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Tapeworm discovery in elasmobranch fishes: quantifying patterns and identifying their correlates

Haseeb S. Randhawa[A,B,C,E] *and Robert Poulin*[D]

[A]Directorate of Natural Resources, Fisheries Department, Falkland Islands Government,
Bypass Road, Stanley, FIQQ 1ZZ, Falkland Islands.
[B]South Atlantic Environmental Research Institute, Stanley Cottage, Stanley, FIQQ 1ZZ,
Falkland Islands.
[C]New Brunswick Museum, 277 Douglas Avenue, Saint John, NB, E2K 1E5, Canada.
[D]Department of Zoology, University of Otago, PO Box 56, Dunedin, 9054, New Zealand.
[E]Corresponding author. Email: hrandhawa@fisheries.gov.fk

Abstract. Most parasites from known host species are yet to be discovered and described, let alone those from host species not yet known to science. Here, we use tapeworms of elasmobranchs to identify factors influencing their discovery and explaining the time lag between the descriptions of elasmobranch hosts and their respective tapeworm parasites. The dataset included 918 tapeworm species from 290 elasmobranch species. Data were analysed using linear mixed-effects models. Our findings indicated that we are currently in the midst of the greatest rate of discovery for tapeworms exploiting elasmobranchs. We identified tapeworm size, year of discovery of the type host, host latitudinal range and type locality of the parasite influencing most on the probability of discovery of tapeworms from elasmobranchs and the average time lag between descriptions of elasmobranchs and their tapeworms. The time lag between descriptions is decreasing progressively, but, at current rates and number of taxonomic experts, it will take two centuries to clear the backlog of undescribed tapeworms from known elasmobranch species. Given that the number of new elasmobranch species described each year is on the rise, we need to re-assess funding strategies to save elasmobranchs (and, thus, their tapeworm parasites) before they go extinct.

Additional keywords: cestodes, linear mixed-effects model, rays, sharks, skates, taxonomic effort, taxonomy, year of description.

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Introduction

It is estimated that between 3×10^6 and 1×10^8 species inhabit our planet (Wilson 2003; May 2010), with more than half the species on Earth parasitising other species (Poulin 2014). More reasonable estimates of global diversity place this number closer to 1×10^7 species (Wilson 2003). Regardless of the exact number, estimating the global diversity on Earth is tricky business (May 1988; Wilson 2003). These are estimates of the biodiversity that might exist, yet the proportion that we actually know is likely to be less than 20% of this estimated diversity (Wilson 2003) and, by all accounts, even this is a generous proportion (see Mora *et al.* 2011). In marine ecosystems, it is estimated that only between one-third and two-thirds of the estimated 0.7×10^6 to 1×10^6 eukaryote species have been discovered and described (Appeltans *et al.* 2012).

Despite parasitic organisms making up a large proportion of the global diversity, the body of literature dedicated to parasites pales in comparison with that dedicated to their hosts, and this is especially true of marine ecosystems (Poulin *et al.* 2016*a*). The relative paucity of studies on the biology of parasitic organisms is primarily attributable to the fact that many have yet to be discovered for many reasons. First, research efforts focusing on parasites and diseases are strongly biased towards specific host groups (Poulin *et al.* 2016*a*). Second, parasites are generally discovered after their hosts (Poulin 1996). Of the rare exceptions, two of the better-documented examples are those of the description of a new genus of a parasitic copepod (Cressey and Boyle 1978) and of a new family of a trypanorhynch tapeworm (Dailey and Vogelbein 1982) found in megamouth sharks (*Megachasma pelagios*), which were published before the host species itself was described in 1983 (Taylor *et al.* 1983). Third, organisms occupying a wider geographical range are more likely to be discovered earlier than those with more restricted ranges (Blackburn and Gaston 1995; Gaston *et al.* 1995; Allsopp 1997; Collen *et al.* 2004; Baselga *et al.* 2010; Randhawa *et al.* 2015). In the specific case of parasites, the host range is analogous to geographical range and parasitic organisms exploiting a wider range of organisms have generally been described before those restricted to fewer hosts species (Poulin and Morand 2004; Krasnov *et al.* 2005; Poulin and

Mouillot 2005). However, for parasites displaying host specificity, i.e. infecting a narrow range of hosts, their geographical range is assumed to mirror that of their respective host(s). Last, free-living organisms are described, generally, on the basis of their external features, and, as such, endoparasites are likely to be overlooked pending examination by a parasitologist.

Recent studies focusing on parasites have identified host range and parasite body size as influencing the probability of discovering new species. In different helminth taxa (acanthocephalans, cestodes, nematodes and trematodes; Poulin and Mouillot 2005) and fleas (Krasnov *et al.* 2005), year of discovery was negatively correlated with host range. Body size of the parasite was also negatively correlated with year of discovery in parasitic copepods (Poulin 1996) and monogeneans parasitic on fish (Poulin 2002), although no such relationship was observed in fish trematodes (Poulin 1996).

Here, we attempt to identify factors influencing the probability of discovering tapeworms from elasmobranch fishes (sharks, skates and rays). The tapeworm–elasmobranch model is ideally suited for the present study. Tapeworms are the most diverse group of parasites to inhabit the digestive tract of elasmobranch fishes (Caira and Healy 2004), with over a 1000 species from 202 genera and nine orders being presently recognised (Caira *et al.* 2017*a*); their length varies by three orders of magnitude, from less than 1 mm to over 1 m (Caira and Reyda 2005) and eight of the nine orders exhibit strict host specificity (i.e. narrow host range), which is an indication of a close association with one or few closely related host species. There are ~1200 described species of elasmobranch fishes (Last *et al.* 2016*a*), of which an estimated ~40% have been examined for tapeworms (Caira *et al.* 2017*a*). It is assumed that parasitological surveys have not been performed for the other species, because nearly all elasmobranch species examined for parasites harbour at least one species of tapeworm (Caira *et al.* 2001). On average, each elasmobranch species is host to six different tapeworm species, of which four exhibit host specificity (Randhawa and Poulin 2010). It is further estimated that there are at least 3600 undescribed species of tapeworm from 'known' elasmobranch fishes (Randhawa and Poulin 2010; Caira *et al.* 2017*a*).

The specific objectives of the study are to (1) test the hypothesis that tapeworm size, tapeworm ordinal affiliation, host biological or ecological features, timing of host description, and host ordinal affiliation influence the discovery of new species of tapeworm from 'known' elasmobranchs, (2) quantify the time lag between the descriptions of elasmobranch fishes and their tapeworms; and (3) test the hypothesis that tapeworm and elasmobranch host features influence this time lag.

Materials and methods

The dataset

The complete list of described and valid tapeworm species from elasmobranch fishes was compiled using Beveridge *et al.* (2017), Caira *et al.* (2017*b*, 2017*c*, 2017*d*, 2017*e*, 2017*f*), Jensen *et al.* (2017), Ruhnke *et al.* (2017*a*, 2017*b*), and the Global Cestode Database (www.tapewormdb.uconn.edu; accessed in September and October 2018). For each tapeworm species, we recorded (1) year of description, (2) tapeworm order to which it is currently assigned, (3) the type host species (and order), (4) year of description of its type host, (5) tapeworm type locality (assigned to a realm and province according to Marine Ecoregions of the World (MEoW) *sensu* Spalding *et al.* 2007), (6) the taxonomic authority and (7) maximum tapeworm length (see Table S1, available as Supplementary material to this paper). Maximum tapeworm length was obtained from the dataset compiled by Randhawa and Poulin (2010) and updated with data from original descriptions for species not included in the aforementioned dataset. However, the authors were not able to access publications from the journal *Zootaxa*; hence, 10 valid species from three different orders were not included in the dataset. In the case of trypanorhynchs, only measurements reported from adult specimens from elasmobranch hosts were included, therefore species for which only larval measurements were published were not included in this study. Host measurements and biological or ecological variables included the following: (1) host maximum length (total length) or disc width; (2) latitudinal range; (3) depth range (preferred depth range when available); (4) depth midpoint, measured as the mid-point of the species' preferred depth range; (5) host order; (6) host type (shark or batoid); (7) habitat (bathydemersal, benthopelagic, demersal, pelagic neritic, pelagic oceanic, reef associated); (8) environment (brackish, freshwater, marine); and (9) climate (deepwater, polar, subtropical, temperate, tropical; see Table S1). Host data were collected from Compagno *et al.* (2005) and FishBase (ver. 06/2018, R. Froese and D. Pauly, see www.fishbase.org, accessed September 2018) (for sharks) and from Last *et al.* (2016*b*) and FishBase (see www.fishbase.org for batoids). Host length was measured as the maximum total length for sharks and batoids of the orders Rajiformes, Rhinopristiformes, Torpediniformes, and three families of Myliobatiformes (Urolophidae, Urotrygonidae, and Zanobatidae), and maximum disc width for the other families of order Myliobatiformes. Host data for trypanorhynch tapeworms correspond to those from the first elasmobranch host from which the adults were recovered, since some species were first described as larvae.

Statistical analyses

The average tapeworm discovery rate from different orders and respective 95% confidence intervals (CI) were calculated using generalised linear models (GLM) with quasi-Poisson error to accommodate the overdispersed and discrete nature of the data. The rate was modelled as

$$S(t+1) - S(t)$$

where S corresponds to the number of new tapeworm species described each year and t corresponds to year. The rate was calculated for distinct periods, e.g. entire dataset (1794–2017), pre-World War (WW) I, between both WWs (1923–1939), post-WWII to molecular era (1950–1985; invention of polymerase chain reaction (PCR) in 1985), since molecular era (1986–2017) and the past decade (2008–2017; Table 1; see Randhawa *et al.* 2015 for explanation as to why these periods exclude 5 years following each WW). We truncated the dataset for these analyses to ensure that the rate was calculated over years including 12 months of published data.

Table 1. Summary of historical tapeworm-species discovery rates from elasmobranch fishes, i.e. number of new species described annually (with 95% confidence intervals), for tapeworm orders infecting elasmobranchs with at least 20 described species as of December 2017

Taxon	1794 to present	Pre–1914	1923–1939	1950–1985	1986–2017	2008–2017
All	4.08 (3.24–5.05)	1.19 (0.66–1.94)	2.41 (1.31–4.00)	6.56 (4.86–8.61)	14.59 (11.53–18.16)	17.56 (14.81–20.27)
Diphyllidea	0.25 (0.16–0.37)	0.02 (<0.01–0.06)	0.06 (<0.01–0.26)	0.33 (0.18–0.56)	1.22 (0.72–1.91)	2.10 (1.00–3.80)
Lecanicephalidea	0.39 (0.24–0.59)	0.12 (0.04–0.26)	0.18 (0.03–0.56)	0.39 (0.13–0.87)	1.72 (0.94–2.84)	3.50 (1.72–6.23)
Onchoproteocephalidea	1.02 (0.72–1.39)	0.16 (0.09–0.26)	0.76 (0.20–1.52)	2.00 (1.41–2.73)	3.63 (2.08–5.79)	3.20 (1.48–5.90)
Phyllobothriidea	0.30 (0.19–0.44)	0.14 (0.08–0.23)	0.24 (0.06–0.61)	0.25 (0.06–0.65)	1.13 (0.58–1.94)	1.30 (0.67–2.24)
Rhinebothriidea	0.68 (0.49–0.90)	0.18 (0.06–0.40)	0.29 (0.06–0.83)	1.75 (1.11–2.61)	1.75 (1.13–2.56)	3.00 (1.56–5.14)
Tetraphyllidea '*relics*'	0.42 (0.29–0.57)	0.15 (0.06–0.29)	0.18 (0.05–0.43)	0.58 (0.28–1.05)	1.53 (0.96–2.29)	1.40 (0.94–1.99)
Trypanorhyncha	0.96 (0.70–1.28)	0.42 (0.24–0.67)	0.71 (0.30–1.37)	1.08 (0.55–1.88)	3.41 (2.19–5.01)	2.80 (1.37–5.00)

Linear mixed-effects models (LMM) were performed using R (ver. 3.4.2, R Foundation for Statistical Computing, Vienna, Austria, see www.r-project.org, accessed October 2018), to assess relationships between two response variables, i.e. tapeworm year of discovery and lag in years between description of elasmobranch host and its tapeworm parasites, and 12 predictor variables. These included the following six fixed effects: (1) maximum tapeworm length; (2) year type host described; (3) host latitudinal range; (4) maximum host length/disc width; (5) depth range; and (6) depth mid-point; and the following six random effects: (1) host order nested within host type; (2) parasite order; (3) parasite type locality (MEoW province *sensu* Spalding *et al.* 2007); (4) climate; (5) host environment; and (6) host habitat. Additionally, we re-ran each LMM as a linear model, i.e. with the random effects removed, to examine differences in the relative importance of fixed effects, compared to when included in a LMM. A multi-model inference approach was performed using the package MuMIn in R (ver. 1.42.1, K. Barton, see http://cran.r-project.org/web/packages/MuMIn, accessed September 2018). Models were ranked according to their Akaike information criterion corrected for small sample-size values (AIC_c). The relative importance and rank of each variable was determined using the AIC_c differences (ΔAIC_c) and Akaike model-averaged weights ($w + (i)$) for all possible model combinations. These were used to determine the best models and the relative importance of each predictor. Model-averaged parameter estimates and 95% CI were computed using MuMIn. The partial r-squared values for each model-averaged parameter were assessed using r2 glmm package in R (ver. 0.1.1, B. Jaeger, see https://cran.r-project.org/package=r2glmm, accessed September 2018), providing insights into the proportion of variance explained by each variable. Second-order interactions were initially included between each possible pair of variables, and compared to models including their single or additive effects using AIC_c. On the basis of these analyses (results not shown), no second-order interaction terms were retained in our analyses.

Given the large number of levels for our random effects, especially for locality (MEoW provinces *sensu* Spalding *et al.* 2007) where $N = 50$, to increase the number of tapeworm species per degree of freedom, we pooled localities into broader geographical categories and assessed the relative importance of each variable, compared to the models including all localities. Seeing no discernible differences (results not shown), we proceeded to use a dataset including all localities. Furthermore, we repeated analyses by including only the five parameters explaining the largest proportion of variance in the data and found no important difference in either the rank or relative importance of each predictor (results not shown). Therefore, results presented below are based on the full complement of variables.

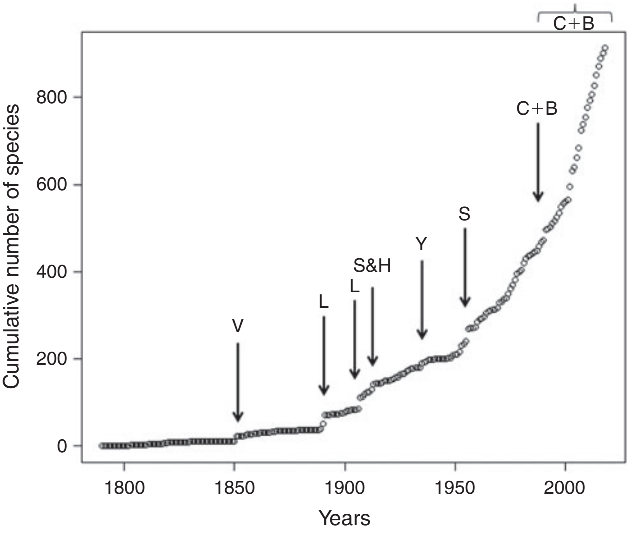

Fig. 1. Cumulative frequency distribution of described number of tapeworm species ($n = 918$) from elasmobranch fishes. Arrows indicate significant contributions made by individuals corresponding to spikes. V, van Beneden; L, Linton; S&H, Shipley and Hornell; Y, Yamaguti; S, Subhapradha; C+B, Caira (and her students) + Beveridge.

Results

The dataset included 918 tapeworm species described between 1794 and 2018, representing all 9 orders known to infect elasmobranch fishes (Fig. 1). Tapeworm ranged in length between 0.475 and 1015.000 mm (mean = 48.2 ± 94.2 mm). Length values were greatly overdispersed, with most of species measuring <40 mm (Fig. 2). Overall, these tapeworms were described from 290 distinct host species. The first tapeworm described from elasmobranchs is the trypanorhynch *Gilquinia*

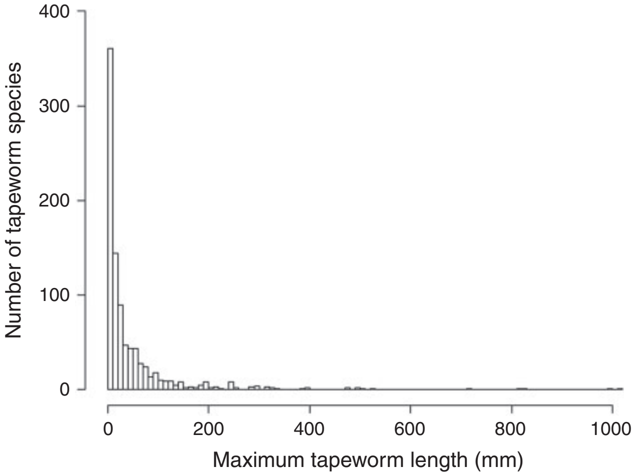

Fig. 2. Frequency distribution of maximum lengths among tapeworm species parasitic in elasmobranch fishes ($n = 918$).

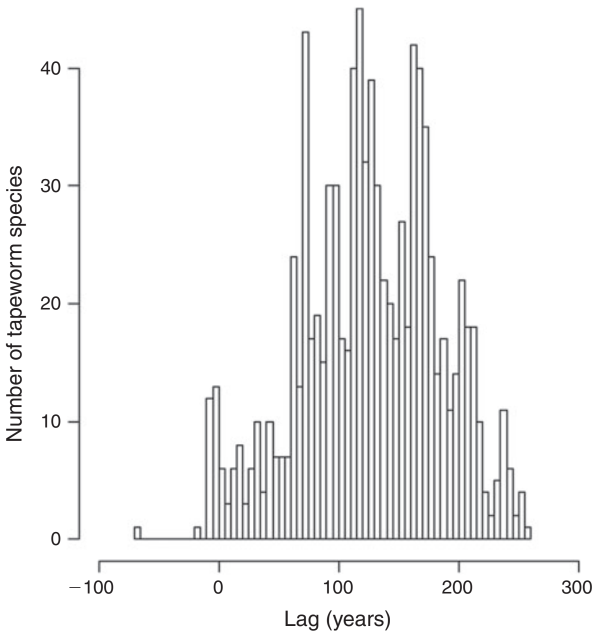

Fig. 3. Frequency distribution of the lag (in years) between the type description of an elasmobranch and that of its tapeworm parasite(s) ($n = 918$).

squali (Fabricius, 1794) from *Squalus acanthias* L. and the most recent ones are also trypanorhynchs, including five species of *Parachristianella* Dollfus, 1946, which were described from a dasyatid, a mobulid, and two potamotrygonids (all batoids of the order Myliobatiformes). Most of the species (97.1%) were described after their host (mean lag = 127 years, s.d. = 58 years), with three species having been described the same year, and 24 having been described before their elasmobranch host (1–68 years) (Fig. 3). The majority of species (median) were described after 1986.

Historically, onchoproteocephalids and trypanorhynchs have the highest rate of species description (Table 1), which is not surprising, given that they are the most speciose orders in our dataset. Prior to WWI, trypanorhynchs were described more frequently than other tapeworm taxa from elasmobranch fishes (Table 1). Over the past decade, there has been a shift, with lecanicephalids being the most frequently described (3.5 species per year), followed by onchoproteocephalids (3.2 species per year), rhinebothriids (3.0 species per year) and trypanorhynchs (2.8 species per year) (Table 1). The overall pattern observed within most tapeworm orders is a significant rise in species description rates since the molecular era (Table 1).

Restricting our data to the 29 MEoW provinces identified as the type locality for at least eight species, we found that there are significant biases (Fig. 4). For instance, 853 of the 918 tapeworm species included in this dataset (92.9%) were described from these 29 localities (58.0%), with 'warm, temperate northeast Pacific' and 'cold, temperate northwest Atlantic' leading the way with 76 (8.3%) and 72 (7.8%) tapeworm species respectively, having been described from elasmobranch fishes. Additionally, surveys of tapeworms from elasmobranchs in tropical countries (e.g. Indonesia, Malaysia), where the greatest host species diversity is expected, have occurred only recently, whereas the majority of early descriptions have occurred from the northern Atlantic (primarily eastern USA and North Sea), northern Pacific (namely western USA and Japan), Mediterranean Sea (France, Italy) and former British colonies (India, Sri Lanka; Fig. 4). These areas are also regions where the most prolific elasmobranch tapeworm taxonomists were based (Fig. 5). Overall, 21 taxonomists (and their students) have described 716 of the species included in this dataset (78.0%), with Janine Caira leading the way with 215 species or nearly one-quarter of all tapeworm species included in this dataset (Fig. 5).

The best model ($\mathrm{AIC_c} = 8918.42$) for tapeworm year of discovery explained 71.9% of the variance and included maximum tapeworm length and year in which the type host was described (in addition to all random effects; Table 2). Some models excluding some of the random effects, but keeping the same two fixed effects, had slightly lower $\mathrm{AIC_c}$ values, but explained a smaller proportion of the variance and had significantly lower log(L) values (in the −4453.0 range compared with −4449.0 for the model selected as best performing). Of all models including all six random effects, a single model was within 2 $\mathrm{AIC_c}$ units and only one other could be considered plausible ($\Delta\mathrm{AIC_c}$ of 0.01 and 7.10 respectively; see Table 2). Our LMM analyses showed that random effects explained 52.6% of the variance in tapeworm year of discovery, whereas year type host described and maximum tapeworm length explained 12.6 and 6.8% of the variance respectively (Table 3). In addition to latitudinal range (explaining 0.4% of the variance), both of these fixed effects were the only ones to have a 95% CI excluding '0' (Table 3). However, maximum tapeworm length ranked as the most important predictor (of the fixed effects; Table 3) and was negatively correlated with the year it was described (Fig. 6; slope = −0.67; $R = 0.32$, $P < 0.001$).

Results of the LMM analyses for the time lag between the descriptions of the elasmobranch host and its tapeworms are very similar to the LMM results for tapeworm year of discovery

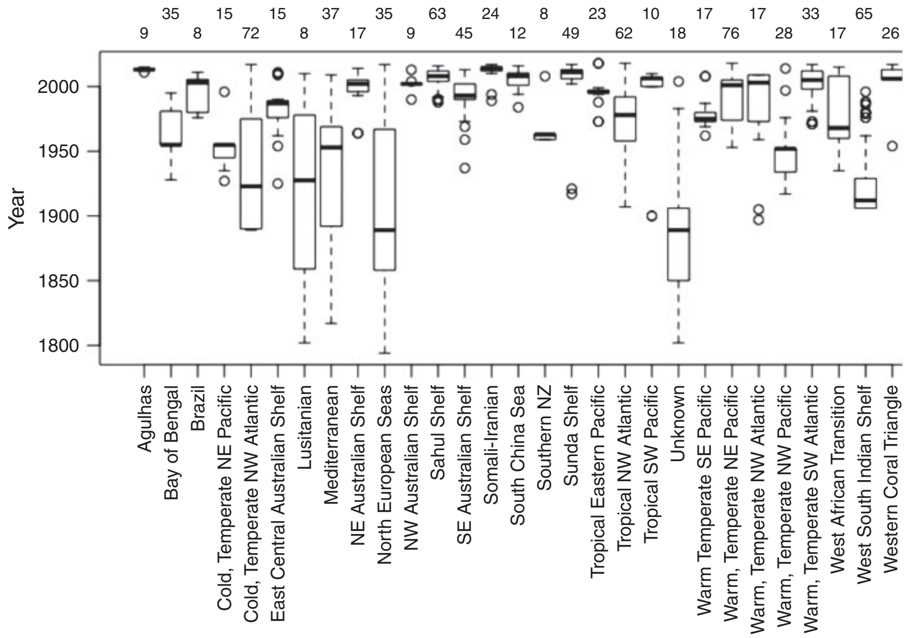

Fig. 4. Boxplots depicting the median year of tapeworm discovery for localities from which at least eight tapeworm species have been described from elasmobranch fishes. Numbers of described species by MEoW province (*sensu* Spalding *et al.* 2007) are listed on the top axis.

(Tables 4, 5). The best model includes the same predictors, but the proportion of variance explained by the best model is 88.9%; random effects explain 32.5% of the overall variance, and year of description of the type host (fixed effect) is ranked as the most important predictor and explains 49.7% of the variance in time lag. The time lag between the descriptions of elasmobranch hosts and their respective tapeworm(s) as a function of the year of description of the elasmobranch type host is plotted in Fig. 7 (slope $= -0.69$; $R = 0.71$, $P < 0.001$), showing that the lag in description between elasmobranch host and its tapeworm(s) is decreasing in most recently described elasmobranchs.

Discussion

The comprehensive dataset we compiled allowed us to thoroughly assess the importance of different host and parasite variables influencing the year of discovery of tapeworm parasites and the time lag between the elasmobranch host and tapeworm descriptions using quantitative tools. It is clear from our results that both the year of tapeworm discovery and the time lag between the description of elasmobranch hosts and their respective tapeworm(s) are largely influenced by (1) the geographical location of the type description of the parasite, (2) the year the elasmobranch host was described, (3) the maximum size of the tapeworm species and, to a lesser extent, (4) its host's latitudinal range. The relative importance of type locality for year of tapeworm species description is not surprising, given that most parasite species are described from temperate areas (Poulin 2010), despite hotspots for host diversity being in the tropics.

For instance, a recent study has found that fewer parasites have been described from hot spots of marine fish biodiversity than would have been expected (Jorge and Poulin 2018). However, Australia has been identified as a hotspot for elasmobranch diversity (Stein *et al.* 2018) and is a country with financial means; thus, it is not surprising that the greatest number of tapeworm species (155 or 16.9%) exploiting elasmobranch fishes have been described from that country (see Table S1). Nevertheless, most areas of high biodiversity, such as Malaysia and Indonesia, are also generally poorer in terms of financial resources. As such, the lag in tapeworm species discovery might be attributable to limited resources in those countries to undertake fieldwork or process samples for scanning electron microscopy and molecular analyses, which are the two methods now commonly used, with the taxonomic quality of type descriptions having increased in contemporary species descriptions (Poulin and Presswell 2016).

Interestingly, the recent initiative Planetary Biodiversity Inventories (PBI) program, funded jointly by the National Science Foundation (NSF) of the USA, the ALL Species Foundation, and the Alfred P. Sloan Foundation to uncover the global tapeworm diversity from all major vertebrate hosts facilitated one of the first focused foray into the examination of elasmobranch fishes in tropical areas (e.g. Southeast Asia), with one of the main objectives being to identify the extent of the tapeworm fauna from these hosts (Caira and Jensen 2017). As such, 215 species of elasmobranchs, many having never before being examined for parasites, yielded the discovery of 148 new species of tapeworms (Caira *et al.* 2017*a*). Many of the taxonomists participating in this initiative are from temperate areas and the funding facilitated their fieldwork into tropical areas (see Caira *et al.* 2017*a*). Therefore, where in the past a taxonomist's field sites might have been located nearer their respective institutions, nowadays, initiatives such as the PBI provide the means necessary to travel overseas to conduct fieldwork.

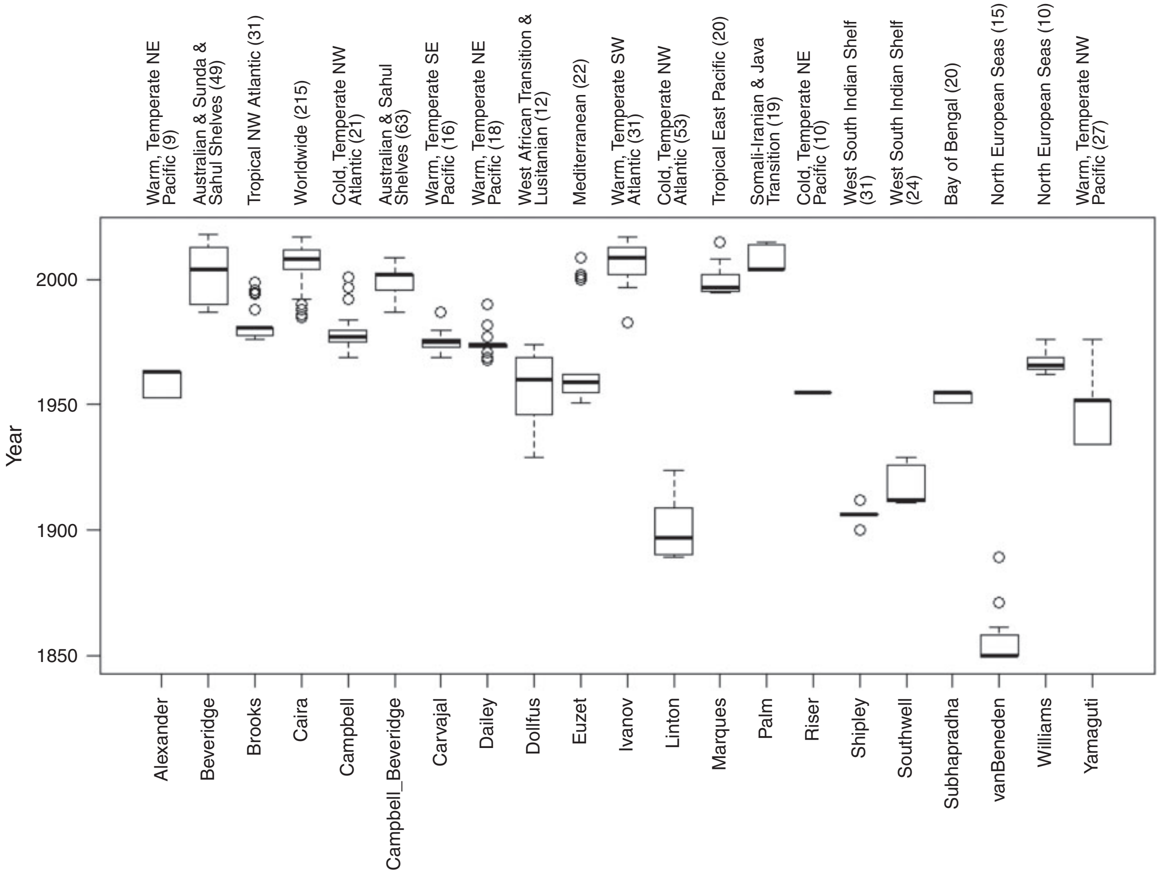

Fig. 5. Boxplots depicting the median year of tapeworm discovery for different tapeworm systematists having described at least nine tapeworm species from elasmobranch fishes. Note that taxonomists have been lumped on the basis of the pedigree of individual researchers when years of activity overlap. For instance, Caira trained Fyler, Jensen, Pickering, Reyda and Ruhnke (to name a few) and all still publish concurrently. These have all been lumped under Caira despite many of these trainees now leading productive careers of their own as tapeworm systematists. Additionally, Campbell and Beveridge each appear separately, but collaboratively, they have described an impressive number of taxa; hence, they appear as a pair to describe their years of collaborative work. In instances where multiple experts have collaborated in species descriptions with no apparent ties, the species has been allocated to the corresponding author. Overall, these 21 tapeworm taxonomists and their students have described 716 of the 918 (78.0%), with Caira having described nearly one-quarter, of species included in this dataset. Localities (MEoW provinces *sensu* Spalding *et al.* 2007) where each author and their students have focused their efforts (number of described species to their name) are listed on the top axis.

Table 2. Summary of the top models to explain year of discovery for elasmobranch tapeworm species on the basis of Akaike information criterion adjusted for small sample sizes (AIC$_c$)

Models include all six random effects and are shown including the number of parameters (K), log-likelihood (log(L)), ΔAIC$_c$, Akaike weights (w$_i$) of each model, and the proportion of variance (% var.) explained by each model given the data

Parameter	K	log(L)	ΔAIC$_c$	w$_i$	% var.
Max. parasite length + year type host described	10	−4449.09	–	0.49	71.86
Max. parasite length + year type host described + latitudinal range	11	−4448.07	0.01	0.48	72.25
Max. parasite length + year type host described + max. host size	11	−4451.62	7.10	0.01	71.87

A stronger partnership between marine ecologists and parasitologists has recently been advocated (see Poulin *et al.* 2016*a*; Blasco-Costa and Poulin 2017), and such close interactions have been facilitated by initiatives such as the PBI and the Chondrichthyan Tree of Life (CTOL) project (also NSF funded). For instance, equally important work was achieved on elasmobranch taxonomy and systematics through the CTOL (e.g. see Naylor *et al.* 2012; Last *et al.* 2016*b*), concurrently to

Table 3. Summary of tapeworm and host features as predictors of year of discovery of elasmobranch tapeworm species

Relative importance of predictors is compared by model-averaged weights (w + (*i*)), rank, parameter estimates, 95% confidence intervals (CI), and partial r^2 values. Bold text indicates predictors where CI excludes '0'

Random effects	Number of levels	Proportion of variance explained (%)
Host order: host type	13	0.69
Parasite order	9	0.79
Locality	50	46.76
Climate	5	2.68
Environment	3	1.35
Habitat	6	0.29

Fixed effects	w + (*i*)	Rank	Estimate	95% CI	Partial r^2
Max. parasite length	**1.00**	**1**	**−0.07094**	**−0.09228 to −0.04959**	**0.0673**
Year type host described	**1.00**	**2**	**0.10918**	**0.06300–0.15560**	**0.1257**
Latitudinal range	**0.49**	**3**	**−0.05473**	**−0.19159 to −0.02966**	**0.0039**
Max. host size	0.02	4	−0.00020	−0.02814–0.00588	0.0001
Depth mid-point	0.01	5	<0.00001	−0.01359–0.01613	<0.0001
Depth range	<0.01	6	<0.00001	−0.00893–0.00987	0.0048

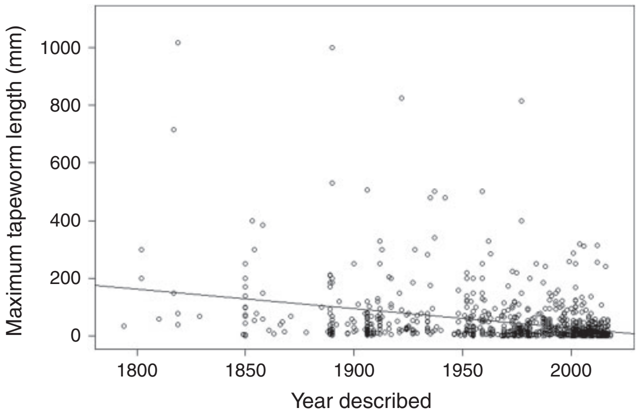

Fig. 6. Relationship between maximum tapeworm length and the year each was described. The line represents the best-fit relationship from a linear regression ($P < 0.001$, $R = 0.32$).

the work conducted on elasmobranch tapeworm discovery (Caira and Jensen 2017).

The PBI also provided sufficient funding to make tools available to ensure the highest-quality descriptions (including scanning electron micrographs and molecular analyses) for all taxa, and the training of the next generation of tapeworm taxonomists. The plea to prevent a shortfall of taxonomy specialists has been made for nearly two decades (Brooks and Hoberg 2000, 2001; Poulin *et al.* 2016*a*) and might be one of the reasons why most host–parasite checklists are far from complete (Poulin *et al.* 2016*b*). This shortfall needs to be addressed before we lose this niche expertise. Initiatives such as the PBI are key to ensuring a global supply of trained professional parasite taxonomists and systematists that will be required to clear the backlog of species to be described from known hosts, let alone those from hosts yet to be discovered. However, once trained, these taxonomists need jobs, and funding priorities need to be re-addressed to ensure the continued employment of taxonomists globally (Poulin *et al.* 2016*a*); no longer can describing species be seen and considered as just a hobby.

The tapeworm species-accumulation curve has yet to reach an asymptote (Fig. 1) because the number of new species being described since the start of the molecular era has increased exponentially (Table 1). This is a pattern mirroring that of species discovery in sharks (Randhawa *et al.* 2015). It is, therefore, statistically impossible to estimate the global diversity of tapeworms yet to be described from known elasmobranchs and, therefore, predict the number of tapeworm taxonomists required to describe this diversity in its entirety. However, the number of tapeworm species yet to be described from known elasmobranch fishes is thought to be at least 3600 (Randhawa and Poulin 2010; Caira *et al.* 2017*a*). Assuming that the rate of tapeworm species descriptions in elasmobranchs remains similar to that in the past decade (17.6 per year; Table 1), it would take over 200 years before we simply clear the backlog of species yet to be described from known elasmobranch fishes.

Unfortunately for taxonomists, the number of elasmobranch species being described each year keeps increasing (Last 2007; White and Last 2012; Randhawa *et al.* 2015) and has yet to reach an asymptote in sharks (Randhawa *et al.* 2015). Although not examined empirically, the same is assumed for batoids. Therefore, it is plausible that we have yet to discover half of all elasmobranch species inhabiting our oceans. The time lag between description of the elasmobranch host and its tapeworm(s) is decreasing (Fig. 5) and ~40% of all known elasmobranchs have been examined for parasites (Caira *et al.* 2017*a*). Recent efforts to uncover both elasmobranch and tapeworm diversity from these hosts have been jointly boosted due to large funding initiatives by both the PBI and CTOL. However, the decreasing time lag was apparent previous to these initiatives and might reflect that taxonomists are catching up on the backlog of tapeworms to be described from elasmobranch hosts.

Table 4. Summary of the top models to explain the time lag (years) between the discovery of elasmobranch and its tapeworm species on the basis of Akaike information criterion for small sample sizes (AIC_c)

Models include all six random effects and are shown including the number of parameters (*K*), log-likelihood (log(L)), ΔAIC_c, Akaike weights (w_i) of each model, and the proportion of variance (% var.) explained by each model given the data

Parameter	*K*	Log(L)	ΔAIC_c	w_i	% var.
Max. parasite length + year type host described	10	−4449.09	–	0.49	88.91
Max. parasite length + year type host described + latitudinal range	11	−4448.07	0.01	0.48	89.30
Max. parasite length + year type host described + max. host size	11	−4451.62	7.10	0.01	88.92

Table 5. Summary of tapeworm and host features as predictors of lag (years) between description of an elasmobranch species and its tapeworm parasites

Relative importance of predictors is compared by model-averaged weights (w + (*i*)), rank, parameter estimates, 95% confidence intervals (CI) and partial r^2 values. Bold text indicates predictors where CI excludes '0'

Random effects	Number of levels	Proportion of variance explained (%)
Host order: host type	13	4.74
Parasite order	9	<0.01
Locality	50	14.71
Climate	5	2.18
Environment	3	3.10
Habitat	6	7.80

Fixed effects	w + (*i*)	Rank	Estimate	95% CI	Partial r^2
Year type host described	**1.00**	**1**	**−0.89070**	**−0.93700 to −0.84440**	**0.4965**
Max. parasite length	**1.00**	**2**	**−0.07094**	**−0.09370 to −0.04959**	**0.0673**
Latitudinal range	**0.49**	**3**	**−0.05459**	**−0.19116 to −0.02977**	**0.0039**
Max. host size	0.02	4	−0.00020	−0.02814–0.00059	0.0001
Depth mid-point	0.01	5	<0.00001	−0.01359–0.01611	<0.0001
Depth range	<0.01	6	<0.00001	−0.00893–0.00987	0.0048

The inverse relationship between body size and year of discovery is a well established pattern in free-living organisms (Gaston 1991; Gaston and Blackburn 1994; Blackburn and Gaston 1995; Reed and Boback 2002; Ferro and Diniz 2008) and, to a certain extent, in parasitic ones (Poulin 1996, 2002). Our results demonstrated that maximum length of tapeworms infecting elasmobranch fishes is one of the most influential predictors of discovery in this group, with larger species more likely to be described first. The maximum size of elasmobranch tapeworms is positively correlated with host size (weight; Randhawa and Poulin 2009). Likewise, large tapeworms infecting elasmobranchs are more likely to be discovered earlier than are smaller ones (Fig. 6). The same is true for shark hosts. For instance, shark species more recently described are generally smaller-bodied than those described earlier (Randhawa *et al.* 2015), therefore larger tapeworms infecting larger elasmobranchs (likely discovered earlier) will likely be discovered before smaller tapeworms infecting smaller-bodied elasmobranch species (likely to be discovered later).

Additionally, the negative relationship between geographical range and year of discovery is another well-established pattern in free-living organisms (Blackburn and Gaston 1995; Gaston *et al.* 1995; Allsopp 1997; Collen *et al.* 2004; Baselga *et al.* 2010). Our results indicated that the latitudinal range, and not depth range, of elasmobranchs does influence the likelihood of their tapeworms being described; tapeworms infecting elasmobranch hosts occupying a wider latitudinal range are more likely to be described earlier. Additionally, latitudinal range was indeed found to influence the time of discovery in sharks where sharks with more restricted latitudinal ranges were generally discovered later (Randhawa *et al.* 2015). In parasites, host range is analogous to geographical range and it is expected that parasites exploiting a wider range of organisms would be described before those restricted to fewer hosts species (Poulin and Morand 2004; Krasnov *et al.* 2005; Poulin and Mouillot 2005). Trypanorhynch tapeworms exhibit a lesser degree of host specificity (Palm and Caira 2008), i.e. they possess a wider host range than do members from most other tapeworm orders exploiting elasmobranch hosts. It is, therefore, not surprising that trypanorhynchs were described generally earlier than were other tapeworms infecting elasmobranch fishes, as is evident from the higher rates of taxa described before WWI and lower rates (relative to other tapeworm orders from elasmobranchs) in the past decade (Table 1). This trend would be exacerbated had we included type descriptions of trypanorhynch tapeworms

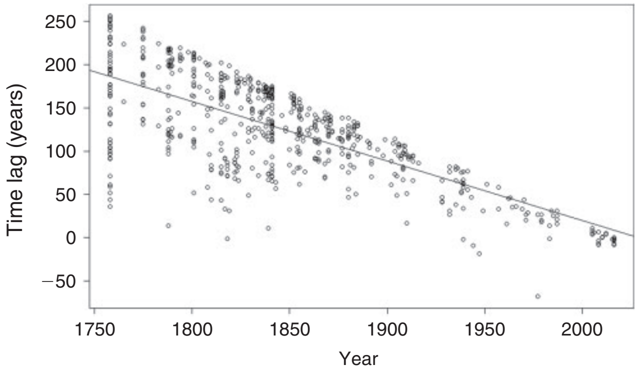

Fig. 7. Relationship between the time lag (in years) between descriptions of the elasmobranch host and that of its tapeworm parasites and the year of description of the elasmobranch type host. The line represents the best-fit relationship from a linear regression ($P < 0.001$, $R = 0.71$).

from teleost hosts, many of which occurred before their discovery in elasmobranch fishes (Palm 2004).

Year of description of elasmobranch species is a strong correlate of the year of discovery of their respective tapeworm(s) and the former is itself strongly correlated with species latitudinal range and, to a lesser extent, size and depth (Randhawa *et al.* 2015). These results are consistent with observations made for other marine organisms by Gibbons *et al.* (2005), whose findings indicated that the geographic range of holozooplankton was the best predictor of date of first description, followed by size and depth. Greater latitudinal range in certain shark species translates into a greater probability of encounter, whereas the mid-point of the depth range of these animals is a proxy for accessibility. Historically, with most fish stocks in decline, fishing efforts have shifted from coastal to offshore–deeper waters (Roberts 2002; Morato *et al.* 2006; Swartz *et al.* 2010). Consequently, the greater fishing effort in these waters has enabled scientists to discover new species from once inaccessible environments. Although these factors influence the likelihood of elasmobranch discovery, tapeworm discovery is also driven by other factors, independent from those influencing that of their hosts.

In conclusion, we are in the midst of a period of maximum species discovery for both elasmobranchs (Last 2007; White and Last 2012; Randhawa *et al.* 2015) and their tapeworms (results presented herein), relative to historical rates (see Table 1). The species accumulation curve of tapeworms infecting elasmobranch fishes has yet to reach an asymptote (Fig. 1), rendering it statistically impossible to predict their global diversity. Furthermore, with a likely large number of hosts not yet described (e.g. Randhawa *et al.* 2015), the task of describing the global tapeworm diversity from the global elasmobranch fauna is a daunting one, especially in the light of the average time lag of 127 years between the descriptions of elasmobranchs and that of their tapeworms. Exacerbating this concern is the fact that elasmobranchs are the most threatened group of marine fishes (Davidson and Dulvy 2017), thus creating a sense of urgency to protect and conserve elasmobranchs (and their respective tapeworms) before they either go extinct or decline to levels where they are unable to sustain parasite transmission. With what we now know, our results suggest that the unknown tapeworm fauna is likely to consist primarily of small-bodied taxa exhibiting strict host specificity and infecting more recently described elasmobranch hosts. However, we caution that without continued investment through programs such as the PBI and without re-assessing funding and recruitment strategies regarding taxonomy and systematics, we are in danger of not having the adequate expertise to tackle this issue. Furthermore, we echo calls encouraging parasitologists to work more closely with ecologists and to undertake fieldwork in areas known as hotspots for biodiversity with few academic institutions in their territory.

Conflicts of interest

Haseeb Randhawa is an Associate Editor for *Marine and Freshwater Research*. Despite this relationship, he did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Marine and Freshwater Research* encourages its editors to publish in the journal and they are kept totally separate from the decision-making process for their manuscripts. The authors have no further conflicts of interest to declare.

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