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**Trematodes of the Great Barrier Reef, Australia: emerging patterns of diversity and richness in coral reef fishes**

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## Abstract

The Great Barrier Reef (GBR) holds the richest array of marine life found anywhere in Australia, including a diverse and fascinating parasite fauna. Members of one group, the trematodes, occur as sexually mature adult worms in almost all GBR bony fish species. Although the first reports of these parasites were made 100 years ago, the fauna has been studied systematically for only the last 25 years. When the fauna was last reviewed in 1994 there were 94 species known from the GBR and it was predicted that there might be 2,270 in total. There are now 326 species reported for the region, suggesting that we are in a much improved position to make an accurate prediction of true trematode richness. Here we review the current state of knowledge of the fauna and the ways in which our understanding of this fascinating group is changing. Our best estimate of the true richness is now a range, 1,100–1,800 species. However there remains considerable scope for even these figures to be incorrect given that fewer than one-third of the fish species of the region have been examined for trematodes. Our goal is a comprehensive characterisation of this fauna, and we outline what work needs to be done to achieve this and discuss whether this goal is practically achievable or philosophically justifiable.

*Keywords:* Trematoda, richness, diversity, Great Barrier Reef, host-specificity, cryptic species

## 1. Introduction

The Great Barrier Reef (GBR) is arguably Australia's greatest natural asset. It is the largest coral reef system globally, stretching for some 1,800 km, and its remarkable complexity harbours the greatest diversity of fishes seen in Australian waters. These fishes are, of course, infected by a significant range of parasites. Rohde (1976) was the first to postulate quantitatively on possible parasite richness of the GBR. He suggested that the (then) 1,000 known fish species of the region were likely to have in the order of 20,000 parasite species. Since this first dramatic prediction, there has been a series of analyses of the possible richness for different components of the parasite fauna in different parts of the tropical Indo-West Pacific (TIWP) (Cribb et al., 1994b; Whittington, 1998; Justine, 2010; Palm and Bray, 2014). Recently Justine (2010) reviewed patterns of richness for a wide range of metazoan parasite groups and suggested that the 1,700 New Caledonian reef fishes are likely to harbour some 17,000 parasite species (excluding protists) of which just 2% are known to science. When such a high proportion of a predicted fauna remains unknown it is difficult to predict the final number accurately. Ironically, predictions of richness generally gain the greatest attention when there is the greatest proportional difference between the known and unknown; few headlines are made by a suggestion that a fauna of 250 species may rise to 252! However, rather prosaically, it is only when a fauna is relatively well known that the predictions or extrapolations of true richness become relatively reliable.

The trematodes of GBR fishes have now been studied for just over a century. The first reports from the region were by S.J. Johnston (1913). In the following 75 years there was a handful of studies by T.H. Johnston, W. Nicoll, W.O. Durio, H.W. Manter, J.C. Pearson and a few others. By 1988 just 30 trematode species had been reported from GBR fishes. In that year systematic study of the fauna began when R.J.G. Lester led the International Congress of Parasitology (ICOPA) parasitological workshop to Heron Island on the southern GBR (Lester and Sewell, 1990). Since 1988 the present authors and colleagues have been involved in a sustained study of this fauna. We calculate that there are now 326 species known from the bony fishes of the region. Cribb et al. (1994b) predicted that GBR fishes may have a fauna of 2,270 trematode species. In the 20 years that followed, much has changed in our understanding of this fauna.

Here, in what is essentially the 100<sup>th</sup> anniversary of commencement of work on this fauna and the 20<sup>th</sup> anniversary of the last overview of its overall composition, we review the

nature of progress towards the biodiversity goal of “understanding the system”. Analyses such as this frequently focus on the generation of a headline figure of predicted true richness for the fauna. Such predictions typically demonstrate that a vast amount of work remains to be done (e.g. Appeltans et al., 2012; Nabout et al., 2013), although we note that Strona and Fattorini (2014) argue that such estimates are frequently overblown. Here, we will attempt to produce such a figure, but we do so with some reticence. This reticence relates partly to the inherent difficulties of such predictions and partly to the emptiness of such attempts (Poulin, 2014). Is it ultimately of importance as to whether there are 1,000 or 2,000 trematodes in GBR fishes, or is what matters the identity of those trematodes, their life-cycles and how they interact with their various hosts? We suspect the latter, but understand the general interest in the former.

## **2. GBR fish trematode fauna**

### *2.1. The data set*

Analyses and remarks made here are based on the parasitological examination of 9,295 individual GBR bony (actinopterygian) fishes belonging to 505 species and 60 families. Although chondrichthyans (sharks, rays and chimaeras) do harbour digeneans, infections are so infrequent that we find that we cannot justify sampling these animals. Collection of trematodes from chondrichthyans is dependent on them being found by workers seeking other groups of parasites (especially cestodes which have radiated widely with the elasmobranchs). Our target fish were caught by line, seine net, barrier net, anaesthetic and spear guns. Over time our approach to the examination of fish has evolved from one that emphasised just the intestinal tract to one that searches for infections under the scales, in the urinary bladder, the circulatory system and the tissues; we can only speculate on how many infections were overlooked in our early years. These fishes were collected almost entirely at Heron Island (5,931 individuals) on the southern GBR and Lizard Island (3,293 individuals) on the northern GBR. Depth of examination of the 505 species has varied dramatically in line with collecting priorities and the ease with which species can be collected. A total of 98 fish species have been sampled at least 30 times but, at the other end of the spectrum, 140 species have been examined only once or twice. Our data set of published reports covers all marine fishes from eastern Queensland, Australia, north of the Tropic of Capricorn. Some of the host fishes reported are not strictly coral reef species but rather than engaging in a complex and

subjective classification of reef and non-reef species, we have analysed all the records of which we are aware from this region.

Table 1 summarises the present state of knowledge of trematodes of the bony fishes of the GBR by family, the numbers of additional species estimated to have been collected by us but not yet reported, and the known level of global richness for the families (including those not yet known from the GBR). Fig. 1A shows the accumulation of trematode species for the fauna over time, Fig. 1B the accumulation of genera, and Fig. 1C the accumulation of new host/parasite species combinations. In total 326 fully identified species from 32 families have been reported and are currently considered valid. The fauna comprises just one species from the subclass Aspidogastrea, *Lobatostoma manteri*, as reported in detail by Rohde (1973); the remaining 325 species belong to the subclass Digenea. The 326 species have been reported in 814 unique host/parasite combinations.

## 2.2. Characteristics of the fauna

Several features emerge from the data set. First, the figures of 326 species and 814 unique host/parasite combinations are substantial ones, comprising approximately 7.5% of the global fauna of trematodes of marine fishes. Tellingly, all three accumulation curves (see Fig. 1) have been almost straight lines for the last 25 years. The fact that there is no hint of a plateau effect (except perhaps for the accumulation of genera) suggests that the end of these accumulations can in no way be considered to be close. A striking feature of the fauna is its taxonomic/phylogenetic diversity as opposed to simple richness (i.e. the number of species). The 326 species are distributed among 156 genera, a mean of only 2.1 species per genus. Of course, the size of a genus is somewhat in the eye of the beholder and in the hands of others the number of genera might be either reduced (lumpers) or increased (splitters), but we think that any such effect could only be marginal. Presently, a remarkable 99 genera are represented by just a single known species on the GBR and a further 33 by just two. Thus, 85% of trematode genera have just one or two species known on the GBR. Despite this, several genera are rich in GBR fishes. The richest genera are *Transversotrema* (Transversotrematidae), *Proisorhynchus* (Bucephalidae), *Stephanostomum* (Acanthocolpidae), *Retrovarium* (Cryptogonimidae), and *Hurleytrematoides* (Monorchidae) with 14, 12, 11, 11 and 11 species recorded from the region, respectively. However, these numbers are relatively low in comparison with richness in genera of some other coral reef fish parasites. For

example, there are already 36 species known for the myxosporean genus *Ceratomyxa* on the GBR (Gunter et al., 2009; Heiniger and Adlard, 2013). In New Caledonia, studies by J.-L. Justine have shown that the monogenean genus *Pseudorhabdosynochus* is exceptionally rich on serranids, including eight species on a single fish species (Justine, 2007). Certainly parasite richness is distributed differently for every major group of parasites in coral reef fishes.

From the data reviewed above, the GBR trematode fauna contains a contrast between a relatively small number of genera that have undergone significant radiations and the vast majority that have not. On the basis of our unpublished collections we predict that this overall pattern will not change with further study. The handful of highly radiated genera have achieved their richness in different ways. *Hurleytrema*, *Prosorhynchus* and *Retrovarium* have radiated within narrow host ranges, being found only in chaetodontids and tetraodontids (McNamara and Cribb, 2009; McNamara and Cribb, 2011), serranids (e.g. Bott et al., 2013), and the closely related haemulids and lutjanids (Miller and Cribb, 2007), respectively. In contrast, the genus *Stephanostomum* is known from six families (e.g. Bray and Cribb, 2003, 2008) and *Transversotrema* from a remarkable 11 (Hunter et al., 2010; Hunter and Cribb, 2012; Hunter et al., 2012). These distributions are at least partly explicable a posteriori in terms of host diet and physiological compatibility, and suggest that speciation has tracked these resources.

In contrast to the few highly radiated genera, most GBR trematode genera have only one or two species. Where such genera are composed of multiple species they are often in hosts that are not closely related, and are often seemingly absent from hosts that would appear to be suitable. For example, the two reported species of the bivesiculid genus *Bivesicula* infect serranids and a pomacentrid (Cribb et al., 1994a). The four species of the lepocreadiid genus *Lepotrema* have been found in five species of pomacentrids, two monacanthids, two balistids and a single blenniid (Bray et al., 1993; Bray and Cribb, 1996, 1998, 2002). In addition, seemingly suitable fishes often lack infections. For example, of 35 pomacentrid species we have examined on the GBR, only one is infected by a bivesiculid (Cribb et al., 1994a) and only one is infected by a gymnophalloid (Sun et al., 2014). These apparently haphazard distributional patterns leave us unable to either explain the distributions or to predict in what other fishes related species might be found in the future.

### 2.3. Host specificity

A key biological attribute of any parasite is its host specificity. Host specificity of GBR fish trematodes was reviewed relatively recently by Miller et al. (2011) who showed that trematode specificity in GBR fishes is overwhelmingly high – either oioxenous (a single host species) or stenoxenous (taxonomically related host species); euryxenous distributions (hosts related only by ecology) are exceptional. Indeed, Miller et al. (2011) found this pattern of oioxenous or stenoxenous specificity to be so strong that they cautioned against the acceptance of any pattern of euryxenous specificity without corroborating evidence from molecular analysis. Two subsequent studies have shown that certain transversotrematid and monorchiid trematodes do indeed have stenoxenous rather than euryxenous specificity as originally reported (Hunter and Cribb, 2012; Searle et al., 2014).

Host specificity takes on great importance if the richness of a parasite fauna is being assessed. Where host specificity is absolutely strict (e.g. most but not all monogeneans), it is plausible to determine mean richness for known host species and extrapolate it to the remainder of the fauna. Where a proportion of the species is shared, it becomes important to understand the rate and nature of sharing. For the trematodes of GBR fishes, the 326 species have been reported in 814 unique host/parasite combinations at a mean of 2.5 hosts per species. The number of hosts ranges from 24 for the lecithasterid *Thulinia microrchis* to only one known host for 175 species. Perhaps the most important aspect of host-specificity is its nature when a large number of closely related host taxa are present. The cases of *Chaetodon* and *Lutjanus* (for which 24 and 17 species have been investigated for trematodes on the GBR, respectively) are instructive in this respect. For the intensively studied monorchiid genus *Hurleytrematoides*, no species has been found in more than six species of *Chaetodon* (McNamara and Cribb, 2011). For the complex of 21 species of cryptogonimids known from species of *Lutjanus*, the cryptogonimid with the lowest known specificity is *Varialvus charadrus*, which has been found in eight *Lutjanus* spp. (Miller et al., 2010b). Thus, even where multiple closely related potential hosts are available, GBR fish trematodes tend to infect only a proportion of the available hosts.

### 2.4. Endemism

Despite its great overall richness, the fish fauna of the GBR has remarkably low endemism. In the context of his estimate that the fish fauna incorporated 1,500 species,



Allen (2008) noted that only 34 were endemic to the region (2.3%). On this basis it might be predicted that the parasite fauna would have similarly low endemicity. Although several species have been shown to have wide distributions in the TIWP on the basis of combined morphological and molecular studies (e.g. Lo et al., 2001; Chambers and Cribb, 2006; Miller and Cribb, 2007), according to our records, a remarkable 45% of GBR fish trematodes have not been reported elsewhere. In addition, there are numerous reports of trematodes from fish species that occur on the GBR but that we have not detected there. For example, the well-studied lutjanid species *Lutjanus fulvivflamma* is reported to have six species of Cryptogonimidae on the GBR (Miller and Cribb, 2007, 2008; Miller et al., 2010a; Miller et al., 2010b), but a further five have been reported from it elsewhere (Hafeezullah and Siddiqi, 1970; Gu and Shen, 1979; Srivastava, 1982; Saoud et al., 1988; Nahhas et al., 1998). In combination, these data might suggest that trematode endemism for the GBR is much higher than for their hosts. However, we suspect that the disparity in proportions of endemism between host and parasite relates significantly to the overall inadequacy of reporting of trematodes throughout the TIWP. We note in particular that reported endemism is exceptionally high for aporocotylids (84%) and transversotrematids (80%). In contrast, GBR Lepocreadiidae have much lower reported endemism (31%). The distinction between these taxa is consistent with the status of the Aporocotylidae and Transversotrematidae as perhaps the least well-studied taxa in the TIWP, and the Lepocreadiidae being one of the best-studied. The system best studied to explore endemism is that of the 20 species of the monorchiid genus *Hurleytrematoides* in chaetodontids in the TIWP. In intensive study at six major localities across the TIWP (McNamara et al., 2012), eight species were found at only one site, however the 10 found on the GBR were all shared with other locations in the TIWP. Overall, it is not yet possible to characterise the level of endemism of trematodes of GBR fishes relative to the remainder of the TIWP except to note that distributions appears to be highly variable and that the field needs attention.

## 2.5. Family level patterns

A handful of trematode families account for well over half of all the richness known from the GBR. Patterns of distribution and richness vary strikingly between these families and here we review what we consider five of the best-known families.

### 2.5.1. *Lepocreadiidae*

The family Lepocreadiidae has the richest known fauna (42 species, 19 genera) of any family of trematodes on the GBR. This relates to its diversity of host families (15 at present) and the fact that the family has received continual attention as new taxa have been found during the last 20 years. The 15 host families represent just two orders, the Perciformes, with 74% of host/parasite records, and the Tetraodontiformes with 26%. It is of interest to note that the taxa in tetraodontiforms appear to form a clade whereas those of perciforms do not (Bray and Cribb, 2012). Lepocreadiids are certainly abundant on the reef, with major reef fish families well represented as hosts. Chaetodontids (16% of records), balistids and acanthurids (each 16%), pomacentrids and serranids (each 8%), ephippids and lutjanids (each 6%) are the major host families. In fact, the only host families which are not always so closely associated with the reef are the Sillaginidae and Carangidae (each 3%) and the Echineidae (1%). The factor in common for these fishes is their diet of invertebrates. However, in turn this makes it surprising that other such fishes (e.g. Lethrinidae and Nemipteridae) appear to lack species of this family entirely.

### 2.5.2. *Cryptogonimidae*

The family Cryptogonimidae has the second greatest reported richness (38 species, 12 genera) for the GBR. A unique attribute of this family is that, for its richness, it has by far the smallest host range, being known from only three fish families in the region. Of these, the Serranidae has a single species, the Haemulidae six and the Lutjanidae a remarkable 31. No other fish/trematode family in this system approaches such richness. This concentration is not an artefact of reporting; we are aware of no cryptogonimid species in any other GBR fish families sampled by us. Concentration of this kind renders targeted collecting far more feasible than for most taxa. The depth of knowledge of this group relates almost entirely to the PhD studies of T.L. Miller (e.g. Miller and Cribb, 2007, 2008; Miller et al., 2010a). Despite the richness characterised to date, we have samples of at least another six species and five genera yet to be reported. Our targeted sampling of lutjanids on the GBR has neglected deep-water inhabiting species of the genera *Etelis* and *Pristipomoides* associated with coral reefs throughout the TIWP. At least seven cryptogonimid species have been reported from these species in other localities in the TIWP, suggesting that the deep-water lutjanids of the GBR may harbour a similarly rich fauna. Overall there remain at least a further 23 lutjanid

species (including Caesioninae) known from the GBR (Randall et al., 1997) which are entirely unsurveyed for cryptogonimids.

### 2.5.3. *Bucephalidae*

Twenty-two species of bucephalids (from five genera) have been reported from fishes of the GBR, and we know of at least another 40 species that have been collected but not formally reported. The family occurs only in piscivores which is explained by the apparent complete restriction of its metacercariae to fishes. On present indications, the Bucephalidae will ultimately prove to be the richest family in GBR fishes. Current knowledge of bucephalids from GBR fishes is mainly a result of PhD research by N.J. Bott and colleagues (Bott and Cribb, 2005b, c, a; Roberts-Thomson and Bott, 2007; Bott and Cribb, 2009; Bott et al., 2013) who reported bucephalids from six teleost families. The greatest reported bucephalid richness on the GBR is that in epinepheline serranids, a dominant and speciose host group. This is especially true of the four species of *Plectropomus*, which are reported to harbour 10 prosorhynchine bucephalid species from two genera (*Neidhartia* and *Proisorhynchus*) (Bott et al., 2013). Several further piscivorous families are known, but yet to be reported, as hosts. A continuing anomaly is that the Lutjanidae, comprising many large and dominant piscivores on the GBR, does not harbour any bucephalid species despite extensive investigation. The reasons for this remain unclear, especially when bucephalids have clearly exploited recent dietary changes to piscivory in families not previously (or not commonly) associated with bucephalids i.e. apogonids (Bott and Cribb, 2005a), labrid cleaner fish (Jones et al., 2004) and blennioid mimic cleaner fishes (Roberts-Thomson and Bott, 2007). Bucephalids from this region appear to be host-specific, at least to the level of host family. We have examined more than 1,500 GBR fishes from families known to be infected with bucephalids (globally), and no bucephalid species have been found in more than one host family.

### 2.5.4. *Aporocotylidae*

The Aporocotylidae, the fish blood flukes, are perhaps the most cryptic of all the trematode taxa found in marine teleosts. They currently comprise eight genera and 25 species in GBR fishes. As adults they occur principally in the circulatory system of the host. Most

species are reported from the heart, but they are also seen in the gills, the body cavity, the kidney and the cephalic blood vessels. The first reports of an aporocotylid from a GBR fish were only published in 1989 (Overstreet and Køie, 1989; Overstreet and Thulin, 1989). A glimpse of the true richness of the group emerged as the result of systematic search in the PhD studies of M.J. Nolan (Nolan and Cribb, 2004, 2006b, a), which reported 20 species (from five genera), and alluded to the presence of a further seven species. This work illustrated that several host groups, most notably the Siganidae, have supported remarkable radiations of two lineages of species whereas many other families remain seemingly free of infection, or almost so. However, infections are often difficult to find and are often only detectable by the discovery of eggs trapped in tissues (Yong et al., 2013). Notably, the uneven host distribution of aporocotylids remains unexplained because, as for all blood flukes, transmission in this group is by direct penetration. It is opaque to us as to why some taxa escape infection from these parasites.

#### 2.5.5. *Transversotrematidae*

Transversotrematids are exceptional trematodes, occupying a unique habitat, the space under the scales of bony fishes. Perhaps because of this, this family seems to have been sought rarely from tropical marine fishes. When the first three transversotrematids were reported from the GBR in 1992 (Cribb et al., 1992), only three transversotrematids were known from marine fishes globally (Witenberg, 1944; Angel, 1969; Manter, 1970). Since then, reported richness on GBR teleosts has grown to 15 as a result of the PhD study of J.A. Hunter (Hunter et al., 2010; Hunter and Cribb, 2012; Hunter et al., 2012). The family is especially rich on lutjanid, mullid and nemipterid fishes. Notably, all but one species belongs to a single genus, *Transversotrema*, which is presently the richest single genus known in the fauna. This richness is completely unparalleled in waters outside Australia but almost certainly this relates to a failure to seek these distinctive parasites elsewhere.

#### 2.5.6. *Understudied taxa*

On the basis of their proportion of the known global trematode fauna, several families in our data set appear to be strikingly under-represented. Two effects are concealed here. First, three families, the Derogenidae, the Fellodistomidae and the Lepidapedidae, appear to

be genuinely depauperate in this region – all three are encountered more frequently in colder and deeper waters (e.g. Campbell and Bray, 1993; Bray and Campbell, 1995; Bray, 2004). In contrast, several other families, the Didymozoidae, Haploporidae, Haplospilichnidae, and Opaeoelidae, are indeed rich in our collections and have simply not received sustained study. The Didymozoidae is perhaps the most glaring case. On the basis of superficial analysis, we have collected perhaps 20 species, in contrast to the six species formally reported from the region. Notably, Yamaguti (1970) reported a remarkable 78 didymozoid species from Hawaii alone. A high proportion of these are parasites of pelagic fishes (especially scombrids) which occur in the waters of the GBR and are likely to be found there as well, should they be sought systematically.

## 2.6. Cryptic species and the molecular revolution – a slow burn

At the time of the last review of the trematodes of GBR fishes (Cribb et al., 1994b), molecular approaches to taxonomy had yet to be applied to any problems of trematode identity in the region. Since then the use of molecular data has increased dramatically and is changing our understanding of many aspects of parasite identity and relationships (Nadler and Perez-Ponce De Leon, 2011). For trematodes of GBR fishes, molecular data have now been applied to a wide range of taxa for the testing of identification hypotheses, inference of phylogenetic relationships, and linking of life-cycle stages. Sequences have been derived from ribosomal (ITS1, ITS2, 18S, 28S) and mitochondrial (*coxI*) DNAs.

Molecular data have become essential to the process of distinguishing species that have limited or no morphological differences for many groups of parasites (e.g. Burger et al., 2007; Jabbar et al., 2013). This cannot, strictly, be said to be the case to date for the trematodes of GBR fishes. In taxonomy, molecular approaches can be said to be at their most powerful when they identify combinations of cryptic species which are either entirely unknown or only suspected. Molecular studies of GBR fish trematodes (based mainly on ITS2 rDNA sequences but also on *coxI* sequences) have, by-and-large, confirmed expectations based on morphological examination rather than revolutionising them (e.g. Nolan and Cribb, 2004; Chambers and Cribb, 2006; Nolan and Cribb, 2006a; Hall and Cribb, 2008; Cutmore et al., 2010; Downie et al., 2011; Rohner and Cribb, 2013). In part this may relate to the observation that so much of the diversity of the fauna is at the genus rather than the species level. Are molecular data thus unimportant? The answer is resoundingly ‘no’ for

three reasons. First, and perhaps most importantly, morphological, biological (especially host identity and geographical source) and molecular data now tend to be gathered and considered almost simultaneously; this approach is at the heart of the so-called “integrative taxonomy” approach (Dayrat, 2005). Such an approach means that the question of whether the species being recognised are only recognised because of the availability of molecular data becomes moot – all the data is used simultaneously (and iteratively) to generate the final taxonomic hypothesis. Second, the molecular data used for identification can also be used for phylogenetic analysis (e.g. Bray and Cribb, 2012; Cutmore et al., 2013) and the matching of life-cycle stages (e.g. Cribb et al., 1998; Lucas et al., 2005; Miller et al., 2009). Third, in several cases molecular data has indeed produced evidence of genuinely cryptic species in GBR fishes (Nolan and Cribb, 2006b; Miller et al., 2010a; Hunter and Cribb, 2012; Cribb et al., 2014; McNamara et al., 2014). The alarming aspect of these latter findings is that the occurrence of cryptic species remains so unpredictable, even with the benefit of hindsight. Poulin (2011) showed that the discovery of cryptic species was proportional to the number of sequences generated, essentially the effort put into finding it, and doubtless there remain more combinations of cryptic trematode species to be found on the GBR as sequences accumulate.

## 2.7. Location, location

The GBR is a nearly continuous group of coral reefs extending from just south of the Tropic of Capricorn and merging north to the reefs of the Coral Sea. The fish composition of the GBR remains similar along its length; richness increases to the north (Russell, 1983), but many species occur essentially everywhere. How are parasites distributed in this huge potential habitat? Our evidence to answer this question is manifestly inadequate as we have only sampled in any detail at two localities, Heron Island in the south and Lizard Island in the north. Of the total of 326 species reported from the GBR, just 66 (20%) have been reported from both sites, although many more remain to be formally reported from the second site or have not been sought there in the appropriate hosts. There is, however, a significant subset of species for which there is positive evidence (from substantial collecting) of restricted distributions. For example, *Phyllodistomum hoggettae* and *Lepocreadium oyabitcha* are both known only from Lizard Island (Bray and Cribb, 1998; Ho et al., 2014) despite the examination of a large sample of their host species at Heron Island. Even more strikingly,

Hunter and Cribb (2012) and Diaz et al. (2013) showed that, in some fish species, species of Faustulidae and Transversotrematidae in the south are replaced by congeners in the north. In both of these cases the two species were readily distinguished by morphology. It remains to be seen whether cryptic variation related to geographic locality on the GBR will prove important.

Overall, our data set is too limited to allow comprehensive analysis of the nature of geographical distribution of trematodes of fishes within the GBR. Importantly, we cannot identify whether differences between the two main collecting sites relate to major paradigms such as latitudinal gradients (Kamiya et al., 2014) or glaciation refugia (van Oppen et al., 2011), or simply to sampling bias that would disappear with more extensive collecting along the length of the GBR. We can certainly conclude, however, that sampling at a single site is inadequate to develop a general understanding of the richness of the whole region.

### **3. A richness prediction = Known + Collected + Unknown**

Predictions of richness often invoke three categories of knowledge of species. Those that are known and characterised (here 326 species), those that are known (collected) but not characterised, and those that have not yet been detected on any level but are suspected to be present. How does our knowledge for GBR fish trematodes relate to the two categories of uncharacterised species?

#### *3.1. Collected but uncharacterised richness*

The first category, collected but uncharacterised species, might be expected to be simple to estimate because the specimens already exist in our collection. This is not the case. Until specimens are stained and mounted, ideally sequenced, and compared carefully with other relevant material, we cannot be certain about how many species are in the collection. In essence, if we had managed to analyse the specimens to that extent we could have written the formal accounts of the species. Thus, for only those few taxa that are under active consideration can we make reliable predictions of the level of uncharacterised richness in our collection. Thus for the Apocreadiidae, six species have been characterised but we are aware of a further 12 and for the Bivesiculidae we are confident that the three known species will rise to eight on the basis of existing collections. Not all taxa will increase so impressively; we

are aware of no further species of Enenteridae, Gorgocephalidae, Hirudinellidae, Sclerodistomidae or several other families. The greatest difficulty arises in the larger, most poorly studied taxa (e.g. Bucephalidae, Didymozoidae, Haploporidae, Monorchidae and Opecoelidae). For these taxa the projections of uncharacterised species held in our collection can only be considered educated guesses based on preliminary sorting and sequencing. In total, our estimates of held but uncharacterised species add an extra 240 GBR trematode species (Table 1). This number suggests that we have characterised approximately 58% of the species known to us.

Published reports of the 326 GBR trematode species have now been made from 265 fish species, a rate of 1.23 species per fish species. Our complete collection of 566 trematode species (published + unpublished) have been from 504 species, a rate of 1.12 per fish species. Given that 28% of the fish species that we have examined have been sampled no more than twice, we conclude that there is significantly more richness to be identified in these species than we have seen to date. Thus, for the fishes that we have examined to date a mean richness of 1.2 trematode species per fish seems conservative. This rate of richness would suggest that the fishes that have been examined (at least to some extent) harbour a minimum of 600 species.

### *3.2. Unseen richness*

How many trematode species in GBR fishes have never been knowingly seen by us or anyone else? Hoese et al. (2006) stated that the total fish richness of the GBR stands at 1,625 species. If we suppose that approximately 100 of these are elasmobranchs (and thus beyond our remit), then perhaps there are approximately 1,000 GBR fish species awaiting assessment for their trematode fauna. The fact that we can begin to use such round numbers hints at the level of inexactitude in the calculations in the remainder of this analysis. What trematodes can be expected in these 1,000 fish species?

A few of the unexamined 1,000 fish are species that we see but have never attempted to collect. However, after 25 years of consistent collecting by a range of methods it becomes increasingly unusual for us to collect previously unexplored fish species. Why is this when there are evidently 1,000 species yet to be examined? The explanation lies in a combination of effects. Several fishes have special conservation protection (e.g. Queensland groper, Barramundi cod, Hump-Headed Maori wrasse and Steep-head parrot fish). Although we are



certainly interested to understand their parasites, we see no special need to seek to sample these species. A second category is fish that are simply rare at the sites that we study (Heron and Lizard Islands). For example, we have only ever seen a single individual of *Chaetodon reticulatus* on the GBR and we did not examine it; we see no prospect that we will ever understand its parasites on the GBR (whereas it is abundant and has been examined in depth in French Polynesia). The third and most important category is fishes that are not rare but are difficult to collect. This category has at least three sub-categories. A number of large taxa are simply difficult and sometimes even dangerous to collect. Preeminent among these are the moray eels (Muraenidae) of which there are at least 29 species known for the GBR (Randall et al., 1997). From examination of just 13 individuals of six species of this family on the GBR we know that they have a rich and distinctive trematode fauna, but their aggression and cryptic habits render them especially poorly known and difficult to collect. In a separate sub-category, there are large numbers of small species (especially gobiids) that are difficult to collect because they live deep amongst coral, in crevices, sand and rubble. Such species are typically collected by ichthyologists by the use of rotenone fish poison at ichthyocide stations. This chemical kills and drives fishes from their habitat, allowing them to be collected with relative ease. Species such as the serranid *Pseudogramma polyacanthum* are often collected abundantly at rotenone stations but J.E. Randall, the doyen of Pacific ichthyologists, comments that he has never observed it alive (Randall et al., 1997). We have never seen this species on the GBR but we have examined specimens that were collected at rotenone stations elsewhere in the tropical Pacific Ocean and have found them to be infected with interesting trematodes. However, the use of rotenone is not permitted on the GBR; we wonder how the parasites of such species will ever be characterised while a prohibition on the use of this effective technique (Robertson and Smith-Vaniz, 2008) remains in place. Finally, those fish species that are found below our effective SCUBA diving [define or insert descriptive words] limit of approximately 20 metres remain inaccessible to us. An important part of this deeper water fauna is the inter-reef fauna — fishes typically only collectable by trawling. We note that of the 172 species of bony fishes listed in the report on seabed biodiversity on the continental shelf of the GBR World Heritage Area (Pitcher et al., 2007), only 10 have been examined by us on coral reefs.

Thus, the unexamined fishes are a complex mix of rare and hard to collect taxa. The many small species can be expected to have low trematode richness, but there remain many

large species to be examined as well. We can predict that the inter-reef fishes will have a fauna quite distinct from that of the more strongly reef-associated species.

### *3.3. An estimate of GBR fish trematode richness*

Our final richness estimate comprises two key components – one in which we are confident, and one of which we are quite uncertain. We think that richness in the fishes already studied to some extent is certain to reach 600 species, and perhaps as high as 800 species if sources of richness such as cryptic species and geographical localisation are greater than presently understood. Richness in the 1,000 unexamined fish species is far more difficult to predict. We think it unlikely that mean richness in these fishes will equal that of those already examined because, on average, they are smaller and rarer and these characteristics are important drivers of parasite richness (Kamiya et al., 2014). We thus suggest that richness per species for these fishes will be in the range of 0.5–1.0. In combination, these figures (600–800 + 500–1,000) suggest that the fauna might comprise 1,100–1,800 trematode species. Although there remains great scope for error in these predictions, it seems unlikely to us that the fauna comprises fewer than 1,000 species or more than 2,000. Notably, this range is below the 2,270 suggested by Cribb et al. (1994b).

Calculation of mean trematode richness for the GBR species has implications for the total mean richness of 20 (all parasites) and 10 (Metazoa only) species per fish species invoked by Rohde (1976) and Justine (2010), respectively, for coral reef fishes. In our experience, trematodes are one of the “big four” in terms of parasite richness in GBR bony fishes. The other highly abundant and rich taxa are the Copepoda, the Monogenea and the Myxozoa. In our experience, other taxa present as adult parasites (acanthocephalans, cestodes, isopods, leeches and nematodes) are relatively minor in their abundance and richness. Given that we find that GBR fishes have a mean trematode richness of ~ 1.2 species, we find ourselves with reservations that the remaining parasite taxa contribute, on average, a further eight to nine metazoan species (Justine, 2010) or 18–19 metazoans and protists (Rohde, 1976) for every fish species.

## **4. The task ahead**

On the basis of the estimates made above, perhaps 19–30% of the GBR reef fish trematode fauna has now been characterised. This leaves a substantial task, one that might take 60–120 years to complete at the present rate of progress depending on how many species are really there to be found. Given the size of the task it is worth considering the value of the exercise.

#### *4.1. Should we even try?*

As species represent the basic unit of evolutionary biology and indeed of natural history, we think that it is critical to know what species of trematodes (and indeed all the other groups of parasites) occur on the GBR as a basis for scientific enquiry. We support the standard argument that naming the species is a first critical step in characterising any biological system, although we do appreciate that it is possible to do significant work without having names on all taxa. From our perspective, we therefore see no reason not to characterise this fauna and every reason to do so. However, as we pull back the view of Google Earth™ from Heron or Lizard Island on the GBR to first see the rest of the GBR, and then progressively the reefs of the rest of the TIWP, we are very much aware of the size of the task of characterising the parasite fauna of all the major sites in this region. In our view, that is presently an unarguably impossible task. Whether it is justifiable or not becomes moot when it is first impossible. We therefore make a case here for a continued concentration on the characterisation of the parasite fauna of the GBR with the intention of achieving some kind of completion.

Our case has two components. First, we think that the GBR offers the best prospects for achieving something close to completion, and as such forming a basis for comparison with other sites in the TIWP. Australia, by way of the GBR, is one of 13 TIWP nations with a bony fish fauna of over 1,000 coral reef species (Allen, 2008). Of these 13, probably only Japan also has the scientific infrastructure to be able to aspire to comprehensive study its parasitic fauna. In terms of the extent to which other sites have been characterised, the only other coral reef sites that can be considered at all well-known are Hawaii and southern Japan. The extent to which the fauna of Hawaii is characterised is especially due to the work of H. Manter, W.E. Martin, M. Pritchard (née Hanson) and particularly S. Yamaguti. However, the work on this fauna was published almost entirely between 1955 (Hanson, 1955) and 1970 (Yamaguti, 1970). As a result none of the species have been characterised by molecular data,

which is now a prerequisite for comparison of species occurring over wide ranges. The fauna of Japan, including that of fishes of the more southerly coral reefs, has also been worked on appreciably, again by S. Yamaguti, but also by S. Kamegai, M. Machida, K. Ogawa, Y. Ozaki, T. Shimazu and others. This fauna is not as clearly a fauna of coral reefs as that of the GBR and also awaits the application of molecular approaches.

The second argument is that we should attempt to characterise the fauna before it disappears. Although some authors are relatively positive about the prospects for the description of the world fauna and flora (e.g. Costello et al., 2013), coral reefs do appear to be especially threatened by environmental change. Coral reefs face threats globally from coral bleaching, ocean acidification, eutrophication, over-fishing, crown-of-thorns starfish, storms and a range of other threats (Lewis et al., 2009; Munday et al., 2010; e.g. Kayal et al., 2012). We note that despite this, the GBR remains one of the healthiest and best protected of the world's reefs and thus remains an excellent study site. It is possible that the fauna that we find so fascinating, ultimately dependent on the existence of healthy coral reefs, is threatened by large-scale extinction locally and globally.

## **5. How to get there from here**

If we accept that characterising this fauna has value, then there are a number of issues to be considered in attacking the task. Here we review issues affecting the implementation of an effective approach.

### *5.1. Every fish species?*

First we can consider whether we need to examine every fish species. As discussed above, trematode specificity in GBR fishes is overwhelmingly high. This means that comprehensive surveying for trematodes requires examination of, effectively, all the fish species present. For example, possibly the most thoroughly collected taxon in our dataset is the butterflyfishes (family Chaetodontidae). We have reported 23 trematodes from 35 species of this family and are aware of at least 10 more in our collection. These trematode species are almost all shared by at least two chaetodontid species and the maximum number found in any one host species is nine (*Chaetodon ulietensis*). Such understanding can only be reached by comprehensive sampling, and we thus see no case for selectively excluding fish species from

analysis. We do see, however, a case to be made that the parasite fauna of representatives of the most characteristic and prominent fishes on the reef should be especially well characterised as a priority.

## 5.2. Prevalence - how many fish?

No GBR fish that we have sampled at least 20 times has been infected with the same trematode species in every individual. Thus, in the search for trematodes and a deeper understanding of their distribution, it is necessary to dissect multiple host individuals, but how many? The issue is of importance because there are matters of efficiency, expense and ethics. Fig. 2 shows randomised species accumulation curves and species richness predictors for real data for seven diverse GBR fish species (Chaetodontidae: *Chaetodon lunulatus*; Labridae: *Thalassoma lunare*; Lutjanidae: *Lutjanus carponotatus*; Nemipteridae: *Scolopsis bilineatus*; Pomacentridae: *Acanthochromis polyacanthus*; Siganidae: *Siganus lineatus*), each sampled 30 times at Heron Island. A sample of 30 gives, statistically, a 95% probability of finding any parasite present in the population at a prevalence of 10% or greater (Post and Millest, 1991). Two observations emerge from these curves. First, the overall combined observed accumulation curve has begun to plateau and to converge with the two richness predictors, suggesting that for these fish we have collected most, but perhaps not quite all, of the trematode species present. The small upward trend evident in two of the curves relates to the fact that the data set contains a number of singleton and doubleton infections. The richness predictors effectively treat these as evidence that there may be undiscovered richness in the system. Second, the effect of the law of diminishing returns is severe. On average, after just two fish have been examined, > 50% of the actual and predicted richness has been discovered. This pattern generates a clear tension in approaches to collecting. Examination of a small number of host individuals will find most of the trematode species; however, a much larger number is required before all of them are found.

From the accumulation curves described above we can predict that, at least for these fish, and probably for most, a sample size of 30 is effective in characterising the trematode fauna of GBR fishes at individual localities (providing that there are no dramatic effects from ontogeny, local distribution or season – all entirely possible and all little studied). Infections that are not detected because they are rare remain a distinct problem. An example comes from a faustulid parasite, *Parayamagutia ostracionis*, of the boxfish *Ostracion cubicus*. We have

examined a large sample of these fishes on the GBR (91), exploring a range of parasitological questions. The first of these was examined in 1986 and produced a single individual of *P. ostracionis*. In a total of 90 further *O. cubicus* examined by us, we have seen only one more infection for an overall prevalence of 2.2%. We conclude that this species is a valid parasite of *O. cubicus* which, for reasons undetectable to us, is strikingly rare. Scarcity of this kind is itself not rare in biology (Jones et al., 2002; Magurran and Henderson, 2003), but for our purposes it poses an essentially insoluble problem.

If indeed it is necessary to examine 30 individuals of each fish from at least two sites to get a comprehensive understanding of the fauna, then a further 60,000 fishes (many hard to get) remain to be examined. Sixty thousand fish, at an optimistic rate of an hour per fish to collect and dissect, translates into a figure of 7,500 field days and much more time in the laboratory.

### 5.3. What should be done – some priorities

If we need to examine another 60,000 fish to characterise the GBR fish trematode fauna then there is certainly room to identify priorities. We think that the best progress might be characterised by

- i) Maintaining continued attention on the best studied families (e.g. Aporocotylidae, Bucephalidae, Cryptogonimidae, Lepocreadiidae and Transversotrematidae) to create a comprehensive basis for comparison with other localities.
- ii) Characterising comprehensively the parasite faunas of key fish species such as the Coral trout (*Plectropomus leopardus*), the Red-throat emperor (*Lethrinus chrysostomus*), the Moon wrasse (*Thalassoma lunare*) and other species that have distinctive parasite faunas.
- iii) Attempting to be consistent in accompanying new species descriptions and reports with molecular data and “back-filling” for those already reported without such data.
- iv) Improving characterisation of the level of similarity between different areas of the GBR.
- v) Making a realistic attempt to explore the importance of small fishes in the richness of GBR fish trematodes.

- vi) Making a realistic attempt to sample the neglected inter-reef fauna.
- vii) Improving the availability of summary information regarding the fauna so as to make the work that has been done more accessible and valuable to others.

Seven priorities is perhaps already too many in the context of the workforce available to tackle these tasks, but it is difficult to distinguish between them in terms of importance. We note with interest, that priorities for the study of parasite faunas in different parts of the world may vary. Perez-Ponce de Leon and Choudhury (2010) make a convincing case that the end is in sight for the characterisation of the helminth fauna of Mexican freshwater fish. In that context they argue that, for that fauna, current priorities should be the least studied fish (whereas here almost no species can be considered fully characterised) and the search for cryptic species (which is here considered important but not a dominant issue).

## **6. Conclusions - beyond the numbers**

At the head of this review we stated that our goal was to work towards the biodiversity goal of “understanding the system”. Although we have shown that there remains a formidable task to characterise all the species in the system, we do not downplay the progress that has been made. We now have a reasonable understanding of the kinds of trematodes that are likely to be found in the most frequently encountered fishes of the GBR. We also have a broad understanding of patterns of host specificity – largely we know what sorts of trematode families will be found in what sorts of fish taxa, even if the details still have the capacity to surprise us. Indeed, some interesting patterns have been noted in this review, e.g. the apparent lack of aporocotylids in many reef fish species, and the unpredictable distribution of cryptic trematode species. The most glaring gap in our understanding of this system is knowledge of life-cycles. These parasites all have at least two hosts, most three and some four. Given the profusion of animals available for involvement in these cycles, the task of elucidating them in any detail is considerably more complex than that of characterising the adults. This perhaps explains why there are still only two completely elucidated life-cycles for trematodes parasitic in GBR fishes (Pearson, 1968; Rohde, 1973) although a range of life-cycle connections have been made (Cribb et al., 1996; Cribb et al., 1998; Lucas et al., 2005), especially by the use of molecular approaches. This field perhaps offers the single greatest challenge for the future.

The task of characterising the biodiversity of the parasites of coral reef fishes is a daunting yet fascinating one. In 25 years of study, knowledge has evolved from a complete absence of understanding of what to expect to a point where the data now create fascinating biological patterns. After many years in this field we have come to recognise that the two finest moments are when we can look at a trematode and say either “I have no idea what that is!”, or, “I know exactly what that is!” The balance of experience is slowly shifting from the former to the latter, but the former is still very much there to be had!

(Board, 2014)

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## Figure legends

Table 1. Numbers of trematode species reported and collected but not reported from Great Barrier Reef (GBR), Australia, fishes. Estimates for known global richness of trematode families predominantly or significantly in marine actinopterygian fishes based on counts in the World Register of Marine Species (2014) and our records.

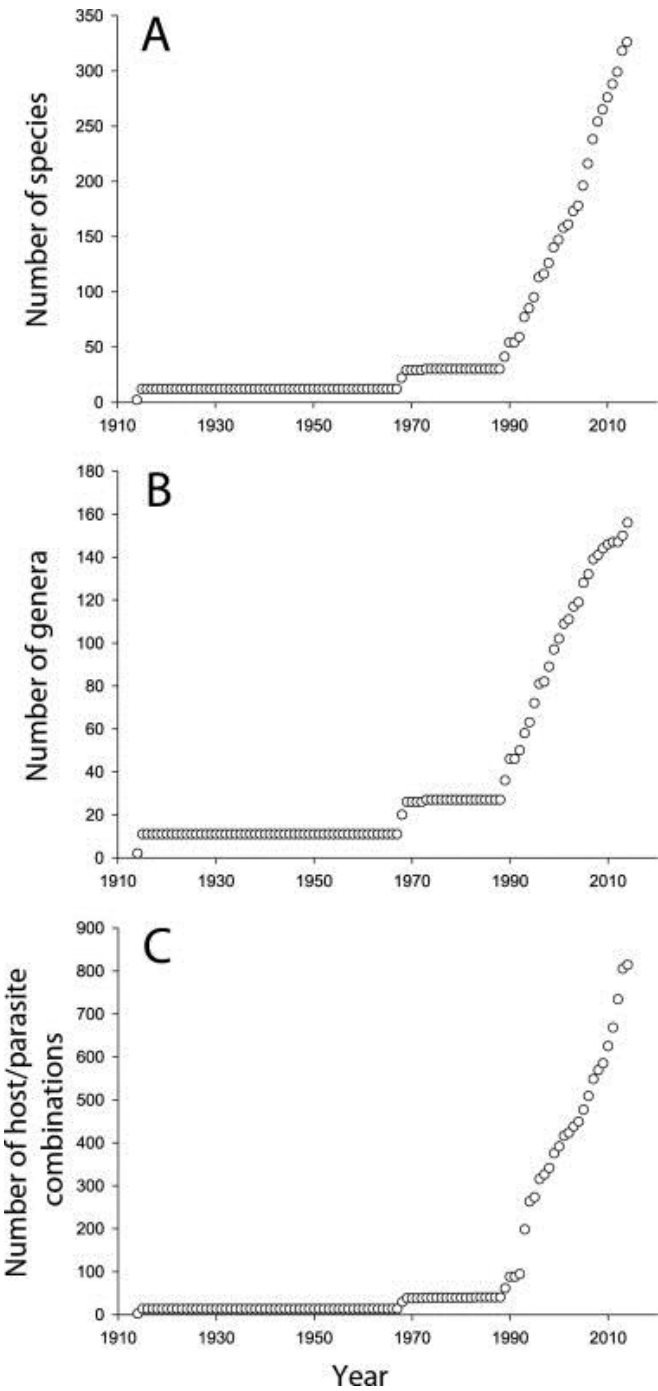
Family	Reported GBR genera	Reported GBR species	Collected GBR species	Reported global species	% World fauna
Acanthocolpidae	5	15	1	199	7.5
Accacoeliidae	0	0	1	27	0.0
Aephniogenidae	3	4	1	21	19.0
Apocreadiidae	4	6	12	87	6.9
Aporocotylidae	8	25	15	118	21.2
Aspidogastridae	1	1	0	10	10.0
Atractotrematidae	2	2	0	2	100.0
Azygiidae	0	0	0	42	0.0
Bathycotylidae	0	0	0	2	0.0
Bivesiculidae	3	4	5	27	14.8
Botulisaccidae	0	0	0	1	0.0
Bucephalidae	5	23	40	380	6.1
Cladorchiidae	0	0	1	4	0.0
Cryptogonimidae	12	38	6	220	17.3
Derogenidae	1	3	1	132	2.3
Deropristidae	0	0	1	6	0.0
Dictysarcidae	0	0	0	8	0.0
Didymozoidae	5	6	20	280	2.1
Enenteridae	2	4	0	32	12.5
Faustulidae	4	13	10	77	16.9
Fellodistomidae	3	3	3	142	2.1
Gorgocephalidae	1	2	0	3	66.7
Gorgoderidae	2	3	2	85	3.5
Gyliauchenidae	6	10	16	42	23.8
Gymnophalloidea (incertae sedis)	1	1	1	4	25.0
Haploporidae	2	3	15	113	1.8
Haplospilichnidae	2	2	11	47	4.3
Hemiuridae	10	15	5	500	3.0
Hirudinellidae	1	1	0	5	20.0
Lecithasteridae	12	18	5	149	12.1
Lepidapedidae	2	4	0	99	2.0
Lepocreadiidae	19	42	8	270	15.6
Mesometridae	0	0	1	9	0.0
Microscaphidiidae	1	1	6	41	2.4
Monorchidae	9	23	13	255	9.0
Opecoelidae	19	27	30	680	4.0
Opistholebetidae	2	3	0	26	11.5
Sclerodistomidae	1	1	0	43	2.3
Sclerodistomoididae	0	0	0	1	0.0
Styphlotrematidae	0	0	0	1	0.0
Syncoeliidae	0	0	0	11	0.0
Tandanicolidae	0	0	0	12	0.0
Transversotrematidae	2	15	3	25	60.0
Zoogonidae	6	8	7	123	4.9

Family	Reported GBR genera	Reported GBR species	Collected GBR species	Reported global species	% World fauna
Total	156	326	240	4361	7.5

1014 % World fauna, GBR reported species as a percentage of known world fauna.

1015

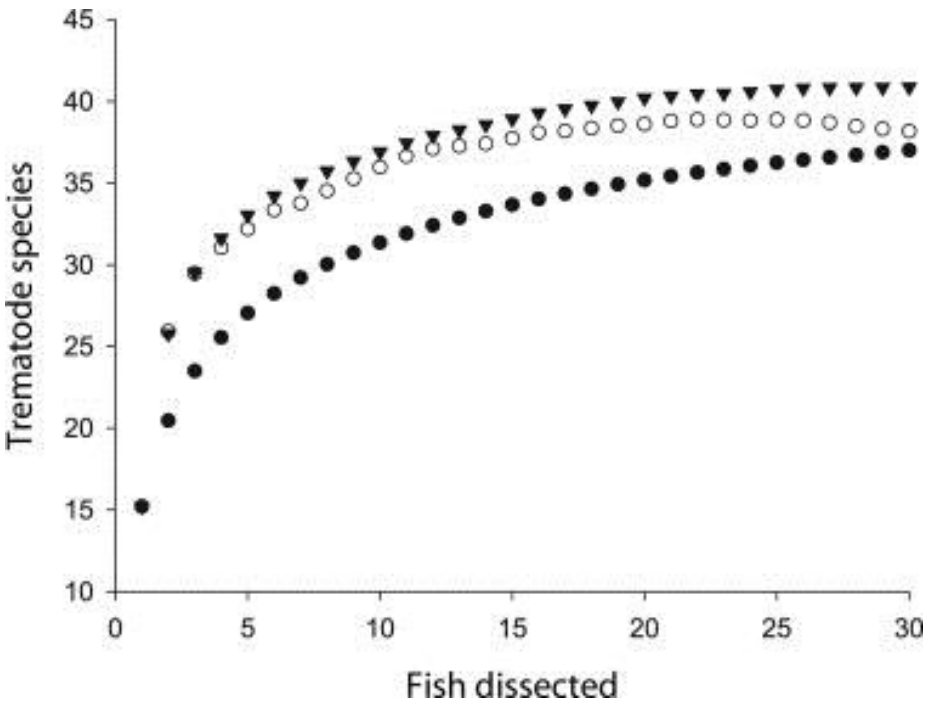
1016 Fig. 1. The study of trematodes from fishes of the Great Barrier Reef, Australia, from 1910.  
1017 The International Congress of Parasitology workshop on the parasites of the Great Barrier  
1018 Reef was held in 1988. (A) Accumulation of species; (B) accumulation of genera; (C)  
1019 accumulation of unique host/parasite combinations.



1020



1021 Fig. 2. Combined randomised (1,000 randomisations) accumulation of species richness  
1022 (actual and predicted) of digenean trematodes in 30 individuals each of seven species (see  
1023 Section 5.2) of Great Barrier Reef fishes at Heron Island, Australia. ● Observed, ○



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