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Invited Review

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 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 Great Barrier Reef 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 Great Barrier Reef 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.

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

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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 100th anniversary of commencement of work on this fauna and the 20th 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), *Prosorhynchus* (Bucephalidae), *Stephanostomum* (Acanthocolpidae), *Retrovarium* (Cryptogonimidae), and *Hurleytrematoides* (Monorchiidae) 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. *Hurleytrematoides*, *Prosorhynchus* and *Retrovarium* have radiated within narrow host ranges, being found only in chaetodontids and tetraodontids (McNamara and Cribb, 2009, 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, 2012; Hunter and Cribb, 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