Journal of Fish Biology (2008) **72,** 189–204
doi:10.1111/j.1095-8649.2007.01695.x, available online at http://www.blackwell-synergy.com

Linking ecology with parasite diversity in Neotropical fishes

J. L. LUQUE* AND R. POULIN†‡

**Departamento de Parasitologia Animal, Universidade Federal Rural do Rio de Janeiro, Caixa Postal 74.508, CEP 23851-970, Seropédica, RJ, Brazil and †Department of Zoology, University of Otago, P. O. Box 56, Dunedin 9054, New Zealand*

(Received 25 February 2007, Accepted 13 September 2007)

A comparative analysis was performed to seek large-scale patterns in the relationships between a set of fish species traits (body size, type of environment, trophic level, schooling behaviour, depth range, mean habitat temperature, geographical range, ability to enter brackish waters and capability of migration) and the diversity of their metazoan parasite assemblages among 651 Neotropical fish species. Two measurements of parasite diversity are used: the species richness and the taxonomic distinctness of a fish's parasite assemblage, including all metazoan parasites, ectoparasites only, or endoparasites only. The results showed that, on this scale, the average taxonomic distinctness of parasite assemblages was clearly more sensitive to the influence of host traits than parasite species richness. Differences in the taxonomic diversification of the parasite assemblages of different fish species were mainly related to the fish's environment (higher values in benthic–demersal species), trophic level (positive correlation with increasing level), temperature (positive correlation with temperature in marine ectoparasites, negative in endoparasites; positive for all groups of parasites in freshwater fishes) and oceanic distribution (higher values in fish species from the Pacific Ocean than those of the Atlantic). The results suggest that, among Neotropical fish species, only certain key host traits have influenced the processes causing the taxonomic diversification of parasite assemblages.

Key words: host phylogeny; Neotropical fishes; oceanic distribution; taxonomic distinctness; temperature; trophic level.

INTRODUCTION

Parasitism plays a central role in fish biology. Parasites influence individual host survival and reproduction, they can alter fish behaviour and migration patterns, and they can even regulate fish populations and affect fish community structure (Gordon & Rau, 1982; Poulin & FitzGerald, 1987; Garnick & Margolis, 1990; Barber & Poulin, 2002). Understanding why certain fish species are plagued by more parasite species than other fish species is thus an important issue in fish ecology. Yet, despite several comparative studies that have tried to link ecological features of fish species to the diversity of parasites exploiting them, a general answer to this question is no closer.

---

‡Author to whom correspondence should be addressed. Tel.: +64 3 479 7983; fax: +64 3 479 7584; email: robert.poulin@stonebow.otago.ac.nz

The main problem is that the results available to date show very little consistency (Poulin & Morand, 2004). For every study suggesting that larger-bodied fish species harbour more parasite species than small-bodied fish (Price & Clancy, 1983), there is another study finding no association between fish body size and parasite species richness (Sasal *et al.*, 1997). For every study pointing to an influence of fish diet on parasite diversity (Bell & Burt, 1991), there is one finding no effect of diet (Poulin, 1995). One reason for these contrasting findings may be that earlier studies often failed to control for two important confounding variables, study effort and the influence of phylogenetic relationships among fish species (Poulin & Morand, 2004). In addition, the vast majority of studies to date have focused on North American and European fish species, which places some limits on the wider generality of any observed patterns. Finally, almost all previous studies have used parasite species richness as their sole measurement of parasite diversity; other facets of diversity, such as the taxonomic or phylogenetic distinctness of the parasite taxa exploiting a fish species, can be more sensitive to host ecology, and can shed further light on what ecological traits of a fish lead to the accumulation of new parasite species.

Here, the relationships between ecological features of host species and parasite diversity are explored among freshwater and marine fish species of the Neotropical region. The data set compiled to this end is not only one of the largest and most extensive ever used for a comparative analysis of parasite diversity but it is also from a previously mostly ignored biogeographical area. The present analyses take into account both sampling effort and host phylogeny, and use both parasite species richness and the taxonomic distinctness of parasite species in an assemblage as measurements of parasite diversity. The biological significance of the main patterns to emerge from these analyses is then discussed in an effort to pinpoint the key drivers of parasitism in fishes.

MATERIALS AND METHODS

PARASITOLOGICAL DATA

The data set used here included all known freshwater and marine fishes from the Neotropical region for which at least four host–parasite associations have been recorded. The following parasite taxa were included: Monogenea, Aspidogastrea, Digenea, Cestoda, Acanthocephala, Nematoda, Pentastomida, Mollusca (glochidia of certain bivalve taxa), Hirudinea, Copepoda, Branchiura and Isopoda. The data set resulted from a search through the Zoological Records and CAB Abstracts databases up to December 2006, as well as the use of other specialized monographs; full details are given in Luque & Poulin (2007). The complete list of references used to generate the data set is available upon request from the authors. In the data set, each entry is a host-parasite record, *i.e.* a known association between a parasite species and a fish species. Several synonymies in the nomenclature of parasite species were detected during the searches and resolved using the most recent taxonomic literature.

HOST DATA

The data set included parasite records from fish species of two large taxa, Actinopterygii (ray-finned fishes) and Chondrichthyes (cartilaginous fishes). Introduced freshwater species, *e.g.* cichlids (*Oreochromis* spp., *Tilapia* spp.), cyprinids (*Carassius* spp., *Cyprinus* spp.)

and salmonids (*Salmo* spp., *Oncorhynchus* spp.) were excluded, because the parasite fauna of exotic fishes is not the one they have acquired over evolutionary time in their area of origin. To solve numerous cases of synonymies among fish species, valid species names were adopted according to FishBase (Froese & Pauly, 2006).

In addition to parasite species richness (known number of metazoan parasite species per fish species), habitat (fresh water or marine) and the maximum total length (L_T; in nearest 10 mm) of each fish species were recorded. The following variables were also scored for each fish species: (1) whether the fish species forms schools or not, with species adopting schooling only in some parts of the year (*e.g.* during the reproductive period) classified as schooling; (2) whether the fish's environment is benthic-demersal, benthopelagic, pelagic or reef-associated; the latter category was not used for freshwater species; (3) the trophic level of the fish species, *i.e.* its position in the food web, determined by the number of energy-transfer steps to that level and estimated from available diet data (Froese & Pauly, 2006); (4) its depth range, measured as the difference between the deepest and shallowest depths at which it occurs (only for marine species); (5) whether or not it occasionally enters brackish or estuarine waters (only for marine species); (6) the mean water temperature of the distribution area of the fish species; (7) its ability to migrate, oceanodromous in the case of marine fishes or potamodromous for freshwater species; (8) its general geographical distribution, whether cosmopolitan-circumglobal, circumtropical or restricted to the Neotropics (only for marine species); (9) whether its geographical distribution extends to South America or to Central America only or both South America and Central America (only for freshwater species); (10) oceanic distribution (Pacific Ocean, Atlantic Ocean or both) in the Neotropics (for marine fishes only).

All this information was obtained from FishBase (Froese & Pauly, 2006), though for a number of fish species about which information was missing, data were obtained from several museum and fish websites and from specific local literature.

As a measurement of the extent of the knowledge about the different fish species, an index of study effort was used, taken as the number of publications on each fish species found in a search of the Zoological Record (1978–2006) electronic database. The Latin names, including all known synonyms, of each species were used as keywords during the searches. This measurement of study effort provides an indirect estimate of the number of fish individuals that were actually examined specifically for parasites, as it generally correlates strongly with that number (Poulin, 2004; Luque & Poulin, 2007). Host sample size is often an important correlate of known parasite species richness (Walther *et al.*, 1995), and a correction for study effort can serve to control for spurious sampling effects.

The continuous variables investigated here (*e.g.* parasite species richness, maximum host body length and study effort), all required $\log_{10}$-transformation ($\log_{10}x + 1$ if zeros were present) to meet the assumptions of parametric statistical tests.

TAXONOMIC DISTINCTNESS OF PARASITE ASSEMBLAGES

The average taxonomic distinctness (Δ^+) of the parasite species recorded (Clarke & Warwick, 1998, 1999; Warwick & Clarke, 2001) was computed for each fish species. This index measures the average taxonomic distance between different parasite species in an assemblage: the greater the value of the index, the greater the average taxonomic difference between species in the assemblage (Luque *et al.*, 2004). This was done in three ways for each fish species: for all parasite species, for endoparasites (trematodes, cestodes, acanthocephalans, pentastomids and nematodes) only and for ectoparasites (molluscs, monogeneans, hirudineans and crustaceans) only.

For the computations of Δ^+, the Taxobiodiv 1.2 programme was used (available from http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2). The computation of this index is based on a taxonomic hierarchy of the parasite species based on the Linnean classification into kingdom, phyla, classes, orders, families, genera and species. For this, the following taxonomies were used: Gibson *et al.* (2002), Olson *et al.* (2003) and Jones *et al.* (2005) for trematodes; Boeger & Kritsky (1993) for monogeneans; Khalil *et al.* (1994) for cestodes; Amin (1985) for acanthocephalans; Anderson (2000) for nematodes; Apakupakul *et al.* (1999) for hirudineans; Ruppert *et al.* (2004) for molluscs; Boxshall & Halsey (2004) for copepods; Martin & Davis (2001) for branchiurans and pentastomids and Bunkley-Williams & Williams (1998) for isopods.

STATISTICAL ANALYSES

Analyses were performed separately for marine actinopterygian, freshwater actinopterygian and marine chondrichthyan species. In the analyses, host phylogeny was taken into account. Closely related host species are likely to harbour similar number of parasite species, and possibly taxonomically related parasite species, *via* inheritance from a common ancestor, and are thus not truly independent statistical observations (Morand & Poulin, 2003). To control for phylogenetic influences when evaluating the effects of host features (*e.g.* body size and schooling or feeding habits) on the evolution of parasite assemblages, the phylogenetically independent contrasts method (Felsenstein, 1985; Harvey & Pagel, 1991) was used. To compute independent contrasts in continuous variables, the PDAP:PDTREE programme (Midford *et al.*, 2005) was used, implemented in Mesquite Modular System for Evolutionary Analysis, Mesquite version 1.12 (Maddison & Maddison, 2006). For categorical variables (*e.g.* schooling behaviour and tolerance of brackish waters), contrasts were computed with the pair-wise comparisons programme for Mesquite version 1.12, using the methodology and algorithm to contrast species pairs in one binary character proposed by Maddison (2000). When the categorical variables studied were not dichotomous (*e.g.* fish environment), a sequence of calculations was performed with binary data to detect possible significant differences between the contrasts.

Contrasts were derived from three host trees (marine actinopterygian, freshwater actinopterygian and marine chondrichthyan fish species) constructed from 69 published studies on the phylogenetic relationships of fishes, mainly molecular phylogenies. Phylogeny of the orders and higher taxonomic levels was based on Nelson (2006). The trees and the list of fish studies used are available as an electronic appendix at http://www.otago.ac.nz/zoology/downloads/poulin/FishParasiteData.xls.

Contrasts were computed on $\log_{10}$-transformed data and all regression analyses were forced through the origin (Garland *et al.*, 1992). Contrasts corrected for the influence of confounding variables (*e.g.* study effort) were obtained by taking the residuals of regressions of a selected variable against the potential confounding variables. Because the aim was to uncover associations between host features and measurements of parasite diversity, a Bonferroni correction was not applied to the results, as it can mask interesting trends worthy of further investigation (Moran, 2003). Only associations significant at the 0·05 probability level are reported hereafter.

RESULTS

The data set included 8766 host–parasite associations involving 651 fish species from the Neotropics (mean ± S.D. 13·5 ± 11·5 parasite records per fish species), all with parasite species richness values ≥ 4. Of these fishes, 338 were marine actinopterygian, 259 freshwater actinopterygian and 54 marine chondrichthyan species. They were distributed among 73 marine actinopterygian, 40 freshwater actinopterygian and 18 marine chondrichthyan families. Table I shows mean ± S.D. of study effort, parasite species richness and Δ^+ for the groups of fishes analysed. The entire data set including all variables for each fish species is available as an electronic appendix (http://www.otago.ac.nz/zoology/downloads/poulin/FishParasiteData.xls).

Whether considering all parasites, only ectoparasites or only endoparasites, there were apparent differences in study effort, and in all three measurements of parasite diversity among the three groups of fishes (see Table I), with

TABLE I. Number (n) of fish species from the Neotropics used in the analyses and their respective mean ± S.D. for study effort, parasite species richness and taxonomic distinctness (Δ^+)

Group of fish	n	Study effort	Species richness	Δ^+
Marine actinopterygian				
All metazoan parasites	338	30·67 ± 76·43	13·84 ± 10·75	78·66 ± 12·21
Ectoparasites	168	45·44 ± 99·30	8·86 ± 5·12	72·27 ± 15·14
Endoparasites	259	33·10 ± 81·99	10·87 ± 7·01	70·02 ± 15·16
Freshwater actinopterygian				
All metazoan parasites	259	31·15 ± 95·62	14·00 ± 13·21	78·64 ± 14·08
Ectoparasites	70	41·09 ± 45·89	9·10 ± 6·49	61·04 ± 19·98
Endoparasites	216	32·85 ± 100·91	12·64 ± 11·41	78·64 ± 11·61
Marine chondrichthyan				
All metazoan parasites	54	32·46 ± 43·94	8·54 ± 4·63	74·01 ± 13·71
Ectoparasites	12	60·00 ± 70·24	7·17 ± 2·29	65·41 ± 15·89
Endoparasites	42	35·19 ± 48·49	7·05 ± 2·95	64·42 ± 13·99

chondrichthyans differing from both marine and freshwater actinopterygians. This, along with the habitat and phylogenetic gaps between these groups, justified treating them in separate analyses.

For both freshwater and marine actinopterygians, parasite species richness correlated with study effort ($r = 0{\cdot}444$, $P < 0{\cdot}001$, $n = 259$; $r = 0{\cdot}453$, $P = 0{\cdot}01$, $n = 338$, respectively) and with the size of the host ($r = 0{\cdot}140$, $P < 0{\cdot}05$, $n = 259$; $r = 0{\cdot}161$, $P < 0{\cdot}01$, $n = 338$, respectively); study effort and host size were not significantly correlated with each other. When correcting species richness for sampling effort by using the residuals of a regression between these variables, parasite species richness was no longer related to the host size (both $P > 0{\cdot}05$). All subsequent analyses used only parasite richness corrected for study effort. For both freshwater and marine actinopterygians, values of Δ^+ were correlated with species richness ($r = 0{\cdot}132$, $P < 0{\cdot}05$, $n = 259$; $r = 0{\cdot}370$, $P < 0{\cdot}001$, $n = 338$, respectively) but not with study effort (both $P > 0{\cdot}05$). Δ^+ is hereafter corrected for parasite richness. Once corrected, Δ^+ did not correlate with host size, for either freshwater or marine actinopterygians (both $P > 0{\cdot}05$). For chondrichthyans, in contrast, parasite species richness and Δ^+ showed no correlation with study effort or host size, and Δ^+ did not correlate with species richness. Thus, for chondrichthyans, no corrections for confounding variables were necessary.

MARINE ACTINOPTERYGIANS

When all metazoan parasites were included in the analyses, a positive correlation emerged between Δ^+ and fish trophic level ($r = 0{\cdot}128$, $P < 0{\cdot}05$, $n = 312$) (Fig. 1), and higher values of Δ^+ were detected in benthic–demersal fishes (number of contrasts = 10, $P < 0{\cdot}05$). Fishes with a distribution restricted to the Neotropics showed higher values of parasite species richness (number of contrasts = 7, $P < 0{\cdot}01$) than circumglobal species. Fishes from the Pacific Ocean showed slightly higher values of Δ^+ (number of contrasts = 19, $P > 0{\cdot}05$)

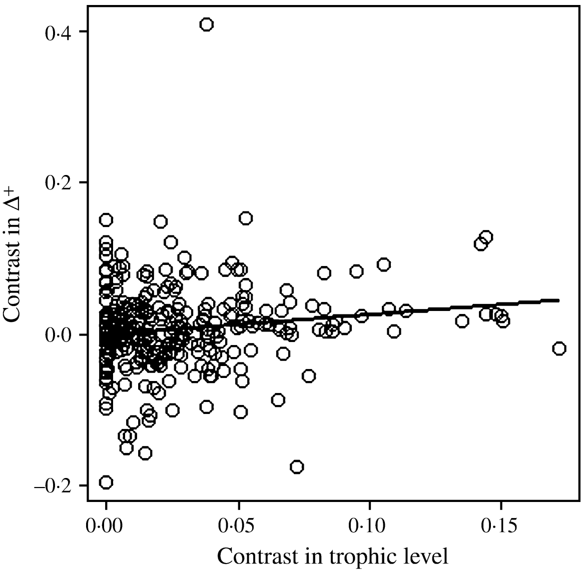

FIG. 1. Average taxonomic distinctness (Δ^+; corrected for parasite species richness) of all metazoan parasites as a function of host trophic level in marine actinopterygian species based on 312 phylogenetically independent contrasts. The curve was fitted by: $y = 0{\cdot}23x$.

(Fig. 2) than Atlantic and amphi-oceanic species. Additionally, values of parasite species richness and Δ^+ were compared with a paired two-tailed *t*-test between congeneric fish species from the Pacific and Atlantic coasts of the Neotropics. Most genera are only represented in one area by a single species, but in cases where two or more species occurred in one ocean the average values computed across all congeneric species present were taken. Taking into account all metazoan parasites, there were no differences between Pacific and Atlantic fish species for either parasite richness (paired *t*-test, d.f. = 38, $P > 0{\cdot}05$) or Δ^+ (paired *t*-test, d.f. = 38, $P > 0{\cdot}5$).

For ectoparasites only, Δ^+ was correlated with temperature ($r = 0{\cdot}152$, $P = 0{\cdot}05$, $n = 167$) [Fig. 3(a)]. No significant differences were detected between Pacific, Atlantic and amphi-oceanic fish species (see Fig. 2). Among endoparasite assemblages, the species richness (number of contrasts = 9, $P < 0{\cdot}05$) was higher in schooling species. Benthic–demersal fishes showed higher values of Δ^+ (number of contrasts = 5, $P < 0{\cdot}05$) than other fishes. The Δ^+ was negatively correlated with temperature ($r = -0{\cdot}135$, $P < 0{\cdot}05$, $n = 258$ contrasts) [Fig. 3(b)] and positively correlated with the depth range ($r = 0{\cdot}124$, $P < 0{\cdot}05$, $n = 258$ contrasts). A direct comparison between Pacific and Atlantic congeneric fishes revealed higher values of Δ^+ in Pacific fishes (paired *t*-test, d.f. = 30, $P = 0{\cdot}01$).

FRESHWATER ACTINOPTERYGIANS

When all metazoan parasites were analysed, significant correlations were observed between the Δ^+ and both fish trophic level ($r = 0{\cdot}179$, $P < 0{\cdot}01$, $n = 258$ contrasts) [Fig. 4(a)] and temperature ($r = 0{\cdot}136$, $P < 0{\cdot}05$, $n = 258$

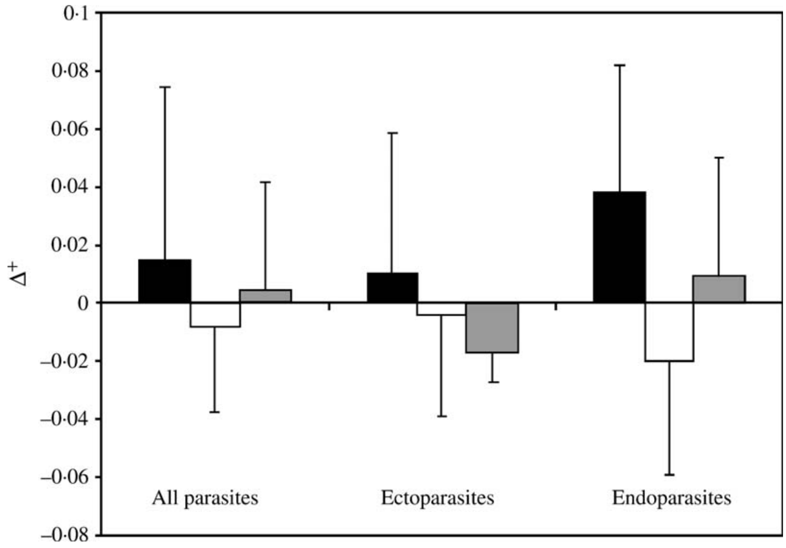

FIG. 2. Mean ± S.E. average taxonomic distinctness (Δ^+; corrected for parasite species richness) of all metazoan parasites ($n = 102$, 193 and 43), ectoparasites ($n = 41$, 103 and 24) and endoparasites ($n = 74$, 155 and 30) in marine actinopterygian species from the Pacific Ocean (■), the Atlantic Ocean (□) and amphi-oceanic species (▨) in the Neotropical region. Measurements of taxonomic distinctness are residuals of the regression of $\log_{10}\Delta^+$ and $\log_{10}$ species richness, and are thus corrected for species richness.

contrasts) [Fig. 5(a)]. The Δ^+ of ectoparasite assemblages was correlated with host size ($r = 0{\cdot}240$, $P < 0{\cdot}05$, $n = 69$ contrasts) and with temperature ($r = 0{\cdot}276$, $P < 0{\cdot}05$, $n = 69$ contrasts) [Fig. 5(b)]. For endoparasite assemblages, parasite species richness was correlated with host size ($r = 0{\cdot}145$, $P < 0{\cdot}05$, $n = 215$ contrasts). The Δ^+ was correlated with trophic level ($r = 0{\cdot}168$, $P < 0{\cdot}05$, $n = 215$ contrasts) [Fig. 4(b)] and with temperature ($r = 0{\cdot}172$, $P < 0{\cdot}05$, $n = 215$ contrasts) [Fig. 5(c)]. The difference in parasite species richness between freshwater fish species from Central America and those of South America detected in Luque & Poulin (2007) and confirmed in this study ($F_{2,258}$, $P < 0{\cdot}001$) disappeared when data were corrected for host phylogeny.

MARINE CHONDRICHTHYANS

There was a negative correlation between host size and parasite species richness in assemblages including all parasite species ($r = -0{\cdot}297$, $P < 0{\cdot}05$, $n = 53$ contrasts). None of the other ecological variables included in this study showed a significant correlation with either of the measurements of parasite diversity for ectoparasite or endoparasite assemblages.

DISCUSSION

Characteristics of host individuals have been identified as key determinants of the probability of acquiring parasites because of their heterogeneity. Using

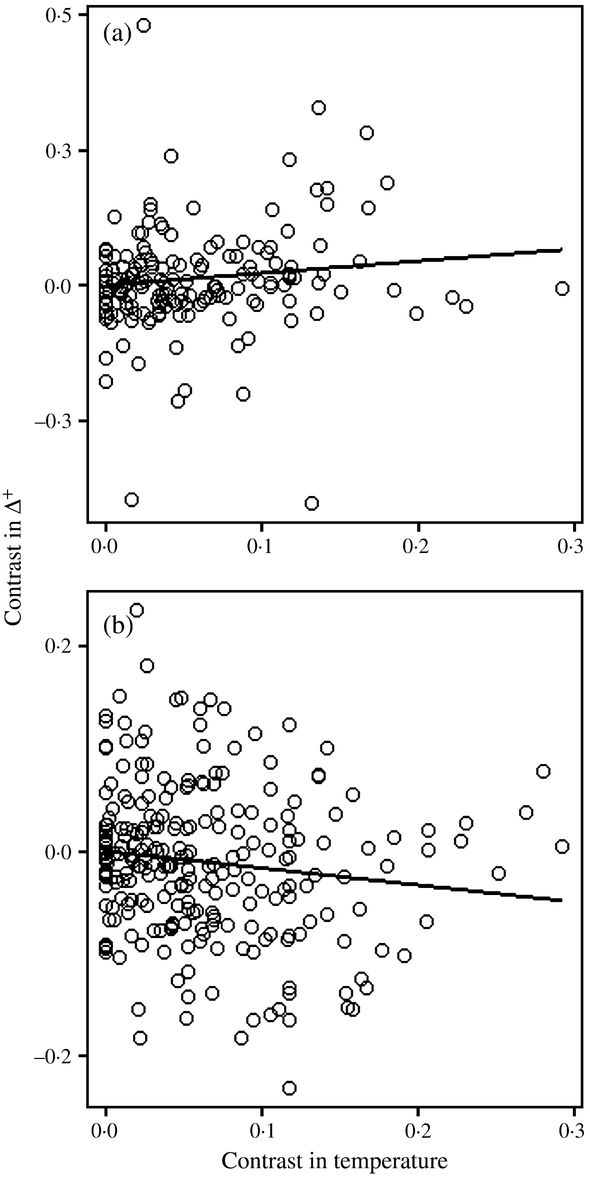

FIG. 3. Average taxonomic distinctness (Δ^+; corrected for parasite species richness) of (a) ectoparasites based on 167 phylogenetically independent contrasts and (b) endoparasites based on 258 phylogenetically independent contrasts, as a function of temperature of the distribution area in marine actinopterygian species. The curves were fitted by: (a) $y = 0{\cdot}271x$ and (b) $y = -0{\cdot}168x$.

the variability of these key features among individual hosts, hosts that are more likely to harbour many parasites can be predicted. The same arguments should hold across different host species, even if in this case parasite acquisition occurs on an evolutionary time scale (Poulin & Morand, 2004). Recent studies searched for correlations between parasite diversity (number of parasite species

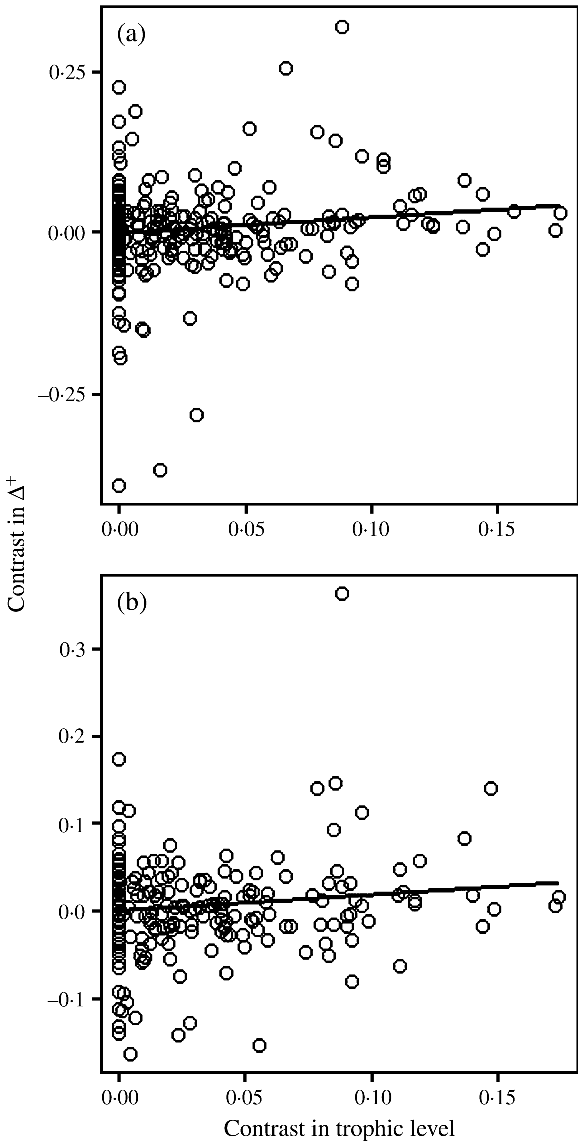

FIG. 4. Average taxonomic distinctness (Δ^+; corrected for parasite species richness) of (a) all metazoan parasites based on 258 phylogenetically independent contrasts and (b) endoparasites based on 215 phylogenetically independent contrasts as a function of host trophic level in freshwater actinopterygian species. The curves were fitted by: (a) $y = 0{\cdot}338x$ and (b) $y = 0{\cdot}244x$.

per host species) and several host features, *e.g.* host size, feeding habits, schooling behaviour and population density (freshwater fishes: Poulin, 2001; Simková *et al.*, 2001; Takemoto *et al.*, 2005; marine fishes: Sasal *et al.*, 1997; Morand *et al.*, 2000; Luque & Poulin, 2004; Luque *et al.*, 2004). Most of these, however, have used only species richness as a measurement of the diversity of parasite assemblages. Species richness is a convenient measurement, but it does not

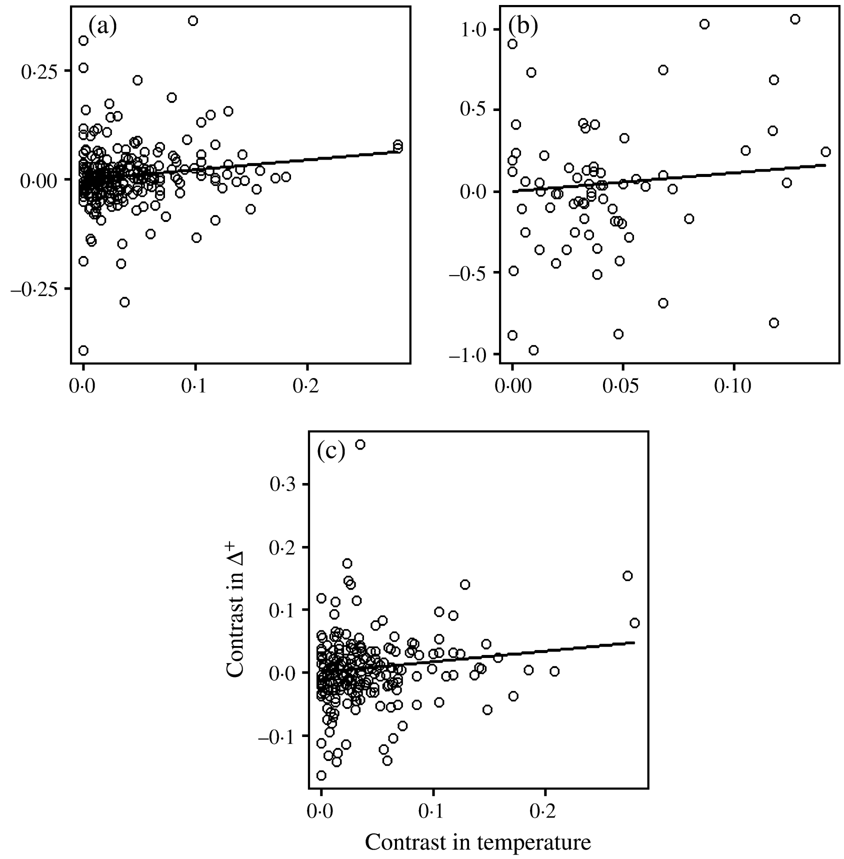

FIG. 5. Average taxonomic distinctness (Δ^+; corrected for parasite species richness) of (a) all metazoan parasites based on 258 phylogenetically independent contrasts, (b) ectoparasites based on 69 contrasts and (c) endoparasites based on 215 contrasts as a function of temperature of the distribution area in freshwater actinopterygian species. The curves were fitted by: (a) $y = 0{\cdot}222x$, (b) $y = 0{\cdot}619x$ and (c) $y = 0{\cdot}214x$.

capture all facets of diversity (Purvis & Hector, 2000), because it ignores the evolutionary relationships among species coexisting in an assemblage (Shimatani, 2001).

The other measurement of diversity used here, the average taxonomic distinctness, focuses on evolutionary relationships among species coexisting in an assemblage and represents the average evolutionary distance among all species. Taxonomic distinctness is seen as a promising tool for biodiversity research and for environmental monitoring and management on a large scale (Ellingsen *et al.*, 2005; Bhat & Magurran, 2006; Leonard *et al.*, 2006). Luque *et al.* (2004) used taxonomic distinctness to assess parasite diversity in marine fishes from Brazil. Although on a local scale, these authors showed that taxonomic distinctness revealed patterns different from those based on parasite species richness, and that shifting the focus from species richness to taxonomic diversity can cast a different light on the evolution of fish parasite biodiversity.

This is the first comparative study of host features as possible determinants of fish parasite diversity that included all marine and freshwater fish species with known parasites from an entire biogeographic realm, in an attempt to distinguish between the possible evolutionary origins of this diversity on a regional scale. At this scale, the Δ^+ was clearly more sensitive to the effects of host traits, mainly the fish's environment, trophic level, temperature and oceanic distribution, than parasite species richness.

Host diet is an expected predictor of parasite diversity in vertebrate hosts (Poulin & Morand, 2004). The use of host trophic level as a continuous variable in the comparative analysis highlighted the relationships between the diversification of the parasite assemblages and the complex marine and freshwater food web over evolutionary time. Trophic level is an accurate index of the location of a host fish in the trophic web (Pauly *et al.*, 1998) and may be a good indicator that fishes at higher levels should be exposed to more infective helminth larvae from a broader range of parasite taxa *via* their diet than those at lower trophic levels over evolutionary time. This should translate in higher parasite colonization rates in high trophic level fishes, pushing up their equilibrium parasite species richness.

The structure and dynamics of food webs allows predictions about the distribution and abundance of parasites, and their influence on food-web structure *via* their regulation of the dominant host species (Marcogliese, 2001, 2002). Independently of the trophic web, however, it is possible that the diversity of parasite assemblages in benthic fishes is higher than in pelagic or reef-associated fishes because the benthic boundary layer is a focal point for parasite exchange among faunas inhabiting different vertical zones in marine habitats (Marcogliese, 2002). Thus, the partitioning of resources in terms of the dietary preferences of fishes and the number of energy-transfer steps to specific trophic levels might contribute to the establishment of more diverse parasite assemblages in benthic-demersal environments, as found in the present analyses. This pattern was stronger when endoparasite assemblages were analysed separately, because helminth endoparasites are usually acquired by ingestion.

Another pattern detected in the present study was the relationship between the Δ^+ of parasites and the mean temperature of the distribution area of the fish species. For marine actinopterygians, considering all parasite species, there was no relationship, but when ectoparasites and endoparasites are analysed separately the relationship became positive for ectoparasites but remained negative for endoparasites. Interestingly, in freshwater actinoperygians the correlation between mean temperature and parasite taxonomic distinctness was clearly positive. The relationship between parasite diversity and local mean temperature has been addressed in several papers dealing with latitudinal gradients in species richness. Poulin & Rohde (1997) suggested that the clear relationship between temperature and the richness of marine-fish ectoparasite communities was not a phylogenetic artefact, but an indication of the importance of temperature in the diversification of fish parasites in the tropics. Rohde & Heap (1998) later confirmed this clear pattern, finding that the species richness of ectoparasite assemblages of marine fishes peaked in warm tropical waters. In contrast, they did not find a correlation between temperature and endoparasite species richness in marine fishes, suggesting that biological differences between ectoparasites and endoparasites can explain this difference. The results generally agreed with the patterns mentioned above, and point to temperature not only as a determinant of parasite species richness in marine fishes but also as a key determinant of the taxonomic diversity of parasite assemblages. In the case of freshwater fishes, the study of Choudhury & Dick (2000) and its refinement by Poulin (2001) showed that temperate freshwater fish species are host to richer assemblages of helminth parasites than tropical freshwater fishes. This suggests a negative relationship between parasite species richness and temperature, counter to those usually seen in plant and animal assemblages. The results, although restricted to the Neotropics, do not indicate any correlation between parasite species richness and temperature, though one exists between the taxonomic distinctness of parasites and temperature for all parasites and for ectoparasites and endoparasites treated separately. This could be explained as for marine parasites, with temperature driving not only the increase in the number of parasite species but also an increase of their taxonomic complexity over evolutionary time, mediated by greater rates of speciation and host colonization (Poulin & Morand, 2004).

The results show higher values of parasite taxonomic distinctness in fishes from the Pacific Ocean than in those from the Atlantic or with an amphi-oceanic distribution, the difference apparently caused mainly by endoparasites. Rohde (1986), using data from extensive surveys in the Pacific and Atlantic Oceans, showed that parasite species richness of marine monogeneans is greater in the Pacific. This difference was tentatively explained by an evolutionary time hypothesis: more species of monogeneans have accumulated in the much older Pacific than in the younger Atlantic Ocean. Rohde (1986) also suggested that an ecological time hypothesis might explain the difference; ice sheets during the last glaciation covered much more of the continental shelf in the Atlantic than Pacific Ocean, possibly extinguishing more parasites in the former than in the latter. More evolutionary time available for the accumulation of species is therefore an alternative explanation for higher species richness (Rohde, 1980). Poulin & Rohde (1997) reviewed these data using a more robust analysis, and confirmed this difference between the ectoparasite fauna from both oceans. Luque & Oliva (1999) compared the parasite communities of two congeneric species of *Menticirrhus* from the South American Pacific and Atlantic Ocean, and found higher values of abundance and parasite richness in ectoparasites from *Menticirrhus ophicephalus* (Jenyns) (Pacific) than *Menticirrhus americanus* (L.) (Atlantic), but the opposite was found with respect to endoparasites, suggesting that this pattern depends on the type of parasites studied. After correcting for study effort and phylogenetic constraints, there were no significant differences in parasite richness between oceans, but values of taxonomic distinctness tended to be higher in Pacific species than in Atlantic and amphi-oceanic species, particularly for endoparasites. These results fit with the arguments of Rohde (1986) and provide a further example of the greater sensitivity of taxonomic distinctness to ecological influences.

Other host features were weakly associated with the diversity of fish parasite assemblages in this study. One of them, host size, previously thought to be a good predictor of parasite diversity, was influential only in endoparasite assemblages of freshwater fishes and in parasite assemblages of marine chondrichthyans. Earlier, Luque & Poulin (2007) used all fishes from the Neotropics with at least one known parasite, and found strong positive correlations of parasite richness with host size for marine and freshwater fishes. Here, only host species with a parasite species richness ≥ 4 were used, eliminating many generally small-bodied fish species with few known parasites. A different picture emerged for parasite taxonomic distinctness, which confirmed the patterns reported by Luque *et al.* (2004) for marine fishes from Rio de Janeiro. Also, as seen by Luque *et al.* (2004), fish schooling behaviour and host depth range had no effect on parasite species richness, but were associated with the taxonomic diversity of parasite species in marine endoparasite assemblages. Possibly fishes living across many depths feed on a wider array of prey species, and thus face colonization by a more diverse group of parasites, than fishes restricted to a narrow depth zone. In addition, for hosts such as fishes, schooling behaviour determines host density, which is a known determinant of parasite diversity (Poulin & Morand, 2004).

On a larger scale, several other determinants can influence the diversity of fish parasites in the region. The Neotropics is far from being a homogeneous region. The coastal areas of the Pacific and Atlantic Oceans are strongly influenced by upwellings and by a complex system of currents. The water circulation pattern in this region renders difficult any exchange of fishes between Central and South America, and many fish species may be organized in different populational units along their distributional range or in a latitudinal gradient with variable parasite assemblages (González & Poulin, 2005; Timi *et al.*, 2005). Moreover, salinity levels fluctuate near the Amazon River (Santos & Carbonel, 2000), and presence of reef barriers in north-eastern Brazil (Feitoza *et al.*, 2005) may also limit the dispersal of fishes and their parasites. Another important disturbance is the El Niño–Southern Oscillation event which causes drastic ecological changes in aquatic ecosystems in the region. These conditions may affect fish species diversity in the area, and may also influence parasite biodiversity. The same applies to freshwater species, with great regions of endemism in South America and in Mexican rivers (Domínguez-Domínguez *et al.*, 2006; Hubert & Renno, 2006; Huidobro *et al.*, 2006), the presence of potamodromous species within the great rivers of South America (Carolsfield *et al.*, 2004), and now a significant number of exotic species in the region. All these may be important factors for parasite species distribution and the diversification of parasite assemblages. Therefore, although host ecology matters, biogeographical factors can also affect parasite diversity.

J.L.L. was supported by a fellowship (N° 200906-2005·4) of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) of Brazil for 1 year of postdoctoral research in the Department of Zoology at the University of Otago, New Zealand.

References

Amin, O. M. (1985). Classification. In *Biology of the Acanthocephala* (Crompton, D. W. T. & Nickol, B. B., eds), pp. 27–72. Cambridge: Cambridge University Press.

Anderson, R. C. (2000). *Nematode Parasites of Vertebrates*, 2nd edn. Wallingford: CABI Publishing.

Apakupakul, K., Siddall, M. E. & Burreson, E. M. (1999). Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and molecular gene sequences. *Molecular Phylogenetics and Evolution* **12,** 350–359.

Barber, I. & Poulin, R. (2002). Interactions between fish, parasites and disease. In *Handbook of Fish Biology and Fisheries* (Hart, P. J. B. & Reynolds, J. D., eds), pp. 359–389. Oxford: Blackwell Publishing.

Bell, G. & Burt, A. (1991). The comparative biology of parasite species diversity: internal helminths of freshwater fish. *Journal of Animal Ecology* **60,** 1047–1064.

Bhat, A. & Magurran, A. E. (2006). Taxonomic distinctness in a linear system: a test using a tropical freshwater fish assemblage. *Ecography* **29,** 104–110. doi: 10.1111/j.2006.0906-7590.04418.x

Boeger, W. A. & Kritsky, D. C. (1993). Phylogeny and a revised classification of the Monogenoidea Bychowsky, 1937 (Platyhelminthes). *Systematic Parasitology* **26,** 1–32.

Boxshall, G. A. & Halsey, S. H. (2004). *An Introduction to Copepod Diversity*. London: Ray Society.

Bunkley-Williams, L. & Williams, E. H. Jr (1998). Isopods associated with fishes: a synopsis and corrections. *Journal of Parasitology* **84,** 893–896.

Carolsfield, J., Harvey, B., Ross, C. & Baer, A. (2004). *Migratory Fishes of South America. Biology, Fisheries, and Conservation Status*. Ottawa: World Fisheries Trust, World Bank & IDRC.

Choudhury, A. & Dick, T. A. (2000). Richness and diversity of helminth communities in tropical freshwater fishes: empirical evidence. *Journal of Biogeography* **27,** 935–956. doi: 10.1046/j.1365-2699.2000.00450.x

Clarke, K. R. & Warwick, R. M. (1998). A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology* **35,** 523–531. doi: 10.1046/j.1365-2664.1998.3540523.x

Clarke, K. R. & Warwick, R. M. (1999). The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Marine Ecology Progress Series* **184,** 21–29.

Domínguez-Domínguez, O., Doadrio, I. & Pérez-Ponce de León, G. (2006). Historical biogeography of some river basins in central Mexico evidenced by their goodeine freshwater fishes: a preliminary hypothesis using secondary Brooks parsimony analysis. *Journal of Biogeography* **33,** 1437–1447. doi: 10.1111/j.1365-2699.2006.01526.x

Ellingsen, K. E., Clarke, K. R., Somerfield, P. J. & Warwick, R. M. (2005). Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. *Journal of Animal Ecology* **74,** 1069–1079. doi: 10.1111/j.1365-2656.2005.01004.x

Feitoza, B. M., Rosa, R. S. & Rocha, L. A. (2005). Ecology and zoogeography of deep-reef fishes in northeastern Brazil. *Bulletin of Marine Science* **76,** 725–742.

Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist* **125,** 1–15.

Garland, T. Jr, Harvey, P. H. & Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41,** 18–32.

Garnick, E. & Margolis, L. (1990). Influence of four species of helminth parasites on orientation of seaward migrating sockeye salmon (*Onchorhynchus nerka*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* **47,** 2380–2389.

Gibson, D. I., Jones, A. & Bray, R. A. (2002). *Keys to the Trematoda*, Vol. 1. Wallingford: CABI International.

González, M. T. & Poulin, R. (2005). Nested patterns in parasite component communities of a marine fish along its latitudinal range on the Pacific coast of South America. *Parasitology* **131,** 569–577.

Gordon, D. M. & Rau, M. E. (1982). Possible evidence for mortality induced by the parasite *Apatemon gracilis* in a population of brook sticklebacks (*Culaea inconstans*). *Parasitology* **84,** 41–47.

Harvey, P. H. & Pagel, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Hubert, N. & Renno, J.-F. (2006). Historical biogeography of South American freshwater fishes. *Journal of Biogeography* **33,** 1414–1436. doi: 10.1111/j.1365-2699.2006.01518.x

Huidobro, L., Morrone, J. J. & Alvarez, J. L. (2006). Distributional patterns of freshwater taxa (fishes, crustaceans and plants) from the Mexican transition zone. *Journal of Biogeography* **33,** 731–741. doi: 10.1111/j.1365-2699.2005.01400.x

Jones, A., Bray, R. A. & Gibson, D. I. (2005). *Keys to the Trematoda*, Vol. 2. Wallingford: CABI International.

Khalil, L. F., Jones, A. & Bray, R. A. (1994). *Keys to the Cestode Parasites of Vertebrates*. Wallingford: CABI International.

Leonard, D. R. P., Clarke, K. R., Somerfield, P. J. & Warwick, R. M. (2006). The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessments. *Journal of Environmental Management* **78,** 52–62.

Luque, J. L. & Oliva, M. E. (1999). Metazoan parasite infracommunities of *Menticirrhus* (Teleostei: Sciaenidae): an amphi-oceanic approximation. *Journal of Parasitology* **85,** 379–381.

Luque, J. L. & Poulin, R. (2004). Use of fish as intermediate hosts by helminth parasites: a comparative analysis. *Acta Parasitologica* **49,** 353–361.

Luque, J. L. & Poulin, R. (2007). Metazoan parasite species richness in Neotropical fishes: hotspots and the geography of biodiversity. *Parasitology* **134,** 865–878.

Luque, J. L., Mouillot, D. & Poulin, R. (2004). Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. *Parasitology* **128,** 671–682.

Maddison, W. P. (2000). Testing character correlation using pairwise comparisons on a phylogeny. *Journal of Theoretical Biology* **202,** 195–204.

Marcogliese, D. J. (2001). Pursuing parasites up the food chain: implications of food web structure and function on parasite communities in aquatic systems. *Acta Parasitologica* **46,** 82–93.

Marcogliese, D. J. (2002). Food webs and the transmission of parasites to marine fish. *Parasitology* **124,** S83–S99.

Martin, J. W. & Davis, G. E. (2001). An updated classification of the recent Crustacea. *Contributions in Science, Natural History Museum of Los Angeles County* **39,** 1–124.

Midford, P. E., Garland, T. Jr & Maddison, W. P. (2005). *PDAP Package of Mesquite. Version 1.07*. Riverside, CA: University of California.

Moran, M. D. (2003). Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100,** 403–405. doi: 10.1034/j.1600-0706.2003.12010.x

Morand, S. & Poulin, R. (2003). Phylogenies, the comparative method and parasite evolutionary ecology. *Advances in Parasitology* **54,** 281–302.

Morand, S., Cribb, T. H., Kulbicki, M., Chauvet, C., Dufour, V., Faliex, E., Galzin, R., Lo, C., Lo-Yat, A., Pichelin, S. P., Rigby, M. C. & Sasal, P. (2000). Determinants of endoparasite species richness of New Caledonian Chaetodontidae. *Parasitology* **121,** 65–73.

Nelson, J. P. (2006). *Fishes of the World*, 4th edn. New York: John Wiley & Sons Inc.

Olson, P. D., Cribb, T. H., Tkach, V. V., Bray, R. A. & Littlewood, D. T. J. (2003). Phylogeny and classification of the Digenea (Platyhelminthes: Trematoda). *International Journal for Parasitology* **33,** 733–755.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. Jr (1998). Fishing down marine food webs. *Science* **279,** 860–863.

Poulin, R. (1995). Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs* **65,** 283–302.

Poulin, R. (2001). Another look at the richness of helminth communities in tropical freshwater fish. *Journal of Biogeography* **28,** 737–743. doi: 10.1046/j.1365-2699.2001.00570.x

Poulin, R. (2004). Parasite species richness in New Zealand fishes: a grossly underestimated component of biodiversity. *Diversity and Distributions* **10,** 31–37. doi: 10.1111/j.1472-4642.2004.00053.x

Poulin, R. & FitzGerald, G. J. (1987). The potential of parasitism in the structuring of a salt marsh stickleback community. *Canadian Journal of Zoology* **65,** 2793–2798.

Poulin, R. & Morand, S. (2004). *Parasite Biodiversity*. Washington, DC: Smithsonian Books.

Poulin, R. & Rohde, K. (1997). Comparing the richness of metazoan ectoparasite communities of marine fishes: controlling for host phylogeny. *Oecologia* **110,** 278–283.

Price, P. W. & Clancy, K. M. (1983). Patterns in number of helminth parasite species in freshwater fishes. *Journal of Parasitology* **69,** 449–454.

Purvis, A. & Hector, A. (2000). Getting the measure of biodiversity. *Nature* **405,** 212–219.

Rohde, K. (1980). Diversity gradients of marine monogenea in the Atlantic and Pacific Oceans. *Experientia* **36,** 1368–1369.

Rohde, K. (1986). Differences in species diversity of monogenea between the Pacific and Atlantic Oceans. *Hydrobiologia* **137,** 21–28.

Rohde, K. & Heap, M. (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.

Ruppert, E. E., Fox, R. S. & Barnes, R. D. (2004). *Invertebrate Zoology: A Functional Evolutionary Approach*, 7th edn. Belmont, CA: Brooks Cole Publishing Company.

Santos, C. P. & Carbonel, C. A. A. (2000). The role of physical factors in the distribution of the monogenean fauna in the midwestern and southwestern Atlantic. In *Metazoan Parasites in the Neotropics: A Systematic and Ecological Perspective* (Salgado-Maldonado, G., Garcia-Aldrete, A. N. & Vidal-Martinez, V. M., eds), pp. 61–75. México City: Instituto de Biologia, UNAM.

Sasal, P., Morand, S. & Guégan, J.-F. (1997). Determinants of parasite species richness in Mediterranean marine fish. *Marine Ecology Progress Series* **149,** 61–71.

Shimatani, K. (2001). On the measurement of species diversity incorporating species differences. *Oikos* **93,** 135–147. doi: 10.1034/j.1600-0706.2001.930115.x

Simková, A., Morand, S., Matejusová, I., Jurajda, P. & Gelnar, M. (2001). Local and regional influences on patterns of parasite species richness of central European fishes. *Biodiversity and Conservation* **10,** 511–525.

Takemoto, R. M., Pavanelli, G. C., Lizama, M. A. P., Luque, J. L. & Poulin, R. (2005). Host population density as the major determinant of endoparasite species richness in floodplain fishes of the upper Paraná River, Brazil. *Journal of Helminthology* **79,** 75–84.

Timi, J. T., Luque, J. L. & Sardella, N. H. (2005). Parasites of *Cynoscion guatucupa* along South American Atlantic coasts: evidence for stock discrimination. *Journal of Fish Biology* **67,** 1603–1618. doi: 10.1111/j.1095-8649.2005.00867.x

Walther, B. A., Cotgreave, P., Price, R. D., Gregory, R. D. & Clayton, D. H. (1995). Sampling effort and parasite species richness. *Parasitology Today* **11,** 306–310.

Warwick, R. M. & Clarke, K. R. (2001). Practical measures of marine biodiversity based on relatedness of species. *Oceanography and Marine Biology Annual Review* **39,** 207–231.

Electronic References

Froese, R. & Pauly, D. (2006). *FishBase*. Available at www.fishbase.org (accessed December 2006).

Maddison, W. P. & Maddison, D. R. (2006). *Mesquite: A Modular System for Evolutionary analysis. Version 1.12*. Available at http://mesquiteproject.org