
Relative abundance	-0.64	-0.13	-0.32	-0.13
Swimming ability	-0.49	0.03	-0.05	0.01
Diet (total food items)	—	-0.39	—	-0.20
Biovolume				
Host body weight	<b>0.85*</b>	<b>0.73*</b>	<b>0.70*</b>	0.48
Relative abundance	<b>-0.69*</b>	-0.57	-0.35	-0.29
Swimming ability	-0.57	-0.36	-0.21	-0.06
Diet (total food items)	—	0.04	—	0.03

\* Significance level,  $P \leq 0.0125$ .

The processes that structure communities of parasites are long-term associations, e.g., they may be reflected in host specificity, in which mutual physiological responses of host and parasites as well as colonizations and extinctions of parasites in host species have taken place (Poulin, 1998a). For example, gill copepods, *Hatschekia* sp. and *Lernanthropus* sp., were specific to their hosts and only present on large hosts (Appendix 1). Probably smaller fish species do not harbor gill copepods because they do not have the appropriate microhabitat for these parasites, e.g., space, flux of water, and aeration. Gill parasites can produce such deleterious effects on small fishes, depressing the ventilation efficiency, that such infections do not generally occur (e.g., Bennett and Bennett, 2001; Ojha and Hughes, 2001). Whereas all parasite species may be able to reach large hosts, perhaps only the most vagile parasites reach small hosts (Poulin, 1998a). This possibility is supported by this study in which mostly gnathiid isopods, which are highly mobile, were found on small wrasses.

In contrast, the indirect transmission of endoparasites depends not only on consideration of available space, but on factors others than body size, such as the identity and abundance of prey and predators (Pulkkinen et al., 1999) or the immune response of the host against parasites (Wakelin, 1984; Larsen et al., 2002). In addition, the transmission of endoparasites from one host to the next is likely to be affected by stochastic factors (Holmes, 1987). Thus, host body size is only one of many important components of the process of colonization and recruitment of endoparasites and presumably, therefore, less important than it is for ectoparasites.

Rohde (2005) postulated that parasite communities are typically nonequilibrium systems. Parasite communities of fishes

generally have low species richness, prevalence, and abundance; they usually are not saturated with species; interspecific competition is low or inexistent; and empty niches are common (Rohde, 1979, 2005). Most of the results gathered in this study indicate that ecto- and endoparasite communities of wrasses are nonequilibrium systems. For example, there was a positive correlation between richness, abundance, and biovolume of parasites (see some results in Muñoz, Muoillot and Poulin, 2006, in which the same data set was used). Also, the random assortment model for niche partitioning was the most common for wrasses (Muñoz, Muoillot, and Poulin, 2006), which suggests that interspecific competition is not important in structuring the parasite communities of these fishes. However, wrasses have a high richness, abundance, biovolume, and prevalence of parasites that make it likely that the parasite community is interactive even if not competitive. To understand better the association between richness, abundance, nonequilibrium, and isolationist or interactive communities, the parasite body size may give some insights about the parasite community structure in different kinds of hosts. For example, wrasses have parasites with small body sizes (see Muñoz, Muoillot, and Poulin, 2006) that may allow high abundance and richness, but at the same time they do not use all the niches available in their hosts. Consequently, parasite species in a community do not compete by resources and they are not saturated with species.

Another point to consider is the potential importance of trophic interactions between wrasses and their predators. The main groups of endoparasites were metacestode and nematode larvae. These parasite groups suggest that wrasses may be food for elasmobranchs and teleosts because they usually are definitive hosts for cestodes and nematodes, respectively (see Anderson,

1992; Khalil et al., 1994). It is known that the abundance of predators can affect the abundance of hosts and probably the parasite transmission from one host to another (Loot et al., 2005). In the case of wrasses, their predators may have an important role in structuring parasite communities because the abundance and diversity of predators may be associated with predation intensity and affect parasite recruitment.

Three wrasse species, *H. melanurus*, *E. insidiator*, and *C. fasciatus*, harbored few parasites in general and notably few cestode larvae. *Halichoeres melanurus* was the smallest fish species collected, so the low level of parasitism may relate to its small body size. However, *E. insidiator* and *C. fasciatus* had the largest body sizes of all the fish examined, so that this variable does not explain their depauperate faunas. *Cheilinus fasciatus* and *E. insidiator* had diets composed of crustaceans (Muñoz, Grutter, and Cribb, 2006), which generally are intermediate hosts for many parasites. However, these 2 species had low richnesses and abundances of cestodes that are unusual for wrasses (see Appendix 1). These observations indicate that perhaps neither fish is eaten regularly by elasmobranchs, and that *E. insidiator* may have no regular predators at all. Both species have low relative abundances at Lizard Island (Green, 1996; Fulton et al., 2001) and low habitat distribution because they usually inhabit the reef slope and base (D. Bellwood, pers. comm.), which may enable them to escape from predators. Thus, we suspect that these species are exposed to infection with cestode larvae, but that a low rate of predation by elasmobranchs (e.g., Simpfendorfer et al., 2001) has meant that there has been no selection for parasite establishment in these fish species. Another explanation may be that these species have a stronger immune response against parasites than other wrasse species.

This study has demonstrated the exceptional complexity of parasite communities of wrasses on the Great Barrier Reef. The differences in parasite composition and their distribution in the fishes are apparently mainly responses to ecological differences rather than to the phylogeny of the hosts. The rich communities of parasites in wrasses may also reflect the high diversity of species in the ecosystem. A diverse ecosystem may exert evolutionary pressure on the parasites to use a wide range of host species because this increases the chances of reaching the definitive hosts. This inference may explain why most wrasses have high parasite richness, prevalence, and abundance and that phylogeny and host ecology do not seem to affect the endoparasite communities. Taken together, we conclude that in a highly complex and diverse system the nature of transmission and recruitment of parasites may affect parasite communities more strongly than in less rich systems.

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#### LITERATURE CITED

- ABBOTT, R. T., AND S. P. DANCE. 1998. Compendium of seashells. Odyssey Publishing, El Cajon, California, 411 p.
- AICKIN, M., AND H. GENSLER. 1996. Adjusting for multiple testing when reporting research results: The Bonferroni vs Holm methods. *American Journal of Public Health* **85**: 726–728.
- ANDERSON, R. C. 1992. Nematode parasites of vertebrates, their development and transmission. CAB International, Cambridge, U.K., 578 p.
- BELLWOOD, D. R., AND P. C. WAINWRIGHT. 2001. Locomotion in labrid fishes: Implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* **20**: 139–150.
- BENNETT, S. M., AND M. B. BENNETT. 2001. Gill pathology caused by infestations of adult and preadult *Dissonus manteri* Kabata (Copepoda: Dissonidae) on coral trout, *Plectropomus leopardus* (Lacepede), (Serranidae). *Journal of Fish Diseases* **24**: 523–533.
- BERNARDI, G., G. BUCCIARELLI, D. COSTAGLIOLA, D. R. ROBERTSON, AND J. B. HEISER. 2004. Evolution of coral reef fish *Thalassoma* spp. (Labridae). 1. Molecular phylogeny and biogeography. *Marine Biology* **144**: 369–375.
- BRUCE, N. L. 1982. Species of *Argathona* Stebbing, 1905 (Isopoda, Corallanidae) new to Australia, with description of two new species. *Crustaceana* **42**: 12–25.
- BUSH, A. O., K. D. LAFFERTY, J. M. LOTZ, AND A. W. SHOSTAK. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* **83**: 575–583.
- CHAMBERS, C. B., T. H. CRIBB, AND M. K. JONES. 2000. Tetracyllidean metacestodes of teleosts of the Great Barrier Reef, and the use of in vitro cultivation to identify them. *Folia Parasitologica* **47**: 285–292.
- CRIBB, T. H., R. A. BRAY, T. WRIGHT, AND S. PICHELIN. 2002. The trematodes of groupers (Serranidae: Epinephelinae): Knowledge, nature and evolution. *Parasitology* **124**: S23–S42.
- FONTENOT, L. W., AND W. F. FONT. 1996. Helminth parasites of four species of aquatic snakes from two habitats in southeastern Louisiana. *Journal of the Helminthological Society of Washington* **63**: 66–75.
- FULTON, C. J., AND D. R. BELLWOOD. 2002a. Ontogenetic habitat use in labrid fishes: An ecomorphological perspective. *Marine Progress Ecology Series* **236**: 255–262.
- , AND ———. 2002b. Patterns of foraging in labrid fishes. *Marine Ecology Progress Series* **226**: 135–142.
- , ———, AND P. C. WAINWRIGHT. 2001. The relationship between swimming ability and habitat use in wrasses (Labridae). *Marine Biology* **139**: 25–33.
- GARLAND, T. J., P. H. HARVEY, AND A. R. IVES. 1992. Procedures for the analysis of comparative data using phylogenetic independent contrasts. *Systematic Biology* **4**: 18–32.
- GEORGE-NASCIMENTO, M. 1987. Ecological helminthology of wildlife animal hosts from South America: A literature review and a search for patterns in marine food webs. *Revista Chilena de Historia Natural* **60**: 181–202.
- , F. GARCÍAS, AND G. MUÑOZ. 2002. Parasite body volume and infracommunity patterns in the southern pomfret *Brama australis* (Pisces: Bramidae). *Revista Chilena de Historia Natural* **75**: 835–839.
- GREEN, A. L. 1996. Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family Labridae). *Marine Ecology Progress Series* **133**: 1–11.
- GRUTTER, A. S. 1995. Comparisons of methods for sampling ectoparasites from coral reef fishes. *Marine and Freshwater Research* **46**: 897–903.
- , AND R. POULIN. 1998. Intraspecific and interspecific relationships between host size and the abundance of parasitic larval gnaithiid isopods on coral reef fishes. *Marine Ecology Progress Series* **164**: 263–271.
- HAYWARD, C. J. 1996. Revision of the monogenean genus *Polylabris* (Microcotylidae). *Invertebrate Taxonomy* **10**: 995–1039.
- HOBERG, E. P., AND A. ADAMS. 2000. Phylogeny, history and biodiversity: Understanding faunal structure and biogeography in the marine realm. *Bulletin of the Scandinavian Society for Parasitology* **10**: 19–37.
- HOLMES, J. C. 1987. The structure of helminth communities. *International Journal for Parasitology* **17**: 203–208.
- JONES, D., AND G. MORGAN. 2002. A field guide to crustaceans of Australian waters, 2nd ed. Reed New Holland, Western Australian Museum, Chatswood, New South Wales, Australia, 224 p.

- KHALIL, L. F., A. JONES, AND R. A. BRAY. 1994. Keys to the cestode parasites of vertebrates. CAB International, Oxon, U.K., 751 p.
- LAMPRELL, K., AND J. M. HEALY. 1998. Bivalves of Australia, volume 2. Backhuys Publishers, Leiden, Netherlands, 288 p.
- , AND T. WHITEHEAD. 1992. Bivalves of Australia, volume 1. Crawford House Press, Bathurst, New South Wales, Australia, 182 p.
- LARSEN, A. H., J. BRESCIANI, AND K. BUCHMANN. 2002. Interactions between ecto- and endoparasites in trout *Salmo trutta*. *Veterinary Parasitology* **103**: 167–173.
- LILE, N. K. 1998. Alimentary tract helminths of four pleuronectid flatfish in relation to host phylogeny and ecology. *Journal of Fish Biology* **53**: 945–953.
- LOOT, G., M. ALDANA, AND S. NAVARRETE. 2005. Effects of human exclusion on parasitism in intertidal food webs of central Chile. *Conservation Biology* **19**: 203–212.
- MORAND, S., T. H. CRIBB, M. KULBICKI, M. C. RIGBY, C. CHAUVET, V. DUFOUR, E. FALIEUX, R. GALZIN, C. M. LO, A. LO YAT, S. PICHELIN, AND P. SASAL. 2000. Endoparasite species richness of New Caledonian butterfly fishes: Host density and diet matter. *Parasitology* **121**: 65–73.
- MUÑOZ, G., AND T. H. CRIBB. 2005. Infracommunity structure of parasites of *Hemigymnus melapterus* (Pisces: Labridae) from Lizard Island, Australia: The importance of habitat and parasite body size. *Journal of Parasitology* **91**: 38–44.
- , AND ———. 2006. Parasite communities and diet of *Coris batuensis* (Pisces: Labridae) from Lizard Island, Great Barrier Reef. *Memoirs of the Queensland Museum* **52**: 191–198.
- , A. S. GRUTTER, AND T. H. CRIBB. 2006. Endoparasite communities of five fish species (Labridae: Cheiliniinae) from Lizard Island: How important is the ecology and phylogeny of the hosts? *Parasitology* **132**: 363–374.
- , D. MUOILLOT, AND R. POULIN. 2006. Testing the niche apportionment hypothesis with parasite communities: Is random assortment always the rule? *Parasitology* **132**: 717–724.
- OJHA, J., AND G. M. HUGHES. 2001. Effect of branchial parasites on the efficiency of the gills of a freshwater catfish, *Wallago attu*. *Journal of Zoology* **255**: 125–129.
- PATERSON, A. M., AND R. D. GRAY. 1997. Host-parasite co-speciation, host switching and missing the boat. *In* Host-parasite evolution: General principles and avian models, D. H. Clayton, and J. Moore (eds.). Oxford University Press, Oxford, U.K., p. 236–250.
- POULIN, R. 1998a. Evolutionary ecology of parasites. Chapman and Hall, London, U.K., 211 p.
- . 1998b. Comparison of three estimators of species richness in parasite component communities. *Journal of Parasitology* **84**: 485–490.
- , D. MUOILLOT, AND M. GEORGE-NASCIMENTO. 2003. The relationship between species richness and productivity in metazoan parasite communities. *Oecologia* **137**: 277–285.
- PRICE, P. W. 1990. Host populations as resources defining parasites community organization. *In* Parasite communities: Patterns and processes, G. W. Esch, A. O. Bush, and J. M. Aho (eds.). Chapman and Hall, New York, New York, p. 21–40.
- , AND K. M. CLANCY. 1983. Patterns in number of helminth parasite species in freshwater fishes. *Journal of Parasitology* **69**: 449–454.
- PULKKINEN, K., E. T. VALTONEN, A. NIEMI, AND K. POIKOLA. 1999. The influence of food competition and host specificity on the transmission of *Triaenophorus crassus* (Cestoda) and *Cystidicola faraonis* (Nematoda) to *Coregonus lavaretus* and *Coregonus albula* (Pisces: Coregonidae). *International Journal for Parasitology* **29**: 1753–1763.
- PURVIS, A., AND A. RAMBAUT. 1994. Comparative analysis by independent contrasts (CAIC), version 2.0. A statistical package for the Apple Macintosh. Available at: <http://www.bio.ic.ac.uk/evolve/software/caic/>.
- RANDALL, J. E., G. R. ALLEN, AND R. C. STEENE. 1997. Fishes of the Great Barrier Reef and Coral Sea, revised and expanded ed. Crawford House Publishing, Bathurst, Australia, 557 p.
- ROBERTS, L. S., AND J. J. JANOVY. 2000. Foundations of parasitology, 6th ed. McGraw-Hill Higher Education, New York, New York, 670 p.
- ROHDE, K. 1979. A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. *American Naturalist* **114**: 648–671.
- . 2005. Parasite populations and communities as non-equilibrium systems. *In* Marine parasitology, K. Rohde (ed.). CABI Publishing, Oxon, U.K., p. 565.
- , AND M. HEAP. 1998. Latitudinal differences in species and community richness and in community structure of metazoan endo- and ectoparasites of marine teleost fish. *International Journal for Parasitology* **28**: 461–474.
- RUSSELL, B. C. 1983. Annotated checklist of the coral reef fishes in the Capricorn–Bunker Group, Great Barrier Reef, Australia. Great Barrier Reef Marine Park Authority, Townsville, Australia, 184 p.
- SANO, M., M. SHIMIZI, AND Y. NOSE. 1984. Food habits of teleostean reef fishes in Okinawa Island, Southern Japan. *The University Museum. The University of Tokyo* **25**: 1–125.
- SASAL, P., N. NIQUIL, AND P. BARTOLI. 1999. Community structure of digenean parasites of sparid and labrid fishes of the Mediterranean Sea: A new approach. *Parasitology* **119**: 635–648.
- SIMPENDORFER, C. A., A. GOODREID, AND R. B. MCAULEY. 2001. Diet of three commercially important shark species from Western Australian waters. *Marine and Freshwater Research* **52**: 975–985.
- SWOFFORD, D. L. 1998. PAUP\* ver. 4.0610: Phylogenetic analysis using parsimony\* and other methods. Software distributed by Sinauer Associates Inc., Sunderland, Massachusetts.
- WALTER, B. A., AND S. MORAND. 1998. Comparative performance of richness estimation methods. *Parasitology* **116**: 395–405.
- WAKELIN, D. 1984. Immunity to parasites. How animals control parasite infections. Edward Arnold, London, U.K., 165 p.
- WESTNEAT, M. W. 1993. Phylogenetic relationship of the tribe Cheiliniina (Labridae: Perciformes). *Bulletin of Marine Science* **52**: 351–394.
- , AND M. E. ALFARO. 2005. Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Molecular Phylogenetics and Evolution* **36**: 370–390.
- WHITTINGTON, I. D., M. R. DEVENNEY, AND S. J. WYBORN. 2001. A revision of *Benedenia* Diesing, 1858 including a redescription of *B. sciaenae* (van Beneden, 1856) Odnher, 1905 and recognition of *Menziesia* Gibson, 1976 (Monogenea: Capsalidae). *Journal of Natural History* **35**: 663–777.
- WILSON, B. 1993. Australian marine shells, prosobranch and gastropods, volumes 1 and 2. Odyssey Publishing, Kallaroo, Western Australia, 778 p.





APPENDIX I. Continued.

	MS	Cfa	Ctr	Cch	Ein	Odi	Hmp	Gva	Tlu	Tja	Tha	Cba	Sba	Sst	Hmn
<i>Bivesticula</i> sp. 2	J										12.5				
<i>Callohelms pichelinae</i>	A						70.0					71.4			
<i>Megacreadium</i> sp.	A	5.6													
<i>Schickhobolotrema</i> sp.	A												7.1		
<i>Deretrema nahaense</i>	A						12.5	25.0	26.7	31.3					
<i>Diphtherostomum</i> sp.	A						6.3	20.0	20.0	6.3					
Nematoda															
<i>Pseudoterranova</i> sp.	L				5.3		5.0	10.0	6.7	12.5					
<i>Hysterothylacium</i> spp. 1															
(probably these are 2 spp)	L	77.8	89.5	34.8	26.3	21.4	5.0								
<i>Hysterothylacium</i> sp. 2	L						10.0	5.0		25.0					10.0
<i>Hysterothylacium</i> sp. 3	L						5.0								
Anisakidae gen. sp.	L			4.3											
<i>Cucullanus</i> sp.	A				5.3	7.1			6.7						
<i>Spirurida</i> gen. sp.	A		15.8	13.0				6.3	15.0	26.7	18.7	25.0		5.6	5.0
<i>Spirocamallanus</i> spp.	A		1.5	21.7				12.5	25.0				7.1		
<i>Procammallanus</i> sp.	A														
<i>Camallanus</i> sp.	J				5.3			56.3	5.0	53.3	37.5	3.1			
<i>Heliconema</i> sp.	L					7.1									
<i>Philometra</i> sp.	A					28.6									
Acanthocephala															
<i>Transvena annulospinosa</i>	A	5.6					15.0			6.7			21.4	16.7	
<i>Hypoehinorhynchus</i> sp.	A								5.0						