Review

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The butterfly effect: parasite diversity, environment, and emerging disease in aquatic wildlife

Robert D. Adlard[1], Terrence L. Miller[2], and Nico J. Smit[3]

[1] Natural Environments Program, Queensland Museum, South Brisbane, QLD 4101, Australia
[2] School of Marine and Tropical Biology, James Cook University, Cairns, QLD 4870, Australia
[3] Unit for Environmental Sciences and Management, North-West University, Potchefstroom 2520, South Africa

Aquatic wildlife is increasingly subjected to emerging diseases often due to perturbations of the existing dynamic balance between hosts and their parasites. Accelerating changes in environmental factors, together with anthropogenic translocation of hosts and parasites, act synergistically to produce hard-to-predict disease outcomes in freshwater and marine systems. These outcomes are further complicated by the intimate links between diseases in wildlife and diseases in humans and domestic animals. Here, we explore the interactions of parasites in aquatic wildlife in terms of their biodiversity, their response to environmental change, their emerging diseases, and the contribution of humans and domestic animals to parasitic disease outcomes. This work highlights the clear need for interdisciplinary approaches to ameliorate disease impacts in aquatic wildlife systems.

Connectivity of aquatic wildlife parasites

It is intuitive that aquatic wildlife systems do not exist as discrete units but rather they interact seamlessly with neighbouring environments through a variety of inputs and outputs that together create a dynamic ecosystem. Although this overarching statement is undeniable and holds true for all sectors of the environment, it is only recently that the intimate links between diseases in wildlife and diseases in humans and domestic animals have been emphasised [1,2]. These observations have prompted transdisciplinary approaches in surveillance, health assessment, and monitoring to provide predictive models allowing timely response to the emergence of disease [3]. Such approaches should ideally also provide early indicators of environmental changes that may impact ecosystem health.

A review on parasitic zoonoses and wildlife [4] focussed further attention on the complex interplay between human and wildlife diseases through the One Health interaction triad and proposed that research into parasite biodiversity in wildlife should not only provide an inventory of parasites, but also include an assessment of the impacts that such pathogens may have on nonwildlife hosts. Equally, similar consideration should be given to the contraflow of human or domestic animal parasites and how they may affect wildlife health.

The aquatic ecosystem, central to this review, is broadly divided in freshwater and marine components. Although the former accounts for only 0.8% of global surface area, it is critical to the survival of many organisms, and is subject to some of the most ecosystem-altering perturbations [1]. By contrast, the marine component covers 71% of the globe, but it too shows recent and relatively rapid environmental changes and acts as the final sink for land-based inputs that impact initially on biodiverse coastal ecosystems.

A survey of the literature shows that parasitologists have focussed their studies on aquatic wildlife through several drivers that include: biodiversity stocktakes; identification of causative agents in events of aquatic wildlife mortality and morbidity; focussed prevention and remediation attempts for aquatic parasites pathogenic in both aquaculture and harvest fisheries; multidirectional aquatic parasite flow between wildlife and aquaculture; and current and projected impacts of often anthropogenic environmental change on the incidence, prevalence, and pathogenicity of aquatic parasites. Given these drivers, we have framed this review to cover aquatic parasites in terms of their biodiversity, response to environmental change, and emerging diseases and disease interactions with nonwildlife species.

Biodiversity of aquatic parasites

Parasites are extraordinarily diverse in aquatic ecosystems, where parasitism likely first arose, long before terrestrial life came into existence. Evidence for such an ancient association is increasingly recognised in the fossil record through distinct pathology or morphologically induced change that parasites cause to their long-dead hosts [5]. The vast diversity and richness of parasites we observe today in aquatic systems reflects this long evolutionary history, with representatives of nearly all known parasitic lineages of life found in marine and freshwater environments [6]. Among the most biodiverse parasites known from aquatic ecosystems are the cestodes, monogeneans, trematodes, and myxozoans, with thousands of species

Corresponding author: Adlard, R.D. (robert.adlard@qm.qld.gov.au).
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known from each group [7]. Many protozoan parasite groups are potentially more diverse than the metazoan groups listed above, but have not yet received the same focussed taxonomic scrutiny [8–14]. Knowledge of this diversity underpins our efforts to examine and characterise in detail the intricate ecology, life cycles, pathological impacts, and evolution of parasites and their hosts in aquatic systems. However, even addressing what parasite species exist in any complex aquatic ecosystem is a daunting task in itself.

How many parasites exist in the aquatic ecosystems of the world?

Recent efforts to estimate the number of parasite species that exist worldwide highlight the difficulties and limitations involved in producing robust estimates and the overwhelming task it is to formally characterise the fauna. Similar to prokaryotic organisms, the genetic, ecological, and biological boundaries that constitute some asexually and sexually reproducing eukaryotic parasite 'species' are often unclear. Biologists [15,16] have debated the limitations of the 'biological species concept', focussing on three elements of concern: (i) taxonomy; (ii) evolution; and (iii) biological diversity assessment, which has led to the designation of an entire field within taxonomy, 'Eidonomy', which seeks to address the 'species problem' [17]. What is clear from the ongoing debate on species definition is that it will likely require whole genomics, informatics technologies, and systems analyses that lie far in the future to adequately address the 'species problem' and facilitate consensus among biologists.

Species have been described as being as fundamental to biology as the elements are to chemistry [18]. This is an eloquent analogy, but based on some estimates [18,19], 5 ± 3 million species exist on Earth today, of which only 1.5 million are formally named, further highlighting the gap to fill before we have as comprehensive an understanding of the biological world as our colleagues do of the chemical world. Our lack of knowledge of the basic 'elements' is particularly emphasised when attempting to estimate the biodiversity of parasite taxa [20–22]. Poulin examined our current understanding of parasite biodiversity [22] by exploring: how many parasite species and active parasite taxonomists are there? And, how does parasite diversity vary across host space and across geographical space? Our understanding of these questions has been fundamentally changed in many ways by recent genetic technologies and analyses, which have revealed a vast diversity of cryptic parasite taxa, as well as detailed information about host specificity, life cycles, and pathology [22,23]. Poulin points out that, despite all we do know about the diversity of parasites, we cannot currently estimate how many parasite species exist with any accuracy in relative or absolute terms [22]. This holds true even for some of the most taxonomically scrutinised parasite groups inhabiting complex aquatic ecosystems (e.g., trematodes of Great Barrier Reef fishes); however, key patterns are emerging that help answer the questions explored by Poulin [20–22].

Ways forward?

Documenting and preserving the biodiversity of the world is a pressing issue, given the threats to many species and ecosystems from a rapidly changing climate, invasive species, and anthropomorphic impacts, some of which we cover here [18]. Parasite taxonomy and systematics provide a foundation for our understanding of parasitism in aquatic ecosystems [16,24–29]. However, characterising this diversity requires substantial human and monetary resources, so most research into the foreseeable future will undoubtedly continue to focus on parasites of human or commercial significance [18,22,26,30,31]. Nonetheless, efforts are being directed towards accelerating and streamlining taxonomic discovery, dissemination, and database compilation, leading to initiatives such as 'cybertaxonomy' or 'evolutionary informatics' [26,28,29,32,33]. It is clear that we do not have the expertise, technology, and resources to formally document and characterise the entire parasite fauna of the aquatic ecosystems of the world. Perhaps an achievable goal for those of us working on aquatic parasites is to make concerted efforts to preserve and lodge as many parasite samples (DNA or whole specimens) as possible into long-term collections (e.g., museums). Preserving more than a scientific description, specimen, or short DNA sequence against future need will help contribute snapshot knowledge of the rich diversity of parasitic life in the aquatic ecosystems of the world [17–19,22,24–26,28,30,33–39]. Given the current actual and potential threats to species inhabiting aquatic ecosystems, it is imperative that such a process be initiated now.

Environmental change

Although heavily debated throughout the previous century, the potential threat of global climate change to living organisms on Earth is now indisputable [40]. The predicted increase in global temperatures has direct abiotic as well as indirect biological consequences. The latter includes shifts in species distribution, timing of reproduction, change in physiological functioning, and change in interspecific relationships [41]. Given the nature and complexity of the parasitic lifestyle, parasites are, as a group, one of the most susceptible to global climate change. This effect is further exacerbated due to parasites usually exhibiting a narrow environmental tolerance and a tight trophic dependency. Parasites of aquatic organisms are sensitive to temperature change [42], because it directly impacts their life cycle, transmission, and host biology. In addition, it also influences their biodiversity and geographical distribution, with both these directly linked to that of their hosts. To date, the main focus of research related to the prediction of the effect of global climate change on aquatic parasites was on vector-borne diseases of humans, with limited information available on the implication of climate change on parasites of wildlife [42].

Climate change: biodiversity and distribution

Parasites are usually excluded from general biodiversity surveys of aquatic ecosystems; however, the parasitic species might in fact constitute half of all biodiversity [43]. Furthermore, despite the bad press that parasites usually receive, it has been shown [44] that a parasite-rich ecosystem equals a healthy one. Thus, it is of utmost importance that we consider the influence of environmental change on aquatic parasite biodiversity and distribution, because