Ontogenetic changes in heterogeneity of parasite communities of fish: disentangling the relative role of compositional versus abundance variability

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SUMMARY

In order to determine how much of the variability in parasite assemblages is driven by differences in composition or in abundance we used multivariate dispersions (average distance from infracommunities to their size class centroid in the multivariate space) as a measurement of β-diversity in infracommunities of *Conger orbignianus*, applying a set of dissimilarity measures with different degrees of emphasis on composition versus relative abundance information. To evaluate comparatively the rate of such changes, we also analysed the effect of host size by regressing differences in β-diversity among size classes against differences in mean fish size. Multivariate dispersions varied along an ontogenetic gradient, its significance depending on the measurement used. Larger fish showed higher richness and abundance; however, smaller fish displayed lower variations in abundance but higher in composition. This could be caused by stochastic encounters at low densities due to the overdispersion of parasites in previous hosts. As fish grow, the composition of their parasite assemblages becomes homogenized by repeated exposure, with abundance thus arising as the main source of variability. Both variables act at different rates, with the exponential decay in the compositional variability as differences in fish size increase being about twice as steep as the decay in abundance variability, indicating that compositional homogeneity is reached faster than abundance heterogeneity as fish grow. Discerning between both variables is crucial in order to understand how community structure is formed by size-dependent variability of host populations.

Key words: *Conger orbignianus*, compositional variability, abundance variability, ontogeny.

INTRODUCTION

For many years, host size has been considered an important determinant of parasite community structure in fish species (Guégan *et al.* 2005; Luque and Poulin, 2008) by affecting parasite diversity through its influence on the rates of parasite speciation and colonization by new parasites at evolutionary and ecological time scales, respectively. However, whereas the relevance of host size as an evolutionary force driving parasite assemblages is still controversial, with many recent papers providing evidence for (i.e. Luque and Poulin, 2007; Timi *et al.* 2010; Poulin and Leung, 2011) and against its importance (i.e. Luque and Poulin, 2008; Timi *et al.* 2011); there is a greater consensus of the effect of fish size at ecological time scales. In fact, ontogenetic changes in the composition of parasite communities in fish host species have been frequently reported (Dogiel *et al.* 1958; Vidal-Martinez *et al.* 1998; Poulin, 2000; Poulin and Valtonen, 2001; Timi and Poulin, 2003; Johnson *et al.* 2004; Pérez-del-Olmo *et al.* 2008).

An increase in both parasite abundance and species richness in larger hosts is a common feature of fish–parasite systems (Poulin, 2000, 2004; Valtonen *et al.* 2010; Timi *et al.* 2011). However, these patterns are far from universal (Poulin, 2007; Luque and Poulin, 2008), probably because hosts inherit parasites from their ancestors, mostly independently of their body size (Poulin, 2007), and because other variables, related to size, may cloud any underlying association between host size and parasite diversity; among these variables, trophic level and longevity have been proposed (Luque and Poulin, 2008; Timi *et al.* 2011; Alarcos and Timi, 2012).

In any case, and independently of the strength and shape of the relationship between fish size and parasite diversity, other size-related patterns of parasite diversity have been recently observed. Indeed, it has been reported that, within given host species, juvenile fish harbour more variable and stochastic parasite assemblages than older hosts (Timi *et al.* 2010), while a similar picture has been observed across species for fish with low trophic level compared to those with higher trophic level (Timi *et al.* 2011). In the first case, this pattern was attributed to the fact that fish begin their life free of parasites and small differences in exposure to

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different parasites can generate substantial differences between individual hosts. Over time, parasite communities become homogenized by repeated exposure (Timi *et al*. 2010). In the second case, it was suggested that fish with low trophic levels display more heterogeneous parasite assemblages because they harbour impoverished assemblages, drawn by stochastic events of encounter at low densities as a consequence of the dilute nature of parasite distributions in previous intermediate invertebrate hosts. The similarity in high-trophic level fish can be reinforced by the accumulation of higher numbers of infective stages acquired as packets of helminth species (Bush *et al*. 1993) that travel together in paratenic hosts along food chains (Timi *et al*. 2011).

The proposed explanations for such patterns involve changes in both the identity and the amount of parasites in the assemblages along an ontogenetic or trophic gradient. However, an important issue remains unsolved: to discern how much of this variability is driven by differences in composition or abundance of assemblages. Here we address this issue by applying multivariate dispersions as a measure of β-diversity of parasite assemblages of the Argentine conger, *Conger orbignianus* Valenciennes, 1837, using a series of dissimilarity measures with different degrees of emphasis on presence/absence versus relative abundance information, which are analysed in relation to changes in fish size (Anderson *et al*. 2006). The original measure of β-diversity (Whittaker, 1960) represents the proportion by which a given area is richer than the average of samples within it. Here we apply the concept of β-diversity proposed by Anderson *et al*. (2006), which considers that β-diversity can be measured as the variability in species composition among sampling units for a given area at a given spatial scale; in other words, it can be measured as the average distance (or dissimilarity) from an individual unit to the group centroid, defined in the principal coordinate space of the dissimilarity measure chosen. The possibility of testing statistical differences of dispersion among size classes (Anderson, 2006), also allows us to study the rate at which similarity in assemblage dispersion tends to decay exponentially with increasing differences in host size. In other words, it allows us to study β-diversity as turnover (Anderson *et al*. 2011), and to measure and compare the rates of such variations as a function of fish size along a gradient that emphasizes compositional versus abundance information.

MATERIALS AND METHODS

Fish samples and parasite inventories

A total of 50 congers, *Conger orbignianus*, were examined for parasites. Fish were caught by trawl in waters off Villa Gesell, Argentina (37°30′ S/56°39′ W) on 20 June 2010. Fish were either kept fresh or were deep frozen in plastic bags at −18 °C until examination. After thawing, congers were measured for total length (cm). Body surface, gills, branchial and body cavities, viscera (stomach, intestine, liver, gall bladder, spleen, heart, gonads and mesenteries), swim bladder, kidneys and musculature were examined with the aid of a stereoscopic microscope. Parasites were recovered, identified and their prevalence and mean abundance were calculated, as well as the total abundance and species richness of each infracommunity, following Bush *et al*. (1997).

Relationships between fish size and parasite population descriptors

The effect of fish size on parasite abundance was analysed for those species with prevalence >10%, as well as for species richness and total abundance by means of Spearman rank correlations. For the same set of parasite species, logistic regressions were used on presence/absence data to determine the effect of fish size on parasite prevalence (Zar, 1999).

β-diversity as a measurement of compositional and abundance variability

Following the protocol of Anderson *et al*. (2006), β-diversity was measured as the variability in species composition among sampling units (individual fish) for a given area (fish sample), and it was calculated as the average distance or dissimilarity from an individual unit to the group centroid, using different distance or dissimilarity measurements, with the centroid being defined in the principal coordinate space of the dissimilarity measure chosen. For delimiting samples, fish were ordered by size and arbitrarily divided into 10 consecutive size groups ($n = 5$ fish each).

To reveal how much of the dissimilarity is driven by compositional difference and how much is driven by differences in relative abundance, we applied a series of dissimilarity and distance measures. These were, in order of their relative emphasis on composition versus abundance information, the Jaccard index of compositional dissimilarity (presence/absence), the Bray-Curtis index, which includes relative abundance information, the modified Gower log 10 which explicitly weights an order-of-magnitude change in abundance the same as a change in species composition, the modified Gower log 2, which weights a compositional change equal to a doubling in abundance and the Euclidean distance on both log-transformed and raw data (Anderson, 2006; Anderson *et al*. 2006, 2011).

The effect of fish size on β-diversity was analysed in 2 ways, with reference to the 2 types of β-diversity as defined by Anderson *et al.* (2011): non-directional variation and directional turnover along a fish size gradient. For non-directional variation, averaged distances to centroids were calculated for each sample (age class) with the different dissimilarity measurements and their values regressed against the averaged fish size in each sample. Since average distances to centroids of different indices were at very different orders of magnitude, to standardize these variables we converted them to relative distances by expressing each value as a percentage of the maximum value for a given index. In this way, the y-axis on all plots had the same scale, which allowed visual comparisons of regression slopes between indices. The analyses were repeated after grouping congers in 5 size classes (10 fish each) and 7 size classes (7 fish each, smallest conger excluded), in order to reassure that results are not an artifact of the arbitrary groupings. This also increased the number of fish per size class in the analyses, but decreased the number of values for regressions. Linear regressions of Euclidean distances on raw data were repeated after log-transformations of average distances to centroids (Log $(x+1)$-transformation for Modified Gower, base 2), to linearize data and because residuals were observed to increase with fish size for some indices in preliminary analyses.

For analysing the effect of host size on β-diversity as turnover, differences in β-diversity among size classes were compared through a multivariate test for homogeneity in multivariate dispersions, with P-values being obtained by permutation of residuals (Anderson, 2006). The variations of β-diversity as a function of host size was assessed by plotting log-transformed differences in β-diversity values against differences in mean fish size between all possible pairs of samples; this procedure was repeated after replacing differences in β-diversity by their P-values. Linear regressions were fitted to each plot, and their slope was used as a measure of the rate of decay in similarity as a function of difference in host size. Since differences of distances to centroids of different indices were at very different orders of magnitude, these variables were also converted to relative distances as in the case of previous analyses. Since data are not truly independent in a statistical sense (each sample was used in more than one pair-wise comparison), and to account for any deviation from normality in data distributions, the significance of all regressions was determined by permutation procedures. All *P*-values are based on 10 000 data permutations.

All analyses were implemented in PERMANOVA+ for PRIMER package (Anderson *et al.* 2008), multivariate dispersions and the significance of their comparisons were applied using the routine

PERMDISP, whereas the routine distLM was used for all regression analyses.

RESULTS

In total 13 909 helminth individuals were recovered from the whole sample. All congers were found parasitized by at least 2 of 21 parasite species. Spores of *Myxidium* sp. were also found in gall bladders at relatively high prevalence (Table 1) but, because only their presence was recorded, myxosporeans were not included in analyses. Twelve helminth species showed prevalences higher than 10%, including 5 intestinal (4 at adult and 1 at larval stage) and 7 non-intestinal larval parasites. The maximum values of prevalence were for *Grillotia carvajalregorum*, *Cucullanus bonaerensis*, *Corynosoma australe* and *Hysterothylacium deardorffoverstreetorum*, with *G. carvajalregorum* and *C. australe* also displaying notably high values of abundance. Eight species showed a significant increase of abundance in larger fish (Table 2). The same species also displayed a higher prevalence in larger fish, except for *G. carvajalregorum*, which was present in 49 out of the 50 congers, and *P. australis*, which show no variations in abundance with fish size (Table 2). A strong positive relationship was observed between fish length and both species richness and total abundance (Rs = 0·54 and 0·59, respectively; both $P < 0·01$).

Analyses of β-diversity as non-directional variability in fish divided in 10 size classes showed that average distance to centroids behaved differentially in relation to fish size depending on the dissimilarity/distance measure used (Fig. 1). Measures emphasizing compositional differences (Jaccard), decreased significantly with increasing fish size (R^2: 0·84, $P < 0·01$); the same pattern was observed after slightly increasing the emphasis on parasite abundance with Bray-Curtis (R^2: 0·55, $P = 0·01$) and modified Gower, base 10 (R^2: 0·70, $P < 0·01$) (Fig. 1A–C). In contrast, analyses emphasizing differences in relative abundances (Euclidean on raw data) indicated the opposite trend: significantly greater variation among large fish compared with smaller ones (R^2: 0·54, $P = 0·02$) (Fig. 1F). In fact, distances to centroids based on Euclidean distances on raw data showed no relationship with fish size ($R^2 = 0·07$, $P > 0·05$), but this was due to the presence of 2 congers harbouring an unusually high number of *C. australe* (1128 and 2364, respectively) and belonging to 2 different size classes; the removal of these outliers yielded the relationship shown in Fig. 1F. Therefore, variation in species composition was greater in smaller congers, while variation in relative abundances was greater in larger fish. The analysis based on modified Gower base 2 (Fig. 1D) showed a tendency to decrease with fish size, while in contrast the analysis based on the Euclidean distances on log transformed abundances

Table 1. *Taxonomic composition, microhabitat, and population descriptors of parasites of Conger orbignianus in the Argentine Sea*

Parasite species	Stage	Microhabitat	Prevalence	Mean abundance ± S.D
Myxosporea				
Myxidium sp	Spores	Gall bladder	34	–
Digenea				
Otodistomum sp.	Metacercaria	Stomach wall	22	0·36 ± 0·88
Prosorhynchus australis Szidat, 1961	Adult	Intestine	58	9·82 ± 18·32
Prosorhynchus sp.	Adult	Intestine	14	1·32 ± 4·65
Acaenodera spinosior Etchegoin, Lanfranchi, Cremonte et Timi, 2006	Adult	Intestine	6	0·42 ± 2·14
Cestoda				
Scolex polymorphus Müller, 1784	Plerocercoid	Intestine	38	4·60 ± 15·67
Grillotia carvajalregorum (Carvajal et Rego, 1983)	Plerocercus	Mesent./gut wall	98	147·16 ± 168·34
Nybelinia sp.	Plerocercoid	Mesent./gut wall	34	0·82 ± 1·65
Nematoda				
Anisakis simplex (Rudolphi, 1809) *s.l.*	LIII	Mesent./gut wall	8	0·12 ± 0·43
Terranova galeocerdonis (Thwaite, 1927)	LIII	Mesenteries	2	0·02 ± 0·14
Contracaecum sp.	LIII	Mesent./gut wall	62	4·72 ± 8·84
Pseudoterranova sp.	LIII	Mesenteries	2	0·02 ± 0·14
Hysterothylacium deardorffoverstreetorum Knoff, Felizardo, Iñiguez, Maldonado Jr., Torres, Magalhães Pinto et Corrêa Gomes, 2012	LIII	Mesent./gut wall	84	5·08 ± 7·16
Hysterothylacium sp. 1	LIII	Mesenteries	2	0·08 ± 0·56
Proleptus sp.	LIII	Stomach wall	4	0·06 ± 0·31
Cucullanus pedroi Timi et Lanfranchi, 2006	Adult	Intest./gut wall	94	6·20 ± 4·65
Capillaria navoneae Timi, Rossin et Lanfranchi, 2006	Adult	Intestine	24	0·46 ± 0·93
Ascarophis marina (Szidat, 1961)	Adult	Intestine	6	0·30 ± 1·39
Hysterothylacium aduncum (Rudolphi, 1802)	Adult	Intestine	2	0·02 ± 0·14
Hysterothylacium sp. 3	Adult	Intestine	2	0·02–0·14
Acanthocephala				
Corynosoma australe Johnston, 1937	Juvenile	Mesenteries	86	95·42 ± 365·94
Corynosoma cetaceum Johnston et Best, 1942	Juvenile	Mesenteries	44	1·14 ± 1·77

(Fig. 1E) showed the opposite pattern. Regression analyses, however, did not detect statistically significant relationships for these indices (R^2: 0·22 and 0·19, respectively; both $P > 0·05$). The slopes of all regressions clearly show this gradual change in the relative importance of composition and abundance in parasite communities as fish grow (Fig. 1). The same patterns were observed after Log-transformation of data, but with slightly increased values of R^2 (except for Bray-Curtis index) and of the significance of regressions (Table 3). All dissimilarity/distance measures displayed the same relationships with fish length after grouping fish into 7 or 5 size classes (Table 3), showing that the effect of fish size on compositional and abundance variability was independent of the arbitrary grouping procedures used.

Analyses of β-diversity as turnover showed an increase in the differences of distance to centroids of parasite communities as a function of increasing length differences between 10 size classes for the same dissimilarity/distance indices that showed significant changes of non-directional variability (Table 4, Fig. 2). The slopes of regression lines showed that the similarity decay for the Jaccard index (Fig. 2A) was about twice as steep as that for Euclidean distance on raw data (2 outliers removed) (Fig. 2F), indicating a stronger change in the variability of community composition than of abundance as fish grow. Exactly the same pattern was observed when differences in distance to centroids were replaced by the P value of multivariate test for homogeneity in multivariate dispersions (data not shown). As the same patterns were observed after grouping fish into 7 or 5 size classes for analyses of β-diversity as non-directional variability, no analyses of β-diversity as turnover were carried out for these two groupings.

DISCUSSION

The present study extends the list of species parasitizing *C. orbignianus* in the Argentine Sea. Tanzola and Guagliardo (2000) reported 10 helminth species in this host from Bahia Blanca, southern Buenos

Table 2. Relationships of the length of *Conger orbignianus* with the mean abundance (Spearmann correlations) and prevalence (logistic regressions) of parasites with prevalence >10% (more than 5 host parasitized)

| Parasite species	Spearman correlation		Logistic regression			
	Rs	P	X2	P	Odds ratio	95% confidence interval
Otodistomum sp.	0·18	>0·05	1·97	>0·05	–	–
P. australis	0·27	>0·05	4·36	0·01 < P < 0·05	1·05	1·00–1·10
Prosorhynchus sp.	0·33	0·01 < P < 0·05	5·70	0·01 < P < 0·05	1·09	1·00–1·19
S. polymorphus	−0·04	>0·05	0·04	>0·05	–	–
G. carvajalregorum	0·58	<0·01	2·91	>0·05	–	–
Nybelinia sp.	−0·16	>0·05	2·05	>0·05	–	–
Contracaecum sp.	0·38	<0·01	10·07	<0·01	1·08	1·03–1·14
Hysterothylacium sp.1	0·67	<0·01	5·30	0·01 < P < 0·05	1·08	1·00–1·15
C. pedroi	0·54	<0·01	9·20	<0·01	1·24	1·00–1·53
C. navoneae	0·34	0·01	7·39	<0·01	1·09	1·01–1·16
C. australe	0·67	<0·01	11·18	<0·01	1·14	1·04–1·25
C. cetaceum	0·59	<0·01	20·43	<0·01	1·15	1·06–1·24
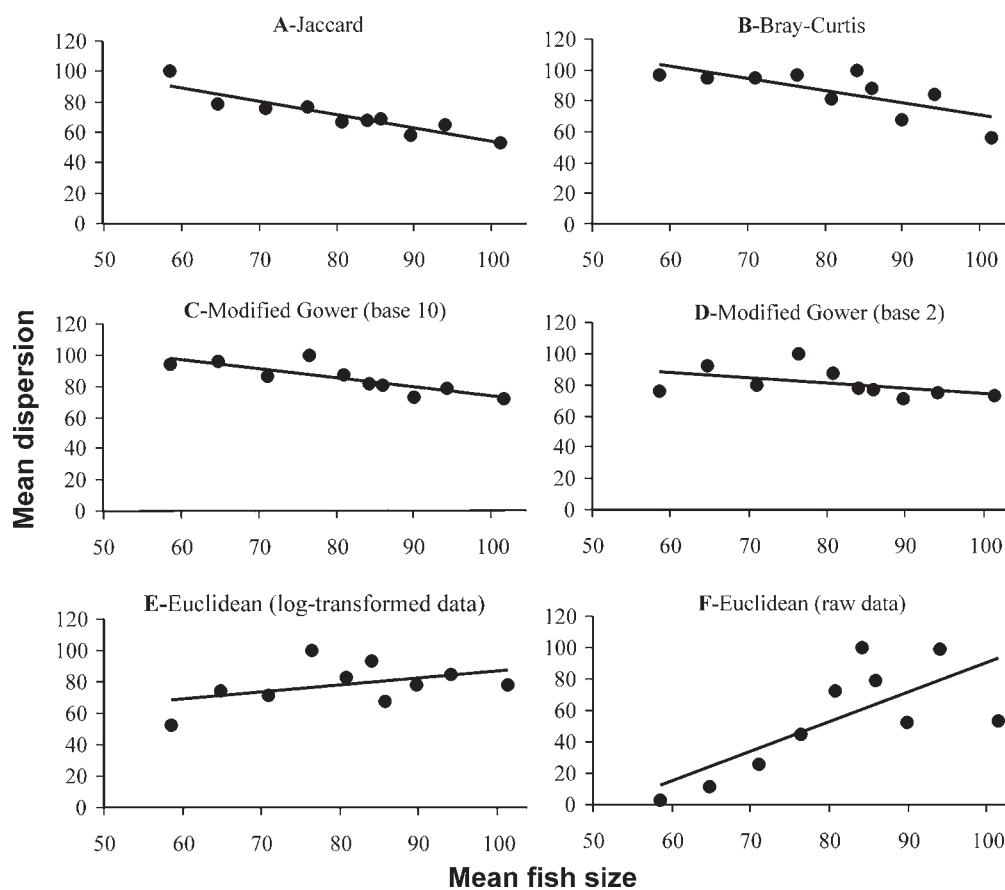
Fig. 1. Relationship between *β*-diversity as non-directional variation of parasite infracommunities, measured as average distance to centroid, and mean size of *Conger orbignianus* classified in 10 size classes, using each of several dissimilarity measures as indicated. Distances to centroids are shown as a percentage of the maximum value for that dissimilarity index.

Aires Province. Later, other species were added to the list by taxonomic studies carried out in waters off Mar del Plata (Etchegoin *et al.* 2006; Timi and Lanfranchi, 2006; Timi *et al.* 2006). In the present paper 13 new host records are reported, including *Myxidium* sp., *Otodistomum* sp., *Prosorhynchus* sp., *Nybelinia* sp., *A. simplex*, *Pseudoterranova* sp., *H. deardorffoverstreetorum*, *Hysterothylacium* sp. 2, *Hysterothylacium* sp. 3, *H. aduncum*, *Proleptus* sp., *A. marina* and *C. cetaceum*.

The Argentine conger is a semelparous species. They reach sexual maturity after living for a period

Table 3. *Regression parameters between fish length and log-transformed distances to centroids of infracommunities of* Conger orbignianus *distributed into size classes with different size ranges and based on dissimilarity/distance measurements with different emphasis on composition versus abundance information*

Disimilarity/distance measure	10 size classes		7 size classes		5 size classes	
	R^2	P	R^2	P	R^2	P
Jaccard	0·87	<0·01	0·92	<0·01	0·96	<0·01
Bray-Curtis	0·54	<0·01	0·65	0·01<P<0·05	0·88	0·01<P<0·05
Modified Gower, base 10	0·71	<0·01	0·78	<0·01	0·91	<0·01
Modified Gower, base 2	0·24	>0·05	0·50	>0·05	0·70	>0·05
Euclidean on log-transformed abundance	0·23	>0·05	0·04	>0·05	0·10	>0·05
Euclidean on raw abundante	0·67	<0·01	0·63	0·01<P<0·05	0·73	0·01<P<0·05

Table 4. *Regression parameters between differences in fish length and differences in distance to centroids of infracommunities of host size classes based on dissimilarity/distance measurements with different emphasis on composition versus abundance information*

Dissimilarity/distance measure	R^2	P	Slope
Jaccard	0·54	<0·01	1·7507
Bray-Curtis	0·11	0·01<P<0·05	0·8922
Modified Gower, base 10	0·34	<0·01	1·5201
Modified Gower, base 2	0·00	>0·05	0·0328
Euclidean on log-transformed abundance	0·02	>0·05	0·3200
Euclidean on raw abundance	0·15	<0·01	0·6779

in coastal waters, cease feeding, decalcify, lose their teeth and migrate to deep waters to spawn in a still unknown region (Figueroa *et al*. 2010). Despite the fact that all congers living in shallow waters can be considered as juveniles, the species richness they reach is one of the highest recorded for fishes in the region, and it is comparable to those of other piscivorous fish with opportunistic habits, such as *Merluccius hubbsi, Cynoscion guatucupa, Percophis brasiliensis* and *Paralichthys patagonicus* (Sardella and Timi, 2004; Timi *et al*. 2005; Braicovich and Timi, 2008; Timi *et al*. 2011; Alarcos and Timi, 2012).

The high species richness harboured by *C. orbignianus*, as well as the high abundance of several parasites, make this host-parasite system a suitable one for analysing the effect of fish size on community structure in terms of both composition and abundance. As expected, a strong increase of both variables was observed with increasing fish length. This kind of relationship is frequently observed in fish–parasite systems, due to larger bodied hosts being able to harbour more parasite species and to sustain a greater number of individuals than small ones; they also provide larger surface areas and more diverse niches for parasite attachment and ingest larger quantities of food with a higher exposure

to infective stages (Guégan *et al*. 1992; Poulin, 2000, 2004, 2007; Valtonen *et al*. 2010). Large fish can also feed on larger prey, broadening the range of potential parasites (Timi *et al*. 2011). Fish of different sizes, but exposed to the same pool of infective stages, acquire therefore qualitatively or quantitatively different parasite assemblages depending on the amount and type of prey they eat. In fact, larger congers tend to be more piscivorous than smaller ones, although carcinophagy is maintained throughout their life-span (Cousseau and Perrotta, 2004). Increasing differences in intraspecific characteristics as fish grow leads them, consequently, to be exposed to increasingly different subsets of infective stages of parasites available in the environment. These differences represent mainly changes in the relative proportions of larval stages acquired as a consequence of changes in the ratio of invertebrates/fish eaten, rather than a replacement of species by shifts in dietary items. On the other hand, the dominance in the assemblages of long-lived parasites, which persist for long periods in the host, indicates that not only fish size, but also age, contribute to the increasing abundance as fish grow.

The observed variability of β-diversity along the ontogenetic gradient, in the shape of average dissimilarities from infracommunities to their size class centroid in the multivariate space, clearly showed that its significance depended on the dissimilarity measure used. It was evident that smaller fish displayed high variation in species composition, while relative abundances of species were more variable in larger hosts. The lower compositional similarity among smaller fish can be a consequence of stochastic events of acquisition of infective stages, which occur in previous intermediate invertebrate hosts at low densities (Marcogliese, 1995, 2002). Over time, repeated exposure can lead to more homogeneous assemblages in terms of composition (Timi *et al*. 2010), with abundance arising consequently as the main source of variability in larger fish.

As suggested for changes observed in β-diversity of invertebrates associated with kelp holdfasts of different size, increased heterogeneity of abundance
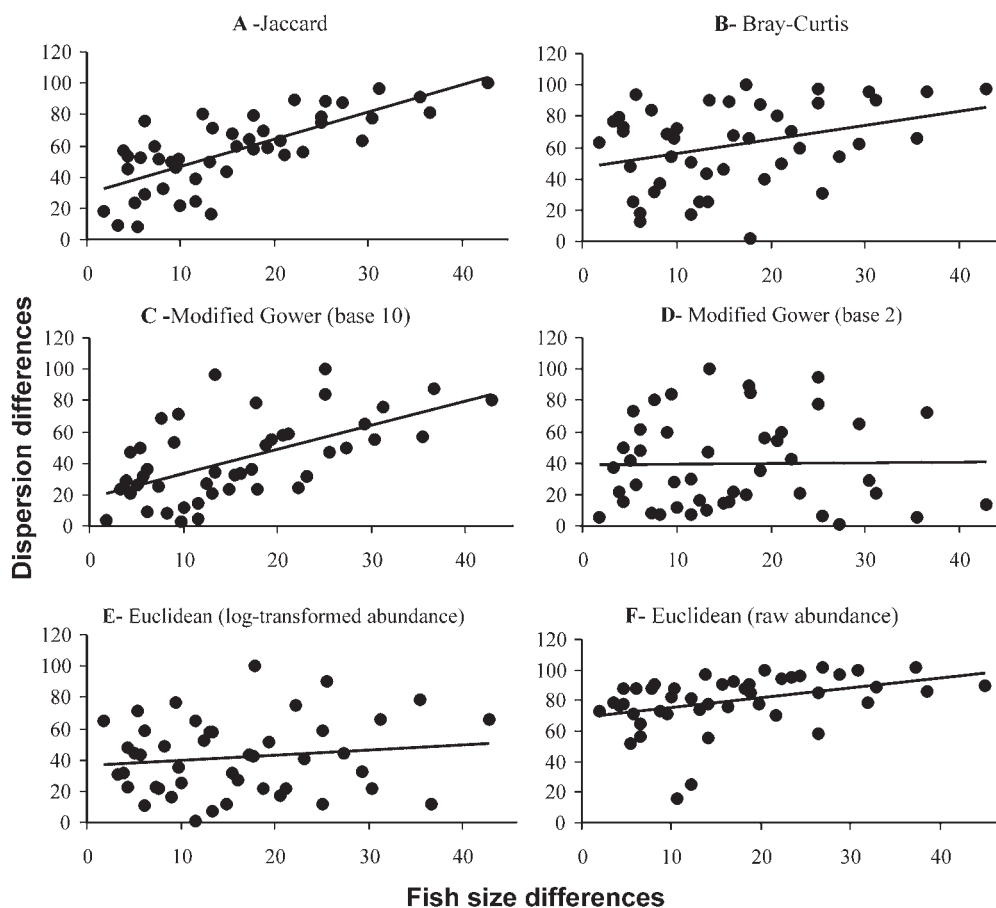
Fig. 2. *β*-diversity as directional turnover of parasite infracommunities of *Conger orbignianus* using each of several dissimilarity measures, as indicated. *β*-diversity measured as log-transformed differences between average distance to centroids, as a function of increasing size differences in body length between two host size classes, calculated across all possible pairs of size classes. Differences between distances to centroids are shown as a percentage of the maximum value for that dissimilarity index.

in larger 'habitats' can also be merely a consequence of Taylor's power law (variance increasing with the mean) (Anderson *et al*. 2006), due to the cumulative effect of long-lived parasites in our host-parasite system. Intrinsic mean–variance relationships in abundances for measuring multivariate dispersion based on different dissimilarity measures and its consequences are still unclear and require further research (Anderson *et al*. 2006). However, biological causes such as differential availability of prey items at microgeographical spatial scales, individual dietary preferences or selectivity, and aggregated distribution of trophically-transmitted parasites in previous hosts, could lead to increasingly variable immigration rates, resulting in the observed patterns. On the other hand, higher variations in extinction rates (parasite death) in larger fish are less probable, because of the dominance of species persisting for long periods, even throughout the entire host life-span.

For each dissimilarity/distance measure, *β*-diversity showed a similar behaviour in relation to host size irrespective of the number of fish in each size class, as well as of the number of size classes. Therefore, these observed patterns reflect real biological processes and are not artifacts due to the arbitrary grouping of fish in size classes, nor to the number of congers in each size class. This was confirmed by performing similar analyses on a sample of anchovies, *Engraulis anchoita* from the same region, divided into 16 size classes of 30 fish each (*unpublished data*). This larger dataset showed patterns of variation of multivariate dispersions, in terms of both composition and abundance, along an ontogenetic gradient similar to those of congers. However, further studies should be based on larger numbers of size classes and including a broader spectrum of fish age or developmental stages (juvenile to adults) in order to determine the specific shape of this kind of relationship along host ontogeny.

Our analyses not only allowed the discernment between the effect of both composition and abundance on the heterogeneity of parasite assemblages along a host ontogenetic range, but also showed that both variables act at different rates. Indeed, the significant exponential decay in the compositional variability as a function of increasing length differences between size classes was about twice as steep as the decay in abundance variability. In other words,

compositional homogeneity is reached faster than abundance heterogeneity as fish grow. This may indicate that a threshold in species richness exists for a given component community, which obviously depends on the pool of potentially infective stages available in the environment. On the other hand, changes in abundance, especially in the proportion of different parasite species (relative abundance), produce a gradual, but continuous increase of heterogeneity as fish grow.

This is, to the best of our knowledge, the first attempt to disentangle quantitatively the relative role of compositional versus abundance variability on heterogeneity of parasite assemblages during fish ontogeny. We acknowledge that analyses were carried out along a restricted portion of the length range of *C. orbignianus*, which in turn do not display marked changes in diet composition at these sizes. Further studies including broader size ranges, as well as host species with different feeding habits, could shed some light on the generality of these patterns, and could lead to the proposal and testing of new hypotheses linking size/age variability in host populations with the development of their parasite communities.

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