# Marine non-parasite rates of description outpace marine parasites

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## Abstract

If, on average, every host species has its own specific parasite, then half of all species should be parasites. However, we found that only 14% of marine animal species are parasites. In this study, we used data from online databases to show that marine parasitic discovery rates are far below those of non-parasitic marine species, and that species discovery rates between marine non-parasitic species and parasites are widening. We examined if this may be a product of taxonomists’ productivity, yet this is at its highest rate ever recorded. However, as more hosts are surveyed, biologists are finding parasite species that have previously been described. These findings suggest that marine parasites may be less host specific than suggested by literature, and that many marine parasites can inhabit whichever suitable host they encounter during their life cycle.

## Introduction

Parasites are increasingly recognized as important components of ecosystems, leading to calls for increased attention for their conservation (Gómez & Nichols, 2013; Spencer & Zuk, 2016). A current challenge for parasitologists and conservationists is to understand the ecological roles played by parasites so as to predict how and which ecosystem functions may be altered by anthropogenic climate change. However, there are fundamental aspects to parasite ecology that are still poorly understood. Chief amongst these is the simple question of how many species are there?

Recent advances in biodiversity informatics are providing the opportunity to address this question for many taxa (Appeltans et al., 2012; Costello, May & Stork, 2013b; Poulin, 2014; Poulin & Presswell, 2016; Chaudhary, Saeedi & Costello, 2016; Costello & Chaudhary, 2017; Arfianti, Wilson & Costello, 2018; Pamungkas et al., 2019). These studies indicate that approximately two-thirds of species on Earth have been described, with the effort and number of authors in these descriptions being at its highest ever recorded (Costello, Wilson & Houlding, 2012, 2013) .

Some predictions into the proportion of parasite species that have been described and are yet to be described vary between one-third to one-half of all species (Price, 1980; Toft, 1986; Poulin & Morand, 2000; Poulin, 2014). These predictions are founded on the assumptions that parasites are highly host specific and that a host can harbour more than one parasitic species (Poulin & Morand, 2004). In addition, hyper-parasitism, where parasites live off other parasites, may further boost parasite species richness (Lucius & Poulin, 2017). However, these predictions have an overwhelming focus on helminth parasites of vertebrate hosts and don’t consider the many other taxa that have transitioned to parasitism (Poulin & Morand, 2004; Dobson et al., 2008; Strona & Fattorini, 2014; Costello, 2016; Poulin & Presswell, 2016; Poulin & Pérez-Ponce de León, 2017; Jorge & Poulin, 2018; Carlson et al., 2020; Poulin, Presswell & Jorge, 2020). These studies have used a variety of methods to estimate these numbers; from collating expert opinion, developing a variety of models and using cumulation curves. One of the common methods for predicting parasite richness is based on the scaling between host and parasite richness, a near-universal pattern across spatial scales and taxonomic groups (Kamiya et al., 2014a,b). This method was first used by Poulin & Morand (2004) who assumed that the scaling of hosts with host-specific parasites is linear. They predicted between 75 000 and 300 000 parasitic helminths of vertebrates. However, Strona & Fattorini (2014) found that this relationship is not linear but follows a power curve. By using this power curve, Carlson et al. (2020) estimated 100 000 to 300 000 species of helminth parasites of vertebrates. Specifically, they predicted that Chondrichthyes and bony fish have only 38% of their potential parasitic helminths described of a potential 41 000 species. However, these predictions are only of helminth parasites of vertebrates.

One paper has analysed global data on parasite diversity. Costello (2016) found that at present, parasites of animals comprise only 5% of named species. The hypotheses proposed to explain this apparent shortage refer to parasites’ cryptic lifestyle, lack of research, paucity of specialized parasite taxonomists, unrecognized synonyms, and under-sampling even within well-studied taxa and locations (e.g. birds, elasmobranchs) (Rohde, 2002; Dobson et al., 2008; Randhawa & Poulin, 2010; Caira & Jensen, 2014; Costello, 2016; Poulin, 2016; Costello & Chaudhary, 2017; Okamura, Hartigan & Naldoni, 2018). By their nature, parasites are often well concealed on or within their hosts, exhibit patchy distributions across and within host populations, and may have few obvious distinctive morphological features, making their discovery and identification difficult (Poulin & Morand, 2004; Okamura, Hartigan & Naldoni, 2018).

Parasitic speciation rates may be different between terrestrial, freshwater, and marine environments due to their intrinsic physical differences (Poulin, 2016; Poulin & Pérez-Ponce de León, 2017). For example, Poulin (2016) showed higher rates of speciation in parasites of freshwater than marine hosts. This is supported by Poulin & Pérez-Ponce de León (2017) who show that freshwater metazoan species hold more cryptic richness than either terrestrial or marine environments. Therefore, pooling diversity predictions across environments, as Costello (2016) did in his study, may also confound the role that each environment individually may have on these predictions. Thus, analyses should distinguish between these environments.

In this paper, by using online registers of species information, we compiled as comprehensive as possible a marine parasite species list. By measuring the rate of description of parasitic and non-parasitic species, we addressed these questions:

* Are there differences between parasite and non-parasite description rates and taxonomic effort in marine species?
* Are there differences in description rates between marine parasites of different functional taxonomic or habitat groups?
* How many parasite species should we expect in the ocean, and how much of that diversity is described?
* Finally, have the rates of discovery between non-parasitic marine species and marine parasites covaried?

## Methods

Parasitism is understood to be a close association of two organisms, in which one (the parasite), during at least one life-history stage, depends on the other (the host) and directly derives some nourishment and/or shelter from it but does not intentionally kill the host (Rohde, 2005). The direct benefit to the parasite is almost always in the form of food, but other benefits have been noted including habitat, shelter, and transport (Poulin, 2014). Microbiologists have focussed on fungi, viruses and bacteria and have considered some of these as parasitic, but for the purposes of this paper we will only consider animal (metazoan) parasites which infest other animals. We exclude animals that feed off plants, such as the many species of plant-feeding insects and nematodes, as these are considered herbivores. We also exclude parasitoid insects because they intentionally kill their host and are therefore considered predators (Rohde, 2005; Costello, 2016). Finally, many of the Chordata and a few Arthropoda species that are included in this dataset are considered as ‘hit and run’ feeders or micropredators (Rohde, 2005), but still fulfil the definition of parasite as they feed off a host at some stage of its life, but typically without killing it.

### Data collection

Parasites are a polyphyletic group. They represent an assembly of organisms that have evolved independently in separate lineages. Therefore, to assemble a full species list of “all parasites” requires an integrated approach. Taxa (e.g., phyla, class, order, family, genus) identified as having chiefly marine parasites were selected and their “downstream” species within that selected taxa were downloaded from the World Register for Marine Species (WoRMS) (Horton et al., 2019) (Figure 1, Table 1). The full dataset if freely available at Morris (2021).

Numbers of free-living marine taxa were collected by downloading full species lists from WoRMS (Horton et al., 2019), and subtracting previously identified marine parasitic taxa. All above lists were downloaded using the *taxize* (Chamberlain et al., 2020) packages in R. The species names were cross referenced with WoRMS using the *worrms* (Chamberlain & Scott, 2020) package in R to determine that all species being analysed are extant “isExtinct ≠ 1”, are marine “is.marine = 1”, and that their species names are accepted “status = accepted”. The year of the original description of each species was used as the year of description throughout the following analyses.

### Taxonomic effort

The author(s) associated with the year of description were collected. The number of authors per year over time is an indicator of taxonomic effort which may influence the rate of description over time. However, it could be biased by changing authorship practices whereby species are increasingly described by two or more authors. Therefore, the *stringr* package (Wickham, 2019) was used to separate the first author if more than one author was present. As such, we only considered unique surnames of first authors per species. Therefore, our author data underestimates the number of people naming new species. In cases where different authors had the same surname, the original descriptions were used to distinguish them from each other. If this was not possible, we only counted a surname for 50 years from first occurrence. The number of descriptions per year divided by the number of first authors of that year was used as a proxy for taxonomic effort.

### Data analysis

ARIMA (Autoregressive Integrated Moving Average) models were used to explore the relationship between marine parasites and non-parasitic marine species rates of description and taxonomic effort. As these data were a time series, current values are dependent on previous values, ARIMA models relate the present value of a series to past values and past prediction errors considering the non-independent nature of time series analysis (Cowpertwait & Metcalfe, 2009). The models fitted conformed to an ARIMA (0,0,1):

No. of descriptions/authors per year ~ (Parasites:Non-Parasites) + s(Year, by = Parasites:Non-Parasites), correlation = corARMA(form = ~ Year| Parasites:Non-Parasites, q = 1)

I compared rates of description for non-parasitic species with parasitic species of the same year to determine if there were any trends in this relationship. It is assumed that parasitic rates of discovery are determined by the rates of discovery in their hosts as a host may need to be described before you can describe its parasite (Poulin & Morand, 2004). A Generalized Additive Model (GAM) was used to test if there was significant co-variation between description rates of parasites to non-parasitic species. These data were then split in 50-year increments from 1750 to 2020 to see if there were any changes in this trend over time. GAM’s fit non-parametric smoothing functions to covariates in a model and allow comparisons between trajectories of the response variable with respect to other factors without the need to fit functions to the data (Wood, 2017). The models were:

Parasites ~ s(non-Parasites)

All ARIMA and GAM models were drawn through *gamm()* and *gam()* functions respectfully within the *mgcv* package (Wood, 2017) and model assessments were visualized and confirmed using *gratia* (Simpson, 2020) package. Once models were fitted and their assessments displayed models conforming to statistical assumptions, model outputs were produced using *modelr* package (Wickham, 2020).

All analysis was conducted in the R environment (R Core Team, 2013) with the use of *tidyverse* (*dplyr*, *readr*, *stringr*, *ggplot2*) (Wickham et al., 2019), along with above mentioned packages.

## Results

In total, 27 699 species of marine parasites were included in this dataset (Table 1). These data were spread across 11 phyla and 23 classes. The group ‘helminths’ (Acanthocephala, Nematoda, and Platyhelminthes) constituted 60% of species within the dataset. The next two largest groups were Arthropoda and Mollusca with 24% and 13% of all species respectively. The final 3% of species constituted Annelida, Chordata, Diceymida, Myxozoa, Orthonectida and three species of Tardigrada.

A total of 202 252 marine animal species were downloaded from WoRMS and the 27 699 parasitic species were removed from that dataset. This resulted in a dataset of 174 553 marine non-parasitic species. Therefore, of all currently described marine animal species 14 % are parasitic.

### Description rates

The earliest descriptions in this dataset are a product of Carl Linnaeus from his early publication *Systema Naturae Vol. 10* (1758), where he described 4,400 species of animal, including 732 non-parasitic marine species and 37 marine parasites. From the early 1800’s until a century later, marine non-parasite description rates steadily outpaced those of marine parasites (df = 1; F = 2413; p < 0.001) (Figure 1a). Both non-parasites and parasites experienced a drop-in description rate during both the World Wars. However, description rates quickly recovered, and surpassed levels seen before these global events.

Within parasitic taxonomic groups molluscs and platyhelminthes have comprised most descriptions with intermittent peaks throughout history (Figure 2a). Helminth’s peaked later in the 1970’s but their rates have been steadily declining since then. Arthropods have steadily increased since the early 1800’s with a peak in the 1980’s. Of the three major taxonomic groups of parasites, molluscs peaked earliest in the late 1950’s and have seen a resurgence in discovery in the last 20 years. Marginally more ectoparasites have been described than endoparasites (13 886 vs 13 813). Between the 1920’s and 1970’s, endoparasite descriptions outpaced those of ectoparasites, but have been declining from the 1970’s and ectoparasitic discoveries have remained constant (Figure 2b).

### Taxonomic effort

There has been an increase in the number of authors over time describing species (Figure 1b). This increase is more pronounced for non-parasitic species than parasitic species (df = 1; F = 3654; p < 0.001). While relatively fewer non-parasitic species are being described in proportion to the number of authors (Figure 1c), descriptions of new parasites have remained constant. These results indicate that number of descriptions per author per year has remained stable for marine parasites yet is on the decline for marine non-parasitic species (df = 1; F = 71.51; p < 0.001).

The parasitic groups with most species also had most authors (Figure 3). Before the 1900’s, ectoparasites had more authors per year than endoparasites, yet from the early 1900’s, endoparasites had caught up and had more authors (Figure 3).

### Parasite vs non-parasite trends

There were similar increases in non-parasitic and parasitic marine species description rates, although five times more non-parasite species have been described than parasitic (Figure 1a). However, this relationship is not linear, and as more non-parasites have been described, relatively fewer parasites have been described (Figure 4). If we compare these rates across half century time periods, we see this relative increase in both description rates for every 50-year period until the 1990s (Figure 5). This is represented by the positive trend line and points migrating upward and to the right in each successive period. However, since the 1990’s, including the current half century, non-parasite description rates are significantly outpacing those of marine parasites (Figure 5). These results show that there are relatively fewer marine parasites being described than non-parasitic (potential host) species.

## Discussion

### How many marine parasitic species are there?

In this paper we focused on marine parasitic species and their associated potential hosts. We found that described parasites currently constitute 14% of marine animal species, and this proportion is decreasing with new species discoveries (Figures 1, 4, 5). That is, the gap between the number of marine parasites and non-parasites is widening because the rates of description of non-parasites are outpacing parasites. Therefore, if we were to scale all marine species currently in WoRMS, with 202 252 described animal species, then we can expect approximately 40 400 species of marine parasites. However, as seen in figure 1a, marine species rates of discovery do not seem to be slowing down anytime soon, and therefore we do not expect their parasite description rates to be slowing down either.

Despite some claiming a crisis in taxonomy (e.g., Brooks & Hoberg, 2001; Pearson, Hamilton & Erwin, 2011), our data and others show that the number of new parasite species described annually has been growing steadily for decades (Poulin, 2014; Poulin & Presswell, 2016). Our results also show that marine parasite discovery rates and number of authors describing parasites per year is still increasing. As seen in figure 1c, the number of parasites described per author has remained constant since the 1800’s (Figure 1c).

Therefore, as taxonomic productivity within parasitology has remained reliably consistent, and that parasite rates of discovery are co-varied with those of non-parasitic species, we believe that the current prediction that one-third to one-half of all species are parasites is an overestimation. According to our analyses, we believe that no more than 1 in 6 marine species are parasitic for the following reasons.

*New discoveries will not alter the global pattern*

Global patterns of non-parasite species are indicating that new discoveries will not alter the global pattern. Biogeographic research on non-parasitic marine species is showing that we do not expect new species discoveries to alter the global pattern of species richness and their biogeography (Costello, May & Stork, 2013a,b; Costello & Chaudhary, 2017; Jorge & Poulin, 2018). Therefore, we expect that parasitic discoveries in these areas will mirror the patterns of non-parasitic species as patterns in spatial variation of parasite species richness tend to match those already well-documented for free-living species (Poulin, 2014; Jorge & Poulin, 2018). This suggests that as further species are described from the marine environment, we expect to find species that are more localized in their distributions, and/or hosts in the case of parasites.

### Less than 1 in 6 marine species are parasites

By comparing all marine parasites and non-parasites at a global scale, our findings contrast with expectations within marine parasite literature. This may be due to previous studies using data collected at local scales or within single taxa. However, our findings do support those of previous analyses of rates of parasite description at larger scales (Costello 2016) and support accumulating evidence that under specific conditions (e.g., changes in geography, host availability), parasites are able to switch hosts more often than may be observed (e.g., Brooks & Hoberg, 2007; Agosta, Janz & Brooks, 2010; Hoberg & Brooks, 2015).

### Hosts are not equal in their suitability for parasites

The best studied parasites are those of vertebrates. These species tend to have large body-sizes and are geographically widespread, thereby providing multiple parasite microhabitats and increased chance for infestation (Costello, 2016). Yet, vertebrates are not representative of all species on Earth. Over 61% of marine species on Earth are arthropods and other macro-invertebrates (Costello, May & Stork, 2013a). Their small body size is a more limiting resource for parasites (Oliva & Alvarez, 2011, Dáttilo et al., 2020) than larger vertebrates and they are often used as intermediate hosts to complete parasitic lifecycles (Leung, Mora & Rohde, 2015). Therefore, as more marine species are sampled for their parasite assemblages, we believe more new species will be discovered in vertebrates than their invertebrate counterparts.

### Better to infect more host species than few

The co-evolutionary tension between parasites and their hosts create unique selection pressures as they continually adapt to survive (Hudson, 2005). These evolutionary moves and counter-moves have been suggested to create highly specialized parasitic organisms, that are uniquely adapted to their host or hosts (Poulin, 2007). However, with the incorporation of molecular and experimental techniques in determining host specificity in parasites, results show that parasites can often infect many more hosts successfully than is seen in nature (Poulin & Keeney, 2007). This is a better evolutionary strategy as most species are geographically rare and rare hosts provide limited opportunities for parasite transmission and evolution. Therefore, parasite host relationships we observe are strongly influenced by the local exposure of hosts to parasites and not solely a consequence of host specificity.

Shifting host distributions and reassembly of communities, as has been happening due to climate change (Lenoir et al., 2020; Chaudhary et al., 2021), may provide new host opportunities for parasites. If so, naïve hosts may suffer pathogenic effects due to lack of behavioural and/or immunological defences against the parasites. Yet, on the other hand, as host species move away from historical distributions, parasites may find it difficult to complete complex lifecycles and as a result, become extinct, releasing host populations. As such, further descriptions of parasites, and parasite host associations, should be part of biodiversity monitoring to aid understanding of how climate change may directly and indirectly (through parasites) impact biodiversity at ecosystem scales.

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