**Introduction and Review**

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Jenny Plan:

Big Data

* The paradigm shift in science toward a data centred approach
* This has pushed science to answer some fundamental questions in new ways
* Use examples from Chhaya (latitudinal theory)
* Big data is particularly good at answering questions about things we know little about … like … for example … parasites.

Parasites

* What are parasites and how are they defined (in this thesis)
* What do we know about parasites (ecosystem engineers…)
* What is currently assumed (that they are super understudied and that there are still many to be discovered … for 1 free living, there is a parasite…)
* What we don’t know (we know a lot about terrestrial but not a lot about marine)
* …and this is compounded and complicated by predicted changes in climate

Climate Change

* How will climate change impact parasites
* But what we don’t know is this in the marine realm

Therefore …

I aim to …

## To be … parasite

Parasitic organisms are typically small cryptic animals concealed on or within their hosts and are often noticed only when their presence causes pathogenicity (illness) in commercially relevant species or pets (Rohde, 2005). In addition to the direct effects they cause to their hosts, ecologists are continually discovering the indirect roles that parasites play in structuring ecosystems (Marcogliese, 2004). But first, what is it to be parasite?

### Defining parasites

Definitions of what constitutes a parasite vary from field to field. The study of parasites is approached from a number of disciplines, including physiology, ecology, epidemiology, veterinary, economics and evolutionary biology. For this thesis, parasitism is understood to be a close association of two organisms, in which one (the parasite), during at least one life-history stage, depends on the other (the host) and directly derives some nourishment and/or shelter from it but does not intentionally kill the host. The direct benefit to the parasite is almost always in the form of food, but other benefits have been noted including habitat, shelter and transport. Microbiologists have focussed on fungi, viruses and bacteria and have considered some of these as parasitic, but for the purposes of this thesis, we will only consider animal (metazoan) parasites which infest other animals. Specifically, we exclude animals that feed off plants, such as the many species of plant-feeding insects and roundworms, as these are considered herbivores. We also exclude parasitoid insects because they intentionally kill their host and are therefore considered predators (Rohde, 2005; Costello, 2016).

### Adaptations to the parasitic lifestyle

Parasites have evolved complex defensive strategies and developed intricate life cycles to improve their survival. Some parasites have developed simple or direct life cycles that involve active transmission via free living larval stages that attach to passing hosts (e.g., Rhizocephala, Ascothoracica, Copepoda, and Monogenea). For example, parasites of the class Monogenea have adapted to living on the skin, fins and gill filaments of fresh water and marine fish (Rohde, 2005). The hermaphroditic adults release eggs into the water column. When the eggs hatch, they release a heavily ciliated larval stage known as an oncomiracidium. These oncomiracidium have numerous posterior hooks and opportunistically latch onto passing hosts, completing their lifecycle. The larval hooks develop into complex holdfast organs or “haptors”, which are specifically adapted to maintain attachment to their preferred host.

In contrast to the simple and direct life cycle of Monogenea, other parasites have developed complex or indirect lifecycles where sexual reproduction occurs in the definitive host and various stages of development and/or asexual reproduction occur in one or more intermediate hosts (e.g., Cestoda, Trematoda, Acanthocephala, Nematoda). For example, *Curtuteria* *australis*, a digenean trematode off the New Zealand coast (Allison, 1979) has two intermediate hosts. Its eggs are released in the droppings of oystercatchers (*Haematopus* spp.), its definitive host. These eggs are ingested by the whelk *Cominella* *glandiformis*, a marine gastropod snail, where they develop into larvae (called redia) in the digestive gland. Once temperatures reach 20˚C, the redia release free swimming larvae (called cercaria) into the surrounding water, which infect the cockle *Austrovenus* *stutchburyi*. In heavily infected cockles, not only is foot tissue replaced by metacercaria cysts, but the size of the foot relative to that of the shell is reduced, leading to the diminished ability of the cockle to bury itself in the sand (Thomas and Poulin, 1998). This alteration in behaviour makes the cockle seven times more susceptible to predation by shorebirds (Thomas and Poulin, 1998). Once consumed by the oystercatcher, the parasite infects the digestive tract, completing its life cycle.

Whether their lifecycles are simple or complex, parasites in both categories have evolved the ability to infect a range of potential micro-habitats that the host’s body may provide. Like the monogenean example above, parasites can infect specific regions of their hosts, including musculature, various organs and cavities and externally in gill chambers, fins, mouth, skin and scales. The traits parasites have developed to survive these micro-habitats include: a reduction in size compared to related non-parasitic species; a reduction or complete loss of sensory and/or locomotory structures; the development of attachment organs so as not to be carried away or cleaned from the host; resistance to host immune systems and/or protection against hostile environments (e.g., cuticles); and specialized reproductive strategies with high reproductive potential (Marcogliese, 2004; Rohde, 2005).

### Parasite-host coevolution

Due to the antagonistic nature of the host-parasite interaction, unique selection pressures are exerted on both the parasite and the host, resulting in parasites that are highly specialized to infect particular hosts. However, there are exceptions, like trypanorhynch cestodes that can infect multiple intermediate host species. This parasite-host interaction creates an evolutionary tension that allows for a delicate equilibrium to be created between the host and the parasite (Hudson, 2005). This evolutionary equilibrium is known as the Red Queen Hypothesis; namely that both parasite and host must continuously adapt to keep up with each other’s adaptations (Morand and Krasnov, 2010). However, creating a defensive strategy against every potential parasitic species would be a costly endeavour for the host. Therefore, it is less costly to allow a moderate level of defence at the expense of slight infection. For a parasite, it is worth having a lower level of pathogenicity within a host, so as to not activate the host’s full defences which allows for improved transmission. It is within these moves and counter moves that we get a glimpse of just how parasites may structure entire ecosystems through their effects on host abundance and/or behaviour.

### Effects of parasites on ecosystems

If we continue with the example of *Curtuteria* *australis*, this parasite controls how energy is transferred through the ecosystem by directly effecting predator-prey interactions (Thomas and Poulin, 1998; Thomas *et al.*, 1998). This is done by limiting the natural behaviour of the whelk to a riskier behaviour. This small change alters the food web dynamics and community structure in the ecosystem. A parasite’s impact on reducing host fitness and modifying competitive and trophic interactions among species have effects on the abundance of different species within that ecosystem and the strength of those interactions between them. Therefore, the parasite impacts the way that energy flows through the ecosystem directly. They do this by imposing additional energetic demands on their host, affecting morphology, behaviour and appearance, reducing fecundity and growth, and they have the ability to cause mortality in weakened individuals.

Parasites can also indirectly modify host biology such that new habitats for other species are formed. Because *Cominella* *glandiformis* can’t bury itself within the sand, it creates a hard substratum on an otherwise sandy beach. While sand is usually a difficult substrate for epibionts (an organism that lives on the surface of another living organism) to colonize, infected cockles provide a habitat for limpets, sea anemones, barnacles and polychaetes. By preventing its host from being able to bury itself in the sand, *Curtuteria* *australis* causes an increase to the relative biodiversity of the area making this species of parasite a localized ecosystem engineer for the New Zealand coastline (Thomas *et al.*, 1998).

When ecologists incorporate parasites into food webs, some obvious effects include a direct increase in overall species richness, an extension of food chain lengths and a proliferation in the number of links between species within the ecosystem network (Hudson, Dobson and Lafferty, 2006). A food web of the Carpinteria Salt Marsh in California found that parasites dramatically increase the links between species (connectance) and improve the functional structure (nestedness) within the ecosystem (Lafferty *et al.*, 2006). These modifications have the ability to improve the stability within the food web and suggest that parasites have an important role in food web structure. The examples show the importance of considering parasites not just in the management and conservation of their hosts but also in the management and conservation of the ecosystems in which they live.

## Global biogeography of parasites

### Latitudinal gradients

Within the marine realm, one of the clearest and well documented geographic patterns is the latitudinal diversity gradient (Hillebrand, 2004). Latitude is a surrogate for temperature and solar radiation (including day length and seasonality), which in turn influences primary and secondary productivity (Costello and Chaudhary, 2017). Chaudhary, Saeedi and Costello, (2016, 2017) reviewed the literature and available global data for 65 000 marine species and concluded that species diversity increased with decreasing latitude. This translates to a diversity gradient with low levels of diversity at the poles and a gradual increase in diversity through the temperate zone toward the tropics.

This increase in diversity is observed in internal parasites, particularly helminths of marine fish (Rohde, 2002, 2010, 2016). Jorge and Poulin, (2018) tested the expected spatial similarity between host and parasite diversity for helminth parasites of vertebrate hosts across the globe, including marine fish. Their results show that although associations were weak, there was a significant positive covariation between host species richness and the number of parasite species reported in the same latitude, supporting the observed latitudinal trends for endo parasites. These results show that as host diversity increases, there is a similar increase in endoparasitic diversity.

Ectoparasites, however, amplify this latitudinal gradient and show an increase in relative diversity compared to their endoparasitic counterparts, with comparatively higher species diversity of monogenean flukes per species diversity of hosts, as latitude decreases (Rohde, 2002, 2016). The most likely explanation, according to Rohde, (2002), for this relative increase in ectoparasitic diversity compared to other parasitic species is due to temperature. Decreasing latitude results in a general increase in temperature and genetic studies have shown that with increasing relative temperature, there is an increase in evolutionary speciation rates in plants and animals (Rohde, 2002; Gillman *et al.*, 2014).

### Longitudinal gradients

Longitudinal gradients of diversity have not been as well documented as latitudinal gradients, but centres for high diversity compared to other areas around the globe have been recorded (Morand and Krasnov, 2010). A primary area is within the Coral Triangle of the Western Pacific Ocean (Asaad *et al.*, 2018). A secondary area is the Caribbean, although this area is not as diverse as the Coral Triangle (Rohde, 2010).

It has become clear that there are barriers to longitudinal dispersal in the oceans, which inhibit the movement of species across the globe. The most effective barrier appears to be the Eastern Pacific Barrier which, due to a lack of islands and a deepening of the thermocline toward the east, reduces the dispersal potential of many species, including parasites, from the western to the eastern parts of the Pacific (Morand and Krasnov, 2010). The “New World Barrier”, represented by the North and South American continents, prevents longitudinal species movement between the eastern Pacific and the Atlantic (Costello and Chaudhary, 2017). These phenomena have been documented for monogenean and copepod parasites of tuna and mackerel species (Rohde and Hayward, 2000).

### Depth gradients

Reviews of marine diversity show an exponential decrease in diversity with depth with a suggested peak at approximately 400 to 500 m (Costello and Chaudhary, 2017). Rohde, (1984)reviewed data of vertical gradients for parasitic species from several authors and concluded that parasite diversity and prevalence becomes poorer with depth. Inshore and open ocean surface fishes have more species of parasite and a greater abundance of parasites than midwater species (Marcogliese, 2002). However, bottom dwelling (benthic) fishes had more species and greater numbers of parasites than midwater (pelagic) species. This is probably due to their food including more infected intermediate hosts, being larger in body size and with a longer life span than midwater species (Rohde, 2010).

There is little knowledge of parasites of the deep oceans. The deep ocean (depths deeper than the continental margin, approximately 200 m) is a hostile environment with low temperatures (2 ˚C average), no light penetration which makes photosynthesis practically impossible and a food supply that is dependent on detritus from the upper levels of the ocean (Costello and Breyer, 2017). This environment is not conducive to high diversity. However, there are exceptions, particularly around hydrothermal vents, whale falls and cold seeps that have an incredible abundance of animals for such hostile environments. Whether parasite abundance is also high in these habitats remains to be studied (De Buron and Morand, 2004).

The latitudinal, longitudinal and depth gradients in marine parasites remain to be analysed at global scales and across all marine parasite taxa. At present it appears they follow the same biogeographic patterns as other species, but confirmation across a broader scale is desirable. Furthermore, the species richness and endemicity of parasites and their hosts are not necessarily linearly correlated. For example, there may be thresholds of host population density where parasites become more or less pathogenic due to dispersal success.

## Parasites’ potential response to climate change

Local studies on heating events indicate that global climate heating may impact parasite biology and ecology. Changes that have been recorded in the protozoan parasite *Perkinsus* *marinus* include an increased pathogenicity in oysters along the east coast of North America during uncharacteristic winter heating events (Harvell *et al.*, 2002). Similarly, warmer winters have led to increased invasions by copepod parasite species on aquaculture farms (Callaway *et al.*, 2012). In some cases, it is the duration of low winter temperatures, rather than the minimum temperature, that is most important for maturation, mortality, and re-infection within some parasite populations (Marcogliese, 2001). An increase in average winter sea surface temperatures will allow parasites to survive through the winter and consequently allow for earlier maturation and increased abundance in the spring.

As temperature increases and biochemical reactions speed up, this increased metabolism is limited by the amount of fuel an organism has access to (Lafferty, 2009). As parasitic organisms depend on their host for food, an increase in temperature has the ability to increase the parasites pathogenicity on the host. Therefore, not only does the host have to deal with their own increased thermal stress, but also an increase in parasite pathogenicity (Marcogliese, 2001). For example, with increases in temperature, dissolved oxygen levels in the water decrease, which increases stress to the fish. Concurrently, a rise in temperature may shorten generation time and increase growth rates of gill parasites (such as monogeneans). The combination of decreased oxygen and increased parasite burden can cause respiratory problems for fish, often resulting in mortality (Marcogliese, 2001).

More importantly, though, global heating have been shown to alter the seasonality and biogeographical range of many species (Hillebrand *et al.*, 2018). These range shifts will undoubtedly affect their associated parasites. This could potentially result in parasitic organisms discovering new hosts and may cause unprecedented pathogenic outbreaks in naïve host populations. In addition, these range shifts could cause local extinctions of parasitic species (in the case of host specialist species) and consequent indirect effects to ecosystems (Strona, 2015).

Climate change is likely to impact parasite communities directly through changes in environmental conditions and indirectly through changes in host species. Therefore, the current challenge for parasitologists and conservationists is to understand the ecological roles played by parasites so as to predict how and which ecosystem functions may be altered as climate changes.

## Aims, Objectives and proposed methodology

This project aims to take advantage of the unprecedented availability of marine species taxonomic and distribution data to study the biogeographic distribution of particular taxonomic (e.g., crustaceans, gastropods, microsporidia) and functional (e.g., helminths) groups of parasites and their hosts. By bringing these data into one holistic global database, macroecological questions surrounding host-parasite relationships can be explored. This information can then be applied to uncertainties surrounding changes in biodiversity, especially impacted by a changing global climate.

Objectives of this study include:

* Online databases will be used to compile a list of parasites and the geographic distributions of their host species. These online databases will include the Global Biodiversity Information Facility (GBIF), Ocean Biogeographic Information System (OBIS), Catalogue of Life (CoL) and the World Register of Marine Species (WoRMS).
* This project will determine the rates of discovery (as descriptions of new species) of identified parasite groups, by both taxonomy (e.g., Family, Order, Class), microhabitat (e.g., ectoparasitic, intestinal, gill, intracellular), and geographic area. These discovery rates will be compared to discovery rates in host taxa. Modelling discovery rates could give us an idea of just how under-sampled marine parasites are. Modelling will be explored to indicate the level of host specificity in marine parasitic groups.
* Species ranges and macro-ecological patterns will be modelled using global environmental data in addition to the newly constructed database. It will allow us to relate the spatial distribution of parasites to their hosts and other marine taxa with corresponding environmental variables. These models will determine if parasites are more or less widespread than predicted and determine whether their distributions are governed by environmental variables or habitat (host) distributions.
* Finally, by using current global environmental data, we will model species distributions under past or future climate change scenarios (e.g., 1900 to 2100) with the inclusion of key parasitic taxonomic groups and their hosts.

### Thesis Outline

The proposed research will be separated into 5 chapters (Table 1).

Table 1: Thesis structure.

|  |  |
| --- | --- |
| Chapter 1: Introductory chapter and literature review | |
| Chapter 2: Database creation | |
| Chapter 3: Host specificity | Chapter 4: Parasite and host biogeography |
| Chapter 5: Modelling distribution changes | |

* Chapter 1: Introductory chapter and literature review

This chapter highlights the important role that parasites play in structuring ecosystems and discussed the implications should these organisms be excluded from future ecological research, particularly in the face of anticipated global climate change. This chapter has discussed the current and future impacts of climate change on biodiversity with particular reference to the potential impacts on parasitic biodiversity.

* Chapter 2: Database creation

By using taxonomic and distribution data, several parasitic taxa within crustaceans (copepods, amphipods, isopods, pentastomids, branchiurans, cirripedes), marine helminths (nematodes, acanthocephalans, trematodes), gastropod molluscs, and other phyla, including their respective hosts, will be collated into a database. These data will be collected from the Global Biodiversity Information Facility (GBIF), Ocean Biogeographic Information System (OBIS), Catalogue of Life (CoL) and the World Register of Marine Species (WoRMS). The database will in turn be complemented and quality controlled using published literature.

This chapter will analyse the species list used to build the database and provide an overall perspective into the relative discovery rates (descriptions of new species) of marine parasites. Aspects regarding rates of description of parasites compared to their hosts; parasite groups by both taxonomy (e.g., Family, Order, Class) and microhabitat (e.g., ectoparasitic, intestinal, gill, intracellular); and geographic area will be explored.

* Chapter 3: Host specificity

Costello (2016) suggests that parasites are more widespread than their hosts and that strict host specificity is probably rare as it is a bad evolutionary strategy. The above database will provide insight into parasite specificity by investigating if there are any correlations between parasitic ecological measures and their associated host specificity measures (e.g.: habitat, lifestyle, lifecycle) and I will also be looking at host ecological measures (e.g.: length, depth range and habitat) and their associated parasite species richness values. This is to determine if parasite or host ecological measures influence a parasites propensity to infest a host. If we can determine key ecological measures that influence a parasites specificity, we are better able to understand how changes in climate might impact host specificity and, as a result, the intricate relationship parasites have with their hosts.

Chapter 4: Parasite and host biogeography

Species Distribution Models (SDMs) will be developed using environmental variables likely to influence parasite species distribution. Variables (e.g., temperature, depth, salinity, dissolved oxygen, pH etc.) will be selected regarding their relevance to the distribution of the parasites, their specific hosts and the biological importance of these variables in affecting the species’ population and diversity. These environmental variables will be compared to the chosen parasite taxa, as these species may infect a broad range of hosts and therefore environmental variables would need to encompass all potential hosts.

A software package called MaxEnt will be used to produce the SDMs. This programme uses a machine learning technique called maximum-entropy modelling for predicting species niches and distributions (Phillips, Anderson and Schapire, 2006). From a set of environmental grids and georeferenced occurrence localities, the model expresses a probability distribution where each grid cell has a predicted suitability of conditions for the species (Phillips, Anderson and Schapire, 2006).

SDMs based on environmental data that coincide with the above dataset (Chapter 2), will allow us to predict species occurrences and see how parasite ranges are governed; either by habitat (host) or by environmental variables directly.

* Chapter 5: Modelling distribution changes due to climate change

Results from chapters 3 and 4 will be used in developing SDMs to predict parasite occurrence changes with changes in climate. Whether parasite taxa are more or less host specific than believed (Chapter 3) and whether their distributions are governed by their habitat (hosts) or environmental variables (Chapter 4), we will be able to use these discoveries to improve the predictions made by SDMs under past and future climate change scenarios. These predictions will give us a more holistic idea of the impact that climate change will have on biodiversity inclusive of parasites.

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