# Parasite-Host Specificity

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## Introduction

The level of host specificity shown by parasites has major implications for their population dynamics, their probability of local extinction, and the likelihood that they can switch to new host species (Bush and Kennedy, 1994; Paterson and Gray, 1997; Poulin, 1998). As such, studies have demonstrated a broad swathe of host specificity strategies employed by parasites in response to speciation events and host ecology (Rohde, 2005; Poulin, 2007). These adaptations range from highly host specific monogenean helminths that can infest specific microhabitats of a host, compared to certain sea lice copepods that are able to infest any species within the salmonid family. The term “host specificity” refers to the number or diversity of host species a parasite is capable of infesting (Poulin and Mouillot, 2003; Wells and Clark, 2019). Therefore, a parasite that infests one host species is highly host specific, and as the number of host species that a parasite can infest increases, so the parasite’s host specificity declines.

### Origins of host specificity

Host specificity can be derived from two key evolutionary processes: cospeciation and host shifting. Cospeciation is where a parasite evolves into two distinct species in response to a host speciation event . This has long been used to explain apparent congruence in host and parasite phylogenies. However, typically, host and parasite phylogenies will not be entirely congruent and parasites will not show strict host specificity. This may be due to one or more parasite species maintaining gene flow within their population, even after a host speciation event. This lack of congruence may also result from host shifting.

Host shifting requires parasites to be exposed to new hosts that exhibit certain levels of physiological and/or behavioural overlap with previous hosts. This allows circumvention of barriers caused by variation in host physiology, behaviour or immunity and therefore the success or failure in the shift. Additionally, host shifting relies on the opportunity for parasites to interact with potential hosts. Therefore, variation in environmental conditions or changes in host distribution could introduce potential hosts to the parasite.

Furthermore, there doesn’t seem to be a directional trend in host specificity, i.e., a trend for parasites to become more host specific or host generalist, the only consistent pattern is that once a parasite has evolved with their host, or has shifted hosts, that they are able to disperse effectively and efficiently. Therefore, host specificity depends as much on opportunities for host shifting as host speciation events.

### Determinants of Specificity

Adamson and Caira (1994) identify 3 distinct determinants of host specificity: microhabitat, external factors and compatibility. Parasites are first and foremost specific to microhabitat. This is obvious in Monogenea and Cestoda which occur in one tissue site of their selected hosts. Host specificity is then further shaped by external factors such as compatibility to its host and the surrounding environment. These are not mutually exclusive, but specificity of particular types of parasites will be dominated by particular types of factors; such as host body size or longevity, host social behaviour or spatial distribution, which have all been shown to influence the ecology of parasites within ecosystems (Poulin, 2007). Additionally, parasite specificity may often be an adaptation. For example, a key feature in parasite life histories is transmission, therefore, parasites would be expected to focus release of their infective stages when susceptible hosts are most abundant. Such peak abundances may occur at different times and/or places for different hosts, thus forcing adaptation and, potentially, specialization.

### Measuring parasite specificity

The measurement of host specificity is of central importance to the study of parasite ecology and evolution (Adamson and Caira, 1994; Poulin, 1998). Researchers need a proper measure of host specificity when comparing different parasite species if we aim to understand why they show different degrees of specialization (Poulin and Mouillot, 2005). Historically, parasite specificity was simply the sum of known host species a parasite has been recorded infesting (Rohde, 1980). As exhaustive datasets are often rarely obtained from the field, by using various diversity and evenness indices (e.g.: Chao, Shannon-Weiner, etc.), this simple measure can be corrected for under-sampling.

However, the measure of parasite range does not consider the phylogenetic relatedness of hosts, and the role that these relationships play in structuring parasite specificity (Poulin and Mouillot, 2003, 2005). There are numerous examples of generalist parasites that are either restricted to a few closely related host species or can exploit completely unrelated host taxa (Rohde, 2005). Therefore, indices of phylogenetic host specificity have been developed and used to determine links within parasite hosts (Poulin and Mouillot, 2003). Whether designed for measuring biodiversity or host specificity, these indices compute either the average or total phylogenetic (or taxonomic in the absence of explicit branch length data) distance between all possible pairs of host species used by a parasite, and estimates their phylogenetic distinctness.

### Impacts of climate change on host specificity

Host specificity is not a fixed trait and has been shown to vary in response to environmental conditions. In the context of global climate change this may have dramatic effects on both the parasite and the hosts that they infest. If we consider that changes in climate are resulting in range shifts of free-living species, and that as these species move, they will be bringing their parasites with them. Therefore, with changes in surrounding environmental conditions, these changes allow for increased interactions with potentially new host species and could result in parasitic species more readily switching to naïve host species. However, if the new conditions are not favourable for the parasite, or the host moves too far away from components that the parasite requires to complete its lifecycle, we may see the extinction of parasites from that host. Either way, both these eventualities have unpredicted consequences on ecosystems and how they function.

In this chapter, I will calculate host specificity measures for parasites of cartilaginous fish. Specifically, I’ll be calculating host range and phylogenetic host specificity (or ‘phylospecificity’; Poulin, Krasnov and Mouillot, 2011), to investigate whether parasites infest more closely related cartilaginous fish hosts than expected by chance. With this measure, a parasite that infests distantly related hosts is a phylogenetic host generalist, whereas a parasite that infests closely related hosts is a phylogenetic host specialist. As changes in climate intensifies, biotic expansion of species has been shown to occur, and parasitic species could either thrive, or become extinct, and it is by calculating host specificity measures that we will get a view of just what might happen to these species.

I will also investigate to see if there are any correlations between parasitic ecological measures and their associated host specificity measures (e.g.: habitat, lifestyle, lifecycle) and I will also be looking at host ecological measures (e.g.: length, depth range and habitat) and their associated parasite species richness values. This is to determine if parasite or host ecological measures influence a parasites propensity to infest a host. If we can determine key ecological measures that influence a parasites specificity, we are better able to understand how changes in climate might impact host specificity and, as a result, the intricate relationship parasites have with their hosts.

## Methods

### Host-Parasite data

We combined data from three publicly available datasets, namely Shark Reference (<https://shark-references.com/>) (Pollerspöck and Straube, 2020), World Register of Marine Species (WoRMS) ([www.marinespecies.org](http://www.marinespecies.org)) (Horton *et al.*, 2019) and the Elasmobranch Host Specimen Database ([www.elasmobranchs.tapewormdb.uconn.edu](http://www.elasmobranchs.tapewormdb.uconn.edu)) (Caira and Jensen, 2017). These data, collectively, resulted in a dataset with 8511 host-parasite interactions, spanning 1323 cartilaginous fish hosts and 2496 parasites. This database was cleaned to only include extant species that occur in the ocean and duplicate records and synonyms were resolved. Taxonomy from WoRMS was used to clarify inconsistencies in taxonomy and in the case of re-descriptions, the original description was used.

Additionally, limiting the dataset to just parasites of cartilaginous fish may skew specificity counts. Therefore, the host-parasite list generated from the above methods was back engineered to develop a host list of potential hosts that go beyond cartilaginous fish. This increased the current dataset to included 765 non-cartilaginous host species to a total of 1323 hosts and an increase to 8511 host-parasite interactions (detailed in Figure 1).

### Sampling effort

Host–parasite data are sensitive to sampling effort: hosts which have been thoroughly sampled for parasites appear to have more parasites than those which have been less well sampled (Gregory et al. 1996), and is certainly the case for these data (stats; figure). To deal with this issue, we focused on well sampled cartilaginous fish, defined as species with at least five different parasites, and evidence for saturation in their parasite accumulation curves (See figures in Appendix S3). These curves were created using the *specaccum* function in the R package *vegan* (Oksanen *et al.*, 2012) as follows. To build accumulation curves, I collected citation counts off Shark Reference (<https://shark-references.com/>) (Pollerspöck and Straube, 2020) database. This database contains scientific bibliography on recent and fossil cartilaginous fishes and their parasites and is the most complete bibliography for this information available. First a paper from Shark Reference for any given cartilaginous fish was randomly sampled (without replacement) and parasite richness for the fish calculated. Next a second paper was randomly sampled and cumulative parasite richness for the fish calculated. This was repeated until all papers had been sampled. The process was then repeated 1000 times per fish. This reduction to only well sampled hosts created an analysis pool to 275 cartilaginous fish hosts, 2078 parasites and 6115 host-parasite interactions.

### Host specificity measures

Three independent variables related to patterns of parasite specificity were calculated, including host range, and two measures of phylogenetic host specificity: average taxonomic distinctness (and the related variation in taxonomic distinctness; ∆+ and Λ+) and net relatedness index (NRI).

*Host range*

Host range is essentially parasite richness, i.e. the number of host species infested by a parasite. This was calculated using the function *specnumber* of the *vegan* package.

*Phylogenetic host specificity*

I investigated whether parasites of cartilaginous fish infest more closely related hosts than expected by chance by using two measures of ‘phylogenetic host specificity’ (or ‘phylospecificity’; Poulin et al. 2011) of each parasite. These measures include taxonomic distinctness, including the related variation in taxonomic distinctness (Warwick and Clarke, 1995; Clarke and Warwick, 2001) and phylogenetic diversity (Faith, 1992; Webb *et al.*, 2002) which is transformed into net relatedness index (NRI).

The average taxonomic distinctness (∆+) is calculated by summing the path lengths through a taxonomic tree connecting every pair of species in the list and dividing by the number of paths. Step lengths are standardized so parasite species connected at the highest taxonomic level (phylum) is set to be equal to 100, with six levels required to reach the lowest taxonomic level (species), such that each step accumulates a value equal to 16.66. The taxonomic categories recorded were: Species, Genus, Family, Order, Class and Phylum. As ∆+ lacks dependence, in mean value, on sampling effort it means these values can be calculated across the full dataset and not just the corrected dataset (Clarke and Warwick, 1998). Variation in Taxonomic distinctness (Λ+) is the variance of these pairwise path lengths and reflects the unevenness of the taxonomic tree (Clarke and Warwick, 1998). Λ+ conveys separate information of how much taxonomic heterogeneity there is among parasite species as it is possible to have two groups of hosts with the same ∆+ value but which differ in their taxonomic range. Note, however, that Λ+ can only be computed when at least 3 host species are infested by a parasite (it always equals zero with 2 species) (Clarke and Warwick, 2001).

To detect a difference in the taxonomic distinctness, for any observed set of species, the 95% ‘confidence funnel’ was obtained for Δ+ and Λ+. This procedure, as defined by Clarke and Warwick, (1998) determines departure from random expectations by comparing measured Δ+ and Λ+ values, respectively, with values of 1000 random selections of the same number of species from the total species pool. This randomization procedure develops an approximation which leads to a 95% confidence funnel against which distinctness values for a set of species (in this case host communities infested by a parasite) can address the question of whether it has a lower or higher than expected taxonomic spread.

The second measurement of phylospecificity is phylogenetic diversity (PD) which leads into net relatedness index (NRI). PD, as initially proposed by Faith (1992), is defined as the total branch length spanned by the taxonomic/phylogenetic tree including all species in a local community. NRI is based on the mean phylogenetic distance (MPD) between all possible pairs of hosts infested by a parasite (MPDobs), where phylogenetic distance is defined as the sum of all intervening branch lengths between two hosts. To allow comparisons among multiple parasites, we standardised these MPD values by subtracting the mean MPD expected for n hosts drawn at random from the host phylogeny across 999 iterations (MPDn) and divide by the standard deviation of the MPD from these 999 randomly drawn n hosts [s(MPDn)]. Finally, we multiplied these values by -1 so that positive values of NRI reflect phylogenetic host specialisation.

NRI = – 1 x ((MPDobs – MPDn) / s(MPDn))

To test for statistical significance in phylogenetic host specificity, we compared MPDobs values with those from the 999 randomly generated MPD values. A parasite was considered significantly phylogenetically host specific if less than 5% of these random MPD values were larger than MPDobs (P < 0.05). We estimated NRI values for each parasite that infested at least two hosts (n = 2078) using the R package *picante* (Kembel et al. 2010).

### Data analysis

Diversity patterns of parasites and their hosts were explored by considering overall parasite data and separating data into the same groupings as chapter 2; functional/ taxonomic groups (Helminths, Arthropods and minor groups), habitat (endo and ecto parasites) and lifestyle (direct and indirect lifecycles). Results were plotted in box and whisker plots and Chi-squared tests were used to determine whether the above groupings had significantly different proportions of phylogenetic host-specialist parasites. Stats were calculated separately to include singleton parasites as specialist species and exclude singleton parasites as specialist species.

*Host species data*

Additionally, by treating each host species as a habitat, we can calculate parasitic species richness (PSR) for each host. Data from FishBase was collated through their R package interface. Specific variables include adult maximum length (mm), adult maximum weight (g), depth range (m) and depth midpoint (m) and their ecosystem zone (demersal, benthopelagic, oceo-pelagic, reef-associated).

To test if host variables are related to phylogenetic specificity measures, Generalized Additive Model (GAM) was fitted using the *mgcv* package in R (Wood, 2017). PSR was used as the response variable, with host length (continuous), weight (continuous), depth midpoint (continuous) and depth range (continuous) as explanatory variables, including marine ecosystem zones (categorical, with 4 levels) (see appendix for more information on variables). To incorporate the dependency of parasites to infest hosts of similar phylogeny, host order was used as a random effect. Number of publications per host was also included as a random effect however it showed little influence on the model (see table in appendix for comparison statistics). As PSR is highly skewed discrete data, a log link function with a negative binomial distribution was used to predict the effects of host variables.

As adult maximum weight and length are co-varied, only maximum adult length was used in model predictions. Additionally, as depth range and depth midpoint were also co-varied, and that the categorical variables provided more information, only depth range was used in model predictions. Therefore, the final model:

*Parasite Species Richness per host (Negative binomial distribution, log link function) ~ s(host length) + s(depth range) + marine ecosystem zones + s(order, bs = ”re”)*

Model assumptions were verified by using a quantile−quantile plot and a histogram of the model residuals as well as plotting residuals versus fitted values. All GAMs were built with the package “*mgcv*” (Wood 2011) using Restricted maximum likelihood (REML) approach. In addition, each model formula included a *gamma = 1.4* term to place a heavier penalty on each degree of freedom to counteract overfitting (Zuur et al. 2009; Wood 2011).

All analyses were conducted in R version 4.0.4 (R Core Team, 2019).

## Results

Almost 42% (536) of all known (1284) cartilaginous fish have had their parasitic communities described. 2446 species of parasites have been described from these surveyed hosts. If this ratio is applied across all cartilaginous fish, there would be over four parasites for every 1 host species (5979 parasites for 1284 host species)(Figure 1, Table 1).

*Host Range*

Parasites of cartilaginous fish infest, on average, 3.357 (median of 2) host species with a minimum of 1 host and a maximum of 79 hosts (digenean: *Helicometrina* *nimia*) (Figure 2). Approximately a third (32.5%) of parasites within this dataset have been recorded to infest one host species, with the remaining parasites known to infest two or more host species. [breakdown across parasitic functional groups?]

By reducing the dataset to include host species that are infested by more than 5 parasitic species (to mitigate the effect of under sampling), only 51.4% of the dataset remains. [What is the breakdown across functional groups?]

### Phylogenetic host specificity

*Phylogenetic distinctness*

The average expected ∆+ value for parasite species is 76.21 (Figure 3a). Most of the calculated ∆+ values were below the expected simulated model of the funnel. 63 % of parasites have ∆+ values that fall significantly outside the expected funnel of the plot, with only three helminths falling above the upper limit of the funnel (*Echinocephalus* *pseudouncinatus*, *Dioecotaenia* *cancellate* and *Parachristianella* *dimegacantha*).

The average Λ+ value for host species is 165.52 (Figure 3b). 66% of the calculated Λ+ values were within to the randomized funnel. Λ+ values that fell outside the funnel fell above the funnel indicating host assemblages are made up of short taxonomic lengths. However, there were species (2 cestodes and a copepod) showing less than lower limit. (*Acanthobothrium* *coronatum*, *Hepatoxylon* *megacephalum* and *Caligus* *rapax*)

[see if there are any trends across group, lifestyle, habitat]

*Phylogenetic diversity*

Of 2078 parasites, 918 were identified as phylogenetic host specialists, i.e. they infest more closely-related chondrichthyan species than expected by chance (Table 1). There were no significant differences among parasite groups (χ2=0.902, d.f.=2,P=0.637; Table 1), habitat (χ2=0.1, d.f.=1,P=0.752; Table 1) or lifestyle (χ2=1.469, d.f.=1, P=0.506; Table 1). When parasites with a single host were included as specialists, differences among groups (χ2=0.797, d.f.=2,P=0.671; Table 1), habitat (χ2=0.181, d.f.=1,P=0.670; Table 1) or lifestyle (χ2=0.443, d.f.=1,P=0.506; Table 1) remained non-significant.

*Host ecological variables*

Model validation indicated that residuals do not show a particular pattern or bias, therefore the model is valid and useful. The model described 28.8% (REML = 852.49, n = 208) of the deviance within the dataset. Smoothing terms were all found to have a significant effect on model fit (figure …). Majority of hosts ranged in length from 25 cm to 760 cm with two outliers at 1520 cm (*Cetorhinus maximus*) and 1700 cm (*Rhincodon typus*) respectively. Even with the two outliers, host length remained a significant contributor to the model fit (edf: 2.626, Chi.sq: 13.78, p = 0.004). Host Depth range (3m to 4000m) also contributed significantly to model fit (edf: 2.486, Chi.sq: 12.43, p = 0.007) with 85% of species in this dataset having a depth range of less than 1000m.

|  |  |
| --- | --- |
|  |  |
| Figure : Predicted GAM plots identifying the additive effect of host length (cm) and host depth range (m) on the probabilities of Parasite Species Richness (PSR). Dotted lines represent 95% confidence intervals with marks along the lower axis representing a single observation. | |

|  |
| --- |
|  |
| Partial effect of marine ecosystem zones on predicted parasite species richness. |

Parametric coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 2.3122 0.1999 11.565 < 2e-16 \*\*\*

benthopelagic 0.8048 0.2365 3.403 0.000667 \*\*\*

demersal 0.6392 0.2081 3.071 0.002131 \*\*

pelagic-oceanic 0.7923 0.2840 2.789 0.005283 \*\*

reef-associated 1.0671 0.2378 4.487 7.22e-06 \*\*\*

For GAM and GAMMs, you must include the effective degrees of freedom of the smoothers and indicate the type of smoothers used (Wood 2006).

There is an ongoing debate in the literature (Halseyet al.2015) over whether P-values should be included. Their interpretation is prone to abuse, and, for most of the frequentist techniques mentioned, P-values are approximate at best. They must be interpreted with care, and this should be emphasized in the paper. An alternative is to present 95% confidence intervals for the regression parameters and effect size estimates and their precision (Halseyet al.2015)

## Discussion

As climate change intensifies and changes in temperature within the oceans causes biotic expansion of species, understanding host specificity of parasites becomes vitally important in predicting effects to these systems (). The measurement of host specificity in parasites is a fundamental measurement in understanding parasite ecology, particularly if these species will be negatively or positively impacted by their new surroundings. Our results show that within the cartilaginous fish, there are more host generalist species than specialists, but that these generalist species are restricted phylogenetically to cartilaginous host species. This is demonstrated by the vast majority (2/3rds) of parasites within this study having 2 or more hosts that they infest, yet, both phylogenetic distinctness and diversity measures indicate phylogenetically specific parasite species.

This has interesting implications for species as they move into new environments. This data shows that there is a strong potential for parasites to switch cartilaginous hosts, but only if they are phylogenetically similar. “has this been seen yet in copepod parasites?”

However, mounting experimental and theoretical evidence suggests that host specificity is not a fixed trait (Poulin & Mouillot 2005; Brooks & Hoberg 2007; Agosta et al. 2010; Nylin et al. 2018) (Agosta, Janz and Brooks, 2010). Parasite specificity has been shown to be dependent on environmental conditions (Fecchio et al., 2019). For host range expansions to occur, a parasite must first be exposed to a novel host species. This exposure will be influenced by environmental conditions that determine host community composition, as variation in host occurrences alters host-parasite contact rates (Canard et al. 2014). Second, adaptation to a new host is required to facilitate transmission. For many parasites, this process is expected to adhere to the principle of ‘ecological fitting’ (Janzen 1985), which states that sharing certain characteristics with previous host species is necessary for successful infestation (Brooks et al. 2006; Davies & Pedersen 2008; Poulin et al. 2011; Clark & Clegg 2017). Yet host traits that influence susceptibility, such as clutch size or breeding behaviour, can fluctuate in response to environmental conditions (Møller et al. 2013).

Our analysis also looked at whether certain host features have allowed some host species to ‘capture’ a narrow or a broad taxonomic range of parasite species, regardless of exactly how many parasite species they have acquired.

Sampling effort. How have I accounted for it …

By using well sampled hosts, thaose that exhibited saturation in their SAC (536 to 273 hosts) species, we believe we take into account the impact that sampling effort has on the data. Therefore, we believe that, in general, larger hosts have more parasite species … independent of sampling effort. However, as much as we tried to take sampling effort into account with these measures, the results are only as good as the amount of sampling being done … and in general sampling is very poor with only 20% of sharks being surveyed and many of these only having a very limited number of parasite assemblage surveys. Therefore, increased sampling would be ideal.

Additionally, the data collected for this chapter was from global databases that depend on …Costello paper about worms…. Therefore the data is only as good as the input and that the collective knowledge placed in these massive datasets are changing the way we currently do science.

Therefore, with that out the way, what did we find

* Any parasite variables that are significant? i.e: are endo parasites more host generalist than specialist … how does this fare across phylogenetic measures?

See wat I can do with this as nothing was significant. But … I wasn’t expecting this to be significant … why…? What information is out there about this. …

* Are there host variables that could explain why parasites are generalist/specialist or is the strongest predictor simply the number of papers published?

YES! The GAM’s show that host variables, such as host length, depth range and environment do play a role in parasite species richness. When results are drawn I can assess this.

#explin why basking and whale are so much lower but the rest are increasing…

#explin why depth range is doing its thing

* Look at this discussion … its kinda what you need! (Luque, Mouillot and Poulin, 2004)

The measures of taxonomic distinctness used here provide a summary of the taxonomic structure, and they suggest possible evolutionary scenarios. For instance, certain feeding habits or living over a broad depth range may facilitate host-switches leading to completely novel host–parasite associations. For a given parasite species richness, this would lead to a taxonomically diverse assemblage. In contrast, parasites in host species with different features (narrow diet and depth range), may have accumulated in part via intra-host speciation, leading to a taxonomically closer set of species. These are only possibilities, of course. As shown by our results, however, shifting the focus from species richness to taxonomic diversity can cast a different light on the evolution of parasite biodiversity.

As we consider the impact of a changing climate on marine species, and have already witnessed species range shifts, this may influence a parasites propensity to switch hosts.

For example: *Sampling effort is a major issue in comparative analyses of parasites because poorly studied hosts will appear to have fewer parasites than well-known hosts (Gregory et al. 1996). We dealt with this issue by focusing on the 35 best-studied primates (of 376 species in the Order Primates; Wilson & Reeder 2005) and find that our analyses still had high power to detect significant phylogenetic host specificity even under heterogeneous parasite sampling. However, we also find that even in these well-studied primates, more effort is needed to sample the full complement of parasites found in most primates, as indicated by only slight saturation in the parasite accumulation curves (Fig. S2). In addition, 205 parasites are found only in one primate species. In some cases, the lack of saturation reflects a truly specialised parasite; in others it likely reflects under sampling of the parasite. This under sampling is also uneven across parasite groups: bacterial parasites are rarely reported, possibly due to lower severity of bacterial diseases compared with viral diseases (e.g. Ebola). Given the past and future implications of emerging parasites contracted from human–wildlife contacts, further research into wildlife parasites is crucial to fill these research gaps.*

And: *Several other methodological issues deserve mention. First, many parasite ‘species’ consist of multiple cryptic species that infect different hosts. Treating these cryptic species as one species could artificially inflate the phylogenetic host specificity of the parasite; however, if a cryptic species complex is phylogenetically host specific, it is likely that its constituent species will be too. In addition, species definitions differ across types of parasite, which makes it difficult to compare phylogenetic host specificity across parasite types. Second, our measure of phylogenetic host specificity only captures one aspect of host specificity in parasites. Poulin et al. (2011) discuss other important factors, including structural (i.e. how the parasite prevalence and abundance vary among hosts) and geographical (i.e. how host use varies geographically) specificity. Third, the mechanisms leading to a pair of hosts sharing two closely related parasites or two distantly related parasites probably differ; however, our methods do not distinguish between these scenarios. If parasite relatedness was considered, we would expect parasite sharing of closely related parasites to be more strongly governed by host phylogeny. We did not consider parasite relatedness due to a lack of suitable parasite phylogenies; however, this should be considered in the future as more comprehensive parasite phylogenies are published (Poulin et al. 2011).*

## Figures and Tables.

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| (a)    (b) |
|  |
| Figure 1: Number of host-parasite associations by (a) parasite taxa and (b) host taxa. |

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| --- |
|  |
| Figure 2: Histogram of host range of parasitic species with box plot above to indicate spread of data |

Appendix

Phylo-specificity (NRI significance) measures. Significant mpd p values

Stats: none were significant. This is with uncorrected dataset.

(chi sq, df, p-value)(w/o singletons; w/ singletons)

Group: (1.420, 2, 0.492; 1.014, 2, 0.602)

Habitat: (0.896, 1, 0.344; 0.828, 1, 0.363)

Lifestyle: (0.077, 1, 0.781; 0.059, 1, 0.808)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | n | specialists | generalists | singletons |
|  |  |  |  |  |
| All parasites | 2269 | 746 | 6 | 871 |
| By group |  |  |  |  |
| Helminths | 1977 | 603 | 6 | 780 |
| Arthropods | 261 | 136 | 0 | 70 |
| Minor groups | 31 | 7 | 0 | 21 |
| By Habitat |  |  |  |  |
| endo | 1748 | 558 | 6 | 666 |
| ecto | 521 | 188 | 0 | 205 |
| By Lifestyle |  |  |  |  |
| direct | 627 | 226 | 1 | 252 |
| indirect | 1642 | 520 | 5 | 619 |

Variables used in GAM

|  |  |
| --- | --- |
| BathyDemersal | Live and feed on the bottom at depths greater than 200 m |
| BenthoPelagic | Living and feeding near the bottom as well as in midwaters or near the surface |
| Demersal | Live and feed on or near the bottom of the sea. |
| PelagicOceanic | Living and feeding in the open sea beyond the continental shelf. Associated with the surface or middle depths of a body of water. In FishBase, referring to surface or mid water from 0 to 200 m depth |
| Reef-Associated | Living and feeding on or near coral reefs |