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Greater diversification of freshwater than marine parasites of fish

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ABSTRACT

The species richness of freshwater environments is disproportionately high compared with that of the oceans, given their respective sizes. If diversification rates are higher in freshwaters because they are isolated and heterogeneous, this should apply to parasites as well. Using 14 large datasets comprising 677 species of freshwater and marine fish, the hypothesis that freshwater parasites experience higher rates of diversification than marine ones is tested by contrasting the relative numbers of species per parasite genus between the regional endohelminth faunas of fish in both environments. The relationship between the number of parasite genera and the number of parasite species per host was well described by a power function, in both environments; although the exponent of this function was slightly lower for freshwater parasite faunas than marine ones, the difference was not significant. However, the ratio between the number of parasite species and the number of parasite genera per host species was significantly higher in freshwater fish than in marine ones. These findings suggest fundamental differences between the way parasite faunas diversify in freshwater versus marine habitats, with the independent evolution of conspecific parasite populations in isolated host populations being a more common phenomenon in freshwater environments.

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1. Introduction

Disparities in species richness between environments, such as the contrast between terrestrial, marine and freshwater habitats (May, 1994; Grosberg et al., 2012; Wiens, 2015), suggest that ecological factors may influence net rates of diversification. For instance, freshwater and marine environments, despite very different areas (approximately 2% and 70% of the Earth's surface, respectively), have very similar overall species richness (Wiens, 2015). The fragmented nature of freshwater habitats, leading to greater habitat heterogeneity and geographic isolation, is a plausible reason for the disproportionately high diversification of the freshwater fauna (May, 1994; Grosberg et al., 2012; Wiens, 2015). If this is true for free-living organisms, it should be also for their parasites, because parasites have very limited dispersal abilities of their own. Indeed, populations of parasite species bound to freshwater habitats by their life cycle generally show greater genetic structuring than those utilising mobile hosts such as birds (Criscione and Blouin, 2004; Blasco-Costa and Poulin, 2013). Restricted gene flow is a prelude to parasite speciation (Huyse et al., 2005), and thus we may expect generally higher rates of speciation in parasites of freshwater hosts with spatially isolated populations, than in those of marine hosts living in an open, more homogeneous environment.

The parasite fauna exploiting a given host species can diversify over evolutionary time through three basic processes: (i) intra-host speciation, whereby a parasite species undergoes sympatric speciation, possibly via divergence in preferences for tissue or within-tissue site of infection; (ii) independent evolution of isolated parasite populations, leading to multiple daughter species across the host's geographical range; and (iii) host-switching, i.e. colonisation by new parasite species 'jumping ship' from other sympatric host species (Paterson and Gray, 1997; Vickery and Poulin, 1998). These processes should leave slightly different signatures in extant parasite faunas. If the first two have been predominant, modern parasite faunas should comprise multiple congeneric species. The taxonomic composition of extant parasite faunas can therefore be used to test for differences between major environments in speciation rates. For example, the number of higher taxa, such as genera, represented in an assemblage is a simple power function of species richness across multiple assemblages, and the exponent of this relationship can reveal differences among environments (Enquist et al., 2002; Passy and Legendre, 2006). Variation in the relative number of species per genus across habitats can also capture the effects of different external pressures on rates of speciation and diversification (Krug et al., 2008). These approaches have been used for parasite faunas before, to make comparisons among those

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using different higher taxa of hosts (e.g., fish versus mammals; Mouillot and Poulin, 2004) or hosts with different life history traits (Poulin, 1999), or among ectoparasite faunas exposed to different climatic conditions (Krasnov et al., 2005).

Here, I test the hypothesis that speciation rates are higher in freshwater parasites than in marine ones, because the isolation and heterogeneity of freshwater habitats should favour independent evolution among separate parasite populations (mechanism (ii) above) whereas the openness of marine systems should facilitate spatial overlap among host species and host-switching by parasites (mechanism (iii) above). The hypothesis is tested using combined datasets on the endoparasitic helminths of fish to seek differences in the relative number of species per genus between the faunas of freshwater and marine hosts. These are ideal model systems to test the hypothesis: freshwater and marine fish are roughly comparable resources, they have endoparasite faunas of comparable sizes and consisting of the same higher taxa of helminths (trematodes, cestodes, nematodes and acanthocephalans). The present findings provide some support for the hypothesis and point toward subtle but universal differences in the taxonomic structure of parasite faunas in marine and freshwater fish hosts.

2. Materials and methods

2.1. Data sources

Compilations of all parasites recorded on given host species in particular geographical areas provide extensive data on the parasite faunas of various host species in different habitats. An internet search, using the keywords ‘host parasite checklist’ and the search engine Google, was conducted to find relevant checklists; additional searches were conducted by replacing ‘host’ with ‘fish’, and ‘parasite’ with ‘helminth’. Of all relevant checklists found, only those that could be downloaded as PDF files or that were available through the University of Otago, New Zealand library were used here. Also, only checklists covering all fish species from a large geographical region (i.e., country or continent) were used, and not those restricted to certain host families or specific localities. Although these checklists do not include all published ones, they represent a large and representative sample of available ones.

When a checklist was updated by a new one published later for the same region, the two were combined with care taken to account for synonymies and changes in species nomenclature. Whether or not they were included in the same or separate checklists, freshwater and marine (including brackish waters) fish were assigned to those two habitat types. Only endohelminth parasites (trematodes, cestodes, nematodes and acanthocephalans) are considered here. I excluded all cases of parasites observed in a host species only through experimental infection, or parasites identified only to the genus level if another congeneric parasite in the same host was identified by a full Latin binomial name. When host subspecies or hybrids between host species were listed as distinct hosts, they were treated as such in the present analyses. Finally, only fish host species with at least two endoparasite species in the surveyed region were included, since those with a single parasite species also harbour a single parasite genus. The resulting global dataset included much more freshwater fish species than marine ones; however, given the very large sample sizes (see Section 3), this difference is unlikely to affect the outcome of the analyses.

For each host species, the information recorded thus included the number of parasite species and the number of parasite genera found on it, its habitat (freshwater or marine) and the geographical region in which its parasite fauna was surveyed.

2.2. Data analysis

Power functions (genera $\propto$ species^{b1}) were fitted to the relationship between the number of parasite genera versus the number of parasite species, among freshwater and marine fish separately. The exponent b_1 captures the rate of increase in generic richness as a function of increasing specific richness: the smaller its value compared to 1, the greater the proportion of congeneric species in rich parasite faunas. The relationships in freshwater and marine habitats were compared using a linear model with log-transformed numbers of parasite genera as the response variable, both habitat and log-transformed numbers of parasite species as fixed factors, and geographical region of origin as a random factor, to account for the non-independence of fish species from the same region and also any possible idiosyncrasies of regional parasite faunas.

In addition, the ratio between the number of parasite species and the number of parasite genera was computed for each fish species. These log-transformed ratios were then used as response variables in another linear model with habitat as a fixed factor and geographical region of origin as a random factor. All analyses were implemented in JMP version 11.0 (SAS Institute Inc., Cary, NC, USA).

3. Results

Information was obtained from 14 datasets representing different geographical regions and/or habitats (Table 1). These involved a total of 677 fish host species, 482 from freshwater habitats and 195 from marine habitats, each harbouring between two and 45 parasite species (see Supplementary Table S1). The taxonomic composition of the parasite faunas was very similar in freshwater and marine habitats, with trematodes dominating in both environments (Fig. 1).

The relationship between the number of parasite genera and the number of parasite species per host species was well described by a power function, in both environments (Fig. 2). The exponent of this function was slightly lower for freshwater parasite faunas ($b_1 = 0.940$, 95% confidence interval (CI) = 0.921–0.959) than for marine ones ($b_1 = 0.966$, 95% CI = 0.937–0.994). The linear model indicated that, not surprisingly, numbers of parasite genera per host were determined by numbers of parasite species ($P < 0.001$; see Table 2), but no difference was detected between freshwater and marine environments ($P = 0.1614$).

In contrast, the ratio between the number of parasite species and the number of parasite genera was significantly higher ($P = 0.0263$) in freshwater fish species than in marine ones (Fig. 3; Table 2). The linear model was run again on a reduced and more conservative data set, from which hosts with only two parasite species were excluded; the results were the same (Table 2), again indicating higher species-to-genus ratios in freshwater fish than in marine ones.

4. Discussion

Freshwater environments account for a very small proportion of the planet’s area compared to oceans, and yet they harbour a similar diversity of free-living organisms, suggesting higher rates of diversification in freshwater than marine habitats (Wiens, 2015). The present results provide some support for the hypothesis that speciation rates are also higher in freshwater parasites than in marine ones, with the number of species per helminth genus being slightly but significantly higher in the parasite faunas of freshwater fish relative to those of marine fish. This is not merely due to taxonomic differences, as the faunas of fish in both environments

Table 1

Summary data on the 14 host-parasite datasets, and details of regressions fitting a power function (genera = b_0 * species^{b_1}) to the relationship between the number of helminth species and the number of helminth genera per fish host species. All b_0 are not significant ($P > 0.08$). All regressions and b_1 coefficients are significant ($P < 0.0001$).

Dataset number	Habitat	Geographical region	No. host species	No. parasite species per host species (range)	b_0	b_1	R^2	Sources
1	Freshwater	Ireland	18	2–22	0.049	0.8096	0.916	Holland and Kennedy (1997)
2	Marine	Germany	47	2–34	0.010	0.9459	0.981	Palm et al. (1999)
3	Freshwater	Latvia	44	2–32	0.016	0.9129	0.977	Kirjusina and Vismanis (2007)
4	Marine	Latvia	17	2–10	0.028	0.9483	0.868	Kirjusina and Vismanis (2007)
5	Freshwater	Czech and Slovak Republics	63	2–45	0.051	0.9932	0.957	Moravec (2001)
6	Freshwater	Turkey	36	2–17	0.003	0.9565	0.961	Oktener (2003, 2014)
7	Marine	Turkey	34	2–8	0.049	0.8801	0.945	Oktener (2005)
8	Freshwater	Bangladesh	26	2–20	0.036	0.8320	0.975	Arthur and Ahmed (2002)
9	Freshwater	Philippines	18	2–12	0.111	1.0190	0.830	Arthur and Lumanlan-Mayo (1997)
10	Marine	Philippines	41	2–7	0.004	0.9517	0.783	Arthur and Lumanlan-Mayo (1997)
11	Freshwater	New Zealand	16	2–15	0.001	0.9591	0.976	Hewitt and Hine (1972), Hine et al. (2000)
12	Marine	New Zealand	56	2–13	0.048	1.0258	0.915	Hewitt and Hine (1972), Hine et al. (2000)
13	Freshwater	Mexico	131	2–44	0.029	0.9235	0.978	Salgado-Maldonado (2006)
14	Freshwater	Brazil	130	2–27	0.013	0.9353	0.878	Eiras et al. (2010)

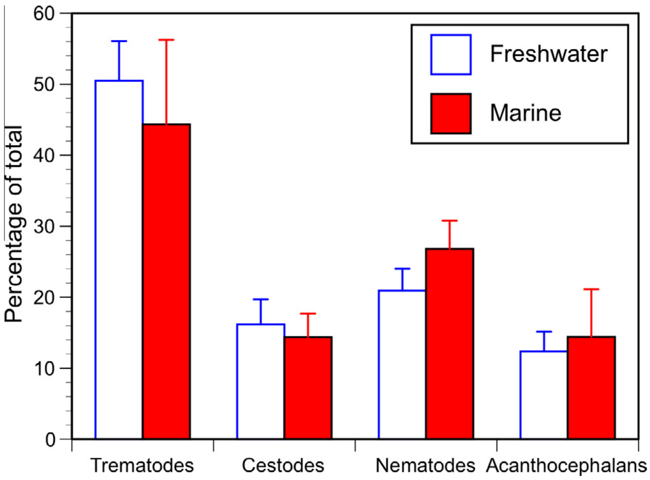

Fig. 1. Percentage (mean ± S.E.) of the total parasite faunas represented by trematodes, cestodes, nematodes and acanthocephalans, across nine freshwater and five marine datasets on endohelminth parasites of fish.

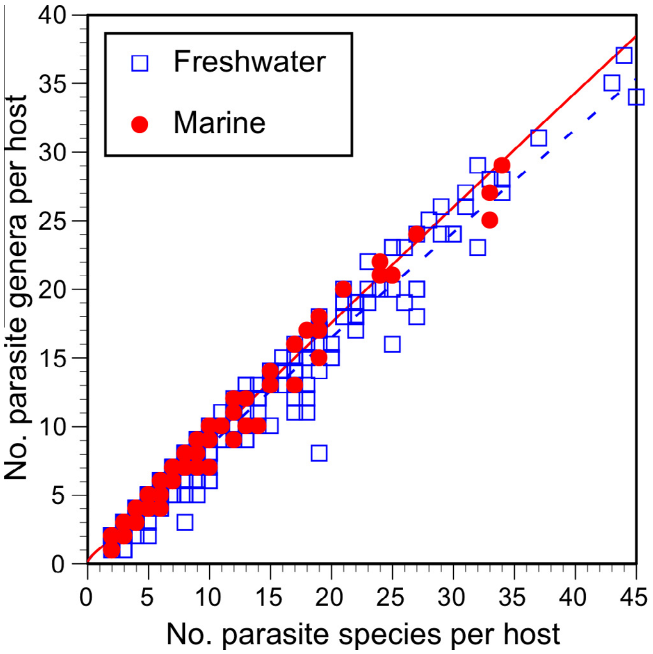

Fig. 2. Relationship between the number of parasite genera and parasite species per host species, across 482 freshwater fish species and 195 marine fish species. For freshwater hosts (open squares, broken line), the power function is genera $\propto$ species$^{0.940}$, and for marine hosts (filled circles, solid line) it is genera $\propto$ species$^{0.966}$.

consist of the same higher taxa of helminths, in approximately the same proportions.

The fragmented nature of freshwater habitats, which leads to substantial genetic structuring among parasite populations (Criscione and Blouin, 2004; Blasco-Costa and Poulin, 2013), is a likely factor promoting diversification in freshwater parasites. With different conspecific parasite populations evolving independently in isolated host populations, the overall parasite fauna of a given fish species, on a large regional scale, is likely to accumulate congeneric species over time. In contrast, in the more open marine environment, the parasite faunas of fish hosts are more likely to diversify by acquiring new species through host-switching. The other evolutionary process that can lead to multiple congeneric parasites exploiting the same host, intra-host speciation, i.e. true sympatric speciation, is also a possibility but seems less plausible. In certain host-parasite systems, large numbers of congeneric parasites, or ‘species flocks’, coexist in single host populations, even single host individuals (Schad, 1963; Kennedy and Bush, 1992; Beveridge et al., 2002; Simkova et al., 2004). However, the conditions required for this sort of extensive sympatric speciation are unlikely to apply broadly to endohelminths in fish hosts.

Several environmental factors can also influence speciation rates. Latitude, a proxy for ambient temperature, is expected to influence speciation rates in ectoparasites, or endoparasites in ectothermic hosts (Rohde, 1992; Krasnov et al., 2005). Here, after power functions were fitted to the relationship between the number of parasite genera and the number of parasite species separately for each of the 14 regional datasets, no correlation was found between the exponent b_1 for each region and the latitude at the centre of the region ($r = -0.129$, $P = 0.659$). Also, the geographical region of origin of each dataset was included as a random factor in all models, and never accounted for much of the variance unexplained by the fixed factors (Table 2). Therefore, latitudinal or regional effects are unlikely to have affected the main findings of the present study, suggesting a general freshwater-versus-marine difference.

Host-parasite checklists were used as sources of data; these do not provide complete inventories of parasite species found on particular host species. However, even if they are incomplete and include only parasites recorded at the time of their publication,

Table 2
Results of the linear models with either the number of parasite genera per host species, or the ratio between the number of species and the number of genera per host as the response variable, showing the effects of the main predictors and the proportion of the remaining variance accounted for by the random factor. Results shown separately for analysis including all fish host species with at least two parasite species exploiting them (2+; $n = 677$), and for that including only hosts with at least three parasite species (3+; $n = 533$).

Fixed factors	Estimate	S.E.	*t*-value	*P*	Random factors	% variance
RESPONSE: Log no. genera						
Intercept	−0.0044	0.0101	0.43	0.6701	Geographical region	8.59
Log no. species	0.9382	0.0090	104.08	<0.0001		
Habitat (freshwater)	−0.0063	0.0045	1.41	0.1614		
RESPONSE: Log species/genus ratio (2+ spp)						
Intercept	0.0490	0.0076	6.43	0.0002	Geographical region	7.93
Habitat (freshwater)	0.0103	0.0046	2.24	0.0263		
RESPONSE: Log species/genus ratio (3+ spp)						
Intercept	0.0557	0.0093	8.01	0.0003	Geographical region	13.65
Habitat (freshwater)	0.0114	0.0051	2.20	0.0287		

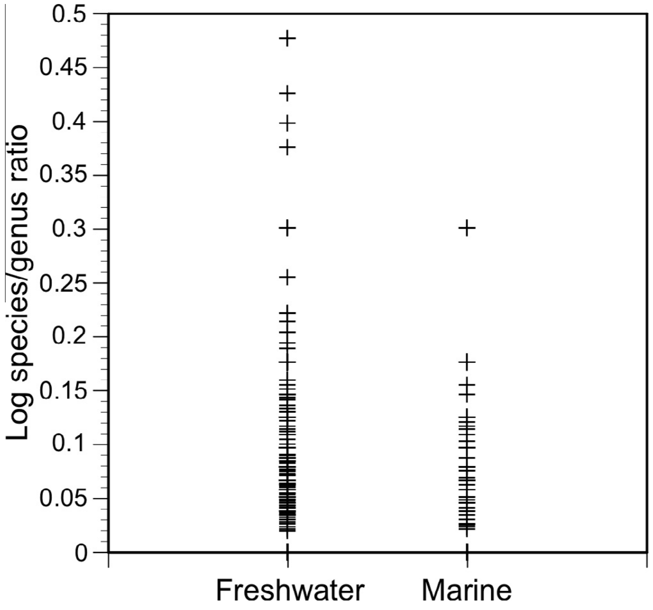

Fig. 3. Ratios of number of parasite species to number of parasite genera across 482 freshwater fish species and 195 marine fish species.

there is no reason to expect that the taxonomic structure (i.e. species-to-genus ratio) of these partial parasite faunas is biased in checklists covering either freshwater or marine environments. One might argue that a parasite 'genus' in freshwater is not necessarily equivalent to a 'genus' in marine habitats, because systematists have not always followed universal rules for lumping or splitting species into one or more genera. However, for the higher parasite taxa covered in this study, very often the same families are represented in both freshwater and marine habitats. The same expert or group of experts have established the nomenclature and classification of these families across habitats, making it very unlikely that biases would exist in favour of one habitat or the other, across vastly different geographical areas.

The datasets used here may underestimate the number of congeneric species in the parasite faunas of fish, because they do not account for cryptic species, i.e. parasite species that are genetically distinct but morphologically indistinguishable from each other (Pérez-Ponce de León and Nadler, 2010; Poulin, 2011). However, cryptic parasite species appear to be very common in freshwater systems (e.g. Locke et al., 2010; Blasco-Costa et al., 2014), thereby reinforcing the pattern observed here. A further test of the hypothesis that parasite speciation rates are higher in freshwater than in marine hosts would involve a phylogenetic approach, in which the rates of diversification and molecular evolution are compared between helminth clades that are predominantly freshwater or predominantly marine. This would complement the small but universal differences in the taxonomic structure of parasite faunas in marine and freshwater fish hosts reported here.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ijpara.2015.12.002.

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