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Host ontogeny and the temporal decay of similarity in parasite communities of marine fish

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ABSTRACT

Geographical distances between host populations are key determinants of how many parasite species they share. In principle, decay in similarity should also occur with increasing distance along any other dimension that characterizes some form of separation between communities. Here, we apply the biogeographical concept of distance decay in similarity to ontogenetic changes in the metazoan parasite communities of three species of marine fish from the Atlantic coast of South America. Using differences in body length between all possible pairs of size classes as measures of ontogenetic distances, we find that, using an index of similarity (Bray-Curtis) that takes into account the abundance of each parasite species, the similarity in parasite communities showed a very clear decay pattern; using an index (Jaccard) based on presence/absence of species only, we obtained slightly weaker but nevertheless similar patterns. As we predicted, the slope of the decay relationship was significantly steeper in the fish *Cynoscion guatucupa*, which goes through clear ontogenetic changes in diet and therefore in exposure to parasites, than in the other species, *Engraulis anchoita* and *Micropogonias furnieri*, which maintain a roughly similar diet throughout their lives. In addition, we found that for any given ontogenetic distance, i.e. for a given length difference between two size classes, the similarity in parasite communities was almost always higher if they were adult size classes, and almost always lower if they were juvenile size classes. This, combined with comparisons among individual fish within size classes, shows that parasite communities in juvenile fish are variable and subject to stochastic effects. We propose the distance decay approach as a rigorous and quantitative method to measure rates of community change as a function of host age, and for comparisons across host species to elucidate the role of host ecology in the development of parasite assemblages.

1. Introduction

The distance decay in community similarity is emerging as one of the most universal patterns in biogeography (Nekola and White, 1999; Soininen et al., 2007). This pattern, i.e. the rate at which similarity in species composition decreases with increasing distance between localities, can shed light on the relative importance of processes such as dispersal or niche-based community structure (Soininen et al., 2007; Morlon et al., 2008). In parasite ecology, pairwise distances between host populations have long been recognized as determinants of how many parasite species they share (Poulin and Morand, 1999). Significant, and sometimes quite strong, negative relationships between parasite community similarity and distance between host populations have been found in both freshwater and marine fish species (Poulin, 2003; Oliva and González, 2005; Fellis and Esch, 2005; Pérez-del-Olmo et al., 2009; Timi et al., 2010), as well as in other host taxa (Poulin, 2003; Krasnov et al., 2005; Thieltges et al., 2009). Both the slope and strength of these relationships are reflections of discontinuities in the landscape or the probability that parasite species disperse among localities via host movements.

To date, the influence of distance on the similarity of parasite communities has mostly been confined to a geographic context. However, there is no a priori reason why only spatial distances should matter. Decay in similarity should occur with increasing distance along any dimension that characterizes some form of separation between communities. For instance, similarity in parasite communities of freshwater fish can decrease with increasing phylogeographic distance between host populations (Seifertova et al., 2008). Substituting geographical distances between localities with genetic divergence between host populations provides a more accurate picture of host movements among localities, and can result in better predictions of the similarity in parasite species com-

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position among those localities. Along the same lines but on a larger scale, when comparing the parasite faunas of different host species, we might predict that their similarity should decrease with increasing phylogenetic distance: closely-related host species should harbour similar parasite faunas, whereas distantly related hosts should not. This is indeed the pattern among some families of freshwater fish, although the trend is weak as it is confounded by convergent ecological traits in non-related host species (Poulin, in press).

Here, we argue that, in addition to geographic, genetic and phylogenetic distances, similarity in parasite communities should also decay as a function of ontogenetic distances. Two age classes of hosts from the same population are separated by developmental time, just as two host populations are separated in geographical space. In fish hosts, different age classes often live in different habitats and have qualitatively or quantitatively different diets; for instance, as young fish grow and as their gape increases, they eat progressively larger prey, and can even switch to completely different types of prey if they shift to new habitats (e.g., Gerking, 1994; Hyndes et al., 1997; Cocheret de la Morinière et al., 2003). This leads to different age classes being exposed to different subsets of the total assemblage of parasite species that can infect a particular host species. Since young fish begin life with no parasites, small differences in their acquisition of parasites as well as stochastic effects should cause young individual hosts to differ more among each other with respect to the composition of their parasite communities than do older hosts, since longer exposure times may homogenize parasite communities. More importantly than differences within age classes, time combined with ontogenetic shifts in habitat or diet should generate differences between age classes. Indeed, ontogenetic changes in the composition of parasite communities in fish host species are commonly reported (Dogiel et al., 1958; Vidal-Martinez et al., 1998; Johnson et al., 2004; Pérez-del-Olmo et al., 2008). However, the rate of change in community similarity as a function of ontogenetic distance, i.e. between adjacent age classes or between very different age classes, has not previously been quantified in a systematic way that would allow comparisons among host species or tests of hypotheses linking host biology to the development of their parasite communities.

Here, we apply the concept of distance decay of similarity developed in biogeography to ontogenetic changes in the metazoan parasite communities of three species of marine fish from the Atlantic coast of South America. We first apply the methodology to comparisons among host age classes to provide a rigorous way to measure rates of community changes as a function of age, and then use distance decay rates to test specific predictions. The three host species investigated are: (i) the striped weakfish, *Cynoscion guatucupa* (Sciaenidae), a coastal demersal fish with opportunistic feeding habits that preys on crustaceans throughout its life, but becoming increasingly ichthyophagous as it grows (Lopez Cazorla, 1996; Sardiña and Lopez Cazorla, 2005a); (ii) the Argentine anchovy, *Engraulis anchoita* (Engraulidae), a small pelagic fish that remains planktivorous throughout its life, such that although larger fish include larger prey items in their diet than small ones, the composition of the diet changes little during the fish's life (Angelescu, 1982); (iii) the whitemouth croaker, *Micropogonias furnieri* (Sciaenidae), a generalist to opportunist benthic feeder with a diet consisting mainly of macroinvertebrates (crustaceans and polychaetes), and staying more or less the same throughout the fish's life (Sardiña and Lopez Cazorla, 2005b; Mendoza-Carranza and Vieira, 2008).

The present study has four objectives. First, we determined whether the similarity in parasite infracommunities (all parasites within individual hosts) is always lowest within young age classes than within older ones. Second, working at the component community level (all parasites within groups of host), we fitted distance decay relationships to comparisons of parasite communities among age classes in each of the three host species. Third, we determined whether similarity between age classes is consistently lower for a given ontogenetic distance among younger age classes than among older ones. Fourth, we tested whether rates of decay in similarity as a function of ontogenetic distance were higher (i.e. steeper negative slope) in fish species with marked ontogenetic shifts in diet (such as *C. guatucupa*) than in those with less pronounced diet changes (like *E. anchoita*). This last objective also served as an evaluation of whether the concept of distance decay could be useful in determining, based on parasite data alone, whether particular fish species undergo substantial diet shifts as they grow toward adulthood.

2. Materials and methods

2.1. Fish samples and parasite inventories

Fish from the three study species were obtained from commercial fishermen in Mar del Plata (Argentina) and Rio de Janeiro (Brazil) (see Table 1). Except for larval stages, our samples covered practically the full range of sizes observed in the wild for each of the fish species. In the laboratory, each fish was measured (total body length); hereafter, fish length is used as a proxy for age, since age and length are strongly correlated in fish because growth does not stop following maturity. Each fish was then examined for ecto- and endoparasitic metazoans, using standard parasitological methods. Identification of parasite species follows earlier studies of these host species (Alves and Luque, 2001; Timi and Poulin, 2003; Timi et al., 2005). The numbers of parasites from each species as well as the species richness were recorded for each individual fish, and their relationship with fish size was evaluated by means of Spearman rank-correlations.

Within each fish species, individual fish were separated into size classes. The body length intervals defining each size class varied among species (see Table 1), and were chosen to ensure both that each size class included sufficient individual fish for accurate estimates of parasite community composition, and that all size

Table 1
Summary data on three fish species and their parasites.

Host species	Sampling locality	Number of fish examined	Range in length (cm)	Number of size classes	Length interval per size class (cm)[a]	Total parasite species richness	Range of parasite richness per size class
Cynoscion guatucupa	Off Buenos Aires Province (Argentina)	924	3–63	11	5	21	3–18
Engraulis anchoita	Off Buenos Aires Province (Argentina)	598	8–19	9	1	12	7–10
Micropogonias furnieri	Off Rio de Janeiro (Brazil)	245	10–69	6	10	34	13–28

[a] Smallest and largest size classes with slightly broader size ranges.

classes consisted of roughly equivalent numbers of individual hosts. In comparisons between size classes, mean abundance values for each parasite species among all fish within a size class were used to compute similarity measures.

2.2. Similarity indices

Similarity in parasite communities was computed (i) among all possible pairs of individual fish within the same size class, and (ii) among all possible pairs of size classes within a fish species. Two indices of similarity were used: the Jaccard index and the Bray-Curtis index (Magurran, 1988). The Jaccard index is based on presence–absence data only and corresponds to the proportion of all parasite species found in two assemblages put together that is shared by both. The Bray-Curtis index also takes into account differences in abundances of each shared parasite species. Both indices have values potentially ranging from 0 (no species in common) to 100 (all species shared, and in the case of the Bray-Curtis index, all having identical abundances). All similarity values were computed using the software Primer v.6. (Clarke and Warwick, 2001; Clarke and Gorley, 2006).

Similarity values computed among size classes were used in the analyses described in the section that follows. In contrast, similarity values obtained among the parasite infracommunities of individual hosts in a size class were compared visually among size classes. Since the number of fish per size class was always large, the numbers of pairwise similarity values per size class were generally in the thousands, or even tens of thousands; thus all ANOVAs (or Kruskal–Wallis tests) and almost all post hoc comparisons between size classes yield significant results reflecting inflated statistical power rather than true biological significance. We therefore opted for a conservative visual assessment of general patterns.

2.3. Similarity decay relationships

The decay in similarity of parasite communities as a function of ontogenetic distance was assessed for each fish species by plotting log-transformed similarity values against body length differences between all possible pairs of size classes. Since the size ranges of the three fish species were very different, the maximum body length difference, i.e. that between the largest and smallest size classes, differed widely among fish species. To standardize this variable, we converted it to relative length difference, by expressing each body length difference between two size classes as a percentage of the maximum value for that species. This way, the *x*-axis on all plots had the same scale, which allowed unbiased comparisons of decay relationships among fish species.

The following analyses were performed separately for the Jaccard index and for the Bray-Curtis index. Linear regressions were fitted to each of the three plots, and their slope was used as a measure of the rate of decay in similarity as a function of difference in body length (i.e. ontogenetic distance). Since the data are not truly independent in a statistical sense (each size class is used in more than one pairwise comparison), and to account from any deviation from normality in data distributions, the significance of each regression was determined with a randomization approach (Manly, 1997), using the RT 2.1 program (Western EcoSystems Technology, Inc., Cheyenne, WY, USA). All *P*-values are thus based on 1000 data permutations. Pairwise comparisons of slopes between the three fish species were performed using the test recommended by Zar (1984) and based on the Student's *t*-test.

In each fish species, size classes were also categorised as either juvenile or adult fish, based on prior information on each species regarding gonad development as a function of fish body length (Angelescu, 1982; Cassia, 1986; Cousseau and Perrotta, 2004). Different symbols are used in the plots to identify pairwise comparisons between two juvenile size classes, between two adult size classes, and between one juvenile and one adult size classes. This allows one to see where these points lie with respect to the regression line, and determine whether similarity between age classes is consistently lower for a given ontogenetic distance among younger age classes than among older ones.

3. Results

In total, 1767 fish of the three species were examined for the present study (Table 1). Within each species, the number of parasite species per individual host (infracommunity richness) tended to increase with fish body length (*C. guatucupa*: $R_s = 0.76$, $P < 0.01$; *E. anchoita*: $R_s = 0.67$, $P < 0.01$; *M. furnieri*: $R_s = 0.58$, $P < 0.01$); the same pattern was observed for total abundance of all parasite species combined (*C. guatucupa*: $R_s = 0.88$, $P < 0.01$; *E. anchoita*: $R_s = 0.60$, $P < 0.01$; *M. furnieri*: $R_s = 0.65$, $P < 0.01$). Thus, host size, i.e. age, does appear important in the development of parasite communities in these host species.

Complete lists of all parasite species and their mean abundance per size class, for each of the three host species, are available in Supplementary Tables S1–3. In each of the three fish species, the parasite community was dominated by one or a few parasite species that had a more important influence on similarity values than other species. In *C. guatucupa*, the larval cestode *Grillotia carvajalregorum* was by far the numerically dominant species. In *E. anchoita*, the most abundant parasites were tetraphyllidean larval cestodes collectively known as *Scolex polymorphus.* Finally, in *M. furnieri*, most infracommunities were dominated by the nematode *Dychelyne sciaenidicola.* Importantly, all these dominant, and most of the other key metazoan species in the parasite communities investigated, are trophically transmitted, making the composition of these communities subject to ontogenetic changes in host diet.

Similarity of parasite infracommunities among fish within a size class differed among size classes. Generally, using the Bray-Curtis index, similarity values were lowest among small fish (Fig. 1). Similarity was higher among large fish, but the highest similarity values were not necessarily observed among the largest size classes (Fig. 1). Using the Jaccard index, similarity was also always lowest in the smallest size class, though it showed an inconsistent association with size among larger classes (results not shown).

In comparisons among size classes, there was a decrease in the similarity of parasite communities as a function of increasing length differences between size classes (Fig. 2). All regressions based on the Bray-Curtis index of similarity were significant (see Table 2). Those using the Jaccard index were only significant for one fish species (*C. guatucupa*) but nevertheless clearly negative for the other two species (Table 2). When comparing slopes among the three fish species, we found that the decay slope for *C. guatucupa* was significantly steeper than that of the other two species (both $P < 0.01$). However, there was no statistical difference ($P > 0.05$) between the slope of *E. anchoita* and that of *M. furnieri*: both were about half that of *C. guatucupa* (see Table 2).

In all plots using the Bray-Curtis index of similarity, points representing pairwise comparisons between two juvenile size classes tend to lie below the regression line, whereas those representing comparisons between two adult size classes tend to lie either on or above the regression line, but still clearly above points for juveniles (Fig. 2). This indicates that for any given ontogenetic distance, or for a given length difference between two size classes, the similarity in parasite communities is almost always high if they are adult size classes, and almost always low if they are juvenile size classes.

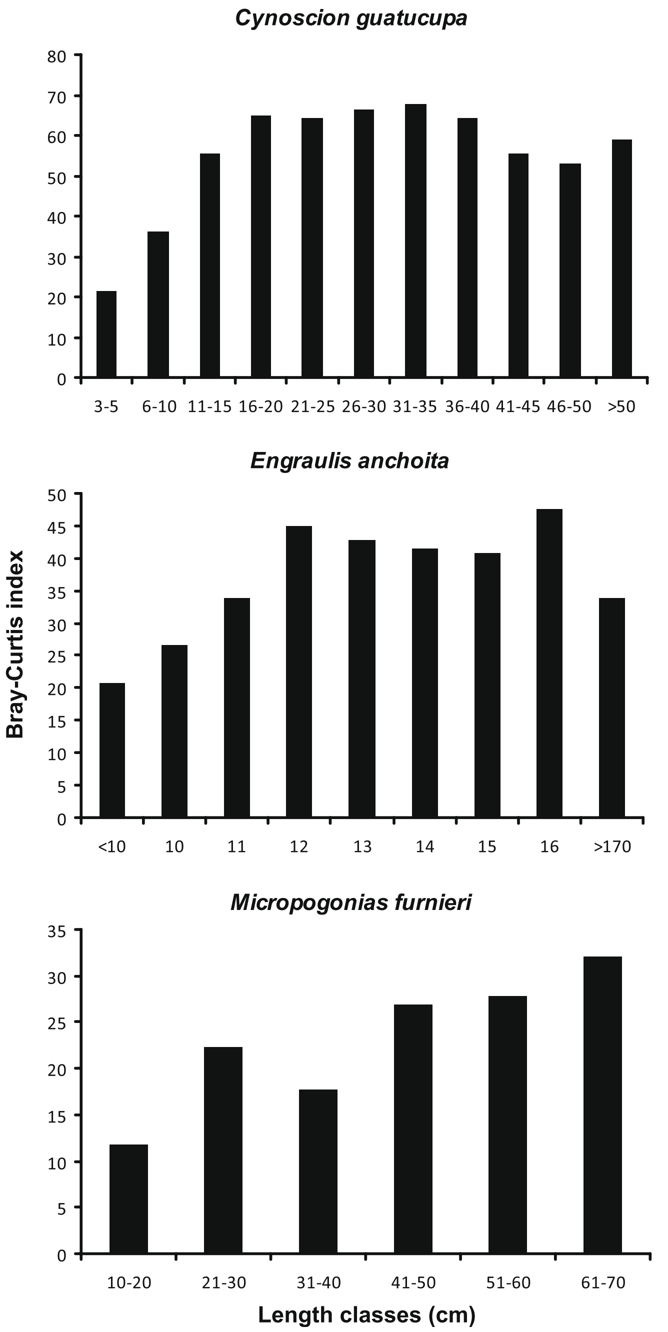

Fig. 1. Average Bray-Curtis similarity values computed among the parasite infracommunities of all individual fish within each size class, for three species of Atlantic marine fish. *Note.* size classes are not the same for the different fish species.

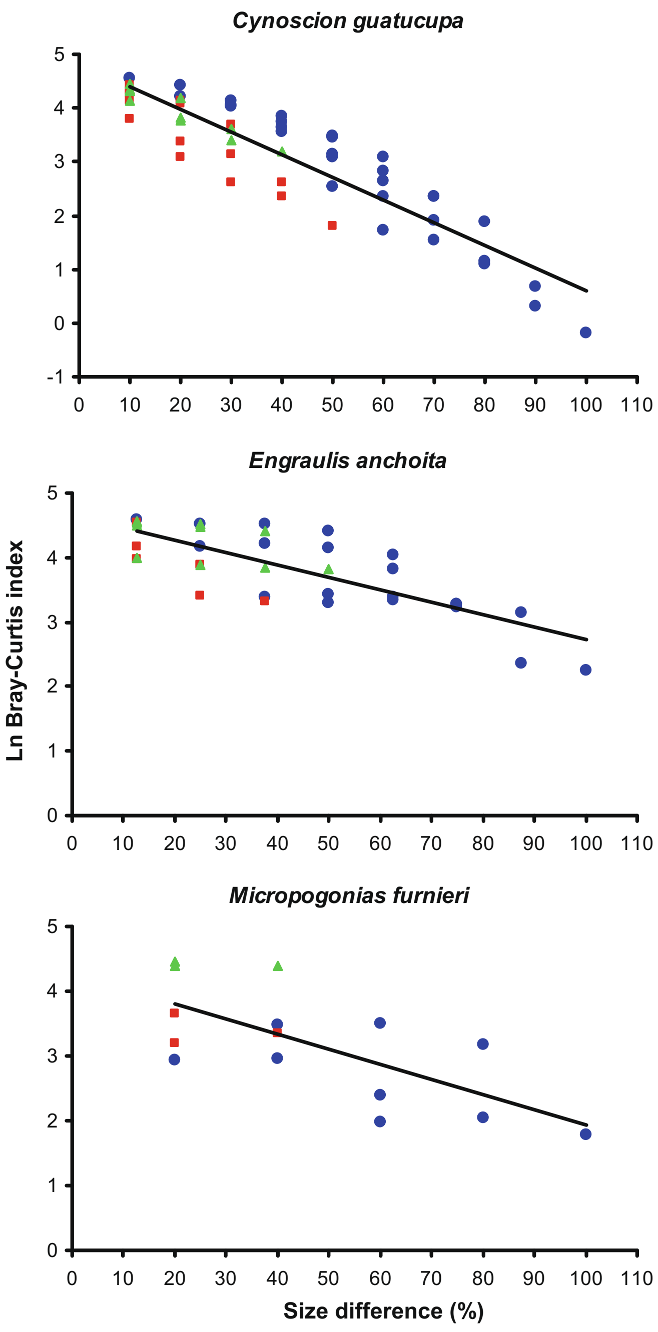

Fig. 2. Decay of similarity, measured with the Bray-Curtis index, as a function of increasing ontogenetic distance, measured as the difference in body length between two host size classes, calculated across all possible pairs of size classes, for three species of Atlantic marine fish. Length differences between two size classes are shown as a percentage of the maximum value for that species. Different symbols are used to identify pairwise comparisons between two juvenile size classes (red squares), between two adult size classes (green triangles), and between one juvenile and one adult size classes (blue circles).

4. Discussion

In natural communities, the process of succession leads to temporal changes in community composition (Connell and Slatyer, 1977). For instance, in plant communities, one possible scenario is that pioneer species first establish on bare ground, and are then gradually replaced over time by species that disperse more slowly or that require specific conditions, such as shading. Any two snapshots of community composition taken at different times would differ, and that difference should be proportional to the length of time between measurements. Similarly, there are ontogenetic changes in the composition of parasite communities in various host species, notably fish (Dogiel et al., 1958; Vidal-Martinez et al., 1998; Johnson et al., 2004; Pérez-del-Olmo et al., 2008). Fish of different age harbour different communities and differences in community composition should be more pronounced when the age difference is large. Earlier studies have reported these patterns but only in a qualitative manner. Here, we applied an approach from biogeography developed to study decay in community similarity as a function of distance, to decreases of similarity as a function of time, or size in the case of fish. This provides for the first

Table 2

Regression statistics for the decay of similarity in parasite communities as a function of increasing ontogenetic distance in three fish species, using two different indices of similarity.

Similarity index	Host species	Number of pairwise comparisons among size classes	Slope	r^2	P
Bray-Curtis	*Cynoscion guatucupa*	55	−0.042	0.83	<0.01
	Engraulis anchoita	36	−0.019	0.62	<0.01
	Micropogonias furnieri	15	−0.023	0.48	0.04
Jaccard	*Cynoscion guatucupa*	55	−0.014	0.32	<0.01
	Engraulis anchoita	36	−0.001	0.07	0.13
	Micropogonias furnieri	15	−0.006	0.21	0.08

time a simple but rigorous quantitative method to measure the rate of community change along host development and to compare these rates across host species.

Our results show that a decay relationship provides a very good fit to comparisons of parasite communities among size classes. Patterns using the Bray-Curtis index (equivalent to the Sorensen index; Magurran, 1988) were clearer than those obtained in analyses using the Jaccard index. This is not surprising, as the Bray-Curtis index incorporates more information about each community, i.e. the abundance of each species as opposed to the presence or absence only, and is less subject to the vagaries of rare species than the Jaccard index. In general, the results obtained here are very comparable to those obtained for conventional similarity decay relationships based on spatial distances as opposed to ontogenetic time (Poulin, 2003; Oliva and González, 2005; Timi et al., 2010). Combined with studies showing that similarity in parasite communities also decays along other dimensions (Seifertova et al., 2008; Poulin, in press), our findings indicate that distance effects are quantitatively similar whatever the distance measure used.

The full value of this approach lies in the fact that it can be used to compare patterns among different host species. Here we compared two fish species, *Engraulis anchoita* and *Micropogonias furnieri*, in which diet shows little change over time as the fish develop from juveniles into adults, with one species, *Cynoscion guatucupa*, in which diet progressively changes from crustaceans to fish as individuals grow larger. We predicted a steeper decay slope in the latter species than in the former two, since the slope reflects the rate at which parasite communities change with growth, and because diet is a key determinant of which parasites a fish is exposed to. Our prediction was confirmed by the results: the slope value for *C. guatucupa* is about twice that for the other two species. As it grows and changes its diet (Lopez Cazorla, 1996; Sardiña and Lopez Cazorla, 2005a), *C. guatucupa* acquires some parasites at an increasingly high rate, and becomes exposed to new ones. Although the larval cestode *Grillotia carvajalregorum* is the dominant species in parasite communities of *C. guatucupa* of all size classes, its abundance is markedly higher in large fish; it is an encysted larval stage that accumulates over time as the fish eat more intermediate hosts. In addition, a monogenean (*Absonifibula estuarina*) is only found in the smallest size classes (Portes Santos and Timi, 2009), whereas two larval cestodes (*Callitetrarhynchus gracilis* and *Dasyrhynchus pacificus*) as well as larval anisakid nematodes (*Anisakis simplex sensu lato*, *Contracaecum* sp., *Hysterothylacium* sp. and *Terranova galeocerdonis*) only appear in mid-sized classes, no doubt a consequence of changes in diet. In contrast, there is no evident disappearance or appearance of parasite species over ontogenetic time in either *E. anchoita* or *M. furnieri*; in these species, dissimilarity in parasite communities results from differences in abundance only. Also, it is important to note that populations of *C. guatucupa* and *E. anchoita* that were sampled are sympatric, and therefore exposed to the same suite of larval parasites, whereas *M. furnieri* were caught in a different faunistic region. Thus, the slope differences observed here are not associated with differences in local faunas. Of course, analyses of more fish species will be necessary to confirm the link between diet shifts and the slope of the similarity decay relationship, since ours included only three host species.

The results of our analyses also demonstrate that juvenile fish harbour more variable and stochastic parasite communities than older fish. Comparisons of infracommunities among small individual fish produce lower similarity values than comparisons among larger individuals; this is true for all three fish species, and with both the Bray-Curtis and Jaccard indices of similarity. Also, in comparisons between size classes, those made between juvenile classes yielded lower similarity values than comparisons made between adult size classes. Therefore, for any given ontogenetic distance, i.e. for a given length difference between two size classes, the similarity in parasite communities is almost always high if they are adult size classes and almost always low if they are juvenile size classes. Young fish begin their life free of parasites and small differences in exposure to different parasites can generate substantial differences among individual hosts, as well as between adjacent size classes. Over time, parasite communities become homogenized by repeated exposure. A similar pattern has been observed in experimental fish, initially uninfected and exposed to natural infections (Vidal-Martinez et al., 1998). Our findings reinforce the assumption that parasite communities in young fish are less predictable than those of older individuals.

In summary, we show that the distance decay of similarity between communities, a phenomenon that applies broadly to parasite communities in geographical space (Poulin, 2003; Oliva and González, 2005; Krasnov et al., 2005; Thieltges et al., 2009; Timi et al., 2010), also applies to parasite community development over host ontology. One important application of this method will be to allow quantitative assessments of the effect of host ecological traits on parasite communities by providing an objective and comparative measure of the rate of change in species composition over time. It may even be possible to infer, from parasitological data alone, whether a particular fish species undergoes marked changes in diet during its life, based on the estimated slope of the decay relationship. This method will be useful to help clarify the link between host ecology and rates of parasite acquisition.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ijpara.2010.02.005.

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