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Aggregation and species coexistence of ectoparasites of marine fishes

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Abstract

Interspecific interaction may lead to species exclusion but there are several ways in which species can coexist. One way is by reducing the overall intensity of competition via aggregated utilisation of fragmented resources. Known as the 'aggregation model of coexistence', this system assumes saturation and an equilibrium number of species per community. In this study we tested the effects of interspecific aggregation on the level of intraspecific aggregation among ectoparasites of marine fishes (36 communities of gill and head ectoparasite species). If parasite species are distributed in a way that interspecific aggregation is reduced relative to intraspecific aggregation then species coexistence is facilitated. We found a positive relationship between parasite species richness and fish body size, controlling for host phylogeny. A positive relationship between infracommunity species richness and total parasite species richness was also found, providing no evidence for saturation. This result supports the view that infracommunities of parasites are not saturated by local parasite residents. The observed lack of saturation implies that we are far from a full exploitation of the fish resource by parasites. Ectoparasites were aggregated at both population and species levels. However, only half of the ectoparasite communities were dominated by negative interspecific aggregation. We found that infracommunity parasite species richness was positively correlated with the level of intraspecific aggregation versus interspecific aggregation. This means that intraspecific aggregation increases compared with interspecific aggregation when total parasite species richness increases, controlling fish size and phylogeny. This supports one assumption of the 'aggregation model of coexistence', which predicts that interspecific interactions are reduced relative to intraspecific interactions, facilitating species coexistence. © 1999 Australian Society for Parasitology. Published by Elsevier Science Ltd. All rights reserved.

Keywords: Ectoparasite communities; Fish; Species richness; Species coexistence; Interspecific aggregation; Intraspecific aggregation

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1. Introduction

The distribution and abundance of species within communities have been the topic of numerous studies [1, 2]. An important debate concerns the role of interactive or non-interactive processes [3]. Hence, communities have been classified as interactive or non-interactive, depending on whether interaction take place or not among the residents of a local habitat. Among community models, interactive communities can be of two types: a niche heterogeneity type, where coexistence is favoured by species-differences in one or more important niche dimensions, or spatio–temporal heterogeneity types (see [4]). While interaction between species may lead to exclusion, there are several ways in which species can coexist—for instance, by reducing the overall intensity of competition via aggregated utilisation of fragmented resources [5, 6]. This has been formalised as the 'aggregation model of coexistence' [7].

The study of parasite communities (compared to free-living organisms) has the advantage that hosts may be considered as individual patches of habitat for parasites and that history, depicted by host phylogeny, can be taken into account. As with free-living communities, the question can be asked as to whether parasite communities are isolationist or interactive [8, 9].

Parasites are generally found aggregated among their hosts [10–12]. Aggregation can be caused by numerous factors [13], among them heterogeneous contacts between sources of infection and hosts and/or differential susceptibility of hosts to parasite attacks. Holmes [14] showed that competition between species exploiting the same resource leads to site segregation or niche restriction. Rohde [15] reasoned that aggregation is the result of selection for improved mate location because highly aggregated parasites have little difficulty in mating even at low densities and/or because mate location reinforces isolation between congeneric species. Rohde [16] also argued that niche restriction is often not the by-product of competition, but is also due to mate location [17]. Using a mathematical approach, Dobson and Roberts [18] concluded that interaction between parasites and their hosts seem to be more important in determining community structure than direct interaction between parasite species (see also [19]). Dobson and Roberts [18] suggested that spatial aggregation, host longevity and population growth rate are crucial mechanisms permitting increases in diversity in parasite communities.

The 'aggregation model of coexistence' postulates that if species (using the same type of resource) are distributed in a way that interspecific aggregation is reduced relative to intraspecific aggregation then species coexistence is facilitated [5–7, 20–24]. The 'aggregation model of coexistence' implies that ecological communities are saturated with species, that is, there is an upper limit (saturation) of local species richness (here, on an individual host) independent of the size of the regional pool (component parasite species). Coexistence of species is facilited as long as intraspecific aggregation exceeds interspecific aggregation (i.e. positive association). This model has been used to explain the distribution and abundance of animals living in patchy and ephemeral resources (and persisting for one or two generations). This model has never been applied to parasites, which also live on patchy resources. In this paper we use the framework of Ives [22] to investigate the effect of interspecific aggregation on the level of intraspecific aggregation. We test the main hypothesis that interspecific interactions should be reduced relative to intraspecific interactions, facilitating species coexistence (i.e. an increase of ectoparasite species richness).

2. Material and methods

2.1. Parasite communities

Data were obtained for 133 communities of gill and head ectoparasites of marine fish from several localities (see Rohde et al. [25]; Hayward, unpublished). Most 'head' parasites live in the mouth cavity and are often found on the gills as well, where they could interact with gill parasites. Ectoparasite communities of host species from tropical waters are probably little affected by time of collection. Host species from cold and temperate waters were collected during the warm season when abundance and diversity of parasites were highest.

We used only parasite communities consisting of at least five species (36 parasite communities), for which the effects of interactions between parasite species would be more easily detected and because the computation of Ives' statistics is problematical for species-poor communities. All parasites in a host individual constitute an infracommunity, and all of the parasites in a given host species population are defined as the component community [8].

2.2. Host saturation and saturated patterns

We applied the framework of regional versus local species richness to parasite communities (see [26]). Local species richness is defined as the mean infracommunity parasite species richness, whereas regional species richness is defined as the component community parasite species richness. A ceiling, i.e. a limit to infracommunity parasite species richness with increasing component community richness, does not necessarily indicate saturation [27], but proportional sampling, i.e. lack of a ceiling, indicates non-saturation, i.e. dependence of infracommunity richness on component community richness.

2.3. Intraspecific aggregation

Ives [22, 24] has suggested a measure of intraspecific aggregation J, that is simply the proportionate increase in the number of conspecific competitors experienced by a random individual relative to a random distribution (following [7]):

$$J_1 = \frac{\sum p_{i=1} \frac{n_{1i}(n_{1i-1})}{m_1} - m_1}{m_1} = \frac{\frac{V_1}{m_1} - 1}{m_1}$$

where n_{1i}, m_1 and V_1 are the numbers in patch i (and p the number of patch), mean numbers and the variance in numbers of species 1. A value of $J = 0$ indicates that individuals are randomly distributed, while a value of $J = 0.5$ indicates a 50% increase in the number of conspecifics expected in a patch compared to the random distribution.

2.4. Interspecific aggregation

To measure interspecific aggregation, Ives [22, 24] derived a similar index, C, which measures the proportionate increase in the number of heterospecific competitors relative to a random association (following [7]):

$$C_{12} = \frac{\sum p_{i=1} \frac{n_{1i}n_{2i}}{m_1 P} - m_2}{m_2} = \frac{Cov_{12}}{m_1 m_2}$$

where Cov is the covariance between a pair of species. When $C > 0$ the two species are positively associated, when $C < 0$ they are negatively associated. The reduction in competition caused by intraspecific aggregation or the relative strength of intraspecific aggregation versus interspecific aggregation, in a pair of species (1 and 2) can therefore be assessed with the quantity (following Shorrocks [7]):

$$A_{12} = \frac{(J_1 + 1)(J_2 + 1)}{(C_{12} + 1)^2}$$

following Ives [22], Jaenike and James [6] and Stevenster [28]. If $A_{\mathrm{ij}} > 1$, intraspecific aggregation is stronger than interspecific aggregation.

We calculated the mean C_{ij} and the mean A_{ij} for each parasite component community.

2.5. Nested structure

We calculated the significance of nestedness structure (i.e. non-random assemblage) for each ectoparasite community (see [29]). The occurrence of significant nestedness structure was compared to ectoparasite species richness and aggregation parameters J, C and A.

2.6. Comparative analysis

One may argue that proximal ecological factors influence prevalence and intensity of parasitism, which are then independent of host or parasite phylogeny. Indeed, there are several arguments to support the view that prevalence (and intensity) of worm infections varies in relation to environment (e.g. temperature). However, values of prevalence and intensity of parasite infections depend on a species' characteristics, which are, in turn, not independent of their phylogenetic relationships [30]. It is therefore necessary to control all epidemiological values (such as species richness, aggregation measures) for phylogenetic confounding effects.

We performed an analysis using phylogenetically independent contrasts with the CAIC 2.0 computer package [31]. We constructed a phylogeny based on the information in Nelson [32] and additional information on the genus *Sillago* (see [33]). Regressions were forced through the origin [34]. This phylogeny provided 19 independent contrasts. All variables except *C* and *J* were log-transformed before contrasts were computed.

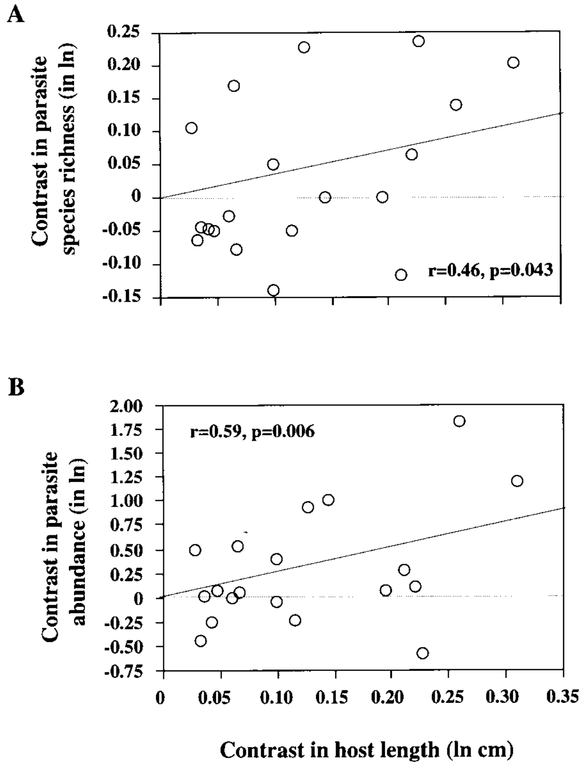

Fig. 1. Relationships between contrasts in fish body size and (A) contrasts in ectoparasite species richness and (B) contrasts in ectoparasite abundance. Nineteen contrasts were derived from a phylogeny of 36 marine fish species.

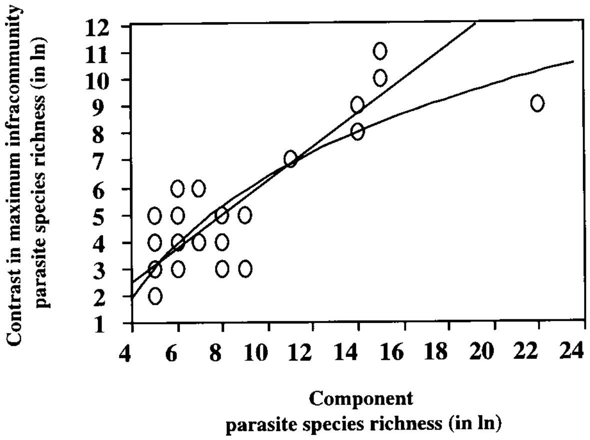

Fig. 2. Relationships between component ectoparasite species richness and maximum infracommunity parasite species richness using cross-species values. A curvilinear relationship is found when using all 36 communities ($Y = -4.815 + 4.87 \times \ln(X)$; $P < 0.0001$, $R_2 = 0.69$), whereas a linear relationship gives the best fit when the upper right point is removed ($Y = 0.057 + 0.623 \times X$; $P < 0.0001$, $R_2 = 0.74$).

3. Results

Host sample size did not correlate with parasite species richness in the case of the 36 fish species harboring at least five parasite species, when not controlling for host phylogeny ($P = 0.29$).

3.1. Component parasite species richness and abundance

Component parasite species richness and parasite abundance correlated positively with host body length (Fig. 1A, B). However, the relationship between component parasite species richness and host body length was not significant using a sign test ($P = 0.49$), i.e. pairs of contrasts with the same signs are not more common than expected by chance.

3.2. Host saturation

A curvilinear relationship was found between maximum infracommunity parasite species richness and component community parasite species richness (Fig. 2) using cross species values, i.e. not controlling for phylogeny. However, this relationship was dependent on one point and a linear relationship gave the best fit between maximum infracommunity parasite species richness and component parasite species richness when this point was removed (Fig. 2). Both mean infracommunity parasite species richness ($r = 0.62$, $P < 0.0038$) and maximum infracommunity parasite species richness ($r = 0.69$,

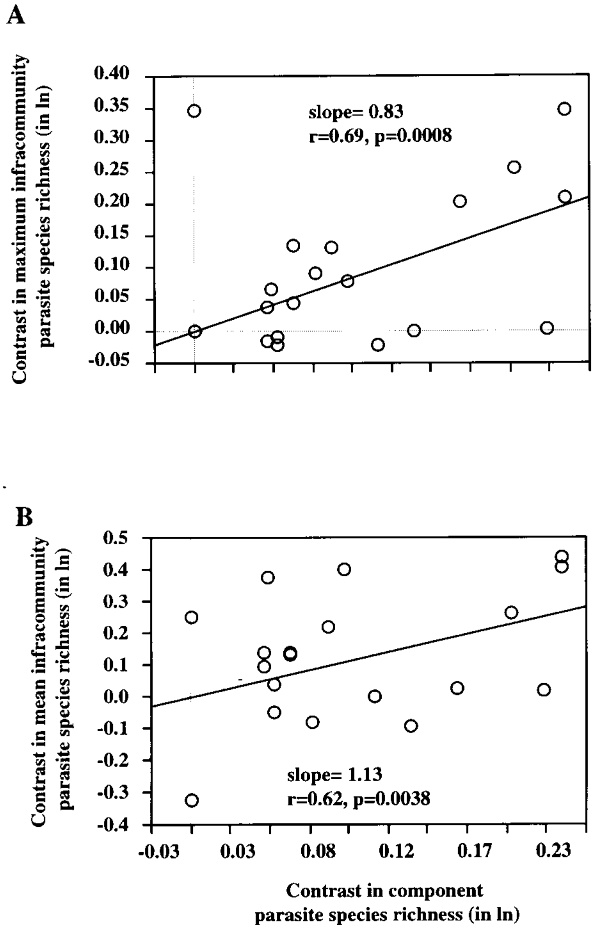

Fig. 3. Relationships between component ectoparasite species richness and maximum infracommunity parasite species richness (A) and mean infracommunity species richness (B). Nineteen contrasts were derived from a phylogeny of 36 marine fish species.

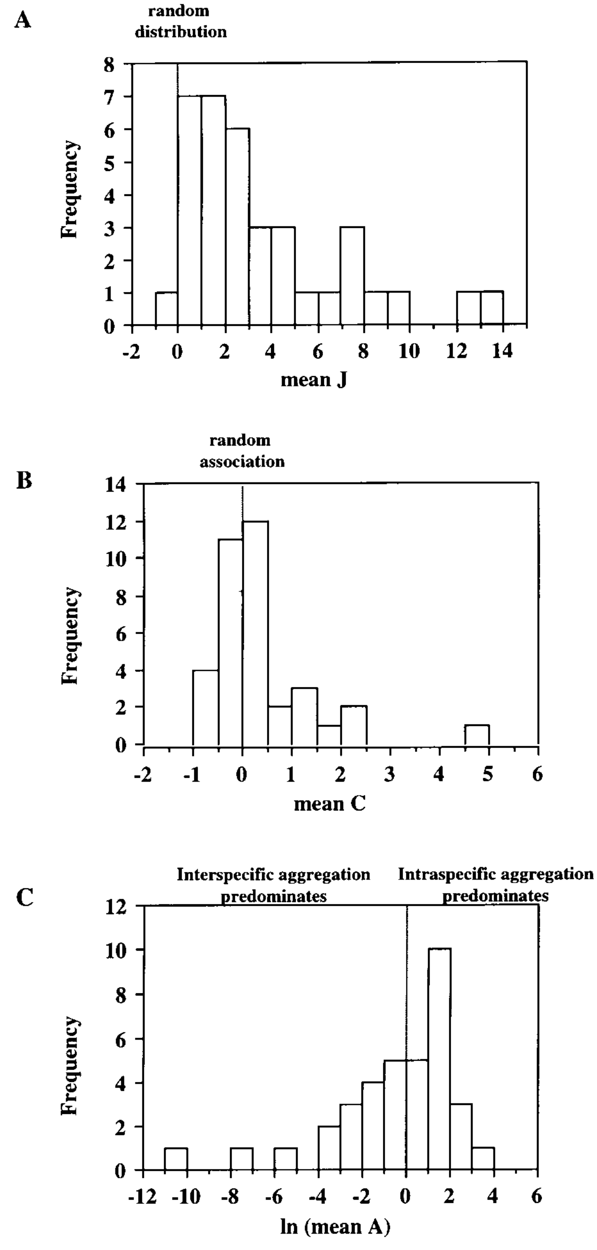

Fig. 4. Frequency distributions of (A) mean intraspecific aggregations J; (B) mean interspecific aggregation C and (C) the mean relative strength of intraspecific aggregation versus interspecific aggregation A (in ln) (mean values calculated for each of 36 communities of gills ectoparasites).

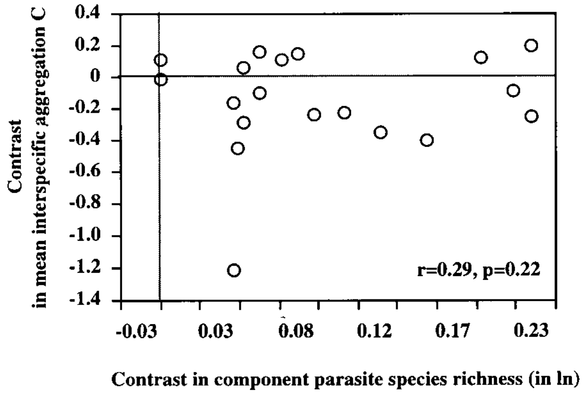

Fig. 5. Relationships between interspecific aggregation C (mean values) and component parasite species richness. Nineteen contrasts were derived from a phylogeny of 36 marine fish species.

$P = 0.0008$), correlated positively with component community parasite species richness (Fig. 3A, B), using independent contrasts. There was no evidence of ceilings, but a proportional relationship between mean infracommunity species richness (or maximum individual species richness) and component community parasite species richness. No slopes differed significantly from 1.

3.3. Parasite aggregation

We calculated for each species of host values of J for each parasite species, and C_{ij} and A_{ij} for each pair of species. Thirty-five of the 36 communities showed a mean $J > 0$ indicating that parasite individuals were aggregated among their hosts at the population level (Fig. 4A).

Fifteen communities showed a mean $C < 0$ (parasite species were on average negatively associated), whereas 21 communities showed a

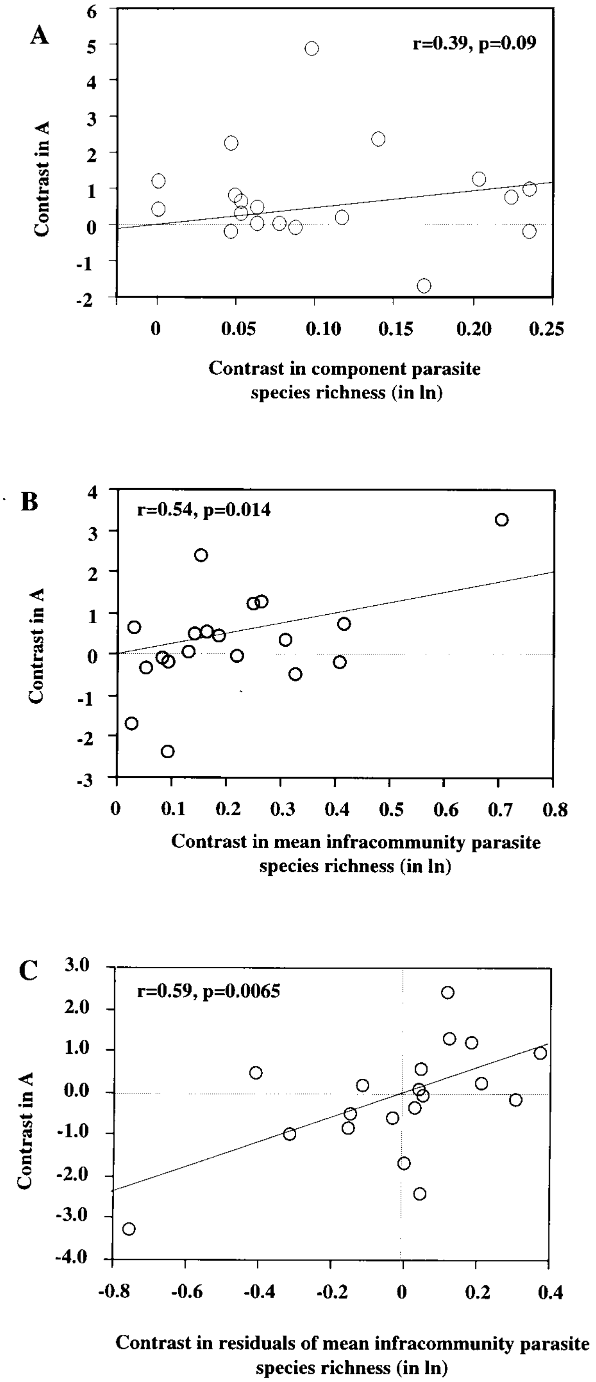

Fig. 6. Relationships between contrasts in relative strength of intraspecific aggregation versus interspecific aggregation (mean value in ln calculated for each of 36 communities of gills ectoparasites) and (A) contrasts in component species richness (B) contrasts in mean infracommunity species richness and (C) contrasts in residuals in mean infracommunity species richness (controlled for fish body size). Nineteen contrasts were derived from a phylogeny of 36 marine fish species.

mean $C > 0$ (parasite species were on average positively associated) (Fig. 4B). Seventeen communities showed a mean $A > 1$ (mean $\ln A > 0$) i.e., intraspecific aggregation was stronger than interspecific aggregation. The other communities showed the opposite trend with interspecific aggregation stronger than intraspecific aggregation (Fig. 4C).

There was no relationship between mean values of J (intraspecific aggregation) and component species richness ($P = 0.67$). We found no relationship between mean values of C (interspecific aggregation) and component parasite species richness, indicating that an increase of species richness does not result in an increase of species aggregation ($P = 0.22$) (Fig. 5). Lack of relationship was also found between maximum individual parasite species richness or mean individual species richness and C. There were no relationships between parasite abundance and A ($P = 0.14$) and C ($P = 0.14$) but a positive correlation between parasite abundance and J ($r = 0.55$, $P = 0.013$).

Parasite species richness did not correlate with A ($P = 0.09$) (Fig. 6A). However, there is a hint of a trend: contrasts in A have the same sign as contrasts in component species richness in 13 of the 17 pairs of contrasts in which contrast in species richness does not equal zero (Fisher's Exact test, $P = 0.049$). This indicates that for 13 of the 17 pairs of contrasts an increase in species diversity is correlated with an increase in intraspecific aggregation. We found a positive relationship between mean values of A and mean infracommunity parasite species richness ($r = 0.54$, $P = 0.014$) (Fig. 6B). Finally, we found a positive relationship between mean values of A and mean infracommunity species richness controlled for fish body size ($r = 0.59$, $P = 0.0065$) (Fig. 6C).

3.4. Nested patterns and parasite aggregation

Fifteen of the 36 communities had significant non-nested structures. Our phylogeny allowed us to obtain 11 contrasts related to a change in nested structure, from random to non-random structure. Neither the acquisition of a non-random structure were related to host length ($P = 0.549$), component parasite species richness ($P = 0.508$), maximum infra community species richness ($P = 0.227$), parasite abundance ($P = 0.549$), J (0.549), C ($P = 0.750$) or A ($P = 0.227$). All the previous results were found when not controlling for host phylogeny.

4. Discussion

Cornell and Lawton [35] suggested that interactions between species are the primary processes determining relative abundance in communities and they cited parasitic helminths as the best examples of such processes (see [36]). However, there is considerable debate on the role of interactions in structuring parasite communities [9].

According to Cornell [4], interactive communities can be classified as niche heterogeneity and spatio–temporal heterogeneity types. Niche heterogeneity models assume that species coexistence is favoured by species differences and also predict saturation (upper limit to species richness). Spatio–temporal models assume that species coexistence is favoured by unpredictable recruitment or aggregated utilisation of fragmented resources.

4.1. Parasite species richness

We found a weak but positive relationship between parasite species richness and fish body size. Poulin and Rohde [37] failed to find this relationship using a large amount of data based on 111 species of marine fish. The difference obtained by ourselves may be due to the fact that we only considered rich parasite species communities, i.e. 36 communities. Also, additional communities have been included in our analysis. We found, as did Poulin and Rohde [37], a positive relationship between fish body size and parasite abundance. A relationship between host body size and parasite species richness was previously found [38–42].

4.2. Community saturation

Several arguments support the view that fish ectoparasite communities are not saturated and form 'little-ordered' assemblages [25]. Rohde [16] (and further references therein) suggested that most gill parasite species live in low-density populations in resource-rich habitats and that many potential niches for ectoparasites of fish are empty. Worthen and Rohde [29] emphasised that ectoparasite communities form unstructured assemblages.

In a recent review Srivastava [43] drew attention to the potential pitfalls when analysing local-regional richness and emphasised that even a cautionary statistical analysis should also be supported by other evidence (such as resource limitation, density compensation, etc.). Rohde [27] also highlighted the many ways in which a curvilinear relationship between local and regional richness can be obtained without the need for species saturation.

We found a curvilinear relationship between maximum infracommunity species richness and component parasite species richness using cross-species values, which may support the view of community saturation. However, this relationship was due to one point and could be artefactual. Removing this point showed that a linear regression was the best fit of the infracommunity species richness–component parasite species richness relationship.

We found a positive relationship between infracommunity species richness and component parasite species richness and no evidence of ceilings using independent contrasts, i.e. no evidence of saturation (but see [27]). This result is in favour of the view that infracommunities of ectoparasites are not saturated by local parasite residents. Since most (97 of 133) communities were species-poor, having less than five species, and were therefore not analysed, non-saturation is likely to be even more pronounced than suggested by analyses of species-rich communities. Our results supplement the analysis of Worthen and Rohde [29] and Rohde et al. [44] who showed the lack of nested patterns in many parasite assemblages. Moreover, we show no relationship between nested patterns and parasite species richness or aggregation parameters (J, C, A) (Rohde et al. [25] found 15 positive and one negative interaction in ectoparasite communities of 102 marine fish species).

4.3. Aggregation and parasite species coexistence

We found that communities with higher parasite species richness also tend to have higher values of A than their phylogenetic sister communities with lower species richness, controlling the effect of fish size. Intraspecific aggregation is stronger than interspecific aggregation which facilitates parasite species coexistence. We found that parasites were aggregated at both population and species levels, which was previously found by Rohde et al. [25]. However, ectoparasite communities are not dominated by negative interspecific aggregation. Using the 36 fish communities, we found the same numbers of ectoparasite fish communities dominated by positive and negative interspecific aggregation.

Total parasite species richness was not correlated with interspecific aggregation (C), which suggests that the increase of parasite diversity has no influence on interspecific aggregation. Finally, using the framework of Ives [22], we found that infracommunity parasite species richness (and to a lesser degree the component community parasite species richness) was positively correlated with the level of intraspecific aggregation versus interspecific aggregation (A). This means that intraspecific aggregation increases compared to interspecific aggregation when component parasite species richness increases, controlling fish size (i.e. niche size). Interspecific interactions are then reduced relative to intraspecific interactions which facilitates species coexistence.

The aggregation model of coexistence assumes saturation and the equilibrium number of community species. The lack of observed pattern of saturation implies that we are far from full exploitation of the fish resource by parasites, in accordance with Rohde and his collaborators' views.

4.4. Structure of ectoparasite communities

There is some evidence that interspecific competition leads to niche restriction in endoparasitic worms, for instance in vertebrate guts [14]. However, several studies concluded to the lack of niche restriction, due to interspecific competition in gills parasites [16, 45]. For example, the recent study of Geets et al. [46] showed that the niche breadth of gill parasites of the fish *Siganus sutor* did not change with increasing abundance of other species present. The results of Geets et al. [46] also indicated that interspecific competition is probably not important for the microhabitat choice of the gill parasites. Our results showed that an increase of parasite species richness did not result in an increase of the level of interspecific aggregation. The power of interspecific competition as an explanation for the structuring of ectoparasite communities is therefore reduced. Our results also show that an increase of species richness was correlated with intraspecific aggregation (corrected for the strength of interspecific aggregation).

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