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Marine Parasites in Island-Like Disturbed Habitats

by

Lauren N. Dykman

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Lauren N. Dykman

B.S., University of California, Santa Barbara (2016)
Submitted to the Department of Earth, Atmospheric and Planetary Sciences
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Abstract

Parasites are taxonomically and functionally diverse members of biological communities, and can play key roles in species interactions, community structure, and ecosystem functioning. For their reliance on host species, parasites are theorized to be particularly sensitive to disturbances that alter host diversity and abundance, especially in isolated habitats, which present challenges to introduction and establishment. In this thesis, I investigate habitat isolation and disturbance as drivers of parasite diversity, with an emphasis on parasite life history strategies related to colonization and persistence. I focus on an island-like, frequently disturbed habitat, deep sea hydrothermal vents at 9°50'N on the East Pacific Rise, to explore the boundaries of parasite persistence in an extreme environment. First, I analyze recovery in the vent community for 11 years after a catastrophic eruption in 2006 to test successional hypotheses in a new setting with distinct fauna and a chemosynthesis-based food web. Second, I compare parasite diversity at isolated, disturbed vents to marine ecosystems that are similarly isolated but undisturbed (atoll sandflat) and both well connected and undisturbed (kelp forest). Overall, parasite diversity within host species was not significantly lower at vents, but the vent community had many fewer parasite species because there are few vertebrate predator species (fish). Parasites with indirect (multi-host) life cycles were relatively diverse in the disturbed environment, which contradicts expectation based on theory. To explore this further, I investigate the three-host life cycles of trematodes at vents, which was the most diverse and abundant parasite taxon. All life stages of the trematode life cycle were discovered in vent fauna and several taxa were traced across multiple life stages via morphology and genetics. Finally, I use a computational model to investigate how different parasite strategies (colonization capability and impact on hosts) contribute to parasite success under a range of disturbance conditions in island habitats. Parasites that reduce host reproduction reached higher densities than parasites that cause mortality across all disturbance frequencies explored, and disturbance facilitated the evolution of more virulent parasites. These studies demonstrate that life history traits and the ability to adapt allow diverse parasite taxa to persist in isolated, ephemeral environments.

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Jason, and AUV *Sentry*. Dedicated people in these agencies and teams made access to the deep ocean possible through many, many sleepless nights. It is a feat comparable to space exploration, and I salute those who make a living pushing the boundaries of our own planet.

Collaboration is one of the most rewarding aspects of the science career. My research benefited greatly from the contribution of mentors and collaborators. I thank my committee members Armand Kuris, Carolyn Tepolt, Serguei Saavedra, and Michael Neubert for hearing countless project iterations and helping me with both the big picture and the tiny details. Many other collaborators contributed ideas, expertise, data, and research assistance. They include, in no particular order, Dana Morton, John McLaughlin, Ryan Hechinger, Zac Tobias, Cory Berger, Bethany Fleming, Kirstin Meyer, Michael Meneses, Mario Fernandez, Henrik Glenner, Jens Høeg, Paola Braicovich, Charles Blend, Daniel Fornari, Rodney Bray, Mike Kinsella, Jyun-Nai Wu, Storm Martin, Norman Dronen, Thomas Cribb, Scott Cuttmore, Tim Shank, Kate Buckman, and John Douglas. I also thank journalists and media specialists Sabrina Imbler, Nicholas Lord, and Daniel Hentz who helped to make my research more broadly accessible.

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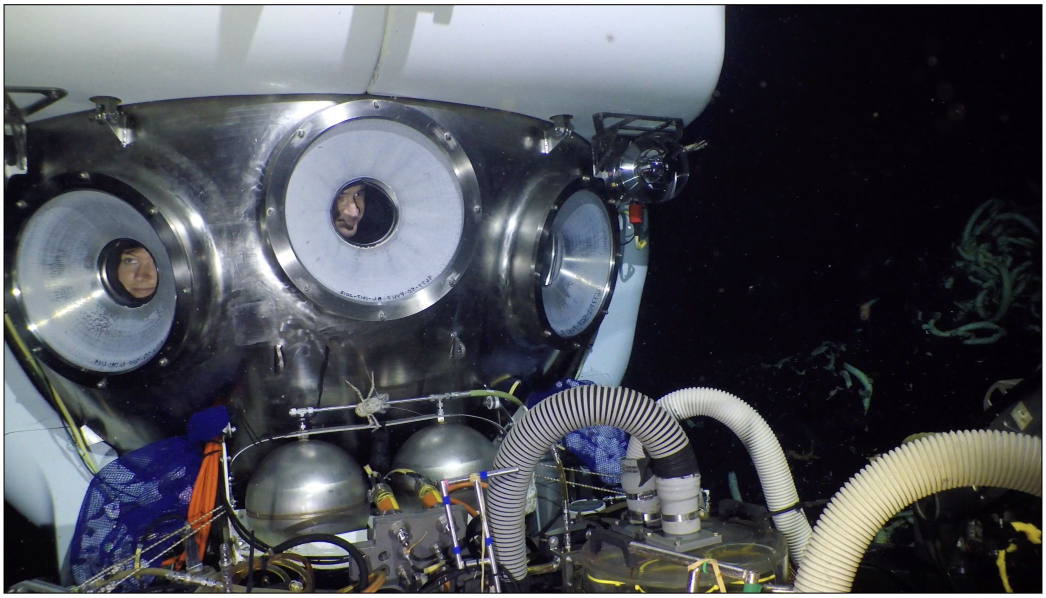
This thesis is dedicated to life and living things. I honor the animals who gave their lives so that I could tell their story, and my deepest hope is that someday this work will give back. I acknowledge the places that sustained my soul. The bike trail and its vantage point on the sea, from the season when ice rims the high tide line to the season that carries the first scent of marsh. The stone pier in Woods Hole Village that provides a vantage point on changing tides, changing ships, and the changing angle of the moon. The noonday haze and turquoise sea of the tropical Eastern Pacific, and the quiet starlight from the bow. The vents at 9°50'N on the East Pacific Rise, where obsidian flows like waves frozen in time mid-break. Where worms bloom like wildflowers.

Finally, most importantly, this thesis is dedicated to my mom and dad, Pat Burger and Derek Dykman, who first introduced me to the ocean. You taught me to walk through this world with my mind and heart open, to care about our world and all living things. You provided the deep ocean of stability from which I could draw during the long process of earning a doctoral degree. This goal took me far away, but through it all we remained close. We always will.



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Chapter 1

Introduction

1.1 Community assembly in island-like, disturbed habitats

Habitat isolation and disturbance are important drivers of patterns in biological diversity (Dayton, 1971; Caswell & Cohen, 1991a; Urban, 2004; Hiebeler & Morin, 2007; Kadmon & Allouche, 2007; Ryser et al., 2019). Theory and observation suggest fewer species occupy habitat patches that are small or distant from other suitable habitats, because these features decrease the likelihood of species arriving and establishing (MacArthur & Wilson, 1967; Simberloff & Wilson, 1969; Thornton, 2007). The persistence of a species in a network of isolated habitat patches connected by dispersal, or "metacommunity" (Leibold et al., 2004), is determined by the balance between colonization and extinction on individual patches. Dispersal is critical for recolonization of isolated habitat patches where populations have gone locally extinct. If habitats are also disturbed, recolonization must be increasingly reliable to assure persistence. Habitats that are island-like and ephemeral are common in nature (Carson et al., 1990; Lafferty et al., 1999; Ebert et al., 2001; Whittaker et al., 2009; Mullineaux et al., 2018), and understanding the processes governing connectivity and persistence are of fundamental interest to biogeography, ecology, and evolution. These questions are also important for conservation (Sasaki et al., 2015), since habitat destruction and fragmentation due to human development is the leading cause of biodiversity loss worldwide (Haddad et al., 2015; Chase et al., 2020).

Some species are better suited to life in isolated, disturbed habitats than others, leading to observed differences in community composition on islands or after disturbances. The variable responses between species to these features are due to differences in the expression of biological traits. Life history traits, such as reproductive output, dispersal strategy, and larval duration, impact the probability of dispersal and colonization, while traits related to habitat preference and feeding method may affect the ability to establish and persist after arrival. It is increasingly recognized that biological traits must be incorporated into theoretical frameworks that seek to explain how the environment determines the distribution of species (Mouillot et al., 2013; Hevia et al., 2017). Only by causally linking physiological or life-history characteristics of organisms to specific environmental stressors can we predict how entire communities might shift in response to environmental change (Kroeker & Sanford, 2022).

Several trait-based theories attempt to explain which types of organisms will be most successful at colonization and establishment during early community assembly on islands or after disturbance. Species with effective dispersal are expected to arrive early in community assembly and be more likely to reach isolated islands (Tsuyuzaki & Del Moral, 1995; Burns, 2005; Fraaije et al., 2015). Species with strategies for rapid reproduction will be more likely to establish (Odum, 1969). Species with tolerance to harsh environmental conditions are likely to survive in early stages of primary succession, when resources are usually low and abiotic stressors high. Conversely, since biological diversity generally increases over time during community assembly (Boit & Gaedke, 2014; Dale & Crisafulli, 2018), species at higher trophic levels, such as predators and parasites, are expected to only establish and increase in diversity once the species they rely on have established. Small habitat area has been shown to restrict food chain length, food web complexity, and, as a consequence, the diversity of top predators (Kadmon & Allouche, 2007; Holt, 2009; Martinson et al., 2012; Galiana et al., 2022). Hence, species that are most reliant on other species for habitat or food, particularly specialist consumers at high trophic levels (Wood et al., 2014; Dharmarajan et al., 2021), may take more time to establish and be less likely to persist in isolated habitats with frequent disturbance.

1.2 Parasites in island-like, disturbed habitats

Parasites have historically been studied as disease agents but are now recognized as an important consumer group in biological communities. They represent a significant proportion of global biodiversity. By some estimates, approximately 40% of eukaryotic species are parasitic (De Meeûs & Renaud, 2002; Dobson et al., 2008), and parasitism evolved 223 separate times in animal taxa (Weinstein & Kuris, 2016). Parasites make up a large proportion of biomass and trophic links in some biological communities (Lafferty et al., 2006; Kuris et al., 2008). It is increasingly clear that ecological studies that omit parasites overlook a large proportion of the interactions that structure biological communities (Marcogliese & Cone, 1997). Despite their strong representation in ecosystems, our understanding of factors driving parasite diversity lags behind that of free-living taxa.

Theory suggests parasites will be less likely to establish on isolated islands and less able to persist in frequently disturbed environments than their hosts. Strict reliance on one or more hosts can be a risky strategy in isolated, dynamic systems, despite the advantages of using another organism as shelter and a rich food source. Consistent with the theory of island biogeography, parasite diversity is expected to be lower on isolated islands due to limited opportunities for introduction, but with the additional layer of reliance on a host. Parasites may not be introduced to isolated habitats with founder hosts (Steadman et al., 1990; MacLeod et al., 2010) and may take time to establish once they arrive (Phillips et al., 2010). In early stages of colonization, when host and parasite population densities are low, parasites are more likely to go extinct before establishing (Anderson & May, 1978). Reliance on a host may also influence the persistence of parasite species once established. Since hosts are essentially small islands (Kuris et al., 1980), parasites encounter patchiness and disturbance on two scales - host and habitat (Fig. 1-1). On the host scale, transmission is a risky period when the parasite may disperse freely in the open environment. Transmission success is a function of the parasite's dispersal strategy and local host densities. As with other obligate symbionts, parasites rely upon persistent host populations and are more likely to go extinct when host populations are small (Bush et al., 2013). On the habitat scale, connectivity between patches is necessary for parasites to recolonize patches where local populations have gone extinct, and ultimately persist in the metacommunity (Fig. 1-1). Effective colonization of both parasite and host is particularly important if habitats are frequently disturbed or far apart. Finally, island habitats offer small areas that may constrain host diversity and food web complexity, limiting the habitat and feeding niches that parasite species could occupy via diversification (Fig. 1-1) (Kadmon &

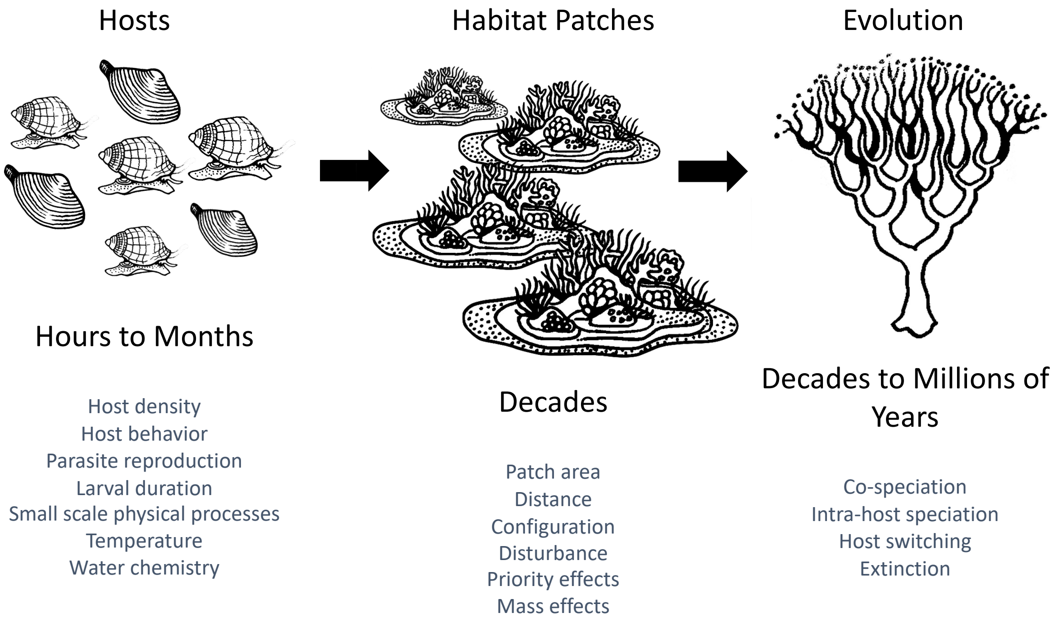


Figure 1-1: Parasites experience habitat patchiness on two scales: host and habitat. Processes determining parasite persistence in ecosystems range from transmission between individual hosts to connectivity between isolated habitat patches. These processes play out on very different spatial and temporal scales. Patterns and processes at both scales are influenced by and feed back to evolution.

Allouche, 2007). The interconnected dynamics with a host make parasite colonization, establishment, and persistence in islands challenging to understand. For the same reason, parasites are an intriguing group of organisms for examining biogeographical patterns and strategies for persistence in challenging environments.

To form general predictions for which parasites will be successful in island-like, disturbed habitats, it is necessary to identify parasite traits that promote persistence. One fundamental difference between parasite taxa is the number of hosts required to complete the life cycle (Dobson & May, 1986; Barrett et al., 2008; Llopis-Belenguer et al., 2019). Parasites with direct (one-host) life cycles (DLC) are expected to be more successful if their suitable host is at a high local population density, which most likely occurs when community diversity is relatively low. Parasites with indirect (multi-host) life cycles (ILC) require multiple host species to be available at the right place and time, so would be favored by a diverse host community (Huspeni & Lafferty, 2004). The relative rates of community assembly for DLC and ILC parasite species have not yet been examined in real successional systems, though several theoretical predictions arise. In successional systems, changes in diversity and composition present a shifting mosaic of potential habitat for parasites, with diversity and food web complexity generally increasing over time (Espínola-Novelo et al., 2020). One might expect DLC parasites and pathogens to be abundant in early succession, when the diversity of the free-living community is relatively low and some species may be highly abundant (Connell & Slatyer, 1977) (Fig. 1-2, DLC Parasite). ILC parasites are expected to increase in diversity later in succession once a rich free-living community has assembled (Fig. 1-2, ILC Parasite). If disturbance is frequent, and communities do not have sufficient time to reassemble, parasites that require multiple host species are likely to go extinct first. Empirical evidence from a number of systems has demonstrated that ILC parasite species diversity decreases with habitat fragmentation (Bitters et al., 2022; Resasco et al., 2019) and the removal of top predators (Wood et al., 2014), but increases after habitat restoration (Huspeni & Lafferty, 2004; Moore et al., 2020). Very few studies have examined the relative success of ILC versus DLC parasite species during community assembly or in disturbed versus undisturbed systems (e.g., Wood et al. 2014), making broad generalizations impossible. To understand which parasite traits best inform parasite response to disturbances requires more observational and experimental evidence from a range of ecosystems that differ in habitat configuration and disturbance frequency.

Another fundamental feature of parasites that may influence colonization and persistence is their impact on the host. If hosts are viewed as islands, parasites are in the unique position of altering the longevity and densities of the islands they inhabit. Parasites may decrease host longevity by exploiting somatic tissue and causing early mortality (hereafter, mortality inducers). Parasites that increase mortality include pathogens, for which the impact on the host is immune-response dependent, and some typical macroparasites, for which the impact on the host is intensity-dependent (Lafferty et al., 2015). Some parasites instead decrease host densities by exploiting reproductive tissue, shutting off host reproduction (hereafter, castrators) (Kuris, 1974; Lafferty & Kuris, 2009). Many theoretical and experimental studies have

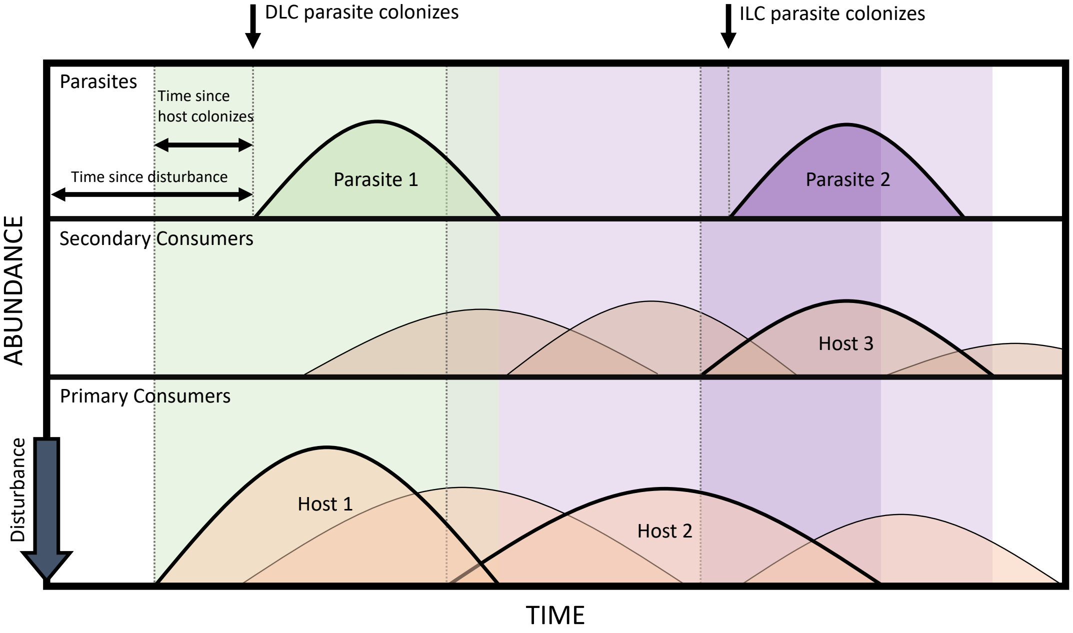


Figure 1-2: A conceptual diagram for host and parasite recolonization after disturbance. In early succession, hosts at low trophic levels that are effective dispersers and fast reproducers dominate available space and may be highly abundant (Host 1). A parasite with a direct life cycle (DLC) that only exploits Host 1, if able to colonize, will find conditions favorable for transmission early in succession when Host 1 is present (green shading). Secondary consumers establish once their prey have established. A parasite with an indirect life cycle (ILC) that passes from a prey (Host 2) to its predator (Host 3) can arrive with one host species (light purple shading), but can only complete its life cycle and increase in abundance when both Host 2 and Host 3 are present (dark purple shading). In theory, there is a lag time between disturbance and the arrival of the host (long arrow), and there may be an additional lag period before the parasite arrives (short arrow). Theory suggests ILC parasites are more likely to find suitable conditions later in community assembly than DLC parasites, so ILC species would go extinct first in frequently disturbed systems.

demonstrated various consequences of different host exploitation strategies on parasite-host evolution and population densities on local scales (Boots & Sasaki, 2002; Hall et al., 2007; Ebert et al., 2004). However, the demographic consequences of different host exploitation strategies have not been directly compared in networks of disturbed habitats. The integration of functional traits into frameworks of parasite biogeography and disturbance ecology is a promising avenue for understanding patterns of biodiversity across a broad range of ecosystems (Poulin, 2021). Some ecosystems and groups of organisms have received heavy research attention, while the integration of functional trait ecology and parasite ecology is just beginning to grow (Llopis-Belenguer et al., 2019).

1.3 The need to understand drivers of parasite diversity

In recent years, the narrative and research focus on parasites has begun to shift. Instead of being studied as disease agents, parasites are now recognized as indicators of a biodiverse ecosystem with a functioning web of interconnected species (Marcogliese, 2005; Hudson et al., 2006). Biodiversity loss, disturbance, and habitat fragmentation are known to alter parasite diversity in a number of ecosystems (Lafferty, 2012; Wood et al., 2014; Bitters et al., 2022; Resasco et al., 2019). For their role as specialist consumers and sensitivity to environmental impacts, parasites might be applied as effective indicators of overall ecosystem health and biodiversity (Dharmarajan et al., 2021; Marcogliese & Cone, 1997; Huspeni & Lafferty, 2004; Hechinger & Lafferty, 2005; Moore et al., 2020). In several marine ecosystems, parasite diversity and parasite-host links have been carefully resolved (Amundsen et al., 2009; Hechinger et al., 2011; Lagrue & Poulin, 2015; McLaughlin, 2018; McLaughlin et al., 2020; Morton et al., 2021), allowing for the first comparisons between different marine ecosystems (McLaughlin et al., 2020). The development and testing of trait-based hypotheses is the promising next step in building a general understanding of how the environment drives patterns in parasite diversity between ecosystems with different conditions.

Despite these practical advances, the number of ecosystems with community-level parasitological data remains low. This limits our ability to test drivers of diversity over broad scales with sufficient statistical power. Parasites are often omitted from biodiversity surveys because they are concealed within hosts, making them far more difficult to collect, process, and identify. They have also only recently been appreciated for their ability to provide insight into ecosystem functioning. Estimates of parasite diversity remain highly uncertain in most systems (Poulin & Morand, 2000), and efforts to discover and describe new species lags behind that of more conspicuous free-living fauna. Parasites are at risk of secondary extinction with their hosts (Dunn et al., 2009), yet parasite extinctions are more likely to go unnoticed (Carlson et al., 2020). Environmental alteration by humans is rapidly exceeding our capacity to explore and understand biological interactions, and our limited understanding of drivers of parasite diversity is a widening research gap (Harvell et al., 2004; Byers, 2021). As humans transport hosts and their parasites around the globe and alter habitat at unprecedented rates (Torchin et al., 2002; De Bellocq et al., 2002; Dunn, 2009; Wikelski et al., 2004), practical interest centers on predicting parasite establishment and persistence in new ranges, and the consequential changes to community structure with the gain or loss of parasites. In an ironic twist of perspective, since parasites make up a large component of global biodiversity and may be more sensitive to change than their hosts, the best conservation policies to preserve the most species may be those specifically directed towards conserving parasites (Carlson et al., 2020). It is critical that we develop a mechanistic framework to predict which parasites will be winners or losers as habitat disturbance and fragmentation intensifies.

In this thesis, I study island-like habitat and disturbance as drivers of metazoan parasite diversity with a focus on parasite life history strategies. I expand the growing body of knowledge on global parasite ecology and biogeography by focusing on a unique marine setting with distinct environmental conditions: deep-sea hydrothermal vents.

1.4 Deep-sea hydrothermal vents: disturbed islands in the abyss

In 1977, the discovery of flourishing animal communities at hot springs on the deep seafloor expanded our concept of the boundaries of life on Earth (Corliss et al., 1979) (Fig. 1-3a). In the decades since, more than 500 deep-sea hydrothermal vent fields have been discovered along oceanic spreading ridges, back arc basins, and intra-plate hotspots (Beaulieu et al., 2013), with an estimated $\sim$ 900 vent fields still undiscovered (Beaulieu et al., 2015) (Fig. 1-3b). Over 700 new species have been described from these unique deep-ocean communities based entirely on chemosynthetic primary production from geothermal emissions (Chapman et al., 2019). New lines of biological inquiry have grown from the study of life under high pressure, extreme temperature, harsh chemicals, and in the absence of sunlight (Childress & Fisher, 1992).

One of the fundamental questions in hydrothermal vent ecology is how vent species persist and maintain connectivity in such isolated habitats (Vrijenhoek, 2010; Mullineaux et al., 2018). Individual vents can be spaced tens to hundreds of meters apart, with vent fields separated by kilometers to hundreds of kilometers (Beaulieu et al., 2013; Baker et al., 2016). Active venting habitat is small in area, usually localized within 100 meters of hydrothermal emission (Arquit, 1990; Levin et al., 2016). The highly localized nature of active vent habitat, coupled with the strict reliance on such habitat by the species that live there, constrains interspecific interactions and feeding relationships to a small area. In such island-like habitat, dispersal is necessary for species to maintain population connectivity between isolated habitat patches (Mullineaux et al., 2018). Many of the animal species at vents, including tubeworms, snails, mussels, and barnacles are relatively sessile as adults, but disperse in the water column during a planktonic larval stage in early life (Adams et al., 2012). For minuscule larvae to locate suitable vent habitat in the unforgiving abyss seems a strategy against all odds. And yet, life persists.

In addition to being isolated, deep-sea hydrothermal vents are also ephemeral and disturbed. Volcanic eruptions provide a large-scale and intense stressor to vent life. The frequency and severity of volcanic disturbance depends on the tectonic setting of the vent field (Rubin et al., 2012). The East Pacific Rise (EPR) is the fastest spreading oceanic plate boundary ($\sim$ 120 mm/y). As a result, volcanic eruptions may occur every 10 to 20 years at some vent fields (Fornari et al., 2012). The most recent documented eruption at the 9°50'N vent field in 2006 paved over 20.8 km^2 of seafloor (Wu et al., 2022) (Fig. 1-4). After such large-scale disturbance, vent species must recolonize from afar in order to ultimately persist regionally (Mullineaux et al., 2010, 2018). Near-decadal disturbance frequency is very different from slow-spreading plate boundaries like the Mid-Atlantic Ridge, where vents may persist undisturbed for hundreds to thousands of years (Sinton et al., 2002; Rubin et al., 2012) and biological communities

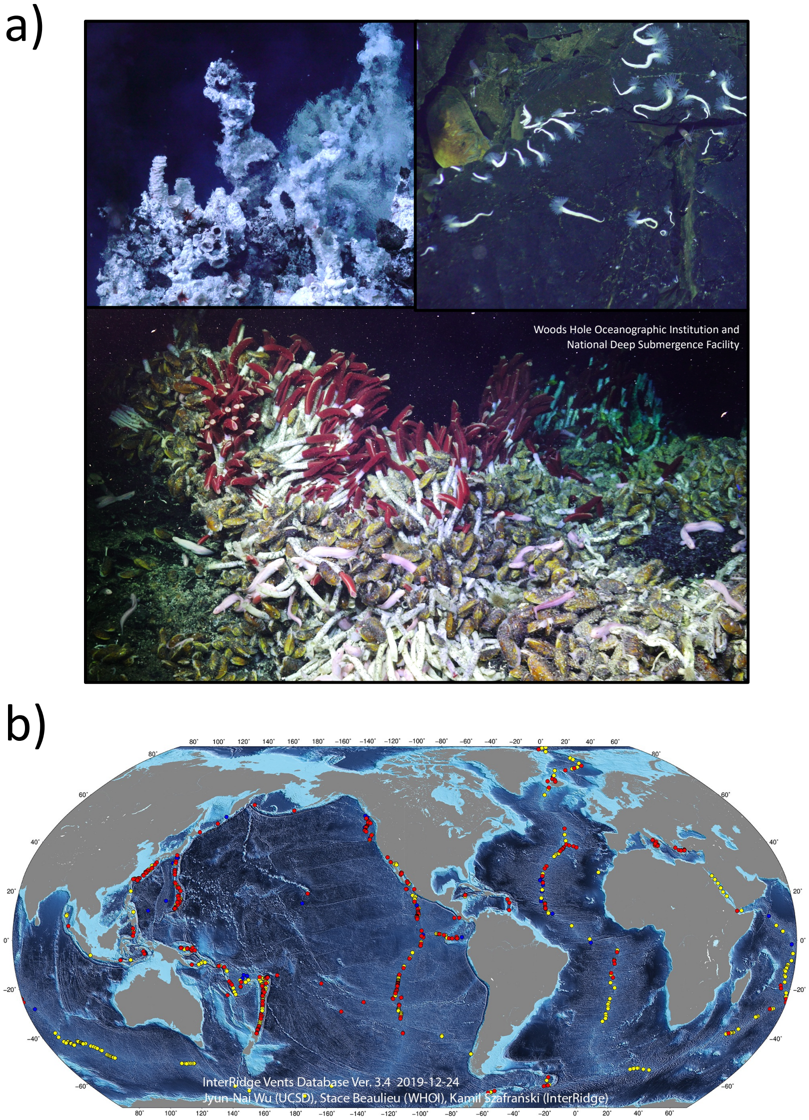
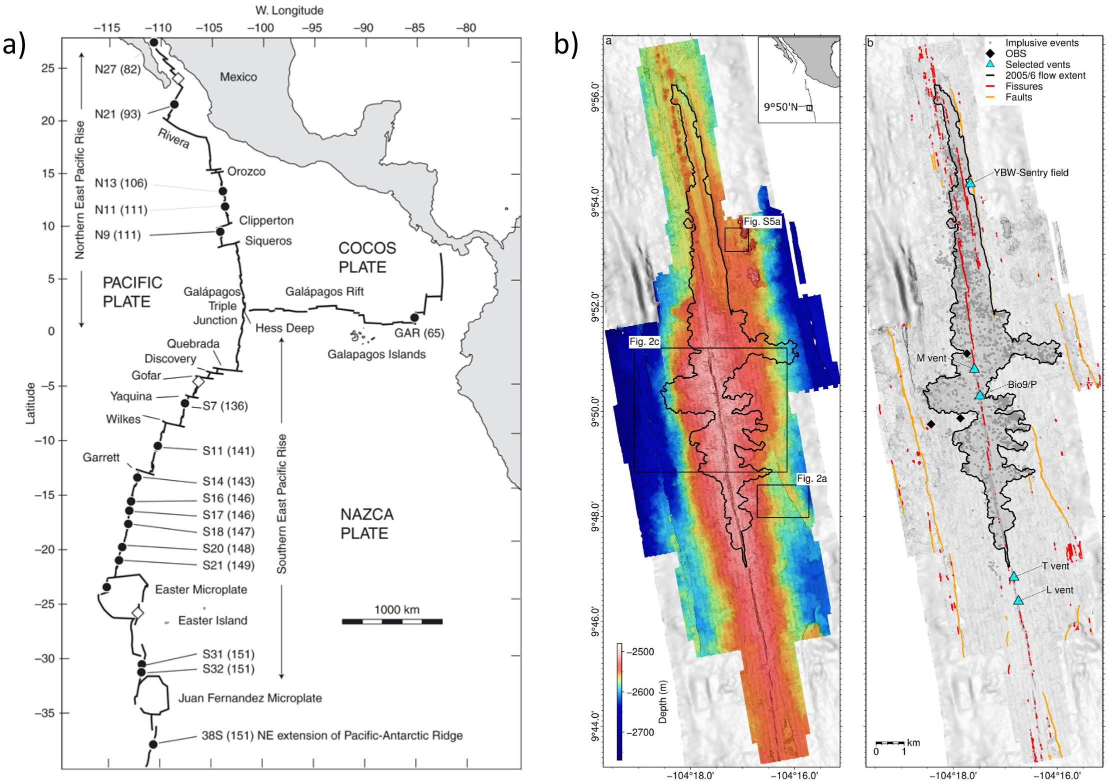


Figure 1-3: a) Hydrothermal vent communities from the East Pacific Rise, including iconic megafaunal species with unique adaptations. *Alvinella* tubeworms (top left) survive temperatures as high as 80°C. Serpulid tubeworms (top right) inhabit peripheral zones where conditions are milder. The giant tubeworm, *Riftia pachyptila* (bottom), does not feed, but instead hosts chemosynthetic endosymbionts that fix carbon. The chemical and thermal tolerances of vent species establish visible zonation patterns in the vent community (Photos: Woods Hole Oceanographic Institution and National Deep Submergence Facility, ROV *Jason*, 2021). b) A map of distributions of active vent fields worldwide taken from Interridge Vents Database Ver. 3.4 (Wu, Beaulieu, and Szafranski 2019-12-24). Red: active, confirmed; Yellow: active, inferred; Blue: inactive.

can be stable on long time scales (Van Audenhaege et al., 2022). Disturbance frequency and vent spacing are expected to be important factors in regulating the geographical distribution of vent species (Mullineaux, 2014). Information on the limitations of species to persist under different disturbance and isolation scenarios is important for understanding current species distributions, and for predicting vulnerability to human impacts such as deep-seabed mining (Amon et al., 2022).



From Vrijenhoek 2010

From Wu et al. 2022

Figure 1-4: The tectonic setting and recent volcanic history of the 9°50’N vent field. a) A map showing the location of the 9°50’N vent field on the East Pacific Rise (adapted from Vrijenhoek 2010). b) A high-resolution map of the 9°50’N vent field showing the extent of the magma flow from the 2006 eruption (black outline) (from Wu et al. 2022).

Due to the challenges of recruitment and persistence in isolated, disturbed systems, we might expect to find few parasites at deep-sea hydrothermal vents. Few parasite species have been discovered at deep-sea vents to date (Fig. 1-5) (Dykman, 2022b). Vent parasites have also received little scientific attention, however, leading early investigators to question whether parasites are truly scarce at vents or whether their scarcity is simply a result of low sampling effort (De Buron & Morand, 2004). This question has remained unresolved. There are many compelling reasons to develop the field of vent parasite ecology. Vents provide an ideal model system to test fundamental expectations for the influence of island-like habitat and disturbance on parasite diversity. Understanding which types of parasites are successful and which are scarce or absent at vents can help identify life history traits that might explain the relative resilience of certain taxa to disturbance. A careful survey of parasite diversity and abundance in a dynamic deep-ocean setting provides an excellent opportunity to test and expand theory, since the majority of theory in marine parasite ecology has been developed in photosynthetic, coastal systems. Finally, since parasites are reliant on host densities and feeding relationships for transmission, parasites provide useful information on ecological relationships between the free-living vent fauna. By resolving parasite-host links and parasite life cycles, this thesis provides a first attempt at understanding the requirements for parasite persistence in frequently-disturbed vent habitats.

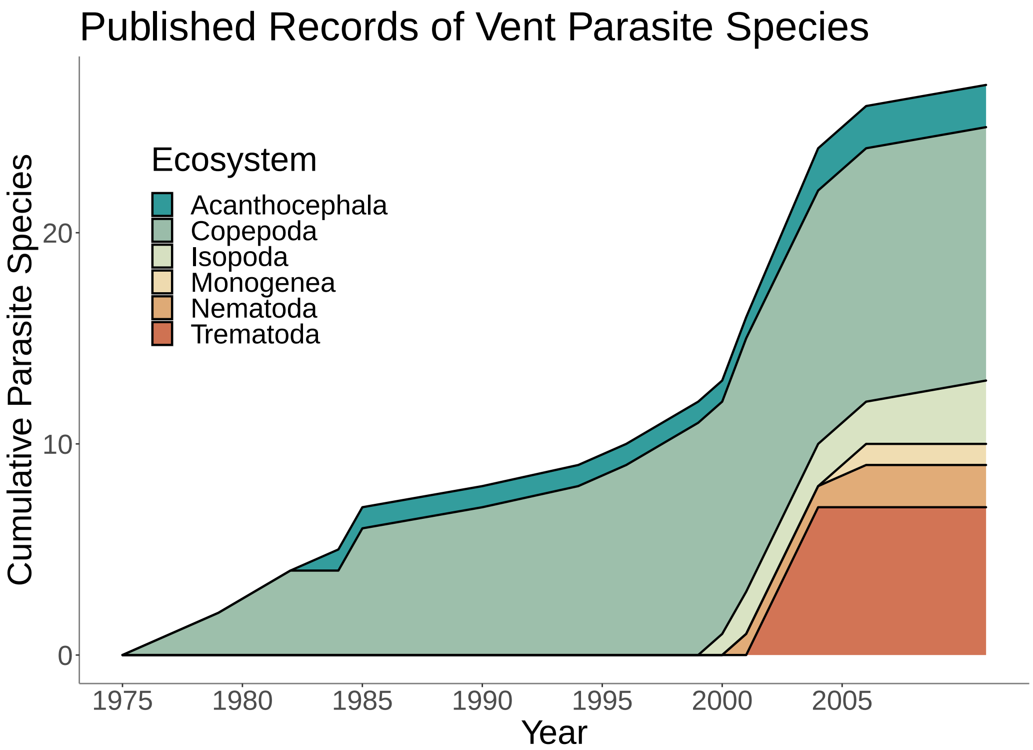


Figure 1-5: Cumulative records of vent parasites reported in the literature by collection year. When collection year was not reported, publication year was used.

1.5 Scope and objectives of the thesis

In this thesis, I test and expand theories of island biogeography, patch dynamics, and disturbance ecology in an under-explored consumer group (parasites) in a novel, extreme ecosystem (deep-sea hydrothermal vents). Specifically, I explore interactions between parasite life history traits (life cycles and impact on the host), landscape features (island configuration and disturbance), and the host community (diversity and functional traits) that structure parasite diversity. I focus on deep-sea hydrothermal vents because they are an excellent example of island-like, disturbed ecosystems. They also have unique fauna and covarying gradients of resources and physical stressors which are expected to drive distinct patterns compared to the more accessible systems where theory has classically been developed. In Chapter 2, I examine the recovery and succession of species composition, functional traits, and diversity over 11 years in a hydrothermal vent invertebrate community following a massive seafloor eruption. I test fundamental concepts in successional and disturbance theory in a new setting, and provide background information on the shifting mosaic of potential hosts that parasites would encounter throughout succession. In Chapter 3, I comprehensively sample for metazoan parasites in the same vent community 13-15 years after the eruption to understand which parasite taxa are diverse at vents and which are scarce or absent. I compare these new data to data from other ecosystems to test the hypothesis that parasite diversity will be lowest in a disturbed, isolated ecosystem (vents), intermediate in an isolated, undisturbed ecosystem (atoll sandflat), and highest in a well-connected, moderately disturbed system (kelp forests). I also test the hypothesis that vents will have relatively fewer parasite species with indirect life cycles and more with direct life cycles due to colonization and recruitment challenges in a frequently disturbed habitat. In Chapter 4, I explore whether trematodes (parasitic flatworms with a three-host life cycle) can complete their entire life cycles in the vent environment. I also use genetic techniques to determine the closest known relatives of vent trematode species, and to assess whether trematode diversity at vents likely arose from one original ancestral species followed by radiation or by multiple original founders. Finally, in Chapter 5, I use mathematical and computational models to compare how disturbance and island-like habitats drive the persistence and adaptive dynamics of parasites that increase host mortality to parasites that decrease host reproduction.

Historically, parasitology has taken a host-centric perspective. If maintaining this tradition, the questions in this thesis would explore how disturbed ecosystems do or do not promote disease transmission and pathology in host populations. Instead, this thesis turns the tables and treats marine parasites as interesting and diverse marine invertebrates in their own right. This thesis is not a narrative of disease. Rather, it is the story of small, resilient animals that eke out a living in seemingly improbable niches, complete audacious life cycles, and traverse between tiny points of refuge in a vast and unforgiving ocean.

Chapter 2

Functional traits provide new insight into recovery and succession at deep-sea hydrothermal vents

2.1 Abstract

Investigation of communities in extreme environments with unique conditions has the potential to broaden or challenge existing theory as to how biological communities assemble and change through succession. Deep-sea hydrothermal vent ecosystems have strong, parallel gradients of nutrients and environmental stress, and present unusual conditions in early succession, in that both nutrient availability and stressors are high. We analyzed the succession of the invertebrate community at 9 °50' N on the East Pacific Rise for 11 years following an eruption in 2006 in order to test successional theories developed in other ecosystems. We focused on functional traits including body size, external protection, provision of habitat (foundation species), and trophic mode to understand how the unique nutritional and stress conditions influence community composition. In contrast to established theory, large, fast-growing, structure-forming organisms colonized rapidly at vents, while small, asexually reproducing organisms were not abundant until later in succession. Species in early succession had high external protection, as expected in the harsh thermal and chemical conditions after the eruption. Changes in traits related to feeding ecology and dispersal potential over succession agreed with expectations from other ecosystems. We also tracked functional diversity metrics over time to see how they compared to species diversity. While species diversity peaked at 8 years post-eruption, functional diversity was continuing to increase at 11 years. Our results indicate that deep-sea hydrothermal vents have distinct successional dynamics due to the high stress and high nutrient conditions in early succession. These findings highlight the importance of extending theory to new systems and considering function to allow comparison between ecosystems with different species and environmental conditions.

2.2 Introduction

Disturbance is a ubiquitous and important driver of biological patterns in most ecosystems. An understanding of the processes influencing the pattern of succession following disturbance has been the focus of a century of research (Clements, 1916; Gleason, 1926; Egler, 1954; Connell & Slatyer, 1977; McCook, 1994), and is of growing practical importance with the recent unprecedented rate of anthropogenic habitat destruction and alteration (Sasaki et al., 2015). While a primary goal has been to identify general patterns of succession (Clements, 1916; Odum, 1969), the complex interplay of biotic and abiotic factors makes such generality difficult. These factors include site condition (Berlow, 1997), the type and supply of initial colonists (Egler, 1954; Sutherland & Karlson, 1977), niche preemption and modification by colonists (Jones et al., 1997; Fukami, 2015), and post-colonization species interactions (Connell & Slatyer, 1977; Farrell, 1991). In many successional systems, physical conditions and resources change over time and drive shifts in community structure by acting on the physiological and nutritional requirements of individual species (Tilman, 1985).

The environment at deep-sea hydrothermal vents differs chemically, physically, and nutritionally from most well-studied successional systems. The hydrothermal fluids reach temperatures of 400°C and, when undiluted by ambient seawater, exhibit low pH, low oxygen, and concentrations of hydrogen sulfide and other chemicals that are toxic to animal life (Childress & Fisher, 1992). These reduced chemicals, however, also provide the energy for microbial chemosynthetic production of the organic matter that fuels the food web. As venting fluid exits the seafloor and mixes with ambient seawater, a gradient is established over which environmental stressors and nutrients vary in parallel (Micheli et al., 2002). Covariance of stress and nutrients is likely an important feature of succession at vents because the source of large-scale disturbance at vents, seafloor eruptions, provides an environment for initial colonists that is physiologically stressful yet also enriched in nutrients in the form of reduced chemicals. This is opposite the trend observed in classic examples of primary succession (i.e., the rocky intertidal, volcanic islands), where the highest abiotic stress (desiccation, limited shelter, high thermal stress) generally co-occurs with the lowest resource availability directly after disturbances (Connell, 1961; Tsuyuzaki & Del Moral, 1995). Thus, for aspects of species succession that are influenced by physiochemical stress and/or nutrition (e.g., body size, physical protection, trophic position), patterns at vents may differ from those in other systems in ways that challenge or broaden existing theory.

Hydrothermal vents on the East Pacific Rise (EPR) are subject to frequent large-scale volcanic disturbance, providing repeated opportunities to study primary succession in the deep sea. The EPR segment between 8° and 10°N is categorized as a fast-spreading center (80–150 mm/yr) (Bird, 2003) and experiences eruptions on a decadal timescale (Rubin et al., 2012). Early stages of succession have been tracked at the 9°50'N vent field on the EPR after two eruptions, one in 1991 (Haymon et al., 1993) and one in 2006 (Tolstoy et al., 2006), which paved over existing invertebrate communities with basaltic pillow lava. Venting flux was vigorous and concentrated following both eruptions, but declined and became more diffuse over time, with a corresponding increase in pH and decrease in reduced sulfur concentration (Le Bris et al., 2006). Visual surveys in the first 3–4 yr following both eruptions showed a repeated pattern of initial microbial colonization, followed by sequential settlement of two different siboglinid tubeworms (*Tevnia jerichonana* and *Riftia pachyptila*) and then mussels (*Bathymodiolus thermophilus*) (Shank et al., 1998; Fornari et al., 2012). Although species assembly patterns have been documented at 9°50'N for early succession (Shank et al., 1998), a comparison with general theory requires longer tracking and consideration of the function, as well as the identity, of the full size-spectrum of invertebrate colonists.

To allow comparison of successional patterns involving systems with distinct conditions and species assemblages, ecologists have used the notion of functional traits (Meiners et al., 2015). The idea is that, by considering the functional role of species rather than just their specific taxonomy, we can gain insight into how organisms affect and respond to features of their environment (Cadotte et al., 2011; Mouillot et al., 2013). Functional trait analysis has proven useful in plant (Reich et al., 1997), insect (Ding et al., 2017), and microbial ecology (Zak et al., 1994), and has recently expanded into oceanic systems (Micheli & Halpern, 2005; Aguilera & Navarrete, 2012; Darling et al., 2012; Stuart-Smith et al., 2013; Teixidó et al., 2004). Here, we use an unprecedented 11-yr colonization time series initiated after the 2006 eruption at the 9°50' N hydrothermal vent field on the East Pacific Rise, combined with a growing trait database for hydrothermal vent invertebrates (sFDvent; Chapman et al. 2019), to test trait-based successional hypotheses in a new setting with the unusual conditions associated with deep-sea eruptions (i.e., high stress and high nutrients in early succession).

We examine a suite of traits and functional diversity metrics that have been observed to change over succession in other marine benthic systems (Greenfield et al., 2016; Bolam et al., 2016; Veríssimo et al., 2017). We explore whether some of these trait patterns diverge from theory, specifically those related to growth, acquisition of nutrients, and provision of habitat. In non-vent systems, where nutrients typically are depleted after a disturbance, small-bodied species colonize first, and biogenic structure (habitat complexity) increases over time (Tilman, 1988; Hirata, 1992; Teixidó et al., 2004). At vents, where a pulse in nutrients occurs during the disturbance, we expect that large-bodied species will be able to grow and create habitat complexity early in succession, thus facilitating the rapid assembly of diverse trophic levels and feeding modes. Later in succession, when venting (and thus nutrients) becomes more diffuse and less reliable, animals with higher mobility may be favored. Other trait patterns are expected to follow established theory. Species with greater external protection are likely to be more abundant in early succession when physiological stressors are highest. Animals with high dispersal potential are likely to colonize earliest, as observed in other patchy, island-like habitats (MacArthur & Wilson, 1967; Tsuyuzaki & Del Moral, 1995; Thornton, 2007), and asexually reproducing organisms, if able to arrive early, will rapidly establish. In addition to traits, we track functional diversity indices over the course of succession to see whether they provide additional information compared to species diversity indices. We discuss the application of these results to vent ecology and conservation, as well as the new insight gained from expanding successional theory to ecosystems with atypical conditions.

2.3 Methods

2.3.1 Biological samples

The post-eruption colonization samples examined for this study were collected from 9°50' N on the EPR at seven time points between November 2006 and April 2017. Sampling focused on P-vent (9.8380° N, 104.2912° W, 2,509 m depth), where the January 2006 eruption had destroyed the local invertebrate community. Colonists were collected from introduced samplers, called “sandwiches” (Fig. 2-1), as described in Mullineaux et al. 2010. Sandwiches were deployed by the deep submergence vehicles *Alvin* and *Jason* across the range of temperatures representative of the environmental and biological zones of the vent field (Micheli et al., 2002). Sandwiches were left on the seafloor for varying intervals between six weeks and four years, based on cruise availability (Fig. 2-2a), and new sandwiches were deployed in the same location as recovered ones, resulting in a continuous time series of colonist abundance.

To characterize the fluid environment at each sandwich, temperature was measured at deployment and recovery by holding a temperature probe at the base for 1–2 minutes until a definite maximum was reached. We used recovery temperature to characterize the thermal environment for subsequent analyses because it reflected the most recent conditions experienced by the community on the sandwiches at the time of collection. From the full set of post-eruption colonization samples, we selected 30 with recovery temperatures of 1.9–6.5°C, as this was the thermal range adequately sampled throughout the full observation period (Fig. 2-2b). Temperatures in the vent field had generally waned over time (Mullineaux et al., 2010), so samples with recovery temperatures greater than 6.5°C were not available after 22 months. This subsampling was necessary to minimize the influence of environmental change, as many vent species have narrow thermal and chemical preferences (Childress & Fisher, 1992), while retaining three to six sandwiches for each time point.

Six pre-eruption samples (recovery temperatures 1.9–6.5°C) that had been collected in 1998 after a 37-month deployment at the nearby site East Wall (9.8421° N, 104.2919° W, 2,506

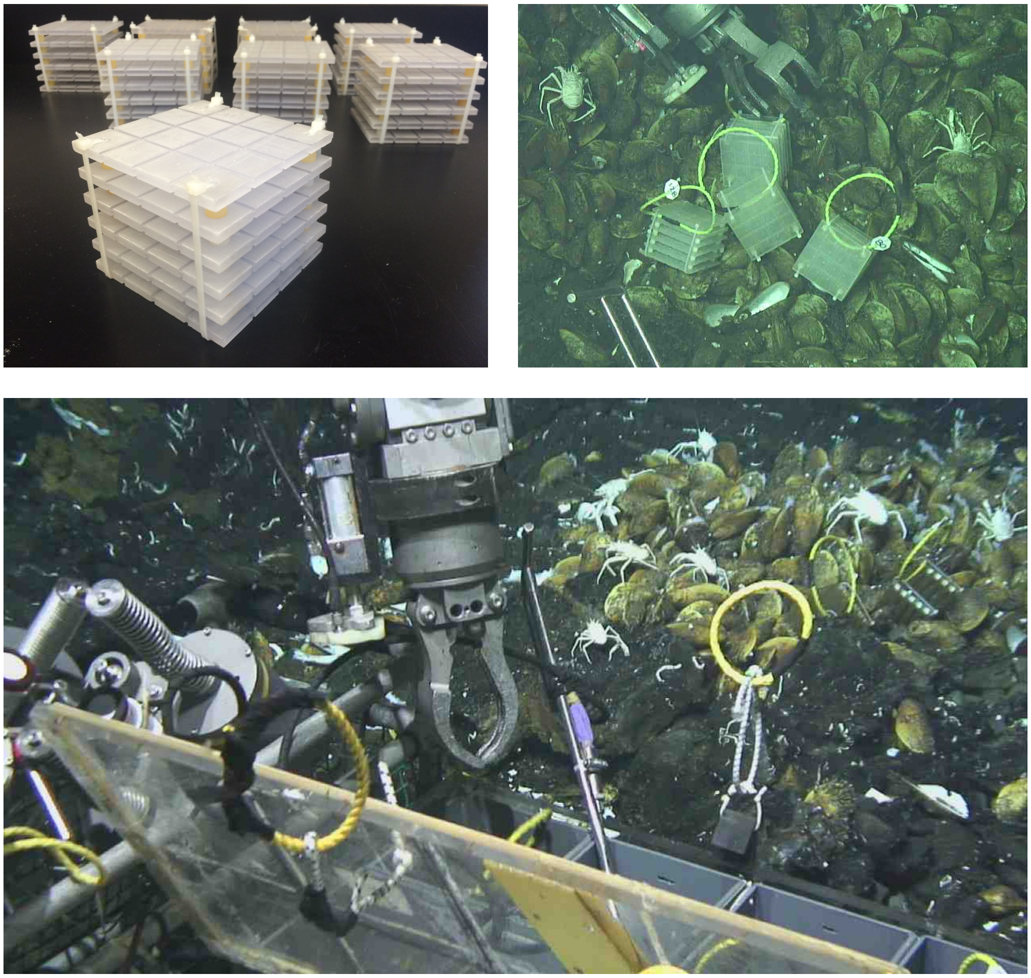


Figure 2-1: Deployment of "sandwich" colonization surfaces using the manipulator arm of DSV *Alvin* and a biobox. Each sandwich was constructed of six stacked 10 cm x 10 cm x 0.7 cm roughened Lexan sheets separated by 1 cm spacers. Counts of colonists on each Lexan sheet were pooled for data entry, so each sandwich constituted a single sample in analysis.

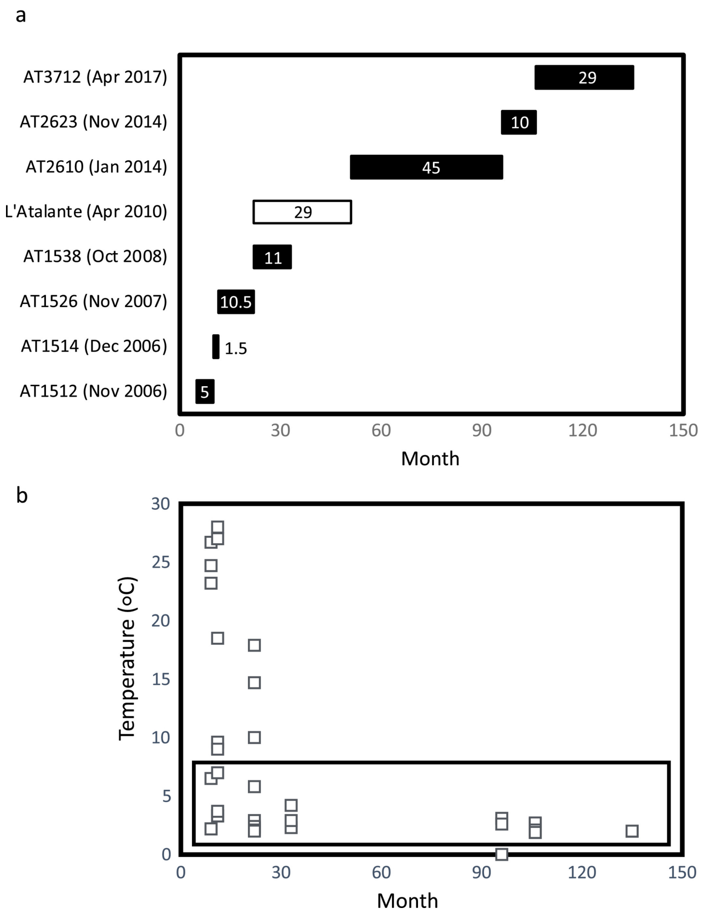


Figure 2-2: (a) Deployment durations of colonization sandwiches in months after the 2006 eruption, labeled by the *Atlantis* or *L'Atalante* recovery cruise. Numbers in the bars indicate deployment duration in months. No data were available for the *L'Atalante* cruise (white bar) as sandwiches were coated with ferrous precipitate. (b) The temperature measured at the base of each sandwich at the time of recovery. The 1.9–6.5°C subset of samples included in analysis are within the black box.

m depth) were also included in the analysis. These samples were basalt colonization blocks rather than sandwiches; however, previous analyses indicate that blocks and sandwiches collect similar colonists (Mullineaux et al., 2010). East Wall was the best available example of a mature community close to P-vent, though the fauna sampled at East Wall may not represent a traditional "climax community" because the site had experienced a prior eruption in 1991 (Shank et al., 1998), 85 months before the sampling.

Sandwiches and blocks were brought to the surface in separate, sealed collection compartments and preserved in 80% ethanol, along with any specimens that fell off in the collection compartments. For each sandwich or block, specimens were visually inspected under a dissecting microscope and identified morphologically to species or the lowest possible taxonomic level. Species-level identification of many juveniles was possible by comparing morphology to adults that retain larval characteristics (Adams et al., 2010). Individuals that were too young to identify to species were grouped by genus or family. For this reason, some individuals of a species might have been categorized differently depending on size (e.g., *Lepetodrilus elevatus* as *Lepetodrilus* spp., *Tevnia jerichonana* as siboglinids). This analysis includes metazoan invertebrates found on sandwiches or blocks, plus individuals found in the collection compartment that were retained on a 1 mm sieve. Counts of individuals per species or higher taxon for each of the 36 sandwiches or blocks used in this analysis (both pre- and post-eruption) are provided as electronic Supplementary File Data S1: CountsPerSpeciesPerSandwich_EPR.csv (Dykman et al., 2021a), and as part of the full sample set (Mullineaux, 2020). Colonist abundances were pooled across all sandwiches or blocks from each recovery date for subsequent analyses.

Of the 68 metazoan invertebrate species or morphotypes encountered, 58 had sufficient trait data to be included in this analysis. *Lepetodrilus* spp. and siboglinid spp. (formerly known as vestimentiferans) were too young to identify to species. These groups were retained because they were abundant in samples and have been identified as important participants in successional interactions (Shank et al., 1998; Mullineaux et al., 2009). Based on genetic sequencing of a subset of individuals, most individuals in the group *Lepetodrilus* spp. are likely *Lepetodrilus tevnianus*, and most individuals in the group siboglinid spp. are likely *Tevnia jerichonana* (Appendix A).

2.3.2 Biological traits

Eight traits were chosen to test our successional hypotheses and explore a range of ecological effects and responses (Table 2.1). Here, we define "trait" as a feature or behavior of a species that affects or responds to its environment, and "modality" as a scoring level reflecting how the organism expresses a given trait. Four traits were taken from the sFDvent Database: maximum adult body size, habitat complexity, trophic mode (i.e., trophic level), and relative adult mobility (Appendix B). Four additional traits were added due to their ecological relevance and common use in functional analyses for aquatic invertebrates. These are external protection, feeding method (i.e., how a species feeds), reproductive type, and larval development (Bolam et al., 2016; Greenfield et al., 2016; Veríssimo et al., 2017). For each trait, a modality was assigned for every species based on literature or personal observation. For the traits from sFDvent, modalities were assigned from the recommended data set, except in cases where we suggested updates. When species identity was uncertain and individuals were identified to a higher taxonomic level (e.g., amphipods), modalities were assigned from a likely species that is found at our site and included in sFDvent. For the four traits not included in sFDvent, we either provided a citation or cited "expert opinion," meaning the modality choice was based on direct observation by one of the co-authors. Although the majority of specimens in our study were juveniles, modality assignments were based on the characteristics of adult organisms due to the availability of data. Modality assignments were fixed for a given species rather than specific to life stages or individuals. For analysis, the abundance of a modality within a trait was taken as the total number of individuals expressing the modality. Modality assignments for each trait and species are available on the Woods Hole Open Access Server (WHOAS) repository at http://doi.org/10.26008/1912/bco-dmo.844993.1 (Dykman et al., 2021b).

2.3.3 Clustering species into functional guilds by similarity in trait modalities

Species were clustered into functional guilds based on the similarity of their modalities for all eight traits. The pairwise dissimilarity of species was calculated using the function gowdis in the R package FD (Laliberté et al. 2014; R version 4.0.3). We chose Gower dissimilarity because it accepts both numerical and categorical data and handles missing values (Gower, 1971). Podani's extension was implemented to include ordinal variables (Podani, 1999). Clusters were computed from the Gower dissimilarity matrix using the hclust function in the R package cluster (Maechler et al., 2019) and plotted as a dendrogram. The cutoff for assigning functional guilds was chosen by optimizing the tradeoff between minimizing within-group distance and maximizing between-group distance. Code for this and subsequent analysis is available online on Zenodo at http://doi.org/10.5281/zenodo.4625160 (Dykman, 2021).

Trait	**Trait type**	**Modality**	**Expected change over succession**
Maximum adult body size	ordered	small (∼1mm) medium (∼10mm) large (∼100mm) very large (∼1000mm)	Unlike in other systems, where early-successional species are generally small (Odum, 1969), large animals will colonize early at vents.
Habitat complexity	categorical	does not add complexity mat forming (<10cm) bed forming (>10cm) open bush forming dense bush forming	Unlike in other systems, where structure forms slowly (Tilman, 1985; Hirata, 1992; Teixidó et al., 2004), structure-forming species will colonize early at vents (Shank et al., 1998).
Trophic mode	ordered	symbiont bacterivore detritivore carnivore S (scavanger) carnivore O (other)	As in other systems, low trophic levels will be abundant in early succession, and a greater number of higher trophic levels will assemble over succession (Margalef, 1963; Odum, 1969; Boit & Gaedke, 2014). We expect the assembly of trophic diversity will progress rapidly at vents due to the high nutrient input.
Feeding method	categorical	non-feeding deposit feeder suspension feeder predator parasite or commensal	As in other systems, symbiont hosts and microbial mat grazers will colonize early when microbial production is highest, whereas suspension feeders, scavengers, parasites, and predators will colonize later. We expect this transition to occur rapidly at vents.
Relative adult mobility	ordered	sessile movement restricted crawler freely mobile	Greater mobility will be favored in late succession when venting flux is less vigorous and more diffuse.
External protection	ordered	soft bodied moderately protected well protected	As in other systems (Connell, 1961), animals will have more external protection in early succession, when environmental stressors are highest. Decreased stress and increased biogenic structure in late succession will facilitate soft bodied organisms.
Larval development	categorical	lecithotrophic planktotrophic brooding direct	As in other patchy, island-like systems, we expect species with limited dispersal potential (brooding and direct development), will not establish until later in succession (Tyler & Young, 1999).
Reproductive type	categorical	gonochoristic hermaphroditic asexual	As in other systems, we expect asexual organisms will be most abundant in early succession, as this is a strategy for rapid population growth (MacArthur & Wilson, 1967).

Table 2.1: The eight selected functional traits and their modalities, including expected change over succession.

2.3.4 Diversity indices

Diversity was calculated for both species and functional guilds using Hill number of order 1 (Hill, 1973), which is the exponential of the Shannon-Wiener index (Jost, 2006). We used this metric because it has an ecologically intuitive interpretation, accounts for varying sample size, and weighs species according to their abundance (Appendix C). For functional diversity, we calculated Rao's Quadratic Entropy (RaoQ), a commonly used index that considers both the relative abundance of species and the functional dissimilarity between species (Rao, 1980). RaoQ was calculated using the function dbFD in the R package FD (Laliberté et al., 2014). Trends in another commonly used metric returned by dbFD, functional richness (FRic), are qualitatively similar, and are provided for comparison with other studies (Appendix C).

2.3.5 Statistics

We used multinomial logistic regression to test the statistical significance of the change over time of both functional guilds and modalities within each trait. These analyses were carried out using the R package nnet (Ripley & Venables, 2011). Briefly, under this model, guild or modality counts are assumed to have a multinomial distribution, with the log of the ratio of the relative abundance of each guild or modality to the relative abundance of a baseline guild or modality being a function of time. To allow for non-monotonic trends in relative abundance, we took this function to be quadratic in time. The model was fit by maximum likelihood, and the significance of the fitted model was assessed by randomization. This involved repeatedly randomizing the samples while keeping the observation times fixed. The regression model was fit to the randomized data, and the P-value was taken as the proportion of 1,000 randomizations for which the randomized deviance was less than the observed deviance. We used randomization because it is insensitive to extra-multinomial variability due, for example, to dependence between individuals. The relationship between diversity indices and time was assessed by ordinary least squares regression with both time and its square as regressors. The significance of the fitted model was taken as the proportion of 1,000 randomizations for which the randomized R^2 value exceeded the observed R^2 value.

2.4 Results

2.4.1 Biological traits

For most traits, the composition of modalities changed over time, often trending toward, or overshooting, the pre-eruption state (Fig. 2-3). The species or taxonomic groups driving these trends typically were siboglinid tubeworms and limpets early in the time series, and a variety of worm and crustacean species toward the end. Counts of colonists collected from colonization surfaces are provided online in Data S1 (CountsPerSpeciesPerSandwich_EPR.csv) with Dykman et al. (2021a) and are a subset of Mullineaux (2020a) from the Woods Hole Open Access Server (WHOAS) repository at https://doi.org/10.26008/1912/bco-dmo.733173.2. Modality assignments for each functional trait are provided on the Woods Hole Open Access Server (WHOAS) repository at http://doi.org/10.26008/1912/bco-dmo.844993.1 (Dykman et al., 2021b).

For the trait "maximum adult body size," large organisms were most abundant both at 9 months and at 96 months or later post-eruption (Fig. 2-3a). The large organisms at 9 months were siboglinid tubeworms, whereas the large organisms at 96 months and later were other polychaetes including serpulid tubeworms and *Nicomache sp.*

In the trait "habitat complexity," bush-forming foundation species were abundant 9 months after the eruption (Fig. 2-3b) and were practically absent thereafter. Bed-forming animals peaked 22 months post-eruption, with the colonization of *Bathymodiolus thermophilus* mussels. Most organisms throughout the time series did not form structure.

In both of the feeding ecology traits, "trophic mode" and "feeding method," modalities changed markedly over time and trended toward the pre-eruption states. In the trait "trophic mode," symbiont hosts were abundant at 9 months, and bacterivores were abundant from 9 months to 33 months post-eruption. Organisms in higher trophic levels, such as detritivores and carnivores, increased over time and were dominant at 96 months and later (Fig. 2-3c). For the trait "feeding method," deposit feeders decreased in abundance around 33 months post-eruption, while suspension feeders such as serpulid species and the barnacle *Neolepas zevinae* became most abundant at 96 months and later (Fig. 2-3d). Carnivores such as the polychaetes *Archinome rosacea*, *Thermiphione risensis*, *Nereis* sp., and the snail *Phymorhynchus major* were similarly most prevalent 96 months post-eruption and later.

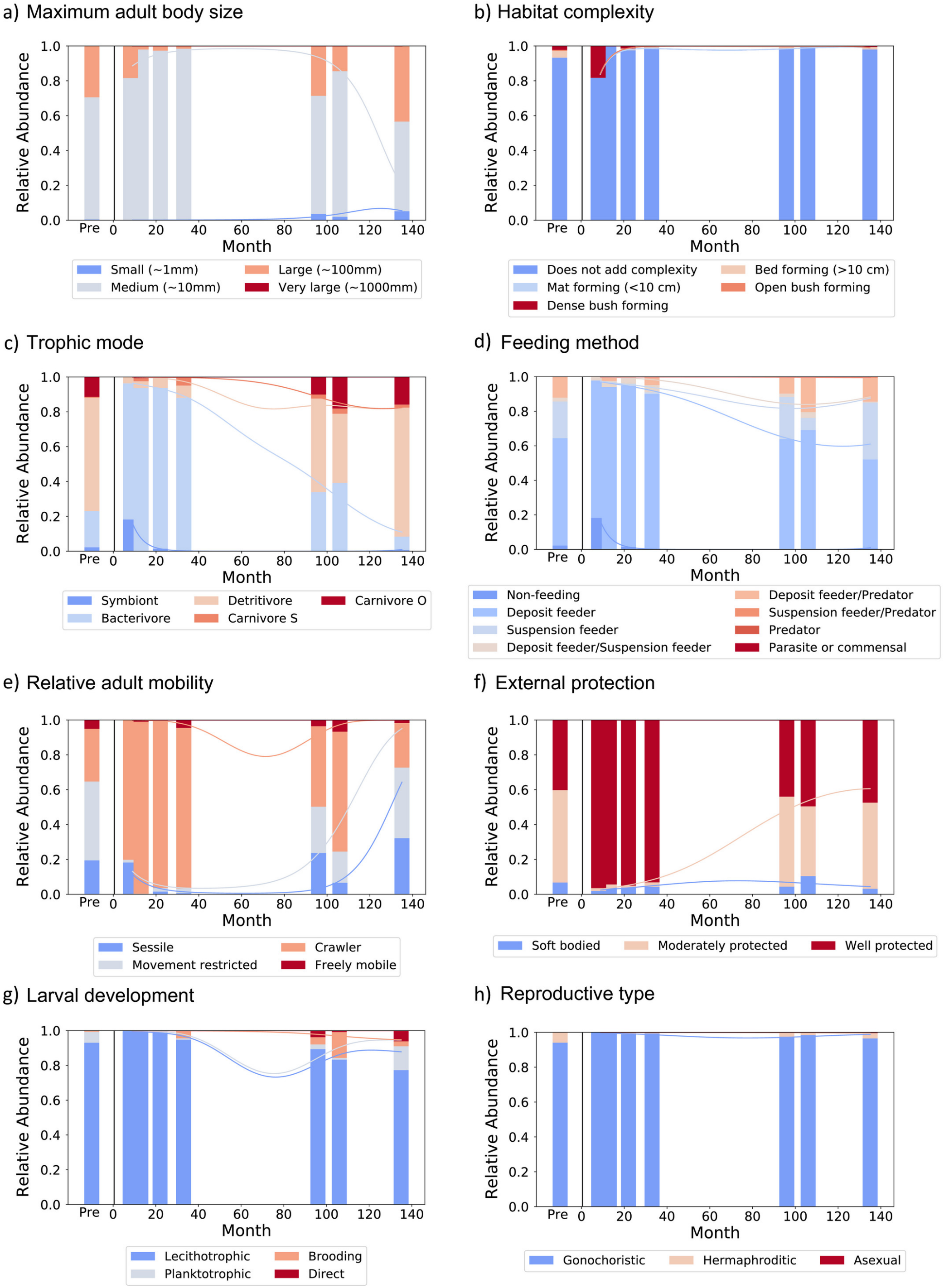


Figure 2-3: The relative abundance of modalities within the traits: (a) maximum adult body size, (b) habitat complexity, (c) trophic mode, (d) feeding method, (e) relative adult mobility, (f) external protection, (g) larval development, and (h) reproductive type. The x-axis shows time in months since the 2006 eruption, with pre-eruption samples plotted to the left of the black line. Best-fit lines were generated by multinomial logistic regression. P values calculated by randomization are provided in Appendix D.

In the trait "relative adult mobility," most organisms early in the time series were crawlers (Fig. 2-3e). Organisms with restricted movement, such as the polychaetes *Amphisamytha galapagensis*, *Nicomache* sp., and *Branchipolynoe* sp., as well as freely mobile organisms, such as amphipods, became more prominent at 96 months and later. Sessile organisms were present both early and late in the time series.

Regarding "external protection," well-protected organisms such as gastropods (i.e., *Lepetodrilus* spp.) and tubeworms were abundant in early samples, but decreased after 33 months (Fig. 2-3f). Moderately protected worms such as *Amphisamytha galapagensis* and *Archinome rosacea* increased in abundance over time, and soft-bodied organisms were most abundant in the middle of the time series.

Within the reproductive trait "larval development," lecithotrophic organisms were most abundant early in the time series and decreased over time, while planktotrophic and brooding development increased (Fig. 2-3g). There was little change in modalities within "reproductive type" (Fig. 2-3h). Of the eight traits tested for significant changes over time, only trophic mode (P = 0.003), feeding method (P = 0.031), and external protection (P = 0.010) showed significant trends under the quadratic model (Appendix D).

2.4.2 Functional guilds

The 58 species retained in our analysis were optimally clustered into 12 guilds (Table 2.2; Fig. 2-4). Guild I, which included large, structure-forming, non-feeding, symbiont-hosting tubeworms, was extremely abundant immediately after the eruption and declined within 33 months. Three guilds, A, B, and F, peaked at 22 months. Guild A included 21 deposit-feeding, crawling bacterivore species; Guild B included deposit feeders and suspension feeders, some of which formed structure; and Guild F included suspension feeders with restricted movement, hermaphroditic reproduction, and planktotrophic larvae. Guilds E, G, and J increased over time. Guild E included moderately protected, mobile scavengers and carnivores; Guild G included sessile or restricted-movement suspension feeders and commensals; and Guild J included well-protected, brooding crustaceans. Time since the eruption was a significant predictor of guild composition (P = 0.029) (Appendix D), which transitioned over time toward the pre-eruption state at 96 months and continued to change thereafter (Fig.2-4b).

Guild	**n**	**Representative Species**	**Modalities**
A	2*	aplacophoran	Small (∼1mm); Moderately protected; Crawler; Does not add complexity; Bacterivore; Deposit feeder; Lecithotrophic; Hermaphroditic
B	21*	*Lepetodrilus tevnianus*	Medium (∼10mm); Well protected; Crawler; Does not add complexity; Bacterivore; Deposit feeder; Lecithotrophic; Gonochoristic
C	4	*Ophryotrocha akessoni*	Medium (∼10mm); Soft bodied; Crawler; Does not add complexity; Detritivore; Deposit feeder/Suspension feeder; Lecithotrophic
D	3*	ophiuroids	Large (∼100mm); Well protected; Crawler; Does not add complexity; Carnivore S; Deposit feeder; Planktotrophic
E	12*	*Archinome rosacea*	Medium (∼10mm); Moderately protected; Crawler; Does not add complexity; Carnivore O; Deposit feeder/Predator; Gonochoristic
F	2	*Bathymodiolus thermophilus*	Large (∼100mm); Well protected; Movement restricted; Bed forming (>10 cm); Detritivore; Suspension feeder; Planktotrophic; Hermaphroditic
G	3*	Serpulid spp.	Large (∼100mm); Well protected; Sessile; Does not add complexity; Detritivore; Suspension feeder
H	2*	*Bythograea thermydron*	Large (∼100mm); Well protected; Freely mobile; Does not add complexity; Carnivore S; Predator; Planktotrophic; Gonochoristic
I	3*	*Tevnia jerichonana*	Large (∼100mm); Well protected; Sessile; Dense bush forming; Symbiont; Non-feeding; Lecithotrophic; Gonochoristic
J	2*	isopods	Medium (∼10mm); Well protected; Crawler; Does not add complexity; Detritivore; Deposit feeder; Brooding; Gonochoristic
K	2*	mites	Small (∼1mm); Moderately protected; Crawler; Does not add complexity; Carnivore O; Deposit feeder; Direct; Gonochoristic
L	2*	anemone	Large (∼100mm); Soft bodied; Sessile; Does not add complexity; Carnivore O; Suspension feeder/Predator; Planktotrophic; Asexual

Table 2.2: Functional groups defined by hierarchical clustering. For each guild, a representative species and its modality assignments are shown, along with the number of species in the guild (n). An asterisk symbolizes that the guild contains at least one group identified at a higher taxonomic level than species, and potentially contains multiple species (e.g., *Lepetodrilus* spp., siboglinid spp.).

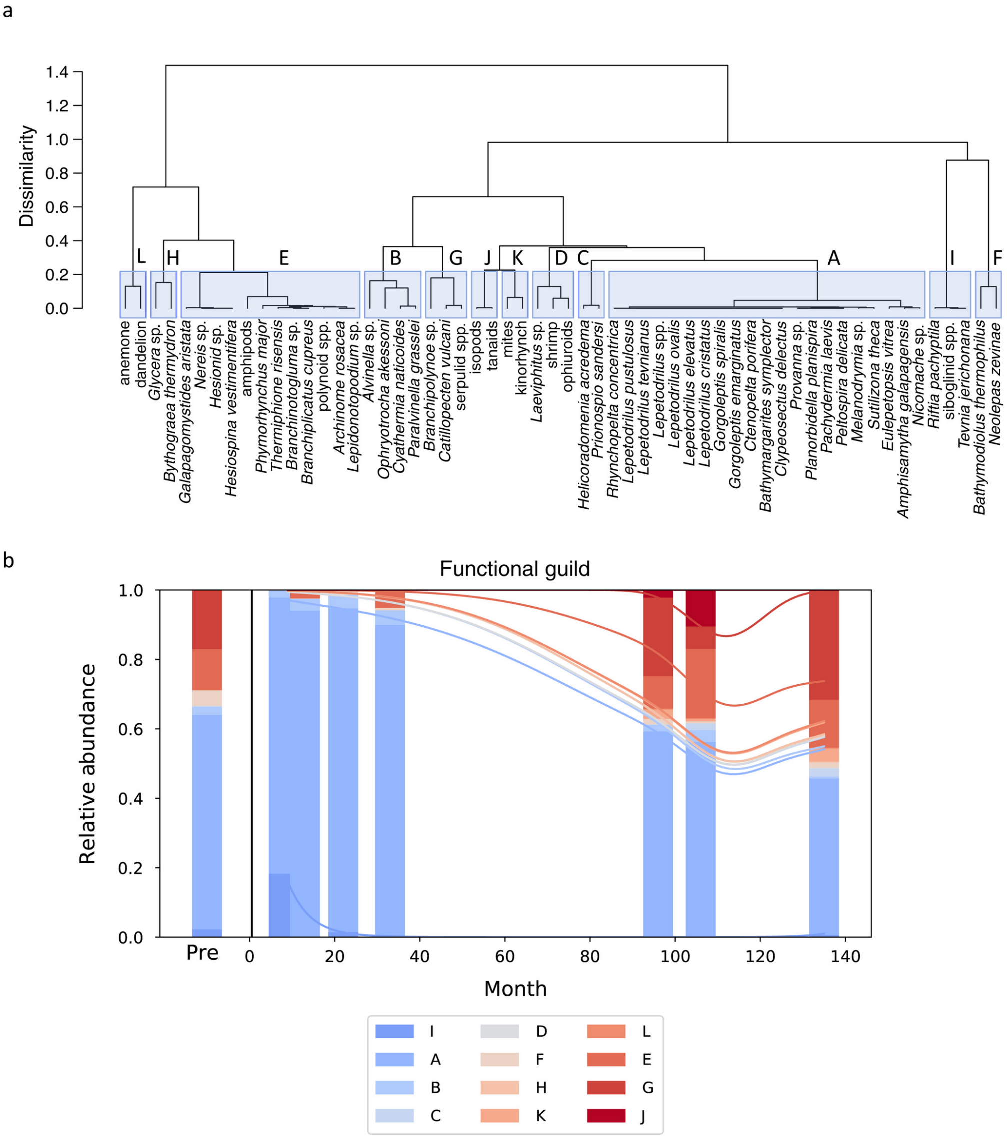


Figure 2-4: (a) A dendrogram of species dissimilarity based on modality assignments for the eight functional traits. The dendrogram was generated by hierarchical clustering using Gower dissimilarity. The y-axis represents dissimilarity between species. (b) The relative abundance of functional guilds in each sample over time, with pre-eruption data shown to the left of the black line. Note that the 96-month sample is similar in composition to the pre-eruption sample, which was collected 85 months after a prior eruption. Best-fit lines were calculated by multinomial logistic regression.

2.4.3 Diversity indices

Both species and guild diversity increased significantly over time (R^2 = 0.78, P = 0.049 for species; R^2 = 0.95, P = 0.009 for guild) and eventually exceeded pre-eruption levels (Fig. 2-5). While species diversity reached pre-eruption levels around 60 months and attained a maxi-

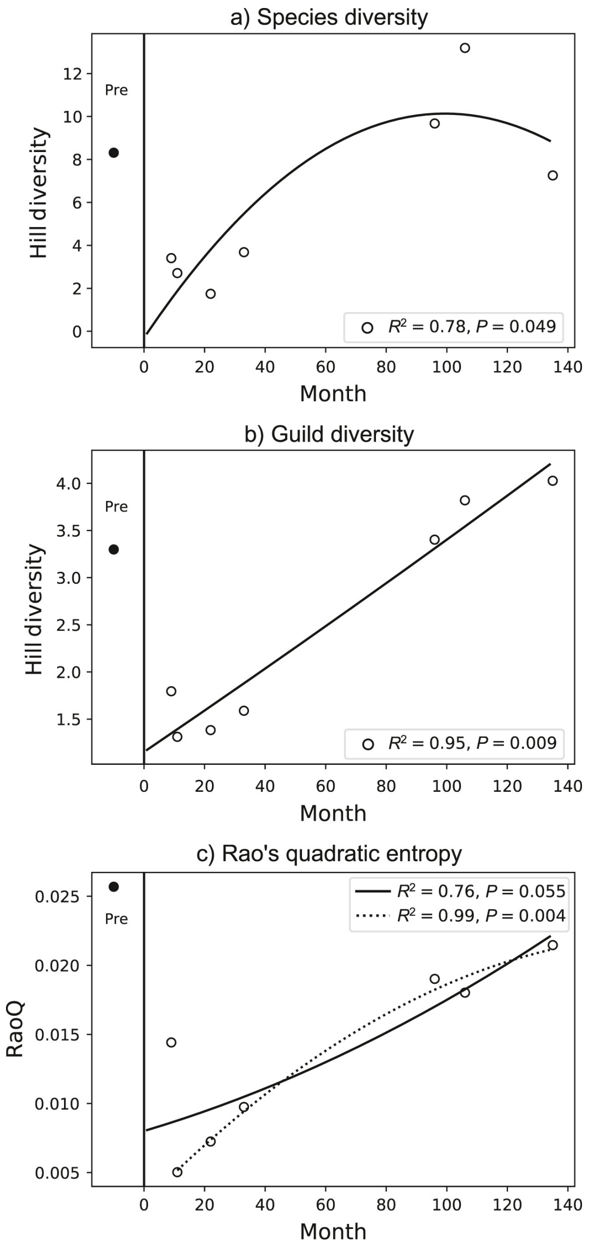


Figure 2-5: Changes in diversity over time: (a) Hill diversity (order 1) for species, (b) Hill diversity (order 1) for guilds, and (c) Rao's quadratic entropy. For all panels, pre-eruption data are plotted to the left of the black line. Best-fit lines were calculated by fitting a quadratic model. In panel c, fit lines are shown both including (solid line) and excluding (dotted line) the outlier at 9 months. P values calculated by randomization are shown in the legend.

mum inflection point around 100 months, guild diversity continued to increase steadily until the final sample at 135 months. RaoQ increased more gradually and had not returned to pre-eruption levels by the end of the time series, although this trend was not statistically significant (R2 = 0.76, P = 0.055) (Fig. 2-5c). The sample at 9 months was an outlier with a high RaoQ compared to the other samples early in the time series, suggesting a rapid, yet temporary, return of functional diversity. When excluding the outlier at 9 months, RaoQ had a significant quadratic relationship with time (R2 = 0.99, P = 0.004) and was beginning to reach an asymptote below the pre-eruption level by the end of the time series.

2.5 Discussion

2.5.1 Testing trait-based successional theories in deep-sea hydrothermal vent ecosystems

Our functional analysis indicates that invertebrate communities at frequently disturbed hydrothermal vents show primary successional patterns that differ from other systems in several key ways. Importantly, the succession of function at vents differs from theory when considering traits related to size, growth, and provision of habitat (foundation species). These patterns are likely consequences of the venting flux associated with volcanic disturbance, which provides nutrients in the form of reduced sulfur that fuels the chemosynthetic-based food web in early stages of succession.

Theory and observation in a range of ecosystems suggest early successional species are often small, due to the harsh abiotic conditions and low nutrient availability after disturbance (MacArthur & Wilson, 1967; Thornton, 2007), while large species establish later, grow slowly, and gradually build habitat structure that supports many other species (Tilman, 1988; Hirata, 1992; Teixidó et al., 2004). Our analysis indicates vent ecosystems represent an exception. Large species, primarily siboglinid tubeworms, were among the earliest colonists. Siboglinids are the largest invertebrates sampled in our time series (0.35 m for *Tevnia jerichonana*; Desbruyères et al. 2006), and they are known for their high growth rates (Lutz et al., 1994) and their role in building dense, bushy habitat structure that supports many species (Govenar & Fisher, 2007). Siboglinids rely entirely on chemosynthetic endosymbiotic bacteria that use reduced sulfur to fix carbon, and accordingly their arrival corresponded with the vigorous venting following the eruption. They were gradually replaced by serpulid tubeworms (which suspension feed) over succession, which suggests the changing chemical environment of the vent field or other transitions in food supply may have driven the dramatic and rapid decrease in large-bodied foundation species early in succession.

Despite the unusually high nutrient input in early succession at vents, the observed changes in feeding traits were consistent with established theory. As in other successional systems (Margalef, 1963; Odum, 1969; Boit & Gaedke, 2014), patterns in feeding traits indicate a transition from high primary productivity and low food web complexity, toward greater food web complexity, more trophic levels, and a greater range of feeding strategies. Although we expected trophic diversity to recover rapidly at vents due to the high nutrient input in early succession, scavengers, carnivores, and suspension feeders only became prominent after 96 months. This indicates that the food web at vents takes longer to recover than expected, which has implications for the persistence of high-trophic-level species in frequently disturbed ecosystems. Prolonged recovery in feeding traits may arise because the patchy nature of vents poses dispersal challenges to some species, and because predators require the prior arrival of prey.

The significant decrease in well-protected organisms (e.g., animals with shells and tubes) late in the time series is consistent with the expectation that external protection allows vent organisms to endure the harsh thermal and chemical conditions in early succession, and thus take advantage of the rich nutritional environment associated with disturbance. Predation is another factor that could influence changes in external protection. We observed predators to increase as succession progressed, which might be expected to result in the elimination of prey that lack external protection. However, highly mobile predators such as crabs are reported to immigrate soon after disturbance (Shank et al., 1998) and may have been important transient scavengers in the vent field in early stages of succession. These wide-ranging adult predators would not have been captured by our sampling methods and might have been responsible for the scarcity of soft-bodied organisms in early succession.

As observed in other patchy, island-like systems (MacArthur & Wilson, 1967; Tsuyuzaki & Del Moral, 1995; Thornton, 2007), we expected vent organisms with brooding and direct development (i.e., no planktonic dispersal stage) to arrive later in the time series due to their limited dispersal potential (Tyler & Young, 1999). According to expectation, vent animals with low dispersal potential were indeed most abundant at the end of the time series. Successional theory also suggests early colonizers are small and rapidly reproducing (i.e., “r-selected” species;

MacArthur & Wilson 1967) in addition to being good dispersers. Contrary to this expectation, unicellular protozoans (ciliates and foraminiferans), which might be considered classic early successional species, typically are not found in the early years of vent succession (Mullineaux et al., 2020). It is likely that the patchy distribution of vent habitat makes dispersal a dominant factor in successional outcomes compared to systems that are less island-like. In our case, species with classic early successional traits (i.e., small body size, asexual reproduction) may not have arrived because they lacked a long-duration planktonic dispersal stage. However, a few individuals of species with benthic and brooding development (amphipods and kinorhynchs) were present in the earliest sample. Since the nearest undisturbed site after the 2006 eruption was 6 km away, this implies that even invertebrates with dispersal limitations have the potential to travel this far within 9 months.

2.5.2 Information from functional diversity indices on processes and timescales of recovery

We tracked two functional diversity metrics over time to see whether they provide additional information on processes and timescales of recovery compared to species diversity indices (Cadotte et al., 2011). Greater functional diversity means a community has a wider range of responses to perturbation and an enhanced ability to maintain structure and stability (Carr et al., 2018). Functional diversity indices are also powerful for their ability to highlight species that disproportionately enhance ecosystem functioning. For example, the relatively high RaoQ in the 9-month sample was largely due to the functional dissimilarity between the groups *Lepetodrilus* spp. and siboglinid spp. (Fig. 2-4a), which were abundant at that time. This demonstrates the colonization of species with distinctive functional roles can facilitate a rapid, albeit transient, recovery of functional diversity in early succession. Most significantly, our study shows that both guild diversity and Rao's quadratic entropy continue to increase 11 yr after catastrophic disturbance, even as species diversity was no longer increasing. This indicates that function at vents may take longer to recover than species diversity and motivates the use of alternate metrics to species diversity when assessing resilience. Moreover, our study shows that species and guild diversity increased beyond our pre-disturbance sample, which indicates the pre-disturbance sample did not represent a maximum assemblage of functions. This finding, along with a similar result for species diversity in a broader set of samples over the same time frame (Mullineaux et al., 2020), reinforces the importance of properly interpreting "baselines" in frequently disturbed systems.

2.5.3 Applications to vent ecology and conservation

Long-term functional analysis leads to several important insights regarding recovery and succession following volcanic disturbance at deep-sea hydrothermal vents. First, eruptions open space for developing communities with distinct trait modalities and functional guilds, and their composition changes markedly over succession. In this conceptual framework, eruptions support a large regional pool of functions by maintaining a patchwork of vents at different stages of succession. Second, functional diversity follows different temporal patterns than species diversity, and takes longer to recover. As in other systems, it is possible that diversity in the EPR community will decline beyond our time series after reaching a peak (Connell, 1978), in which case decadal volcanic disturbance at the EPR may play a role in maintaining high species and functional diversity. Finally, there was striking similarity in trait and guild composition between the pre-eruption sample, collected 85 months after the 1991 eruption, and the samples collected 96 months after the 2006 eruption. This is a compelling indication of predictable, repeating patterns in the recovery of function over succession at this vent field. These insights motivate the expansion of long-term monitoring programs to test trait-based hypotheses later in succession and at hydrothermal regions with different species and conditions.

Several features of our sampling protocol limit resolution on successional processes. Colonization surfaces were deployed in series for short intervals, which did not allow a mature community to develop on any given sandwich or block. This means our sampling regime did not capture the interspecific interactions that influence succession when space is limited. Sandwiches were also deployed for variable times, which means the community on the surfaces were at various stages of maturity at recovery. However, there was always open space on recovered sandwiches, even those deployed for years, so we do not expect deployment duration led to significant exclusion of colonists. The timing of spawning events and stochastic larval supply determine the composition of settlers to some extent in all colonization experiments (Sutherland & Karlson, 1977; Underwood & Chapman, 2006). Because many vent invertebrates spawn continuously or asynchronously (Tyler & Young, 1999), and because most sandwiches were deployed for more than a year, we expect this reduced the influence of large random recruitment events on results. Sandwiches also undersample animals with certain modalities, such as highly mobile species or large adults. As in all functional analyses, the traits used in this study may have failed to capture all subtleties in niches. Trait information for most deep-sea species remains incomplete or low in certainty. In our case, we expect taxonomic uncertainty for species within the major abundant groups that drove patterns (e.g., siboglinid spp. and *Lepetodrilus* spp.) did not lead to uncertainty in functional interpretations because modalities for these species were well-described, and species within each group tended to have similar modalities for the traits we examined. We expect our analysis can be updated as trait and taxonomic data become more refined.

An understanding of recovery processes in deep-sea ecosystems has increasing practical application due to the development of seabed mining. In order to predict how endemic vent fauna will respond to anthropogenic disturbance, the patterns and drivers of succession after natural disturbance must first be understood (Boschen et al., 2013). Our data indicate modalities related to high community productivity, such as large body size, symbiont-hosting, and structure-forming were particularly abundant directly after the eruption. Mining at deep-sea vents differs from natural disturbance by imposing direct damage, seabed alteration, and sediment plumes (Van Dover, 2014) without necessarily promoting new venting. Thus, recovery from anthropogenic disturbance will likely depend on the timing and location of mining disturbance in the vent field and whether mining stimulates new venting. The combination of long-term colonization data and functional traits is an important advance for assessing resilience and developing successional theory that allows comparison between ecosystems. Frequent disturbance, atypical stress and nutrient conditions, and unique resident fauna make hydrothermal vents a compelling new system in which to expand successional research and broaden existing theory.

2.6 Acknowledgements

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2.7 Co-Authors and Prior Publication

This chapter was previously published in *Ecology* by Wiley Periodicals LLC on behalf of Ecological Society of America. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Dykman, L. N., Beaulieu, S. E., Mills, S. W., Solow, A. R., & Mullineaux, L. S. (2021). Functional traits provide new insight into recovery and succession at deep-sea hydrothermal vents. Ecology, 102(8), e03418.

2.8 Data Availability

Dates and locations of colonization sampler deployments and recoveries (Mullineaux 2020b) are available from the Woods Hole Open Access Server (WHOAS) repository at https://doi.org/10.26008/1912/bco-dmo.733210.3. Counts of colonists collected from colonization surfaces are provided online in Data S1 (CountsPerSpeciesPerSandwich_EPR.csv) with Dykman et al. (2021a) and are a subset of Mullineaux (2020a) from the Woods Hole Open Access Server (WHOAS) repository at https://doi.org/10.26008/1912/bco-dmo.733173.2. Modality assignments for each functional trait are provided online in Data S1: ModalitiesPerTraitPerSpecies_EPR.csv in Dykman et al. (2021a) and in Dykman et al. (2021) on the Woods Hole Open Access Server (WHOAS) repository at http://doi.org/10.26008/1912/bco-dmo.844993.1. Scripts used for this analysis are provided on Zenodo at http://doi.org/10.5281/zenodo.4625160 (Dykman, 2021).

Chapter 3

Parasite diversity in an isolated, disturbed marine ecosystem

3.1 Abstract

Habitat isolation and disturbance are important regulators of biodiversity, yet it remains unclear how these environmental features drive differences in parasites diversity between ecosystems. We tested whether the biological communities at deep sea hydrothermal vents have reduced parasite diversity compared to less isolated and less disturbed habitats, and whether these habitat features favor parasite taxa with direct life cycles. We surveyed the parasite fauna of the biological community at the 9°50'N hydrothermal vent field on the East Pacific Rise and compared it to similar data sets from a well-connected ecosystem (Santa Barbara kelp forests) and an isolated, undisturbed ecosystem (Palmyra Atoll lagoon sandflats). Parasite richness within host species did not differ significantly between ecosystems, though it broadly followed the expected trend, being highest in the well-connected system, intermediate in the isolated undisturbed system, and lowest in the isolated disturbed system (vents). Total parasite richness in the vent community was limited by the low number of fish species and short food chains. Parasites with indirect life cycles (ILCs) had a greater species richness at vents than expected due to a high richness of trematodes, while other ILC parasite taxa were scarce (nematodes) or absent (cestodes). These results demonstrate the ubiquity of parasites, even in an extreme environment, and point towards different responses between taxa to disturbance.

3.2 Introduction

Parasites are now recognized as a dominant component of global biodiversity (De Meeûs & Renaud, 2002; Dobson et al., 2008) and an important consumer group that can have a keystone influence on ecosystems (Hatcher et al., 2014). They modify the survival, phenology, and behavior of individual hosts (Miura et al., 2006; Bates et al., 2010), alter the demographics and distribution of host populations (Lafferty, 1993), influence the composition, structure, and function of biological communities (Mouritsen & Poulin, 2005; Grewell, 2008; Kuris et al., 2008), and drive host evolution (Auld et al., 2016). Increasing evidence suggests that ecosystems without parasites would function entirely differently (Wood & Johnson, 2015; Morton & Silliman, 2020).

Ecosystem features, such as disturbance and habitat isolation, can drive parasite diversity. Parasites may be more tightly bounded by geographic constraints than their hosts because the critical steps of dispersal and colonization rely on the right hosts being available at the right time. For example, parasites sometimes lag behind their hosts during range expansions (Phillips et al., 2010; Hopper et al., 2014) or are left behind during species introductions (Brown & Wilson, 1975; Torchin et al., 2003; Blakeslee et al., 2013). In remote, island-like habitats, where species must colonize from afar, parasites may not arrive with initial founder host individuals (Lopes et al., 2018) or may not be able to establish until hosts reach a threshold population size (MacLeod et al., 2010). Theory suggests island-like habitats may filter for certain types of parasites based on their life histories (Bataille et al., 2018). For example, parasites with indirect (multiple-host) life cycles (ILC) may be slower to invade or establish in isolated habitats than parasites with direct (one-host) life cycles (DLC) because they require multiple, sometimes obligate, host species to first establish and reach threshold densities (Dobson & May, 1986). A decreased diversity of ILC parasites has also been observed after disturbances that alter host diversity and abundance (Dunn et al., 2009), such as the removal of top predators by fishing (Wood et al., 2014). Conversely, the diversity of ILC parasites has been shown to increase with host diversity after habitat restoration (Huspeni & Lafferty, 2004; Moore et al., 2020).

Deep-sea hydrothermal vents are island-like, ephemeral habitats, making them a compelling system in which to study the impact of isolation and disturbance on parasite diversity. The geothermal activity that fuels vent communities is patchily distributed, resulting in small habitat areas which support discrete populations connected by dispersal (Mullineaux et al., 2018). Venting activity can be dynamic, with relatively short-lived habitat patches compared to other island systems (Whittaker et al., 2009). On fast-spreading plate boundaries such as the East Pacific Rise (EPR), large volcanic disturbances appear to occur on decadal time scales (Rubin et al., 2012) and eradicate animal life over several square kilometers (Shank et al., 1998; Wu et al., 2022). This requires the entire community to assemble anew by recolonization from surrounding undisturbed sites, a process which may continue for decades (Mullineaux et al., 2020; Dykman et al., 2021a). The island-like nature of vent habitat poses dispersal and colonization challenges for all vent life, but is likely to be particularly difficult for parasites due to their reliance on hosts. If parasites lag behind hosts in colonization and establishment, certain parasite species may be slow to establish or fail to persist in vent metacommunities where habitat patches are frequently disturbed or far apart.

Features of the biological communities at vents may further limit the colonization, establishment, or persistence of parasite species. First, vent communities are characterized by a relatively low richness of free-living species (Van Dover, 2000). This limits opportunities for parasite introductions into vent ecosystems with founder host species and constrains the niches into which parasites can radiate once established. Second, vent communities have relatively simple food webs and a low number of vertebrate predator species (Voight, 2000). Most parasite species with indirect life cycles have one or more life stages that are passed up food chains when one host consumes another. Many ILC parasite taxa, including acanthocephalans, cestodes, nematodes, and some trematodes, transmit through multiple fish species, living as encysted intermediate life stages (cystacanths, metacestodes, larvae, and metaercariae, respectively) in prey fish hosts, and maturing as sexually reproducing adults in the definitive host (a vertebrate predator). The low vertebrate diversity at vents is expected to constrain the diversity of parasites with indirect life cycles by prohibiting parasite species that require multiple vertebrate hosts from completing their life cycles.

Consistent with the expectation that features of vent ecosystems may limit parasite diversity, few parasite species have been reported from vents. The most recent review of metazoan vent parasites worldwide (De Buron & Morand, 2004) included only seven described species and three unpublished accounts. Since this review, an additional five copepods, five trematodes, one monogenean, one nematode, and one isopod have been reported in published literature (Thesis Chapter 1, Fig. 1-5) (Dykman, 2022b). The rate of less than one new parasite species per year is remarkably low compared to the over 700 new free-living species (~ 42 species per year) described since the discovery of animal life at vents in 1977 (Chapman et al., 2019).

Although isolation, disturbance, or simple food webs might limit parasite diversity at vents, the scarcity of reported vent parasites may simply be due to low research effort. Relatively few studies have sampled for parasites from a host population in deep benthic ecosystems (Campbell et al., 1980; Powell et al., 1999; Ward et al., 2004), even fewer from a host population at vents or seeps (Terlizzi et al., 2004; Tunnicliffe et al., 2008), and none from a comprehensive range of host taxa from a single vent community. Without quantitative, community-level data, it remains impossible to test whether parasite diversity is truly reduced at vents or to draw any meaningful conclusion about factors driving parasite diversity in vent ecosystems.

We quantitatively sampled the biological community at the 9°50'N hydrothermal vent field on the East Pacific Rise (EPR 9N) to investigate the drivers of parasite diversity at vents. Its location on a fast-spreading plate boundary that experiences large-scale eruptive disturbance every 10-20 years (Rubin et al., 2012) allows us to examine how features of parasite diversity differ in an extreme, island-like, and disturbed environment. We compare the vent data to coastal marine benthic ecosystems that differ in their degree of disturbance and isolation, and for which parasitological data were collected using similar methods: kelp forests on the coast of Santa Barbara, California, USA (Morton et al., 2021) and the lagoon sandflat of Palmyra Atoll in the Line Islands Archipelago (Vidal-Martínez et al., 2012, 2017; McLaughlin, 2018; González-Solís et al., 2019; Soler-Jiménez et al., 2019).

We use these data to first test the hypothesis that parasite richness will be lowest in island-like, disturbed habitat (vents), intermediate in isolated, undisturbed habitat (atoll lagoon sandflats), and highest in well-connected, moderately disturbed habitats (kelp forests). Second, we ask whether there are relatively more parasite species with direct (one host) life cycles than indirect (multi-host) life cycles at vents due to the additional challenges multi-host parasites must overcome to establish and persist. Finally, we test whether the vertebrate top predators at vents (fish) have a lower variety of intermediate parasite life stages to explore whether simple food webs may limit the trophic pathways that ILC parasites use to complete their life cycles.

3.3 Methods

3.3.1 Biological collections

Animals were collected from deep-sea hydrothermal vent sites at the East Pacific Rise 9°50'N vent field (EPR 9N) during two cruises, one in December of 2019 (AT42-21) using HOV *Alvin* and one in March of 2021 (RR2102) using ROV *Jason*. In this region, "vent sites" are discrete areas of warm-water outflow. Faunal communities within a vent site usually extend ~100 meters around a central venting orifice (Levin et al., 2016). Individual vent sites are separated by tens to hundreds of meters of bare basalt characterized by relatively low faunal biomass and species composition more similar to the ambient seabed than an active vent community (Levin et al., 2016). Samples were collected 13-15 years after a massive seafloor eruption in 2006 paved over vent sites at the EPR 9N vent field (Tolstoy et al., 2006; Wu et al., 2022), after which their biological communities had to completely reestablish (Mullineaux et al., 2010).

We collected potential hosts from 12 vent sites including nine in the EPR 9N vent field proper (Bio-vent, M Vent, Zeta Garden, Teddy Bear, Crab Spa, Tica Vent, Riftia Mound, P Vent, East Wall) and two ~7 km further south (V Vent and L Vent) (Appendix E). We sampled hosts from a range of thermal zones (Micheli et al., 2002) and substrate types, including basalt and active sulfide chimneys, to capture the range of primary potential host species in the ecosystem, and to increase the chance of encountering parasite species that are patchily distributed in host populations. Large tubeworms and mussels were collected into sealed, insulated bioboxes using the manipulator of the HOV or ROV. Mobile hosts such as fish, crabs, and squat lobsters were collected using suction samplers or box-style crayfish traps baited with tubeworm and mussel tissue and left overnight on the seafloor. Small crustaceans, mollusks, and polychaetes were gathered opportunistically from geological samples or directly targeted with suction sampling or grabs.

3.3.2 Dissections

Potential hosts were dissected fresh aboard the ship or frozen at -80°C immediately after arrival at the surface. Dissections followed standard methods for detecting metazoan parasites (Kuris et al., 2008; McLaughlin, 2018; Morton et al., 2021) (Appendix F). Briefly, all tissue of each host was thoroughly examined by squashing between two glass plates and examining under a dissecting scope illuminated by transmitted light. Metazoan parasites were assigned a species or morphogroup name and counted. Expert taxonomists were consulted to assure morphogroups were distinct to a species level. If there was uncertainty as to whether a symbiont was parasitic, we determined parasitic status based on three criteria: the symbiont must be 1) found living in close association with a potential host and not elsewhere, 2) have specialized morphology for feeding or attachment, and 3) be embedded within host tissues and have evidence of feeding on host tissues. All dissection data for the EPR 9N vent field fauna are available on BCO-DMO at https://www.bco-dmo.org/dataset/879118 (Dykman et al., 2022).

3.3.3 Comparison data sets and parasite life cycle assignments

We compared the vent data to similar dissection data sets from two other marine benthic ecosystems: kelp forests on the coast of Santa Barbara, California (Morton et al., 2021) and the intertidal lagoon sandflats of Palmyra Atoll, Line Islands Archipelago (Vidal-Martínez et al., 2012, 2017; McLaughlin, 2018; González-Solís et al., 2019; Soler-Jiménez et al., 2019) (Fig. 3-1). These ecosystems differ from EPR 9N vents in their combination of disturbance regimes, isolation, and the richness of their free-living fauna (Table 3.1). Collectors and dissectors for all three data sets were trained in the same lab group and followed similar protocols. In all data sets, specimens were collected haphazardly over several years at a range of collection sites, often targeting the numerically or functionally dominant free-living species in the system. In the Palmyra Atoll sandflats and Santa Barbara kelp forest data sets, some hosts were collected as part of standardized density surveys. All three studies were designed to be unbiased regarding host species expected to have more or fewer parasites.

The three data sets were filtered following a consistent protocol to facilitate comparison (Appendix F). Only host species with a sample size of ten or more individuals were included in analyses to assure a decent sample size of each host species while retaining at least two species in each ecosystem and host group. We focused on four host taxonomic groups: crustaceans, fishes, mollusks, and polychaetes. For the vent fishes *Thermarces cerberus* and *Thermichthys hollisi* we were only able to collect nine and two fresh individuals, respectively. To increase sample size, we supplemented our collections with specimens collected from the same sites during prior cruises: two whole frozen *T. cerberus* collected in April of 2017 during cruise AT37-12 (dive A4897); and preserved gut contents of 22 *T. hollisi* collected in February of 2007 during cruise AT15-15 (dive A4317) (Buckman, 2009). This study includes metazoan parasites, omitting microbial pathologies and symbionts that are not parasitic. We adopt the "consumer strategy" definition of a parasite as an organism that feeds on only one individual resource at a single life stage (Lafferty & Kuris, 2002). The metazoan parasite groups included in analysis were Acanthocephala, Cestoda, Copepoda, Isopoda, Monogenea, Nematoda, Rhizocephala, and Trematoda. Each parasite species or morphogroup retained for comparative analyses was categorized as having a direct (single-host) or indirect (multi-host) life cycle based on direct observation or published literature (Appendix F). Life cycle assignments and citations are available in BCO-DMO at https://www.bco-dmo.org/dataset/879253 (Dykman, 2022a). Scripts for merging the three data sets and performing the analyses in this study are available in GitHub https://github.com/ldykman/VENT_PARASITES_EPR.

3.3.4 Comparing parasite richness at vents to other marine ecosystems

We examined two components of parasite species richness to test whether parasite diversity is low at deep-sea hydrothermal vents compared to other ecosystems. The first component, parasite richness within host species, examines whether a free-living species at vents will, on average, host fewer parasite species than a free-living species in the other two ecosystems. Here, we apply an *ad hoc* approach to test the null hypothesis H_0 that parasite richness within host groups is the same in the three ecosystems against the alternative hypothesis H_1 that parasite richness within host groups follows the ordering kelp forest > atoll sandflat > vent, suggested by biogeography theory. To account for the dependence of observed parasite rich-

	Kelp forest	Atoll sandflat	Vent
ECOSYSTEM FEATURES			
Isolation	Well-connected to kelp forests along the coast and adjacent habitat (Morton et al., 2021).	Extremely isolated, nearest sandflat 376 km away on Kiritimati Atoll (McLaughlin, 2018).	Extremely isolated, vent fields spaced tens to hundreds of kilometers apart (Mullineaux et al., 2018).
Disturbance	Moderate; storms, wave action, and fishing (Byrnes et al., 2011; Reed et al., 2011).	Minimal; no permanent human settlement or fishery, some military development (McLaughlin, 2018).	Frequent and intense; seafloor eruptions (Rubin et al., 2012).
Food webs	Complex; support commercial fisheries, top predators include bird, elasmobranch, and marine mammal species.	Intact; high top predator biomass including bird and elasmobranch species (Stevenson et al., 2007).	Relatively simple; top predators are two fish and two crab species (Cohen & Haedrich, 1983; Buckman, 2009).
HOST SPECIES EXAMINED			
Crustacea	2 (n=25)	5 (n=200)	6 (n=712)
Fish	12 (n=195)	23 (n=574)	2 (n=26)
Mollusca	12 (n=379)	12 (n=1578)	10 (n=919)
Polychaeta	2 (n=79)	4 (n=285)	10 (n=507)
Total	28 (n=678)	44 (n=2637)	28 (n=2164)
COLLECTION DATA			
Collection dates	Oct 2012 - July 2017	July 2009 - July 2012	Feb 2007 - Apr 2021
No. collection days	31	38	23
No. collection sites	8	10	15
Geographic range	12 km	4 km	7 km

Table 3.1: Information on key features of the three ecosystems expected to drive parasite diversity, the number of host species and host individuals (in parentheses) included in comparative analyses, and additional geographic and temporal information on the specimen collections.

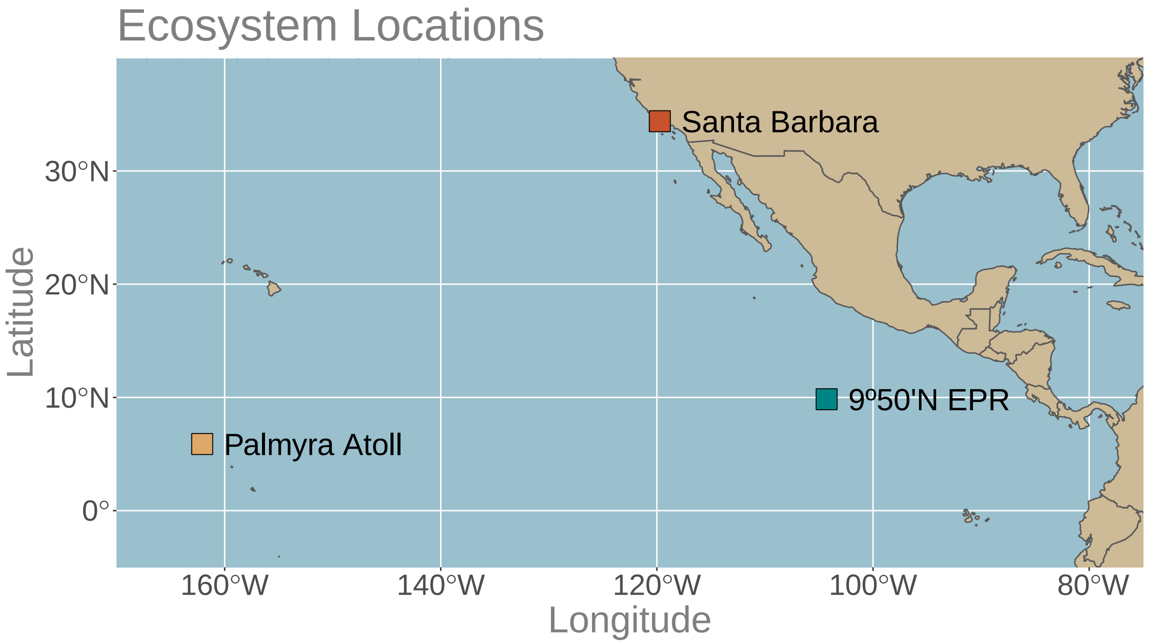

Figure 3-1: A map of the locations of the three comparison data sets from benthic communities in the Pacific Ocean.

ness on the number of host individuals examined, parasite richness within host species was estimated using the Chao2 species estimator using the chao2 function in the R package "fossil" (Vavrek, 2011). Chao2 has been shown to be the most effective estimator of parasite community richness (Teitelbaum et al., 2020). We analyzed this variable using a nonparametric rank analysis-of-covariance (ANCOVA) model (Lawson, 1983) using host group and ecosystem as fixed factors and the rank of average host species length as a covariate (Appendix G). This covariate is included to account for the dependence of observed parasite richness on the size of the host individual (Guégan et al., 1992; Iyaji et al., 2009) (Appendix G, Fig. G-2). Significance was assessed by randomizing the assignment of the species within host groups to ecosystems. All analyses were performed in R v4.2.1 (R Core Team, 2022).

Second, we analyzed the relationship between parasite richness and host richness in the three ecosystems using traditional species accumulation curves. The points on these curves represent estimates of mean parasite richness in fixed numbers of host species. Curves were generated using the equations from Solow & Smith (1991) (Appendix H) with the number of host species as the sampling unit. Separate curves were produced for fish and invertebrate hosts. When analyzing parasite richness across host species, one factor that could lead to overestimates of richness is erroneously counting different life stages in indirect life cycles as separate species. Some life stages in the three data sets were not identified to species and were assigned separate morphogroup IDs from the adults. Separating fish and invertebrates for analysis avoided this source of error for ILC species that pass from invertebrates to fish. To account for parasite species that pass through multiple fish species or multiple invertebrate species, we omitted life stages that were potentially redundant with other life stages within fish and invertebrate hosts from species accumulation curves.

3.3.5 Comparing the proportion of parasite species with direct and indirect life cycles

We tested the null hypothesis that the proportions of parasite species with direct life cycles (DLC) are the same across ecosystems using a standard chi squared test applied to contingency tables. When significant differences were found ($p < 0.05$), we conducted pairwise tests to determine which pairs of ecosystems differed using the Bonferroni correction for multiple tests. We treated fish and invertebrate host species separately and omitted parasite life stages that might be redundant with other stages in a host group from life cycle analyses. This subsetting removed several ILC larval morphogroups from the kelp forest data but did not qualitatively change results. Finally, we generated species accumulation curves for each parasite taxonomic group to examine which parasite taxa drove differences in richness in the two life cycle categories. We focused on fish hosts for this analysis since fish hosted the greatest number of parasite species from the widest range of taxa. As with diversity analyses that look across host species, potentially redundant life stages were omitted from this analysis.

3.3.6 Evidence of trophic relationships from parasite life stages

We tested the null hypothesis that the proportions of parasite morphogroups in different life-stage categories are the same across ecosystems using a standard chi squared test applied to contingency tables. As before, we treated fish and invertebrate hosts separately and, when significant differences were found, conducted pairwise tests to determine which pairs of ecosystems were different using a Bonferroni correction for multiple tests. We hypothesized that we would find relatively few parasite species in intermediate stages (acanthocephalan cystacanths, larval nematodes, cestode metacestodes, trematode metacercariae) and relatively more in the adult stage in vent fishes, since the short food chains and low richness of vertebrate predators at vents may preclude parasite species that use fish as intermediate hosts. Since this analysis focuses on life stages rather than total species richness, all larval morphotypes were included. As before, when significant differences were detected ($p < 0.05$), the direction and magnitude of the difference was assessed by checking the residuals, and pairwise tests were conducted between every combination of the three ecosystems.

3.4 Results

3.4.1 Summary of EPR 9N vent fauna surveys

I dissected 2,215 potential host individuals of 51 species from the EPR 9N vent field (Table 3.2). These included 10 crustacean, 2 fish, 14 mollusk, and 25 polychaete species. Dissections revealed 14 adult metazoan parasite morphogroups and nine larval morphogroups in five of the major marine parasite taxa included in this study (Fig. 3-2). These were two adult acanthocephalans, one adult copepod, one adult nematode, one larval nematode, one adult rhizocephalan, nine adult trematodes, seven trematode metacercariae, and one trematode sporocyst. Dissections also revealed non-parasitic symbionts: several copepod species that may be commensals or micropredators, nemertean egg predators, and the commensal scaleworm *Branchipolynoe symmitilida*. All dissection data for EPR 9N vent field fauna are available on BCO-DMO at https://www.bco-dmo.org/dataset/879118 (Dykman et al., 2022).

3.4.2 Comparing parasite richness between marine ecosystems

Parasite richness within host species broadly followed the hypothesized order, being highest in kelp forests, intermediate at the atoll lagoon sandflats, and lowest at vents, but these differences were not significant (2-way ANCOVA with ordered alternative, R-sq = 0.67, p = 0.39) (Fig.

Host Species	n	Acan	Cest	Cope	Isop	Mono	Nema	Rhiz	Trem
Crustacean									
Alvinocaris lusca[*]	10	0	0	0	0	0	0	0	90(1)[†]
Amphipod spp.[*]	22	0	0	0	0	0	0	0	0
Bythograea thermydron[*]	36	0	0	0	0	0	0	0	6(2)[†]
Cyanagraea praedator	5	0	0	0	0	0	0	0	0
Dahlella caldariensis	4	0	0	0	0	0	0	0	0
Halice hesmonectes[*]	235	0	0	0	0	0	0	0	0
Isopod sp.	1	0	0	0	0	0	0	0	0
Munidopsis cf. recta[*]	19	0	0	0	0	0	0	26(1)	0
Neolepas zevinae	7	0	0	0	0	0	0	0	0
Ventiella sulfuris[*]	390	0	0	0	0	0	0.3(1)[§]	0	0.3(1)[†]
Fish									
Thermarces cerberus[*]	11	64(2)	0	18(1)	0	0	27(1)	0	100(6)
Thermichthys hollisi[*]	24	0	0	0	0	0	8(1)	0	92(4)
Mollusk									
Bathymargarites symplector[*]	99	0	0	0	0	0	0	0	6(2)[†]
Bathymodiolus thermophilus[*]	42	0	0	0	0	0	0	0	0
Cyathermia naticoides[*]	65	0	0	0	0	0	0	0	0
Eulepetopsis vitrea[*]	100	0	0	0	0	0	0	0	5(1)[‡]
Lepetodrilus cristatus	5	0	0	0	0	0	0	0	0
Lepetodrilus elevatus[*]	349	0	0	0	0	0	0	0	0
Lepetodrilus ovalis[*]	38	0	0	0	0	0	0	0	5(2)[†]
Lepetodrilus spp.[*]	76	0	0	0	0	0	0	0	0
Lepetodrilus tevnianus[*]	18	0	0	0	0	0	0	0	0
Neomphalus fretterae[*]	31	0	0	0	0	0	0	0	0
Nodopelta sp.	1	0	0	0	0	0	0	0	0
Provanna ios	2	0	0	0	0	0	0	0	0
Rhynchopelta concentrica[*]	62	0	0	0	0	0	0	0	0
Turneroconcha magnifica	1	0	0	0	0	0	0	0	0
Polychaete									
Alvinella caudata[*]	12	0	0	0	0	0	0	0	0
Alvinella pompejana [*]	84	0	0	0	0	0	0	0	0
Amphisamytha galapagensis[*]	94	0	0	0	0	0	0	0	19(1)[†]
Archinome rosacea [*]	71	0	0	0	0	0	0	0	4(1)[†]
Branchinotogluma hessleri[*]	21	0	0	0	0	0	0	0	0
Branchinotogluma sandersi[*]	14	0	0	0	0	0	0	0	7(1)[†]
Branchiplicatus cupreus	2	0	0	0	0	0	0	0	0
Branchipolynoe sp.	5	0	0	0	0	0	0	0	0
Branchipolynoe symmytilida[*]	23	0	0	0	0	0	0	0	9(2)[†]
Galapagomystides aristata[*]	26	0	0	0	0	0	0	0	0
Hesiolyra bergi	1	0	0	0	0	0	0	0	0
Hesionid sp.	1	0	0	0	0	0	0	0	0
Hesiospina vestimentifera	1	0	0	0	0	0	0	0	0
Lepidonotopodium fimbriatum	7	0	0	0	0	0	0	0	0
Nereis sandersi	7	0	0	0	0	0	0	0	14(1)[†]
Nereis sp.	1	0	0	0	0	0	0	0	0
Nicomache sp.	1	0	0	0	0	0	0	0	100(2)[†]
Ophryotrocha akessoni	2	0	0	0	0	0	0	0	0
Paralvinella grasslei [*]	110	0	0	0	0	0	0	0	0
Polychaete sp.	3	0	0	0	0	0	0	0	67(1)[†]
Polynoid sp. A	7	0	0	0	0	0	0	0	0
Polynoid sp. B	9	0	0	0	0	0	0	0	0
Riftia pachyptila[*]	52	0	0	0	0	0	0	0	0
Tevnia jerichonana	2	0	0	0	0	0	0	0	0
Thermiphione risensis	6	0	0	0	0	0	0	0	33(2)[†]

Table 3.2: Summary of dissection data from EPR 9N vent fauna. Sample size (n) is shown next to the host species name. Prevalence (% host individuals infected) and parasite species richness (in parentheses) are shown for the eight major parasite taxonomic groups in this study. Keys: * = host species included in comparative analysis; † = trematode metacercaria; ‡ = trematode sporocyst; § = nematode larva.

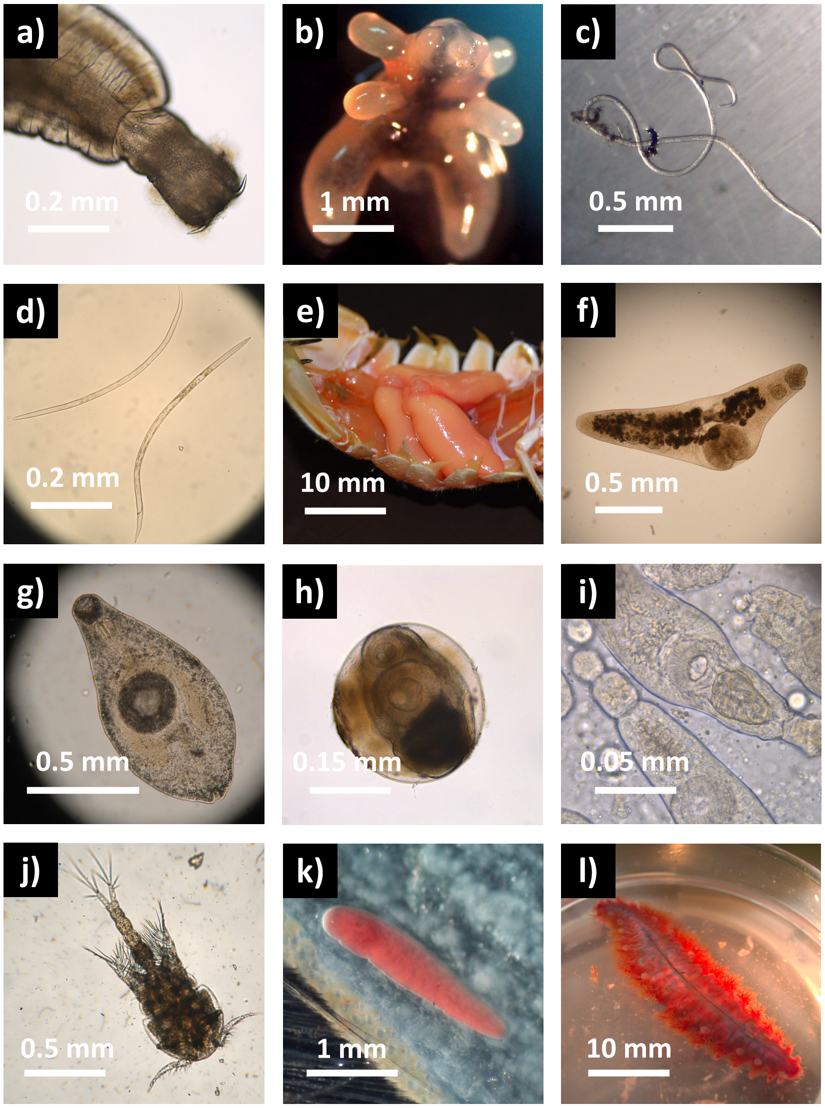

Figure 3-2: Photographs of parasite, commensal, and egg predator species encountered in dissections of EPR 9N fauna: a) Acanthocephalan from the gut of the fish *Thermarces cerberus*; b) Copepod (Family Chondracanthidae) from the mouth of *T. cerberus*; c) Nematode from the gut of *T. cerberus*; d) Nematode larvae from the amphipod *Ventiella sulfuris*; e) Rhizocephalan (genus Paratriangulus) in the abdominal muscle of the squat lobster *Munidopsis cf. exuta*; f) Adult trematode (Family Opecoelidae) from the gut of *T. cerberus*; g) Adult trematode (Family Opecoelidae) from the gall bladder of *T. cerberus*; h) Trematode metacercaria from the abdominal muscle of the shrimp *Alvinocaris lusca*; i) Trematode sporocyst from the gonad of the limpet *Eulepetopsis vitrea*; j) Commensal or micropredator copepod from the gills of *B. thermophilus*; k) Nemertean egg predators, likely of the genus *Ovicides*, from the limb axillae of the crabs *Bythograea thermydron* and *Cyanagraea praedator*; l) Commensal scaleworm *Branchipolynoe symmitilida* from the mussel *Bathymodiolus thermophilus*.

3-3a). The relationship between parasite richness and host richness for fish hosts followed a similar trajectory in the three ecosystems (initial slope of the line), but the low number of vent fish species constrained the total number of parasite species in the vent community (end point of line) (Fig. 3-3b). The relationship between parasite richness and host richness for invertebrate hosts was lowest at vents and greatest at the atoll lagoon sandflat (Fig. 3-3c).

3.4.3 Comparing the richness of parasites with direct and indirect life cycles

Most of the parasite species in each of the three ecosystems had indirect life cycles. The relative number of parasite species with DLCs and ILCs was significantly different between the ecosystems for fish hosts (χ^2 (df = 2) = 7.9, p = 0.020) (Fig. 3-4a) but not for invertebrate hosts (χ^2 (df = 2) = 3.1, p = 0.21) (Fig. 3-4b). The proportion of parasite species with indirect life cycles was greater in vent fish than expected under the null model and was more similar to kelp forests than to the atoll lagoon sandflat.

Differences between ecosystems in the proportion of DLC to ILC parasite species were driven by a few parasite taxa, and patterns were not consistent across parasite taxa within the same life cycle category (Fig 3-5). Among DLC parasites, copepod richness at vents was similar to the atoll lagoon sandflat while monogeneans were absent at vents. Among ILC taxa, nematodes were low in richness and cestodes were absent at vents, while acanthocephalan and trematode richness was comparable between vents and the coastal ecosystems.

3.4.4 Composition of parasite life stages in fish hosts

The relative number of parasite morphogroups in adult versus intermediate (acanthocephalan cystacanths, larval nematodes, cestode metacestodes, trematode metacercariae) life stages was significantly different between the ecosystems for fish hosts (χ^2 (df = 2) = 8.99, p = 0.01) (Fig. 3-6a) but not invertebrate hosts (χ^2 (df = 2) = 2.47, p = 0.29) (Fig. 3-6b). Vent fish hosted only adult parasites and lacked the acanthocephalan cystacanths, larval nematodes, trematode metacercariae, and cestode metacestodes that were common in fish from other ecosystems. Among invertebrates, the most notable differences between ecosystems were: an ab-

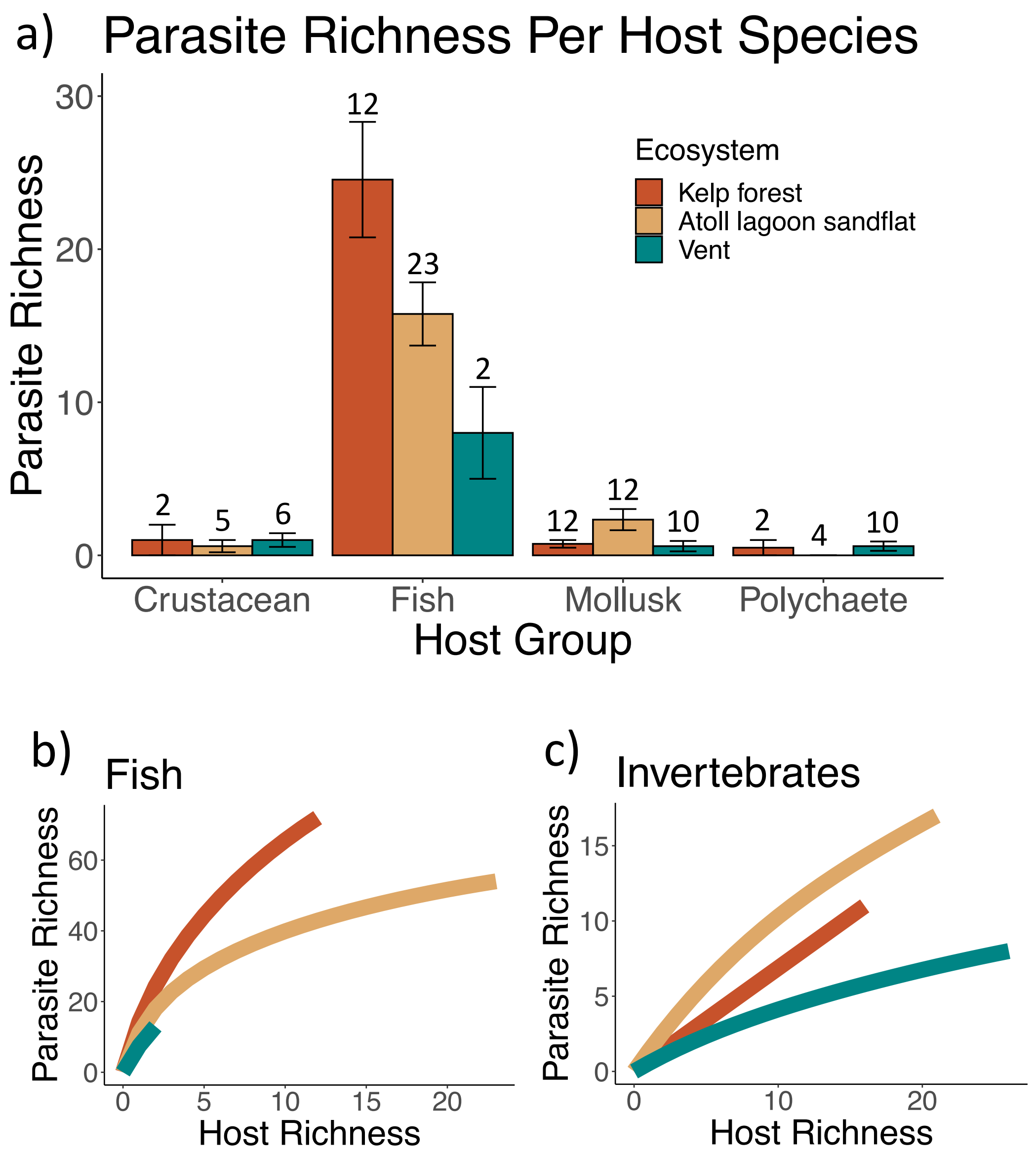

Figure 3-3: a) Mean (± SE) estimated parasite richness within host species in each ecosystem and host group. The number above the error bar is the number of host species included in the ecosystem and host group. Parasite species accumulation curves as a function of the number of host species sampled for b) fish hosts and c) invertebrate hosts.

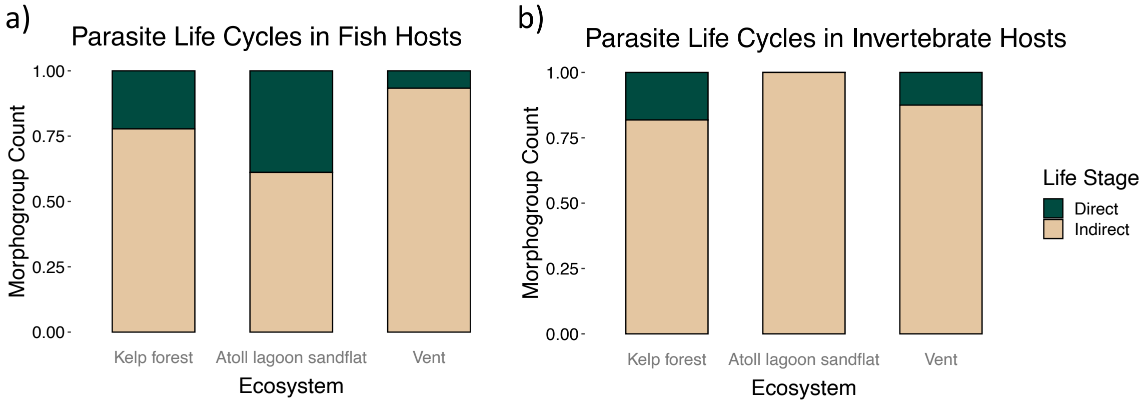

Figure 3-4: The relative number of parasite species with direct and indirect life cycles in the three ecosystems in a) fish hosts (χ^2 (df = 2) = 6.72, p = 0.03), and b) invertebrate hosts (χ^2 (df = 2) = 3.12, p = 0.21). The proportion of parasite species with indirect life cycles was greater in vent fish than expected under the null model and was more similar to kelp forests (χ^2 (df = 2) = 0.52, p = 0.47) than to the atoll sandflats (χ^2 (df = 2) = 2.82, p = 0.09).

sence of trematode sporocysts yet a high number of metacestode morphogroups in the kelp forests; a high number of sporocyst morphogroups at the atoll lagoon sandflat; and an absence of cestode metacestodes yet a high number of metacercarial morphogroups at vents.

3.5 Discussion

3.5.1 Challenges of recruitment in an island-like disturbed habitat

The isolation of vent habitats is expected to challenge the recruitment and persistence of parasite species. Differences in parasite richness in free-living species between the three ecosystems were not statistically significant despite following the hypothesized order suggested by island biogeography theory (Fig. 3-3a). This demonstrates the ubiquity of parasites in biological communities, even in an extreme setting. Of the four host groups examined, parasite diversity in fish hosts most closely followed the expectation based on habitat isolation (Fig. 3-3a). Fish likely provide the most integrated sampling of regional parasite diversity because they are highly mobile and acquire many of their parasites through feeding, thus accumulating parasites over space and time. Santa Barbara kelp forest fish species had the highest parasite

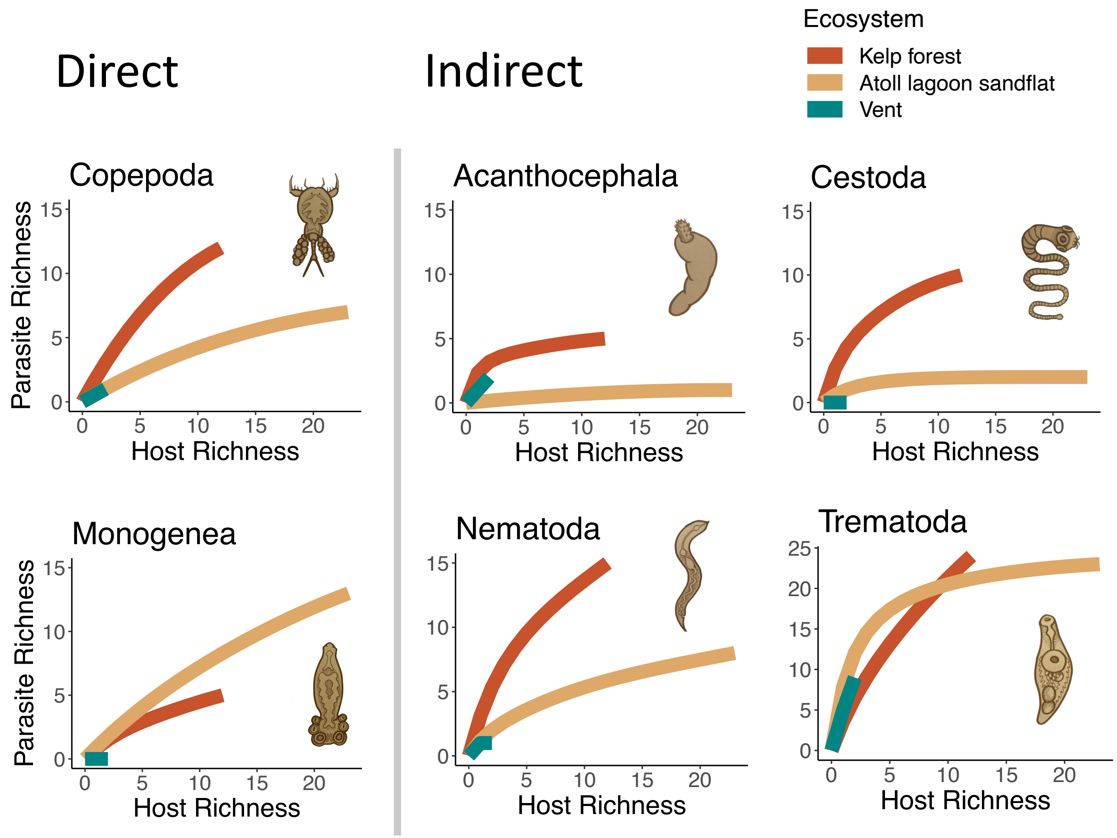

Figure 3-5: Species accumulation curves for the six parasite taxa found on fish as a function of host richness. Parasite taxa are grouped by whether their species generally have direct or indirect life cycles.

richness because their habitat is connected to kelp forests along the coast and interacts with adjacent intertidal, pelagic, and estuarine areas (Morton et al., 2021). Although fish species in Palmyra sandflats move between some adjacent habitats (coral reef, pelagic), Palmyra Atoll is comparable to vents in its small area (~ 4 km^2) and extreme isolation from the nearest sandflat, which is 375 km away on Kiritimati Atoll (McLaughlin, 2018) (Table 3.1). That parasite diversity in vent fish was comparable to fish in less isolated and less disturbed systems suggests that vent fishes may be highly effective dispersal agents and may offer more connectivity between vent fields than has been appreciated. The extent to which vent fishes move among vent fields is unknown, however the feeding spheres of *T. cerberus* and *T. hollisi* have been inferred from otolith chemistry (Buckman, 2009) and likely do not extend much into adjacent habitats (Cohen & Haedrich, 1983).

Extreme, frequent disturbance is another factor expected to reduce parasite diversity at

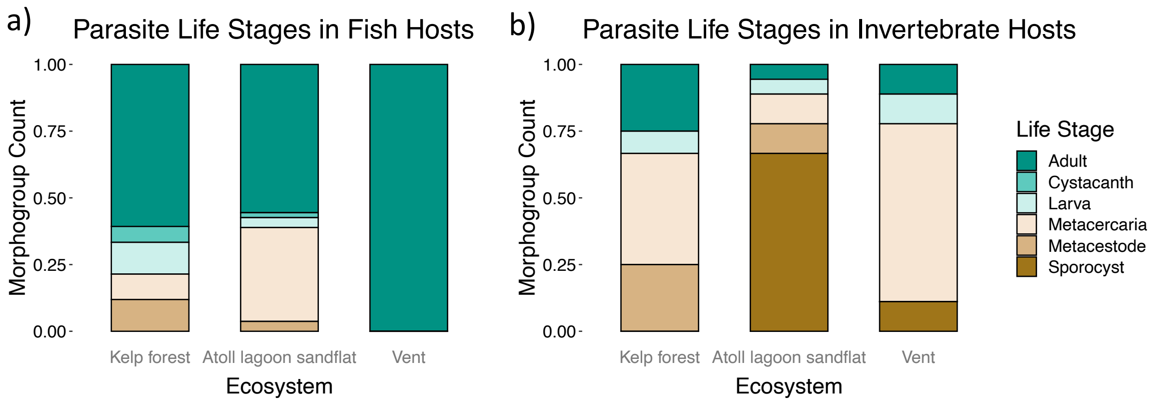

Figure 3-6: The relative number of parasite life stages in the three ecosystems in a) fish hosts (χ^2 (df = 2) = 8.99, p = 0.01) and b) invertebrate hosts (χ^2 (df = 2) = 2.47, p = 0.29). Note, the figure shows the taxonomic identity of different intermediate parasite stages, but the statistical test compared only the proportion of morphogroups in the adult stage versus the intermediate stage. For fish hosts, pairwise tests were performed between vents and the other ecosystems with a Bonferroni correction. Vents were distinct from kelp forests (χ^2(df = 2) = 6.08, p = 0.014) and the atoll lagoon sandflat (χ^2(df = 2) = 7.17, p = 0.0074).

EPR 9N vents. Patterns of parasite richness in invertebrate hosts (Fig. 3-3c) correlated with the relative levels of disturbance in the three ecosystems, with Palmyra being least disturbed and vents being the most. Differences in parasite diversity between fish and invertebrate hosts could result from their distinct modes of infection: fish are often infected by feeding on other hosts, whereas invertebrates are infected by encountering dispersive parasite stages. Parasites may take longer to colonize and spread in the invertebrate community after disturbance, since transmission among invertebrates is more a function of relative host densities than of host feeding rates. Since our samples of the vent community were taken 13-15 years after the 2006 eruption, the community was already in advanced stages of recovery (Mullineaux et al., 2020; Dykman et al., 2021a). Additionally, parasite prevalence (the proportion of host individuals infected) in host species, did not differ significantly between the three ecosystems (see Appendix I for prevalence methods and results). These lines of evidence suggest time since the disturbance does not entirely explain the reduced parasite richness in vent invertebrates. Local hydrographical conditions may also influence the probability of parasite larvae encountering a host: vents and kelp forests are open systems with significant water flow, while the atoll lagoon is a more enclosed system with greater entrainment.

3.5.2 Successful life histories in island-like, disturbed habitats

Due to challenges of recruitment in island-like, transient habitats, we expected to find relatively more parasite species with direct (one-host) life cycles than indirect (multi-host) life cycles at vents compared to other ecosystems (Dobson & May, 1986). Instead, we found more parasite species with indirect life cycles than expected at vents (Fig. 3-4). This result was driven by the high richness of trematodes and the absence of monogeneans (Fig. 3-5). This finding is inconsistent with the theoretical expectation that island-like habitat filters parasite species based on the number of hosts they use in their life cycles. Rather, our results indicate the establishment and persistence of parasites on islands is determined by the specific ecological requirements of parasite taxa, including opportunities for introduction and life cycle completion within the available host species (Malcicka et al., 2015).

Some aspects of ILCs may be advantageous in disturbed habitats, allowing certain taxa to persist. In general, ILCs allow parasites to maximize different fitness costs at different stages (Benesh et al., 2021), with higher transmission rates in small intermediate hosts (which are often more abundant) and greater growth and reproduction in definitive hosts (which are often large and long-lived). Trematodes may be particularly successful in disturbed environments because they have an asexual cloning stage, which allows for multiplication in small intermediate hosts, while also using fish, a highly mobile host group, for long-distance dispersal. Bottom-up nutrient enrichment in estuarine ecosystems is associated with high trematode densities, likely because it increases the abundance of gastropod intermediate hosts (Johnson & Heard, 2017). Trematode species richness and biomass are also high in these estuarine ecosystems (Lafferty et al., 2006; Kuris et al., 2008). This same mechanism may enhance trematode transmission at vents, where venting activity provides a rich bottom-up source of energy with an abundance of gastropods as first intermediate hosts for trematodes. DLC parasites were much less diverse at vents than expected. We encountered only one parasitic copepod species and one rhizocephalan species. Monogeneans were conspicuously missing at vents despite being speciose in the other ecosystems and found in fish hosts as deep as 5,000 meters (Campbell et al., 1980). Their absence may be explained by ineffective larval dispersal, low host densities, high host specificity, or sensitivity to the chemical environment. The low diversity of direct life cycle parasites at vents could indicate that reliance on a single, often highly specific, host species may be a relatively inefficient strategy in isolated disturbed environments.

3.5.3 The effect of simple food webs and low diversity of top predators

The relatively short food chains and low diversity of vertebrate predators at vents (Cohen & Haedrich, 1983; Voight, 2000) are expected to restrict parasite diversity by limiting the potential pathways for ILC parasites to complete their life cycles. Our data reveal that vent fish lack the encysted intermediate parasite stages of acanthocephalans, cestodes, nematodes, and trematodes that are common in marine fish in other ecosystems (Fig. 3-6a). These differences cannot be explained by the deep-sea setting alone, since metacestodes and larval nematodes have been found in fish from 1,000-5,000 meters depth (Campbell et al., 1980; Ñacari & Oliva, 2016; Costa et al., 2016). The absence of intermediate parasite life stages in vent fish is likely a signature of short food chains and restricted vertebrate diversity. Kelp forests and the atoll lagoon sandflat have many more fish species and trophic links than do vent ecosystems. Parasites in other ecosystems also use other vertebrate taxa – sharks, birds, and marine mammals – as final hosts. The relatively low number of vertebrate species may constrain total parasite diversity in vent ecosystems by limiting available parasite habitat and opportunities for introduction into the vent environment. For a specific example, most marine cestodes use sharks as definitive hosts. The absence of cestodes at vents may result from sharks avoiding vent habitat or a lack of deep-sea sharks in the EPR region. Taken together, diversity trends with the limited number of fish hosts (Fig. 3-3b) and the absence of intermediate parasite life stages in vent fishes (Fig. 3-6a) suggest that total parasite diversity in the community is largely constrained by the available number of host species and trophic links. The reduced diversity of endemic vent predators may be a direct result of the small habitat area (Holt, 2009; Martinson et al., 2012) or the challenges of vertebrate species adapting to tolerate a harsh chemical environment.

3.5.4 Conclusion

Broadening comparative studies to extreme environments is useful for testing the generality and exceptions of ecological patterns and offers insights into causes for exceptions. Our study reveals that parasite diversity in vent hosts is comparable to two coastal marine ecosystems, despite vent habitat being more isolated and more disturbed. This indicates the previously low encounter rate of vent parasites was largely due to lack of sampling effort, and provides additional evidence of the ubiquity of parasites, even in extreme environments. Contrary to expectation, parasites with indirect life cycles were relatively diverse at vents due to the success of trematodes, whose life strategy may allow for effective dispersal and rapid establishment. Finally, we found that the number of host species and trophic pathways available for parasites to complete their lifecycles were important regulating factors for parasite diversity at vents and may also explain the scarcity or absence of some ILC parasite taxa. Since EPR 9N is disturbed at a high frequency that is not typical for most vent fields, additional insight into processes will be gained by investigating more vent fields with different disturbance frequencies and assemblages of potential host species.

3.6 Acknowledgements

This work is dedicated to the deep-sea hydrothermal vent fauna whose beauty inspires us and whose sacrifice made this work possible. Research was funded by NSF OCE BIO-1829773, NSF OCE BIO-1948580, the WHOI Hill Fund, and the WHOI Grassle Fellowship Fund. We thank the crew of R/V *Atlantis* and R/V *Roger Revelle* and the technicians and pilots of ROV *Jason*, HOV *Alvin*, and AUV *Sentry* for making field sampling possible. We thank John McLaughlin, Ryan Hechinger, Kevin Lafferty, Dana Morton, Kate Buckman, Timothy Shank, and Gorka Sancho for contributing data and providing input on analyses. We thank Michael Meneses, Bethany Fleming, and Caitlin Plowman for their help processing samples. We thank Mario Fernandez for designing and building a high-capacity suction sampler for ROV *Jason*. We thank Stace Beaulieu and Susan Mills for guidance in data collection and tidying. We thank Charles Blend, Paola Braicovich, Rodney Bray, Henrik Glenner, Jens Høeg, and Mike Kinsella for species identification and description. Finally, we tip our hat to all the deep-sea parasitologists who have

boldly gone before us into the uncharted depths of oceans and guts.

3.7 Co-Authors and Prior Publication

This chapter has been submitted as a manuscript to the journal *Proceedings of the Royal Society B*. The text of this chapter was copied directly from the submitted manuscript and formatted to fit thesis guidelines. The co-authors on this manuscript are Lauren S. Mullineaux, Armand M. Kuris, Carolyn K. Tepolt, and Andrew R. Solow. LD performed field and laboratory work, assembled the vent parasite database, analyzed the data, and wrote the manuscript. AK conducted preliminary sampling at EPR 9N and contributed parasitology expertise. LM and CT supported sample collection and processing. AS developed statistical analyses and the supplementary methods description and wrote the paragraph on statistical methods in the main text. All authors provided input on the manuscript and analyses.

3.8 Data Availability

The data that support the findings of this study are openly available in BCO-DMO. Dissection data from EPR 9N hydrothermal vent fauna are available at https://www.bco-dmo.org/dataset/879118. Life cycle assignments and citations for all parasite species included in analyses are available at https://www.bco-dmo.org/dataset/879253. Data on the vent parasite species reported in literature prior to this study are available at https://www.bco-dmo.org/dataset/879266. Scripts used for this analysis are available on GitHub at https://github.com/ldykman/VENT_PARASITES_EPR.

Chapter 4

Morphological and genetic evidence that digenetic trematodes complete indirect life cycles in an island-like and ephemeral deep-sea habitat

4.1 Abstract

Parasites with indirect life cycles (ILCs) are expected to be sensitive to environmental disturbances because they require multiple host species from very different taxa to complete their life cycles. For this reason, the presence of ILC parasites in an ecosystem contains valuable information on overall diversity, species interactions, and ecosystem functioning, which is especially useful in systems that are difficult to sample. In this study, I examine all life stages of a diverse parasite group with ILCs (digenetic trematodes) in a highly disturbed habitat (deep-sea hydrothermal vents) to determine what hosts they use, and whether they complete their entire life cycles within the habitat. I also explore the phylogenetic relatedness of these newly discovered species to close deep-sea relatives to understand whether digenean diversity at vents arose from one or more founding clades. Digenean sporocysts, cercariae, metacercariae, and adults were sampled from deep-sea hydrothermal vent fauna from the 9°50' N vent field on the

East Pacific Rise. The different life stages of several morphogroups were compared morphologically and genetically with 18S and 28S barcoding sequences. The vent digeneans formed two distinct genetic clusters, one in Family Opecoelidae and one in a clade sister to Opecoelidae, indicating digenean diversity at the sampled vents arose from at least two introductions. One sporocyst matched genetically with adult morphogroups in Opecoelidae and two metacercariae matched with adults in the sister group to Opecoelidae, yet a full life cycle was not completed. Close genetic and morphological relatedness of the vent species suggests radiation within vent systems and potential host-switching events. This analysis of the hosts used in indirect life cycles provides information on conditions for parasite persistence in an isolated, disturbed ecosystem, and suggests potential routes of introduction into the vent environment.

4.2 Introduction

Parasite diversity and abundance provides valuable information about ecosystem functioning and relationships between hosts (Combes, 1996). Since parasites rely on hosts, they are sensitive to environmental disturbances that alter host diversity, density, or trophic structure (Lafferty, 1997; Wood et al., 2014). For this reason, parasites have recently been used as indicators of environmental degradation (Lafferty, 1997; Marcogliese, 2005), and conversely, successful restoration (Huspeni & Lafferty, 2004; Moore et al., 2020). Parasites with indirect life cycles (ILCs) are especially informative of ecosystem function because they require multiple hosts from a wide range of taxa in order to reproduce and ultimately persist (Blasco-Costa & Poulin, 2017). The critical step of transmission between hosts occurs multiple times in one generation, and can require a range of processes including transmission as larvae in the environment (Combes et al., 1994) or trophic transmission when one host feeds on another (Marcogliese, 2002). For their many different hosts and transmission steps, ILC parasites are expected to be less able to persist in disturbed habitats and less likely to establish in isolated habitats (Dobson & May, 1986).

Digenea is a diverse and abundant group of parasitic flatworms in Class Trematoda with indirect life cycles involving two to three host species. Digeneans are excellent subjects for investigating the ecological and evolutionary consequences of complex life cycles, as they have distinct host requirements, modes of transmission, and impacts on the host at each stage. The first life stage in the digenean life cycle is the sporocyst (Fig. 4-1b), which invades the gonad of a molluscan first intermediate host. A single infection results in the degradation of reproductive tissue and castration of the host, with consequences for host population dynamics and demographics (Miura et al., 2006). The sporocyst asexually clones and releases free-swimming larvae called cercariae (Fig. 4-1c). Since cercariae are short-lived and disperse as planktonic larvae, evidence of efficient transmission between the first and second intermediate host might indicate the host species live in close proximity. Cercariae encyst within the second intermediate host (a polychaete, mollusk, crustacean, or small fish) as a metacercaria (Fig. 4-1d). These may have little impact on the host at low intensities, but can significantly reduce host vitality or alter host behavior at high intensities (Lafferty & Morris, 1996; Stier et al., 2015; Bates et al., 2010). The life cycle is completed through trophic transmission, when a vertebrate definitive host eats the second intermediate host, and the metacercaria develops into a sexually reproducing adult in the digestive tract (Fig. 4-1e). Linking the adult stage in the definitive host to the metacercaria in the second intermediate host indicates a durable feeding relationship between predator and prey. For rare host specimens, this often provides more time-integrated and reliable information on trophic interactions than gut content analysis alone (Kuris et al., 2015). The complex interconnection with many species, and niche shifts at each step, demonstrates that a digenean can only be understood as the sum of its parts.

Knowledge of all the hosts required to complete parasite life cycles can provide valuable information on species interactions, especially in ecosystems that are difficult to sample. Despite compelling reasons for resolving life cycles, digeneans are usually described only by the morphology of the adult (Blasco-Costa & Poulin, 2017). Life cycle studies were a central focus of parasitology in the 1950s-1960s, but the marked decrease in life cycle work in the decades since has inspired a call to "resurrect an old tradition" (Blasco-Costa & Poulin, 2017). The completion of life cycles, which requires the linking of all life stages, is usually achieved through a combination of morphological description, experimental infections, and, more recently, matching of genetic sequences by DNA barcoding. Life cycle description is particularly difficult in large, open systems like the deep sea (Bray, 2020), where host species can be highly mobile and patchy, species occurrences and ranges are poorly known, and animals generally cannot

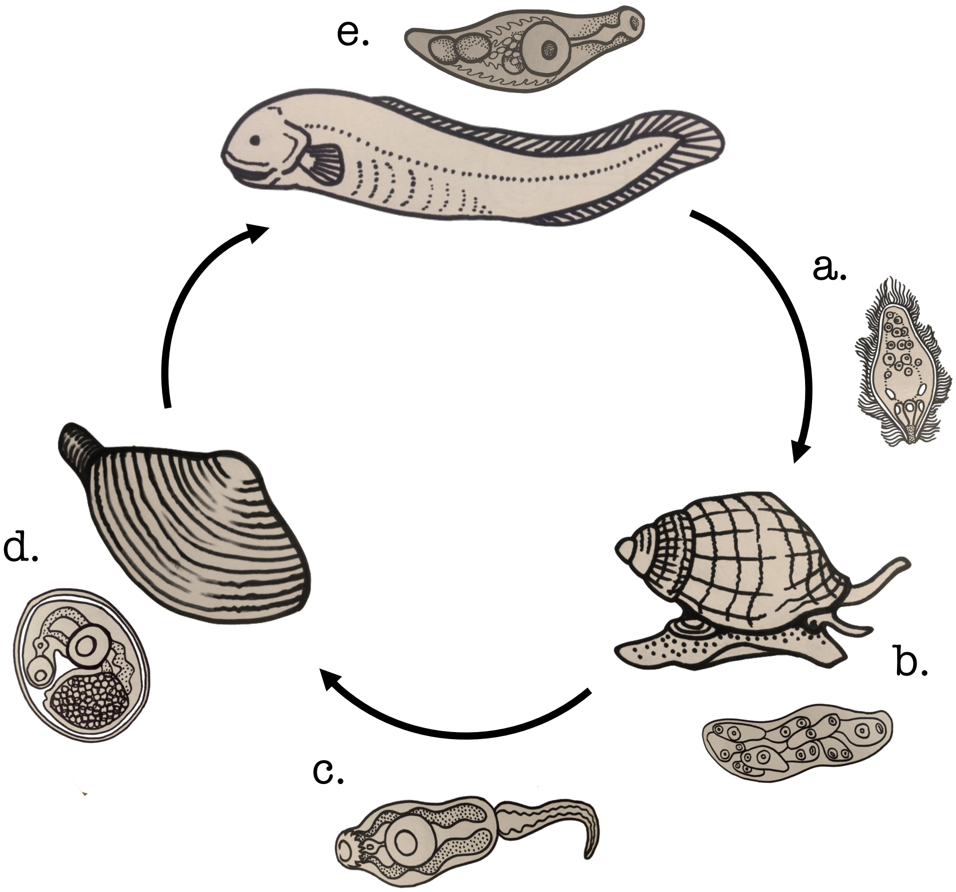

Figure 4-1: A generic trematode life cycle. Eggs are shed in the host feces and hatch into a ciliated larva called a miracidium a). The miracidium penetrates a molluscan first intermediate host, in this case a marine snail, and forms asexually reproducing clones called sporocysts b) in the host gonad or digestive gland. Sporocysts shed free-living larvae called cercariae c). Cercariae actively seek a second intermediate host, which can be from a wide range of taxa including mollusks, fish, polychaetes, and crustaceans. The cercaria penetrates and encysts as a metacercaria d). The metacercaria infects the definitive host when the definitive host feeds on the second intermediate host. The adult trematode e) develops in the digestive tract of the vertebrate definitive host (in this example a deep-sea fish) and sexually reproduces, shedding eggs with host feces to begin the cycle anew.

be kept alive in culture. For this reason, the life cycles of ILC deep-sea parasites have never been resolved to date, yet this information has the potential to provide broader insights into ecosystem structure and function in settings that are difficult to access.

Deep-sea hydrothermal vents are island-like, ephemeral habitats, making them a compelling system to explore the boundaries of persistence for ILC parasites. Vent habitats have a well-constrained area and unique endemic fauna. The potential host species tend to spend their adult lives close to centers of active venting and disperse as planktonic larvae. Since the interspecific interactions and feeding spheres of vent species are constrained to a small area, it is likely that vent parasites, if able to persist, will complete their entire life cycles in the vent environment. Recent investigation into parasite diversity at deep-sea hydrothermal vents on the Northern East Pacific Rise (Chapter 3) revealed several abundant digenean parasite species (in the adult stage) in the vent-endemic fishes *Thermarces cerberus* and *Thermichthys hollisi*. Five digenean species (also in the adult stage) have previously been described from the vent fish *T. hollisi* from the Southern East Pacific Rise (Bray et al., 2014). These results contradict the expectation that the island-like, disturbed nature of vent habitat would challenge the introduction, establishment, and persistence of ILC parasites (Dobson & May, 1986). Observation and dietary analysis indicate vent fish live and feed almost exclusively in vent habitat (Buckman, 2009), making it likely that their parasites use vent invertebrates at other life stages. Despite this, no intermediate digenean life stages have previously been reported at vents. Since adult digeneans are common in deep-sea fishes in general, it is impossible to determine whether the parasites found in *T. cerberus* and *T. hollisi* are endemic to vents without demonstrating that they can complete all stages of their life cycle in vent hosts.

In this study, I report the recent discovery of four life stages in the digenean life cycle – sporocyst, cercaria, metacercaria, and adult – of multiple species from the 9°50'N hydrothermal vent field on the East Pacific Rise (EPR 9N). This study has two objectives: first, to morphologically and genetically match life stages to determine whether the newly discovered digenean species complete their life cycles in the vent environment; and second, to place the new vent species in the phylogenetic context of other deep-sea digenean species to investigate potential origins of introduction into the vent environment. In addition to contributing to basic knowledge of parasite-host interactions at vents, the results of this study are broadly relevant in demonstrating the feasibility of ILC species establishing and persisting in an extreme, disturbed, and isolated setting.

4.3 Methods

4.3.1 Biological collections and dissections

Vent fauna were collected from a range of environmental zones at 12 vent sites in the 9°50'N vent field, East Pacific Rise. Specimens were collected using HOV *Alvin* and ROV *Jason* during three research cruises AT37-12 (April, 2017), AT42-21 (December, 2019), and RR2102 (March, 2021). Collection sites included Bio-vent, M Vent, Zeta Garden, Teddy Bear, Crab Spa, Tica Vent, Riftia Mound, P Vent, East Wall, V Vent, and L Vent. Briefly, specimens were brought to the surface in sealed, insulated boxes and either dissected fresh aboard ship or frozen at -80°C for later dissection on shore. All tissues of each host specimen were thoroughly examined under a dissecting scope by pressing the tissue between two glass slides and illuminating with transmitted light. Cercaria larvae were collected in water sieved over 124μm mesh from a sealed collection container that had contained a settlement surface with juvenile invertebrates. Further detail on faunal collection and dissection methods are presented in Thesis Chapter 3 Table 3.2 and Appendix F.

4.3.2 Morphological description of trematode life stages

Digenean life stages were initially assigned to morphogroups based on morphological characteristics such as shape, size, and presence or absence of key features. For each morphogroup encountered, features including total length (TL), total width (TW), oral sucker length (OSL), oral sucker width (OSW), ventral sucker length (VSL), and ventral sucker width (VSW) were measured from a subset of specimens using a compound microscope with an ocular micrometer. For metacercariae, cyst length (CL) and cyst width (CW) were also recorded. When possible, metacercariae were removed from their cyst to measure dimensions of the developing worm including oral sucker and ventral sucker length and width. For sporocysts, dimensions were taken for both the mother sporocyst and the daughter rediae. Several representative individuals of each morphogroup were photographed using a Zeiss Axiostar or Nikon camera attached with a C-mount. Specimens were then preserved in 95% ethanol and frozen at -80°C for molecular analysis.

4.3.3 Molecular analysis

DNA was extracted from ethanol-preserved specimens using the DNeasy Blood and Tissue Kit (QIAGEN, Beverly, Massachusetts) following the manufacturer's Quick-start protocol for tissue with the modification of using 35μL Buffer AE for the elution step rather than 200μL. PCR was performed in 25μL reaction mixtures containing 12.5μL of GoTaq G2 Colorless Master Mix (Promega Corporation, Madison, Wisconsin) (1.5 mM $MgCl^{2+}$ and 200μM of each dNTP in the final reaction volume), 2.5μL of each primer (1μM in the final reaction volume), 6.5μL nuclease free water, and 1μL of 0.03-10 ng/L sample DNA. Partial 18S sequence (581-601 bp) was amplified with the primers 18S9modF (5'-GAT CCT GCC AGT AGT CAT ATG CTT G-3') and 18S637modR (5'-TAC GCT WYT GGA GCT GGA GTT ACC G-3') (Moszczynska et al., 2009; Van Steenkiste et al., 2015). Partial 28S sequence (1211-1251 bp) was amplified with the primers ZX-1 (5'-ACC CGC TGA ATT TAA GCA TAT-3') or LSU5' (5'-TAG GTC GAC CCG CTG AAY TTA AGC A-3') and 1500R (5'-GCT ATC CTG AGG GAA ACT TCG-3') (Tkach et al., 2003; Bray et al., 2009). The following touchdown cycling protocol was used for all reactions: 95°C for 3 min; 14 "touchdown" cycles of 95°C for 30 s, 65°C to 52°C for 30 s (decreasing 1°C each cycle), and 72°C for 1 min; 20 cycles of 95°C for 30 s, 52°C for 30 s, 72°C for 1 min; and a final extension at 72°C for 7 min. Successful amplification was confirmed with gel electrophoresis and PCR product was sent to Sequegen DNA Sequencing (Worcester, Massachusetts) for Sanger sequencing in both directions. Raw sequence data was cleaned and consensus sequences built using Sequencher v5.4.6 (Gene Codes Corporation, Ann Arbor, Michigan). Sequence identity was checked using the online Basic Local Alignment Search Tool (BLAST) v2.13.0 (Altschul et al., 1990) using the megablast tool against the nr/nt database with an e-value cutoff of 0.05 and default settings.

4.3.4 Phylogenetic Analysis

Reference sequences were gathered from NCBI, including the closest matches in the NCBI nr/nt database to the new species, all sequences from known vent digeneans (Bray et al., 2014), and other deep-sea digenean genera in the same families (Sokolov et al., 2019, 2020; Bray, 2020). Due to the paucity of deep-sea digenean sequences, the 18S and 28S genes were analyzed separately to allow for the inclusion of more taxonomic diversity in each analysis. When possible, the same reference species were used in both analyses. However, the trees contain some different species because many reference species only had an available sequence from one gene. *Echinostoma revolutum* was used as an outgroup for consistency with prior studies (Sokolov et al., 2019). Sequences were aligned using the software clustalo v1.2.2 (Sievers & Higgins, 2021; Goujon et al., 2010) and manually trimmed to remove all gaps. After alignment and trimming, a 475 bp segment was used for 18S analysis and a 1040 bp segment was used for 28S analysis with full coverage. Trees were generated using the software iqtree v2.2.0 (Nguyen et al., 2015). Branch supports were estimated using the ultrafast bootstrap with 1,000 replicates (Hoang et al., 2018) as in Sokolov et al. (2019), and the best fit model was selected based on the BIC using the program ModelFinder v2.2.0 (Kalyaanamoorthy et al., 2017). The best model for the 18S tree was TNe+R2 (BIC = 3340.284) and the best model for the 28S tree was GTR+F+R3 (BIC = 18277.663) based on the BIC. The next best models were TNe+I+G4 (BIC = 3342.458) and TIM3e+R3 (BIC = 18282.034) for the 18S and 28S trees, respectively. When possible, two to three individuals from each morphogroup were included in preliminary analyses to assure morphospecies assignments were consistent. If all individuals in a morphogroup were genetically identical, only one individual in the morphogroup was retained in the final tree figures for simplicity.

4.4 Results

4.4.1 Digenean species and life stages from vent communities on 9°50'N on the East Pacific Rise

Dissections of 51 species from the 9°50'N vent communities on the East Pacific Rise revealed nine morphologically distinct adult trematodes, seven metacercariae, and one sporocyst (Table 4.1). Examination of the wash from recovered settlement surfaces also revealed three morphologically distinct cercarial types. The adult trematodes were found in the stomach, intestines, and gall bladder of the vent fishes *Thermarces cerberus* and *Thermichthys hollisi*. Metacercariae were found in the shrimp *Alvinocaris lusca*, the crab *Bythograea thermydron*, the gastropods *Bathymargarites symplector* and *Lepetodrillus ovalis*, and the polychaetes *Amphisamytha galapagensis*, *Archinome rosacea*, *Branchinotogluma sandersi*, *Nereis sandersi*, *Nichomache* sp., Polychaete sp. (unidentified), and *Thermiphione rissensis*. Of the parasite morphospecies and life stages collected, high-quality consensus sequences were obtained from eight adult, two metacercarial, one sporocyst, and one cercarial morphotype (Table 4.2). The eight adult morphospecies that were sequenced were distinguished based on differences in characteristics including overall size, body shape, relative oral and ventral sucker dimension and position, size and position of eggs, testes configuration, and the presence and position of a Manter's Organ (Yamaguti et al., 1971) (Fig. 4-2). Six of the adult morphogroups were stained and mounted for formal taxonomic description (Charles Blend, pers comm., Blend & Dykman in prep), which allows resolution of finer features used in digenean taxonomy such as relative position of the seminal vesicle, position of the uterus, and size of eggs. Remaining uncertainty in species identification and discernment of morphogroups will be discussed.

4.4.2 Morphological and phylogenetic matching of trematode life stages

The parasite species at EPR 9N form two distinct taxonomic clusters, and several of the intermediate life stages match very closely to adult life stages both morphologically and phylogenetically. The first cluster falls within Family Opecoelidae. Its position relative to other species in the family is well supported in the 28S tree (bootstrap support value = 97), but poorly supported in the 18S tree (bootstrap support value = 39). It contains the two adult morphospecies DIGE08 (Fig. 4-2g) and DIGE16 (Fig. 4-2h) from the gut of the eelpout *T. cerberus* and the sporocyst SPOR01 (Fig. 4-3c) from the gonad of the glass limpet *Eulepetopis vitrea*. The adults and sporocyst have identical sequences in the region of 18S and 28S gene examined (594/594 and 1231/1231 bp, respectively). Based on formal taxonomic analysis of stained and mounted samples, several morphological characters of the adults DIGE08 and DIGE16 are consistent with the genus *Mesobathylebouria* established by Martin et al. (2018a). These include "a less robust body, smooth testes, and the cirrus pouch reaching the midlevel of the ventral sucker" (Charles Blend, pers comm, Dykman & Blend in prep). Based on a BLASTn search of the partial 28S gene, however, the new species had 99% (1192/1193 bp) similarity to *Neolebouria georgiensis* (28S: MH892478.1) (bootstrap support value = 100) from the icefish *Trematomus pennellii* in the Weddell Sea, Prince Gustav Channel, Antarctica (Faltỳnková et al., 2017). The newly discovered species only shared 92% (1143/1237 bp) similarity with *Mesobathylebouria lanceolata* (28S: KJ001210) (bootstrap support value = 100). Therefore, we place these new species in the genus *Neolebouria* with fairly high confidence.

The genus *Mesobathylebouria* was established by Martin et al. (2018a) to "encompass species that are morphologically similar to *Neolebouria* but were from the lower epipelagic and mesope lagic zones" (Charles Blend, pers comm). Five of the eleven species previously in *Neolebouria* were reclassified as *Mesobathylebouria* when genetic data revealed that *N. georgiensis* and *Neolebouria* (now *Mesobathylebouria*) *lanceolata* did not cluster together. Our new material from deep-sea vent fish is the first test of the recent reclassification of *Neolebouria* and creation of *Mesobathylebouria* by Martin et al. (2018a). Disagreement between genetic and morphological evidence suggests further revision of the genera is warranted. The next closest matches to our new material were *Podocotyle atomon* (28S: MH161437.1) from fish in the North Pacific and *Allopodocotyle margolisi* (18S: KU320583.1, 28S: KU320596.1) from a grenadier in the North Atlantic. The previously described vent digenean *Buticulotrema thermichthysi* (18S: KF733987.1; 28S: KF733984.1) (Bray et al., 2014) was 97% (1194/1234 bp) similar to our new material. It forms a sister group to the *Neolebouria* cluster (bootstrap support value = 95%), along with *Gaevskajatrema halosauropsi* (18S: AJ287514.1, 28S: AY222207.1) from the deep-sea fish *Halosauropsis macrochir*.

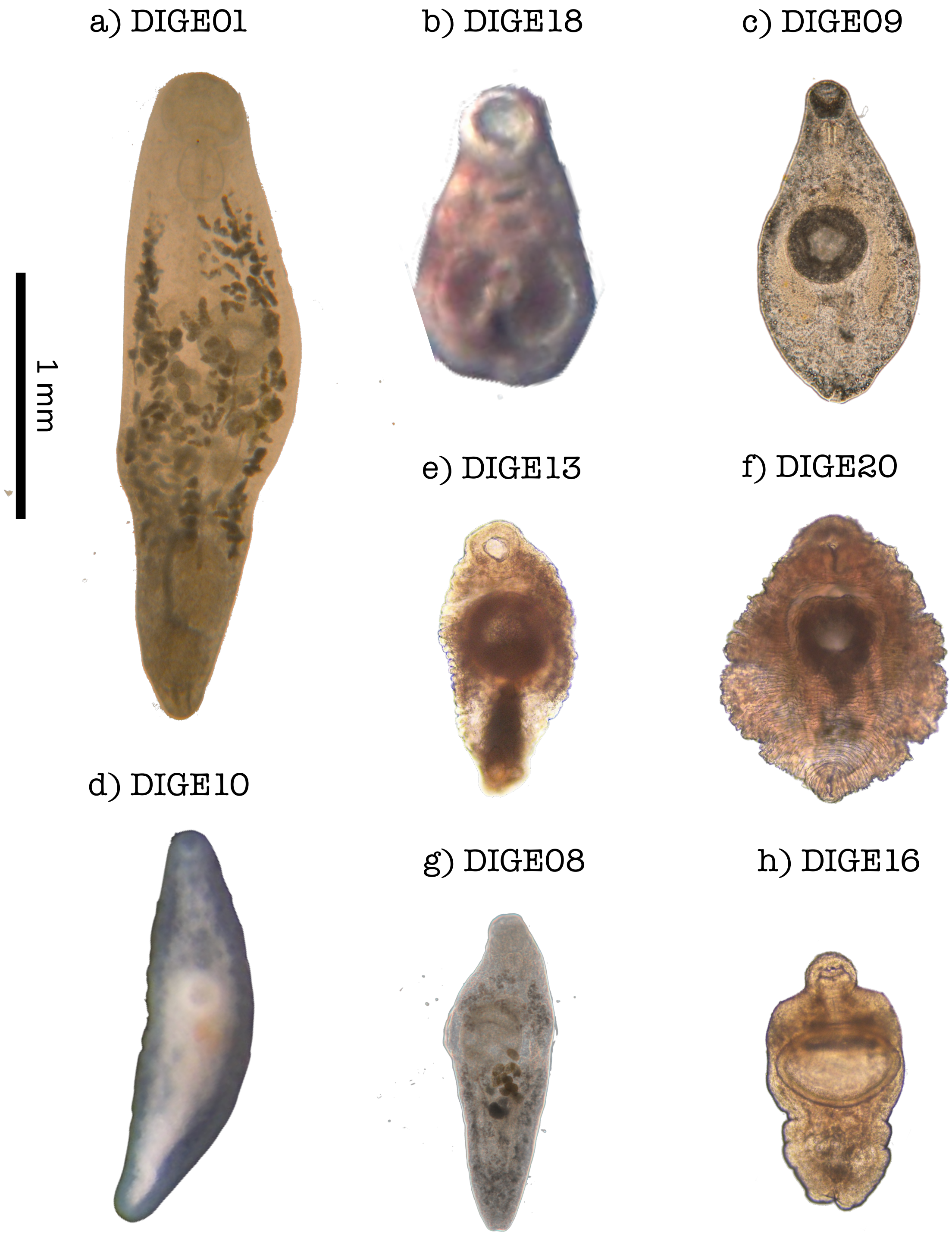

Figure 4-2: Images of the adult parasite morphotypes included in phylogenetic analyses. The scale bar is 1 mm long.

Figure 4-3: Images of the intermediate life stage morphotypes included in phylogenetic analyses. The metacercariae META01 (a) and META08 (b) are shown both encysted (left) and excysted (right). The scale bar for the metacercariae and the sporocyst is 400 μm, and the scale bar for the cercaria is 200 μm.

The rest of the adult and metacercarial morphogroups cluster within a sister group to Opecoelidae, Xiphidiata *incertae sedis* (Sokolov et al., 2019). This group contains species morphologically and genetically consistent with genera *Biospeedotrema* and *Caudotestis*. The four adult morphospecies DIGE09 (Fig. 4-2c), DIGE10 (Fig. 4-2d), DIGE13 (Fig. 4-2e), DIGE20 (Fig. 4-2f) are genetically similar to each other and to metacercaria META01 (Fig. 4-3a) from the shrimp *Alvinocaris lusca*. These morphogroups are genetically identical in the 18S tree (494/494 bp) and 99% (1210/1228 bp) to 100% (1228/1228 bp) similar in the 28S tree. The four adult morphogroups share features with *Biospeedotrema* originally described from vent specimens collected from the Southern East Pacific Rise (Bray et al., 2014). DIGE09 was found only in the gall bladder of *T. cerberus*, and DIGE20 was found in the gall bladders of *T. cerberus* and *T. hollisi*. They are morphologically similar, but differ in their "egg size, vitellaria distribution relative to testes, cirrus pouch extent relative to ventral sucker, and body shape", which is "broadly pyriform or oval" for DIGE09 "vs. squat cf. *B. parajolliveti*" for DIGE20 (Charles Blend, pers comm). DIGE10 and DIGE13 are numerically dominant in the intestine of *T. hollisi*. DIGE10 is distinguished by its long, fusiform body, small ventral sucker, and small oral sucker. DIGE13 is distinguished by its large oral and ventral suckers relative to the other morphogroups in the genus. The body is somewhat fusiform, rounded anteriorly, bulging near the ventral sucker, and tapering posteriorly. This morphogroup has a prominent, dark pigmented Manter's Organ. The morphology of the excysted metacercaria META01 matched most closely to DIGE13, for its large ventral sucker, wrinkled tegument, and dark pigmented area in the posterior body.

It remains unclear whether the new *Biospeedotrema* morphogroups form a complex of closely related species, or whether they are one species with much variation (Charles Blend, pers comm). Based on a subset of stained and mounted specimens, there is considerable variability within each morphospecies in the key feature of the genus. None of the morphogroups can be definitively keyed out as one of the described species, *B. parajolliveti*, *B. biospeedoi*, or *B. thermichthysi*, because the new morphogroups share a mixture of the morphological features of two described species in Bray et al. (2014) (Charles Blend, pers comm). The genetic similarity of the morphogroups discussed above also leaves ambiguities as to the distinctness of the species. The most similar 28S sequences in the NCBI nr/nt database were *B. jolliveti* (28s: KF733985.1) (100% agreement, 1241/1241 bp) and *B. biospeedoi* (28S: KF733986.1) (99% agreement, 1238/1241 bp) from *T. hollisi* from vents on the Southern EPR (Bray et al., 2014). The next closest sequences were *Caudotestis dobrovolski* (28S: MN437379.1) (Sokolov et al., 2020) and *Zdzitowieckitrema incognitum* (28S: MF398366) from the Antarctic fish *Muraenolepis marmorata* collected from the Amundsen Sea, Cooperation Sea, Weddell Sea, and Ross Sea (Sokolov et al., 2019).

A subcluster branching from the *Biospeedotrema* cluster in Xiphidiata *incertae sedis* contains two adult species and one metacercarial type with morphology suggesting *Caudotestis* (Cribb, 2005). These are DIGE01 (Fig. 4-2a) and DIGE18 (Fig. 4-2b) from the vent fish *Thermarces cerberus* and the metacercaria META08 from the polychaete *Branchipolynoe symmitilida* (Fig. 4-3b). The adults share a relatively large, terminal oral sucker, large pharynx, and small ventral sucker. The body is elongate for DIGE01 and pear-shaped for DIGE18. Eggs are small and ovular, located near the ventral sucker. Testes are located posteriorly and are arranged in-line. Based on three stained and mounted specimens, the presence of uterine seminal receptacle and median to sub-median genital pore were confirmed, which is consistent with the genus (Charles Blend, pers. comm.). The metacercaria META08 was morphologically closest with DIGE01 for its elongate body, relatively large terminal to subterminal oral sucker, and relatively small ventral sucker. It had 99% genetic agreement with the adult sequences in the 18S gene (a clean 28S sequence for META08 was not obtained). 28S sequences from the new vent *Caudotestis* species do not group closely with the only *Caudotestis* sequence available in GenBank, *Caudotestis dobrovolski* (28S: MN437379.1) from a Scorpaeniform fish off Simushir Island, Northwestern Pacific Ocean (Sokolov et al., 2020) (98% agreement (1180/1202 bp), bootstrap support value = 100). The inconsistency among new molecular evidence suggests the characters of the genus may require revision. One *Caudotestis* species, *C. ventichthysi*, has been described from an EPR vent fish (Bray et al., 2014), but no sequence is available for this species. Formal comparisons of these morphogroups to nominal species of the genus are still ongoing.

The single cercarial morphotype with a high-quality consensus sequence fell within Opecoelidae but was genetically distant from the vent species (96% agreement (460/477 bp) with DIGE08). It was most closely related to *Opegaster ditrematis* (18S: KY471300.1) (99% agreement (491/497 bp), bootstrap support value = 95) from the South China Sea, Malaysia (Elshawesh et al. unpublished). These formed a clade with *Magnaosimum brooksae* (MG813906.1) and *Paci-*

Parasite Morphospecies	Host Species	n	Prevalence	Intensity	Sequences
ADULT					
DIGE09 (*Biospeedotrema*)	*Thermarces cerberus*	11	91	1-25 (8.2)	28S (2)
DIGE10 (*Biospeedotrema*)	*Thermichthys hollisi*	24	64	1-144 (72.1)	18S (3), 28S (4)
DIGE13 (*Biospeedotrema*)	*Thermichthys hollisi*	24	77	1-113 (34.2)	18S (3), 28S (1)
DIGE20 (*Biospeedotrema*)	*Thermarces cerberus*	11	18	10-11 (10.5)	
	Thermichthys hollisi	24	38	1-59 (19.1)	18S (2)
DIGE01 (*Caudotestis*)	*Thermarces cerberus*	11	64	1-6 (3.6)	18S (2)
DIGE18 (*Caudotestis*)	*Thermarces cerberus*	11	9	51 (51.0)	18S (2), 28S (2)
DIGE08 (*Neolebouria*)	*Thermarces cerberus*	11	73	2-120 (26.9)	18S (2), 28S (1)
DIGE16 (*Neolebouria*)	*Thermarces cerberus*	11	18	3-131 (67.0)	18S (2), 28S (1)
DIGE11	*Thermichthys hollisi*	24	45	1-8 (4.5)	
METACERCARIA					
META01 (*Biospeedotrema*)	*Alvinocaris lusca*	10	90	1-344 (107)	18S (2), 28S (3)
	Bythograea thermydron	36	3	1 (1.0)	
META08 (*Caudotestis*)	*Branchipolynoe symmytilida*	23	4	1 (1.0)	18S (1)
META04	*Branchipolynoe symmytilida*	23	4	1 (1.0)	
META05	*Amphisamytha galapagensis*	94	18	1-7 (2)	
	Archinome rosacea	71	4	4-10 (6.3)	
	Bathymargarites symplector	99	4	1-4 (2.0)	
	Bythograea thermydron	36	3	2 (2.0)	
	Lepetodrilus ovalis	38	3	2 (2.0)	
	Nicomache sp.	1	100	3 (3.0)	
	Thermiphione risensis	6	33	3 (3.0)	
META06	*Branchinotogluma sandersi*	14	7	3 (3.0)	
	Lepetodrilus ovalis	38	3	3 (3.0)	
	Polychaete sp.	3	67	4-5 (4.5)	
	Thermiphione risensis	6	17	6 (6.0)	
META11	*Nereis sandersi*	7	14	1 (1.0)	
META14	*Bathymargarites symplector*	99	2	1-2 (1.5)	
	Nicomache sp.	1	100	1 (1.0)	
CERCARIA					
CERC01	NA	NA	NA	NA	18S (1)
CERC02	NA	NA	NA	NA	
CERC03	NA	NA	NA	NA	
SPOROCYST					
SPOR01 (*Neolebouria*)	*Eulepetopsis vitrea*	100	5	1 (1.0)	18S (5), 28S (5)

Table 4.1: Prevalence and intensity (range and average) of the digenean species and life stages encountered during dissections of vent host species.

Table 4.2: Collection location and host data for specimens with genetic sequences. Latitude and longitude in decimal degrees, depth in meters.

Parasite Species	Host ID	Cruise	Dive	Site	Latitude	Longitude	Depth	Gene	Sequences
ADULT									
DIGE09 (*Biospeedotrema*)	*Thermarces cerberus* 11	RR2102	J2-1318	Crab Spa	9.83992536	-104.2915604	2511	28S	28S.THCE11.09.03.LSU5
	Thermarces cerberus 12	RR2102	J2-1318	Crab Spa	9.83992536	-104.2915604	2511	28S	28S.THCE12.09.01.LSU5
DIGE10 (*Biospeedotrema*)	*Thermichthys hollisi* 01	RR2102	J2-1311	L Vent	9.7712087	-104.2791306	2530	18S	18S.THHO01.10.02 18S.THHO01.10.03 18S.THHO01.10.05
								28S	28S.THHO01.10.02.LSU5 28S.THHO01.10.03.LSU5 28S.THHO01.10.05.LSU5 28S.THHO01.10.06.LSU5
DIGE13 (*Biospeedotrema*)	*Thermichthys hollisi* 01	RR2102	J2-1311	L Vent	9.7712087	-104.2791306	2530	18S	18S.THHO01.13.01 18S.THHO01.13.02 18S.THHO01.13.03
								28S	28S.THHO01.13.01.LSU5
DIGE20 (*Biospeedotrema*)	*Thermichthys hollisi* 02	RR2102	J2-1312	V Vent	9.78793175	-104.2830233	2513	18S	18S.THHO02.20.01 18S.THHO02.20.02
DIGE01 (*Caudotestes*)	*Thermarces cerberus* 01	AT37-12	A4897	Crab Spa	9.83997072	-104.2915493	2506	18S	18S.THCE01.01.02 18S.THCE01.01.03
DIGE18 (*Caudotestes*)	*Thermarces cerberus* 05	AT42-21	A5047	Tica Vent	9.8401303	-104.2916867	2519	18S	18S.THCE05.18.02 18S.THCE05.18.03
								28S	28S.THCE05.DIGE18.01.LSU5 28S.THCE05.DIGE18.01.ZX1
DIGE08 (*Neolebouria*)	*Thermarces cerberus* 02	AT37-12	A4897	Crab Spa	9.83997072	-104.2915493	2506	18S	18S.THCE02.08.02 18S.THCE02.08.03
								28S	28S.THCE02.DIGE08.01
DIGE16 (*Neolebouria*)	*Thermarces cerberus* 05	AT42-21	A5047	Tica Vent	9.8401303	-104.2916867	2519	18S	18S.THCE05.16.01 18S.THCE05.16.03
								28S	28S.THCE05.DIGE16.01.LSU5
METACERCARIA									
META01 (*Biospeedotrema*)	*Alvinocaris lusca* 05	RR2102	J2-1320	Crab Spa	9.83995872	-104.2915527	2507	28S	28S.ALLU05.META01.01.ZX1 28S.ALLU05.META01.02.ZX1
	Alvinocaris lusca 07	RR2102	J2-1320	Crab Spa	9.83995872	-104.2915527	2507	18S	18S.ALLU07.META01.01 18S.ALLU07.META01.02
								28S	28S.ALLU07.META01.01.LSU5
META08 (*Caudotestes*)	*Branchipolynoe symmytilida* 09	AT42-21	A5048	Teddy Bear	9.8417595	-104.291813	2521	18S	18S.BRSY09.META08
SPOROCYST									
SPOR01 (*Neolebouria*)	*Eulepetopsis vitrea* 018	AT42-21	A5047	Tica Vent	9.8401505	-104.2917156	2518	18S	18S.EUVI018.SPOR01
								28S	28S.EUVI018.SPOR01.LSU5 28S.EUVI018.SPOR01.ZX1
	Eulepetopsis vitrea 025	RR2102	J2-1305	Tica Vent	9.84007461	-104.291608	2515	18S	18S.EUVI125.SPOR01
								28S	28S.EUVI125.SPOR01.ZX1
	Eulepetopsis vitrea 036	RR2102	J2-1307	Riftia Mound	9.83827047	-104.2913152	2515	18S	18S.EUVI036.SPOR01
								28S	28S.EUVI036.SPOR01.ZX1
	Eulepetopsis vitrea 061	RR2102	J2-1309	V Vent	9.78797617	-104.2829808	2514	18S	18S.EUVI061.SPOR01
								28S	28S.EUVI061.SPOR01.ZX1
	Eulepetopsis vitrea 071	RR2102	J2-1318	Tica Vent	9.84005326	-104.2916205	2515	18S	18S.EUVI071.SPOR01
CERCARIA									
CERC01	NA	AT37-12	A4896	P-vent	4625	77993	2506	18S	18S.CERC01.182.01

ficreadium serrani (KU320589.1) (bootstrap support value = 79). The close association with shallow-water species from the Western Pacific could indicate either that additional digenean diversity at vents remains undiscovered or that it was captured accidentally during transit through the non-vent environment.

4.5 Discussion

4.5.1 Evidence for the completion of indirect life cycles in an isolated ephemeral habitat

Digenean early life stages in vent invertebrates match genetically and morphologically to adult life stages in vent fish, which provides preliminary evidence that vent parasites very likely complete all steps of a three-host life cycle in active vent habitat. Matching of parasite life stages indicates potential intimate and durable feeding relationships between vent-endemic species. The metacercaria META01 (*Biospeedotrema*), found encysted in high densities in the vent shrimp *Alvinocaris lusca*, was genetically identical to the adult species DIGE09, DIGE13, DIGE10, and DIGE20 in Genus *Biospeedotrema*. Species of this genus are mostly found in the vent fish *Thermichthys hollisi*, with the exception of DIGE09, which lives in the gall bladder of *Thermarces cerberus* (Table. 4.1). *T. hollisi* lives and feeds in the periphery of active venting habitat (Buckman, 2009), and very likely obtains its heavy infections by eating shrimp and other crustaceans. The metacercaria META08 (*Caudotestis*), was found in the commensal scaleworm *Branchipolynoe symmitilida* living inside a *Bathymodiolid* mussel. This metacercaria matches most closely both genetically and morphologically to DIGE01 (*Caudotestis*) from the Zoarcid fish *Thermarces cerberus*. This indicates that the Zoarcid vent fish, which live mainly in intermediate to high-flux zones, are infected by eating small polychaetes. Since commensal scaleworms are protected by the mussel host and are therefore difficult for predators to access, this host may have been a “dead end” for transmission. It is unknown whether *T. cerberus* feeds on vent mussels, but it is unlikely the fish would be able to access the tissue inside a living adult mussel. This parasite species likely completes its life cycle by using a broader range of polychaetes in the vent community.

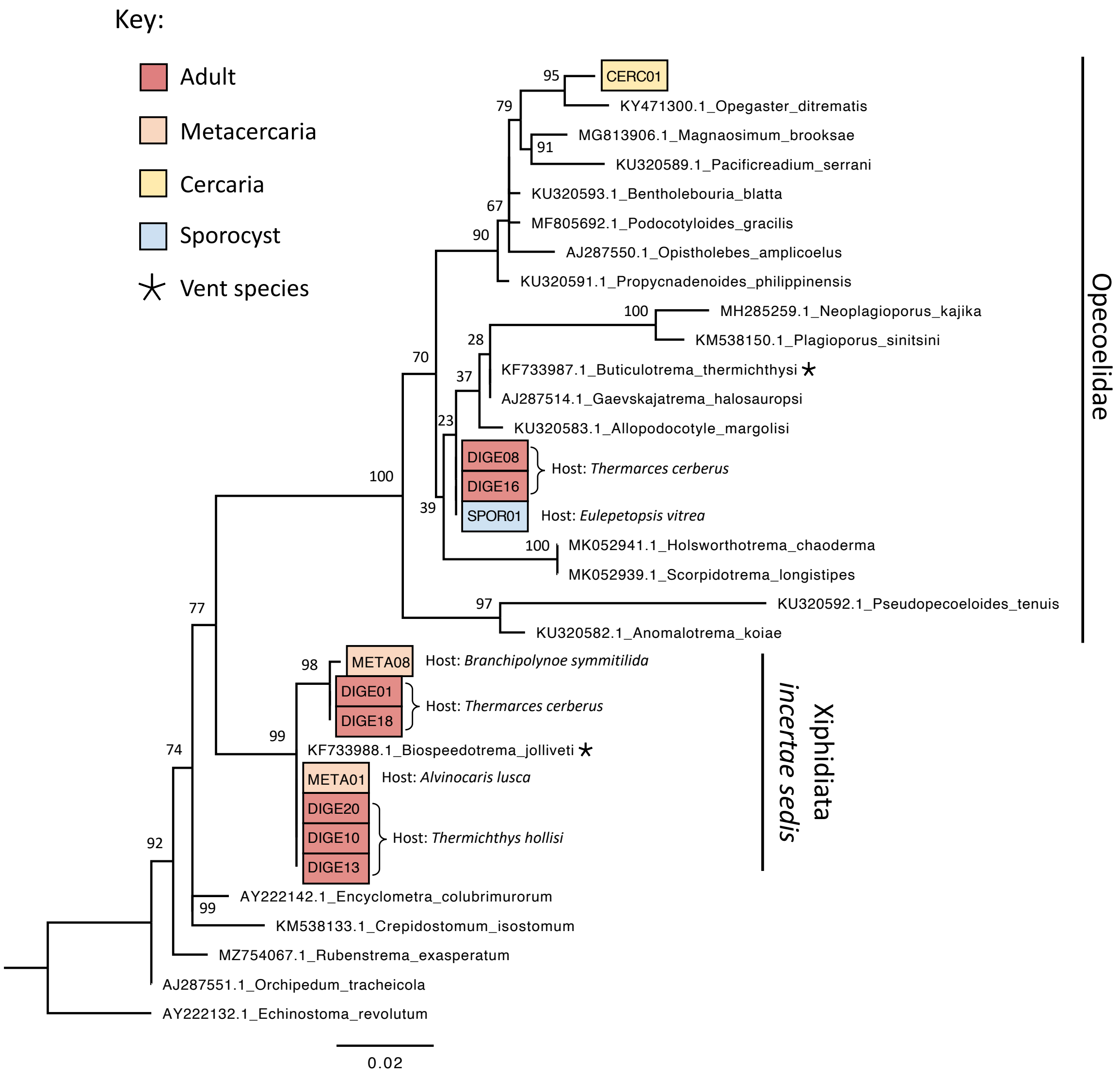

Figure 4-4: Phylogenetic tree resulting from maximum likelihood analysis of the partial 18S rDNA alignment. This analysis includes species closely-related to the new vent material, other known deep-sea genera, and *Echinostoma revolutum* as an outgroup. Support values were generated with 10,000 bootstraps. The new vent parasite species are shown in colored boxes with the life stages color coded, and the host species is listed to the right. Previously-described vent digenean species are denoted with an asterisk (*). The scale bar indicates the expected number of substitutions per site.

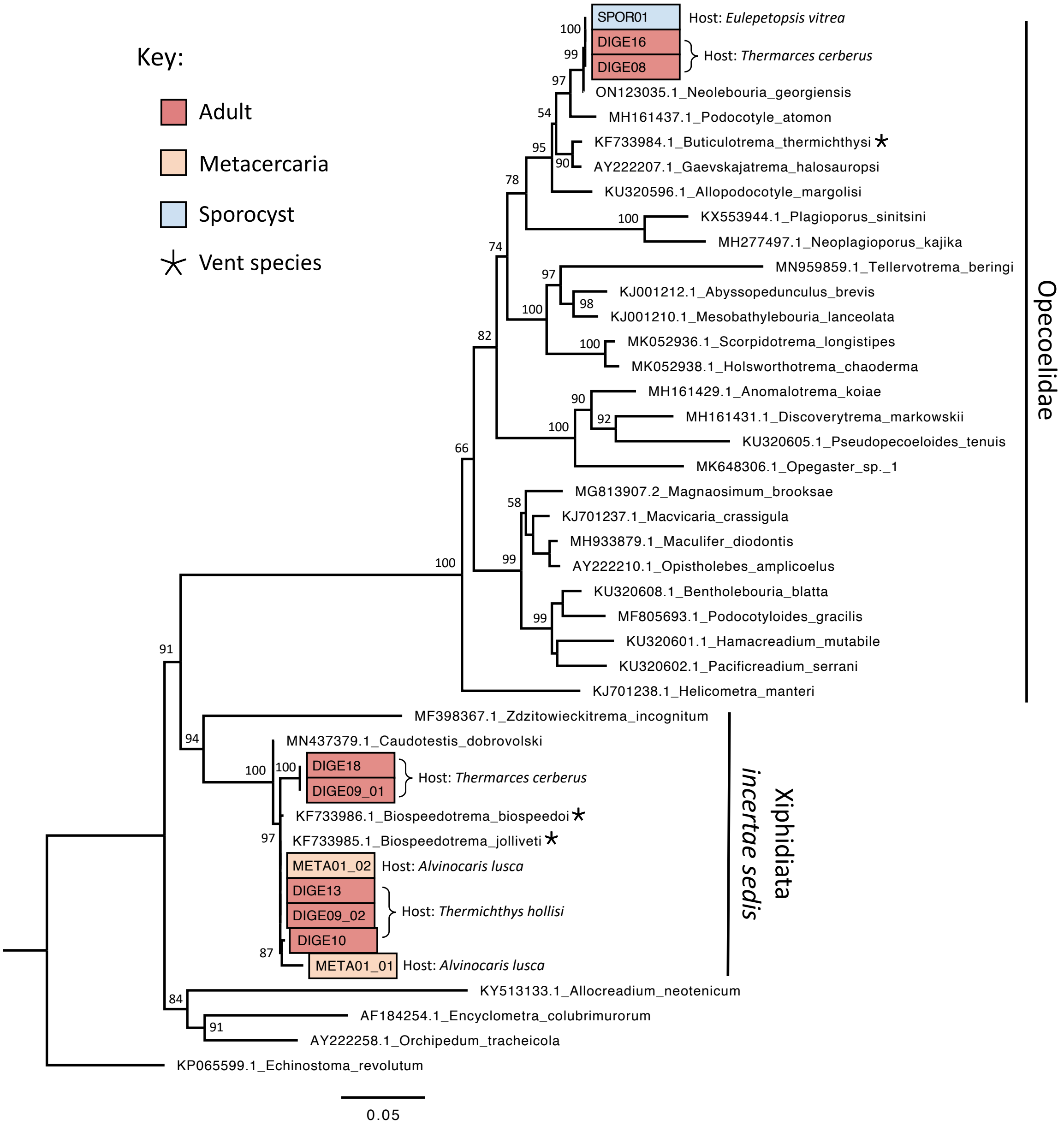

Figure 4-5: Phylogenetic tree resulting from maximum likelihood analysis of the partial 28S rDNA alignment. This analysis includes species closely-related to the new vent material, other known deep-sea genera, and *Echinostoma revolutum* as an outgroup. Support values were generated with 10,000 bootstraps. The new vent parasite species are shown in colored boxes with the life stages color coded, and the host species is listed to the right. Previously-described vent digenean species are denoted with an asterisk (*). The scale bar indicates the expected number of substitutions per site.

The only sporocyst discovered in the vent community, SPOR01 (*Neolebouria*), matches genetically with the adult species DIGE01 and DIGE18 in Genus *Neolebouria*. The second intermediate host in this life cycle remains an unresolved question, since none of the metacercariae matched *Neolebouria* genetically or morphologically. The linking of a sporocyst to a metacercaria was the only link in the life cycle missing in this study, but would provide useful information on species interactions and habitat suitability for parasite transmission. Transmission between the first and second intermediate host is by free-living cercaria larvae, which have a very short planktonic duration (~ 24 hr) and are sensitive to chemical and thermal stress. *E. vitrea* and the small invertebrates found to host metacercariae inhabit the cooler peripheral zones of the vent field (Mills et al., 2007), which may partly explain their suitability as hosts for parasite stages that transmit as larvae. In other ecosystems, high reduced sulfur and heavy metal concentrations damage free-living parasite stages (Cross et al., 2001; Tobler et al., 2007), although some parasites can tolerate such conditions (Riesch et al., 2020). It is possible that the harsh chemical environment at vents provides a "refuge" from parasitism for those species adapted to life in high-flux zones. Further sampling to resolve the within-site distribution of parasite life stages will help clarify the role of thermal and chemical zonation in structuring areas of heightened parasite transmission within the vent field.

Although evidence indicates that digenean parasites very likely complete their life cycles at vents, several factors prevented the description of a single complete life cycle. To date, we have only successfully sequenced a subset of the morphogroups and life stages discovered. In some cases, this was due to small sample sizes and tissue volumes, especially for metacercariae. Some morphogroups did not amplify well with the given primers and PCR protocol. Work to test approaches to extract DNA from very small sample volumes is ongoing, and successful sequences will likely be obtained once a new protocol is optimized. A second, unresolved problem is that several species were morphologically distinct yet genetically identical in the barcoding regions examined. The lack of genetic variation in the 18S and 28S genetic regions between species that are morphologically distinct is unusual but not unheard of in digenean taxa (Martin et al., 2018b). Inconsistencies between different barcoding genes have recently been encountered (Thomas Cribb, pers comm), hinting at a more complicated story in the evolution of different genes within Opecoelidae. If 18S and 28S are insufficient to detect species-level differences in vent digenean taxa, they cannot be applied to match life stages within a specific species. The ITS2 and Cox1 genes may be more effective at resolving species (Martin et al., 2017) and will be the focus of future investigation. Sequences will also be obtained from a greater number of individuals in each morphogroup to capture intra- and interspecific variation. Finally, although this was a comprehensive survey for vent digenean life stages, the intermediate life stages were often at low prevalence ($\sim 5\%$), and additional sampling at vents is encouraged to collect a greater sample size for sequencing. Specifically, only one sporocyst morphogroup was encountered, and more would need to be found to demonstrate multiple trematode species complete life cycles at vents. Further sampling should target the small invertebrates that inhabit intermediate zones, particularly the gastropods that may host sporocysts. With further sampling and protocol development, it is very likely that a complete life cycle will be described for a vent parasite species.

4.5.2 Phylogenetic evidence for the origins of vent digenean diversity

Phylogenetic analysis suggests that digenean diversity at EPR 9N vents arose from multiple founder events with potential host-switching. First, a clade of closely related species in the genera *Biospeedotrema* and *Caudotestis* span a geographic range of at least 3,000 kilometers along the East Pacific Rise (Bray et al., 2014). The range of this clade along the EPR and the genetic similarity between species suggests connectivity of mobile fish hosts between distant vent fields on evolutionary timescales. Ancestors of this clade may have been introduced to vents with ancestors of *T. hollisi*, spread geographically, and radiated within the vent environment. The partitioning of parasite fauna between the two vent fish species is consistent with evidence that the two fish species have distinct diets and occupy different habitats (Buckman, 2009). The preference of *T. hollisi* for peripheral habitats might indicate it is more comfortable moving between vent fields than the Zoarcid *T. cerberus*, which could explain the 3,000 km known geographic range of the parasite genera inhabiting *T. hollisi*. *Biospeedotrema* species have so far only been found at vents, so it remains possible this genus is endemic to vents. Collections of non-vent fish species from nearby seafloor habitats are needed to clarify the endemicity of *Biospeedotrema* species to vent ecosystems.

A second group of vent digenean species in the genus *Neolebouria* appear to have originated independently from the *Biospeedotrema/Caudotestis* clade, and provide a glimpse into an intriguing evolutionary story. The vent species DIGE08 and DIGE16 are very closely related to *Neolebouria georgiensis* from a grenadier fish in Antarctic waters. The ecological and geographic distance between our vent species and *N. georgiensis* is noteworthy given their genetic similarity. This might suggest the genus is globally distributed and some species are very generalist. Introduction into the vent environment could have occurred with the ancestors of *T. cerberus*, or a more recent host-switching event from more generalist deep-sea fishes. We also know that the first intermediate host in this life cycle is the glass limpet *E. vitrea*, which provides an important link in the story, yet leaves the open puzzle as to when and how *Neolebouria* invaded chemosynthetic limpets. The genus *Eulepetopsis* (Family Neolepetopsidae) currently contains only two species, *Eulepetopsis vitrea* from the East Pacific Rise, and *Eulepetopsis crystallina* from the Central Indian Ridge (Chen et al., 2022), both of which are endemic to active venting habitats. All three genera in family Neolepetopsidae (*Eulepetopsis*, *Paralepetopsis*, and *Neolepetopsis*) are endemic to chemosynthetic seafloor features, including active vents and inactive sulfide mounds (Chen et al., 2022). The exploitation by digeneans of a gastropod family that is endemic to chemosynthetic ecosystems is intriguing and unexpected. The possibility that *Neolebouria* diversity at vents arose from cospeciation with an ancestral Neolepetopsid species should be explored further. A host switch into a chemosynthetic limpet remains possible (Araujo et al., 2015), but may present an evolutionary challenge: in species introductions and range expansions, ILC parasite species often cannot establish until a suitable first intermediate host is introduced, as reviewed in Bauer & Hoffman (1976). If some aspect of *E. vitrea*, whether in evolutionary history or physiology, makes this a viable host for sporocysts, this species should be sampled further, since some gastropod species are first intermediate hosts for many digenean species (Kuris, 1990). Investigation of other Neolepetopsid species from chemosynthetic habitats would provide greater insight into the route of invasion of *Neolebouria* species into vent ecosystems.

Placing the new vent species in a phylogenetic context hints at two potential host-switching events that may have occurred during diversification in vent ecosystems. First, most *Biospeedotrema* species parasitize *T. hollisi*, except for DIGE09 (*Biospeedotrema*), which inhabits the gall bladder of the Zoarcid *T. cerberus*. Second, two *Caudotestis* species appear to have branched from the *Biospeedotrema* clade in *T. hollisi*, but instead parasitize *T. cerberus*. Since this study looks only at barcoding genes, which may not sufficiently resolve more recent evolutionary changes, these lines of inquiry remain speculation. In the future, comparison of hosts and their parasites across a broader geographic range, including vent and nearby non-vent host species, would help clarify the host specificity and potential origins of vent parasite species. Genomic techniques that can estimate the time of evolution into the vent environment of parasites and their hosts (e.g., Sun et al. 2019) would help clarify the relative times of transition between host species, and the role of different hosts as vectors for introduction.

4.6 Conclusions

This study demonstrates parasite species with indirect life cycles persist and reproduce in a frequently disturbed, isolated ecosystem. The matching of life stages points towards intimate and durable feeding relationships between vent fish and invertebrate prey. Phylogenetic comparison to closely related deep-sea species suggests at least two separate ancestral digenean clades were introduced to the vent environment. The large known geographic range and close genetic relatedness of species in one of these clades suggests considerable connectivity between vent fields on the East Pacific Rise. Greater detail on the host requirements and evolutionary origins of vent parasites are limited by the amount of available data on deep-sea parasites. Similar sampling efforts should be conducted at vent fields along the East Pacific Rise to better understand parasite species ranges, connectivity, and potential routes of introduction into the vent environment.

4.7 Acknowledgements

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Chapter 5

Disturbance and habitat configuration drive parasite persistence and adaptation in island-like habitats

5.1 Abstract

Parasites rely on hosts, which are island-like, ephemeral resources. Hosts, in turn, often live in metapopulations, distributed among discrete habitat patches connected by dispersal and subject to local extinction events due to habitat disturbance. Parasites may be more vulnerable to habitat disturbance than their hosts since they are affected both directly, through increased mortality, and indirectly, through reduced host density (which reduces transmission). Parasites also impact their host by increasing mortality or eliminating reproduction, leading to potential shifts in optimal parasite strategies as disturbance intensifies. Here, I address the question: How do parasite colonization potential (good colonizer versus poor colonizer) and mode of host impact (increasing mortality versus castration) interact to influence occupancy, persistence, and adaptation under different disturbance scenarios in island-like habitats? I compare a spatially implicit patch occupancy model to a spatially explicit, stochastic cellular automaton model. The spatially explicit model tracks changes in parasite occupancy (fraction of habitable cells occupied) in networks of habitat patches connected by dispersal, both on

the level of individual patches and at the landscape level. I also impose a tradeoff between colonization and impact on the host, such that parasites that harm their hosts more are also more effective colonizers. In this model, parasites reached the highest occupancy in infrequently disturbed habitats by being poorer colonizers and minimizing their impact on the host, and in frequently disturbed habitats by being better colonizers at the cost of harming hosts more. Castrators reached higher occupancy than mortality inducers overall, but they were more negatively impacted by disturbance, especially in island-like habitats. For this reason, the occupancies of castrators and mortality inducers were similarly low at high disturbance frequencies, and both went extinct at similar disturbance frequencies. Of the parasite strategies compared, mortality inducers that are poor colonizers went extinct first, and castrators that are good colonizers persisted under the highest disturbance frequencies. Despite slight differences in persistence between the parasite strategies explored, all persisted across a broad range of disturbance frequencies. This result is consistent with the observation that a range of parasite taxa and consumer strategies are found in isolated ephemeral habitats like deep-sea vents. Disturbance showed a strong effect on adaptive dynamics, making it easier for mutant phenotypes that are better colonizers to invade, while habitat isolation had no discernible impact on adaptation in this model. These results help interpret observed patterns in parasite diversity in disturbed habitats, and build predictions for which types of parasites will remain if disturbance or fragmentation intensifies.

5.2 Introduction

Habitat patchiness and disturbance are important regulators of species diversity and abundance (Simberloff & Wilson, 1969; Dayton, 1971; Denslow, 1980; Caswell & Cohen, 1991b; Hill & Caswell, 1999), particularly for species like parasites with strict feeding and habitat niches (Steadman et al., 1990; Morand & Guégan, 2000; MacLeod et al., 2010; Resasco et al., 2019; Lafferty & Kuris, 2005). Isolation and disturbance can impact parasites directly, by impeding dispersal and causing direct mortality (Ebert et al., 2004; Hanke et al., 2021), or indirectly, by decreasing the density of hosts through the same mechanisms (Bitters et al., 2022). Since hosts are essentially small ephemeral islands (Kuris et al., 1980), parasites live in isolated, disturbed habitat on two scales. Importantly, parasites can impact the individual longevity and population density of their host by increasing mortality or decreasing reproductive output (Scott & Dobson, 1989; Fredensborg et al., 2006; Lafferty & Kuris, 2005). The feedback between parasite and host is likely to result in complex outcomes in the ability of parasite species to persist under frequent disturbance and may drive distinct adaptive dynamics for parasite life history traits under different disturbance scenarios.

Despite the apparent challenges of life as a parasite in island-like, disturbed habitats, parasites are still found in such settings, including ephemeral tidal pools (Bengtsson & Ebert, 1998; Ebert et al., 2001), seasonal pools in the African Savannah (Nezhybova et al., 2017), and disturbed deep-sea hydrothermal vents (Thesis Chapter 3). What biological traits allow some parasites to exploit such habitats? Both theoretical (Morand & Guégan, 2000) and observational (Bataille et al., 2018) studies suggest that island habitats filter for certain types of parasites based on their life history traits. For example, in field studies, parasites with traits to make them good colonizers (i.e., rapid larval output, high transmission) are more effective at establishing after introduction to islands (Clark & Clegg, 2015), and more readily avoid stochastic extinctions when host populations are still small (MacLeod et al., 2010). High colonization rates are increasingly important as disturbance intensifies because disturbed habitat patches must be recolonized from undisturbed neighboring patches quickly enough to prevent extinction in the habitat network. Both experiment and theory show parasites whose interactions with hosts are constrained to a more local scale evolve lower virulence (Boots & Mealor, 2007; Webb et al., 2007). Theory also predicts that parasites in island-like habitats would evolve to minimize their impact on hosts, because higher mortality is more likely to cause host extinction in a small habitat area (Wikelski et al., 2004), thus removing the resource the parasite relies on (Morand & Guégan, 2000). Despite this evidence, it is still unclear how habitat isolation and disturbance interact to drive parasite populations on large scales, or whether they impose different adaptive pressures on parasite life history traits.

Several key parasite life history traits are likely to interact to influence colonization, establishment, and persistence on disturbed islands. One primary difference between parasites is the nature of the parasite's impact on the host, imposed partially by the tissue the parasite targets. Some parasites exploit host somatic tissue, causing pathology and increasing host mortality as the parasite takes more resources. Parasites that increase mortality include some pathogens, microparasites, macroparasites, and parasitoids (Lafferty et al., 2015). Others exploit host reproductive tissue (i.e., castrators), which compromises or eliminates the host's ability to reproduce (Kuris, 1974; Hurd, 2001; Lafferty & Kuris, 2009). These strategies have distinct demographic consequences for parasite-host population dynamics. However, these strategies are seldom compared, and their consequences for persistence and adaptation in isolated and disturbed habitats is not known. Another key life history trait parasites might maximize is the tradeoff between their colonization ability (transmission) and the level of harm to the host (virulence). Since parasites take resources from the host to fuel their own growth and reproduction, there is a theorized tradeoff between the parasite's reproductive output and the damage it causes to its host (Anderson & May, 1982; Roff, 1993; O'Keefe & Antonovics, 2002). This tradeoff has been extensively demonstrated experimentally in viruses and microparasites (Ewald, 1983; Laine & Barrès, 2013; Ben-Ami, 2017) and is beginning to be empirically demonstrated in macroparasites (Davies et al., 2001; Medica, 2002). It is unknown how disturbance or habitat configuration affect the relative persistence of parasites when their energetics are constrained by limited host resources.

Here, I investigate whether island-like, disturbed habitats select for different types of parasites than habitats that are unstructured or undisturbed. Hereafter in this study, I use "parasite strategy" to mean a combination of the expression of two traits: the nature of impact on the host (castrator versus mortality inducer), and the colonization coefficient (a continuous range, but often referred to as "poor" or "good" colonizer for simplicity). Similarly, I define "parasite type" to mean a parasite species or set of species with a certain combination of traits, for example, parasites that are "castrators and good colonizers." To interpret the origins of parasite diversity on disturbed islands, I consider both ecological and evolutionary processes (Cornuault et al., 2012). On ecological timescales, if a parasite species is introduced to a habitat with its host, the parasite with its current set of traits will either persist under the environmental conditions or go extinct (MacLeod et al., 2010). If the parasite species can persist after introduction, it may evolve in its new setting if slight variations in its traits confer a competitive advantage against the dominant phenotype.

Mathematical models have been used extensively to explore the impact of habitat fragmentation and disturbance on parasite occupancy (Gubbins & Gilligan, 1997; Keeling, 1999; McCallum & Dobson, 2002; Hiebeler & Morin, 2007; Webb et al., 2007; Jesse et al., 2008; Su et al., 2009; Reigada et al., 2015; White et al., 2018), yet very few compare multiple parasite strategies with the aim of explaining diversity patterns in biological communities. Most models focus on either castrators or mortality inducers, without comparing the dynamics of these two strategies that are common in nature. Even fewer explore interactive effects between isolation and disturbance, even though most habitats in nature are becoming more fragmented and disturbed (Chase et al., 2020). Due to the wide taxonomic and functional diversity of parasites in most biological communities, including those of economic and cultural importance (Kuris et al., 2008; Behringer et al., 2020; Godwin et al., 2021; Morton et al., 2021), current patterns and future change in parasite distribution can only be interpreted with a flexible framework that compares parasite species with different combinations of traits and effects on host demographics.

I use mathematical and computational models to compare parasites with different combinations of traits related to colonization capability and the nature of their impact on the host. I impose an energetic tradeoff in parasite traits by assuming parasites that transmit more effectively (i.e., produce more larvae or larvae more competent at colonizing hosts) also harm their host more by consuming more host resources (Fig. 5-1) (i.e., Alizon & van Baalen 2005, Ben-Ami 2017). First, I hypothesize that mortality inducers will be less able to persist under frequent disturbance than castrators because they impose an additional source of host mortality. Second, I hypothesize that infrequent disturbance will favor parasites that decrease colonization and harm to the host, whereas frequent disturbance will favor parasites that increase colonization and harm to the host. Third, I expect disturbance and island-like habitats will shift adaptive dynamics, but in opposing directions: disturbance will favor the evolution of parasites with higher transmission and virulence (Alizon & van Baalen, 2005; Nidelet et al., 2009), while island habitats will drive evolution towards "prudent" strategies with low virulence and low transmission (Claessen & de Roos, 1995; Morand & Guégan, 2000; Boots & Mealor, 2007) (Fig. 5-1). I expect these opposing forces will compete, but which will dominate dynamics under different scenarios is an open question this study will address.

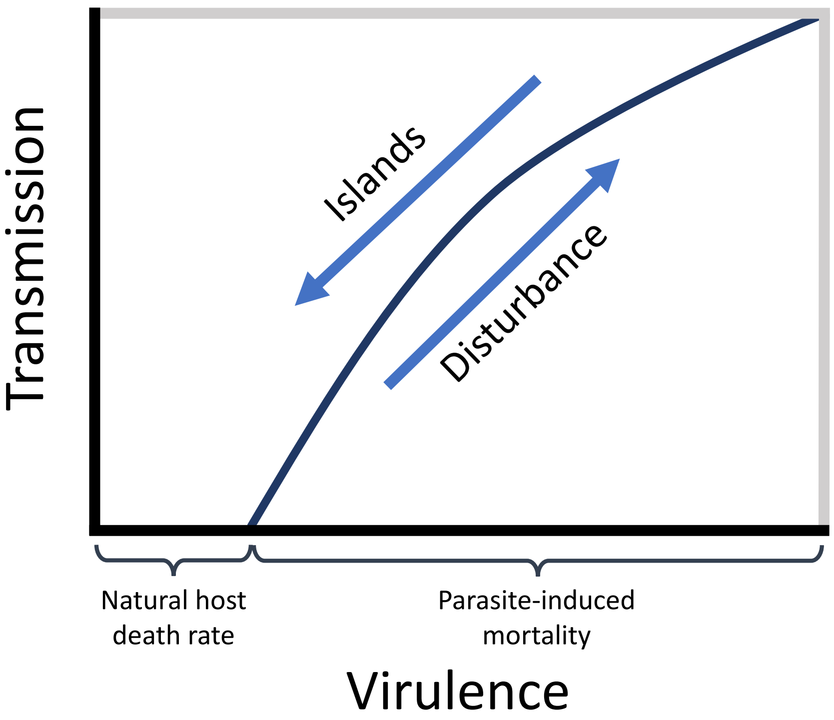


Figure 5-1: A conceptual diagram for how islands and disturbance will influence parasites whose traits fall on the classic transmission-virulence tradeoff (adapted from Alizon & van Baalen 2005). Disturbance will favor parasites with higher transmission and virulence (Alizon & van Baalen, 2005; Nidelet et al., 2009), and lead to evolution in the same direction, whereas islands will have the opposite effect (Claessen & de Roos, 1995; Morand & Guégan, 2000; Boots & Mealor, 2007).

5.3 Methods

5.3.1 The patch occupancy model

I develop a patch occupancy model to understand the influence of disturbance on parasite occupancy (number of patches occupied) and persistence (whether the parasite goes extinct). This model includes four patch states with each patch on the scale of an individual host (Table 5.1). In State 0 the patch is suitable and unoccupied; in State 1 the patch is suitable and occupied by an uninfected host; in State 2 the patch is suitable and occupied by a parasitized host; and in State 3 the patch is unsuitable. The dynamics can be described by a system of discrete-time nonlinear equations (Eq. 1, Fig. 5-2):

$$x_0(t+1) = (1-C_h)x_0(t) + \delta_s x_1(t) + \delta_i x_2(t) \tag{1a}$$

$$x_1(t+1) = C_h x_0(t) + (1-\delta_s)(1-C_p)x_1(t) + m_p(1-\delta_i)x_2(t) \tag{1b}$$

$$x_2(t+1) = C_p(1-\delta_s)x_1(t) + (1-\delta_i)(1-m_p)x_2(t) \tag{1c}$$

$$x_3(t+1) = x_3(t) \tag{1d}$$

Here, x_n denotes the proportion of patches in state n (Table 5.1). In this model, I assume new hosts colonizing empty patches are uninfected (i.e., vertical transmission does not occur), and parasites subsequently colonize uninfected hosts from infected hosts, as is common for aquatic species that host macroparasites (McCallum et al., 2004; Giménez-Romero et al., 2022). There are two sources of host mortality: biological mortality (i.e., from old age, predation, etc.) and external disturbance. The mortality rates of susceptible and infected hosts are denoted as δ_s and δ_i, respectively. Host mortality occurs if the host dies naturally, or if the host does not die naturally but there is a disturbance. These equations are: $\delta_s = m_s + D(1-m_s)$ and $\delta_i = m_i + D(1-m_i)$.

In this model, a parasite may die naturally, returning the host to the unparasitized state (x_1). Death of a host, whether from biological mortality or disturbance returns patches occupied by parasitized and unparasitized hosts back to the empty, habitable state (x_0). This model assumes a static proportion of suitable to unsuitable habitat, and suitable habitat can

	Definition
States	
0	suitable, unoccupied
1	suitable, occupied by susceptible host
2	suitable, occupied by infected host
3	unsuitable
Variables	
x_0	proportion of patches in state 0
x_1	proportion of patches in state 1
x_2	proportion of patches in state 2
x_3	proportion of patches in state 3
Parameters	
d_s	colonization coefficient of susceptible host
d_i	colonization coefficient of infected host
d_p	colonization coefficient of parasite
C_h	colonization probability of host
C_p	colonization probability of parasite
m_s	mortality of susceptible host
m_i	mortality of infected host
m_p	mortality of parasite
D	disturbance probability
δ_s	combined sources of mortality for susceptible host
δ_i	combined sources of mortality for infected host

Table 5.1: Definitions of states, state variables, and parameters.

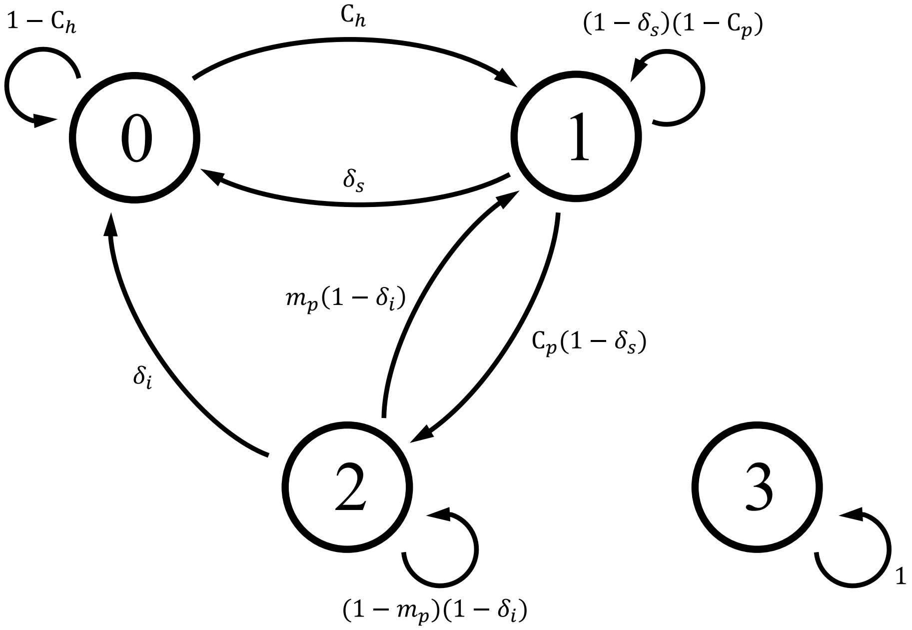


Figure 5-2: Transition diagram for the patch occupancy model. State 0: suitable, unoccupied; State 1: occupied by susceptible host; State 2: occupied by infected host; State 3: unsuitable. Parameters and variables are defined in Table 5.1.

be recolonized immediately after disturbance. Uninfected hosts colonize unoccupied suitable patches (State 0) at a probability C_h. This assumes hosts are relatively sedentary as adults and colonize as dispersive juveniles or larvae as in many marine systems (McCallum et al., 2004). Parasites colonize uninfected hosts (State 1) at a probability C_p. The colonization of an empty patch by a host (C_h) or a host by a parasite (C_p) is described by a Poisson process (Eq. 2) (Hill & Caswell, 1999):

$$C_h = P\left[\text{at least 1 colonist arrives}\right] = 1 - e^{-(d_s x_1(t) + d_i x_2(t))} \tag{2a}$$

$$C_p = P\left[\text{at least 1 colonist arrives}\right] = 1 - e^{-d_p x_2(t)} \tag{2b}$$

The colonization parameters d_p, d_s, and d_i determine the shape of the colonization probability functions of the parasite, susceptible host, and infected host, respectively. For example, a parasite is more likely to colonize a susceptible host if d_p is higher, and is unable to colonize a host if $d_p = 0$. In this model, d_p is an aggregate term that incorporates many biological processes involved in colonizing a host, such as larval output, larval activity or habitat-seeking, and infectivity. The ways in which real parasite species might increase d_p in the context of energetics and adaptation will be considered in the discussion.

5.3.2 The cellular automaton model

A spatially explicit cellular automaton model was developed to compare the impact of disturbance in the spatially implicit patch occupancy model to a scenario in which parasites and hosts live in island-like habitats and dispersal is relatively localized. The environment is a 250 x 250 cell grid where each grid cell can hold an individual host. The landscape is generated by randomly placing circular "islands" of suitable habitat, each with an area of ~ 200 cells (radius $= 8$) on a background of unsuitable habitat such that their edges are at least one grid cell apart. As in the patch occupancy model, the suitable grid cells in the islands are initially randomly assigned in equal proportion to states 0, 1, and 2. To explore the effect of limited dispersal relative to the patch occupancy model, I set the scale of dispersal to allow recolonization of only neighboring islands. To test the influence of habitat configuration, island placement was confined to a sub-area of the grid that can be set as either square or rectangular while maintaining the same total area and island density. This allows comparison of parasite persistence in island-like habitats that are evenly clustered, such as seep habitat or nodules on the abyssal plain, to those arranged along a linear feature, such as a plate boundary or coastline (Fig. 5-3).

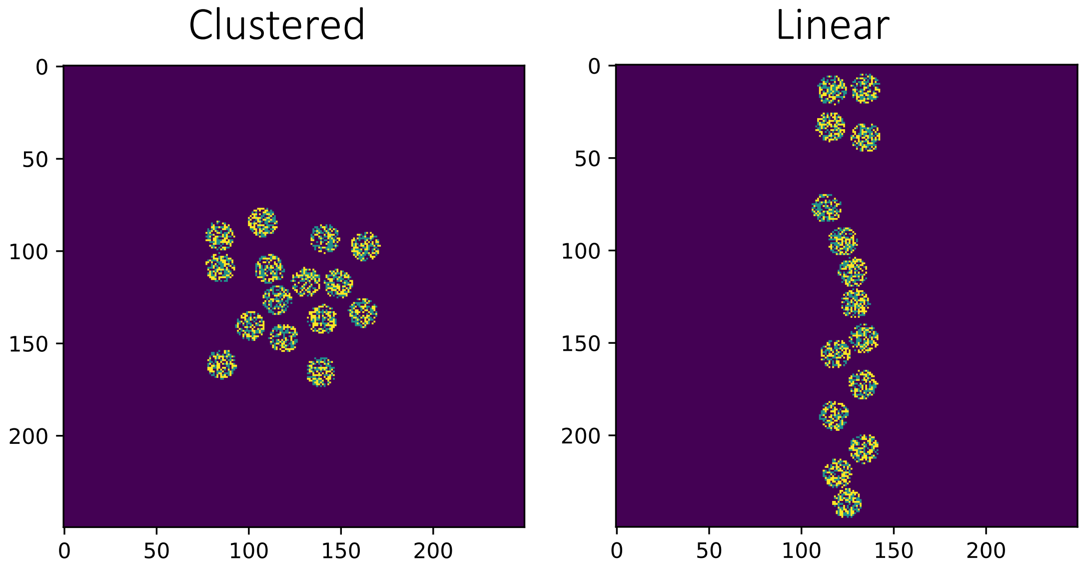


Figure 5-3: Examples of an initial randomly generated landscape with suitable habitat (circles) in clustered (left) and linear (right) configurations. Here, unoccupied grid cells (both suitable and unsuitable) are dark purple, grid cells occupied by an uninfected, susceptible host are light blue, and cells occupied by an infected host are yellow.

The cellular automaton model is stochastic and discrete in time. At each time step, all habitable grid cells are updated simultaneously according to transition rules and probabilities for colonization, mortality, and disturbance. These transitions follow the same rules as in the patch occupancy model, but with several key differences because the model is spatially explicit and stochastic. First, colonization probabilities C_h and C_p are calculated for each grid cell at the beginning of each time step t before any cells are updated, such that colonization probability at time step $t+1$ is based on the state of the grid at time t. C_h and C_p are calculated with the same equations as the patch occupancy model (Eq. 2), except that the proportion of cells contributing host and parasite colonists is calculated within a radius r from the focal cell, rather than the entire landscape. The dispersal radius sets the extent of connectivity across the landscape, anywhere from local ($r = 1$ for the eight nearest neighbors) to completely global ($r = 124$, which is equivalent to the patch occupancy model). In this study, the dispersal radius was set to $r = 15$ such that every island could be recolonized, but only from its nearest neighbors. After colonization probabilities are calculated, cell transitions are based on the relative probabilities of colonization or mortality. Since the probabilities of all possible transitions must sum to one, transitions were determined based on where a random number falls on a uniform distribution in the range 0 to 1.

A key difference from the patch occupancy model is that disturbance occurs in a separate step after the biological processes are complete. Disturbance impacts entire islands by setting all grid cells in an island back to State 0 (unoccupied, suitable). At each time step, each island has an independent, random chance of being disturbed based on whether a number randomly drawn from a uniform distribution between 0 and 1 is less than the disturbance probability D. As in the patch occupancy model, habitable grid cells can be recolonized immediately after disturbance. After the biological dynamics and disturbance have occurred, all cells are updated synchronously, and population data are recorded.

5.3.3 Parasite occupancy and persistence

First, I examine how disturbance influences the occupancy (fraction of habitable patches occupied) and persistence (whether the parasite goes extinct) of castrating and mortality-inducing parasites. I used the patch occupancy model to compute equilibrium occupancy along a range of disturbance frequencies ($D = 0.0$ to $D = 0.3$) and parasite colonization coefficients ($d_p = 0$ to $d_p = 10$) in unstructured habitat. The maximum colonization coefficient explored, $d_p = 10$, was selected as a biologically reasonable upper limit that allowed for parasite persistence based on exploratory sensitivity analyses. I imposed a concave-down relationship between parasite colonization coefficient (transmission) and the impact on the host (virulence) as is broadly used in the literature (Lion & Boots, 2010; Alizon & van Baalen, 2005). The tradeoff function used was $d_i = d_s - (e^{\alpha d_p} - 1)$ for castrators (Fig. 5-5a) and $m_i = m_s + (e^{\beta d_p} - 1)$ for mortality inducers (Fig. 5-5b) based on the tradeoff equation in Lion & Boots (2010). α and

β are arbitrary coefficients that determine the slope, which I set such that no harm is caused to the host when $d_p = 0$ ($d_i = d_s$ for castrators, $m_i = m_s$ for mortality inducers) and maximum harm is caused to the host when $d_p = 10$ ($d_i = 0$ for castrators, $m_i = 1$ for mortality inducers) (Fig. 5-5a&b).

I compared the results of the patch occupancy model to the cellular automaton model to understand whether parasite occupancy or the threshold for persistence shift when habitat is structured as islands. I ran spatial simulations using the same initial conditions and examined four parasite types across the same range of disturbance frequencies. The parasite types were: castrator, poor colonizer ($d_p = 4$); castrator, good colonizer ($d_p = 8$); mortality inducer, poor colonizer ($d_p = 4$); mortality inducer, good colonizer ($d_p = 8$). The parasite colonization coefficients defining "good disperser" and "poor disperser" were based on results of the previous patch occupancy analyses.

In all model runs, 70% of patches were unsuitable ($x_3 = 0.7$), and the remaining 30% of suitable habitat was divided evenly between the three remaining states ($x_0 = 0.1, x_1 = 0.1, x_2 = 0.1$). The model was run for 500 time steps, which was always sufficient to achieve equilibrium (or pseudoequilibrium for the stochastic model) within the parameter space explored. Occupancy at equilibrium of the parasite ($\hat{p}_p$) was calculated at the end of each run as the proportion of patches containing a parasite divided by the proportion of suitable habitat patches: $\hat{p}_p = x_2/(x_0 + x_1 + x_2)$. In all model runs, the following conditions were imposed: $d_s = 2.0$, $m_i = 0.1$, $m_p = 0.1$. The susceptible host colonization coefficient $d_s = 2.0$ was chosen as it was found to be sufficient for host persistence across the disturbance frequencies explored. Mortality rates $m_s = 0.1$ and $m_p = 0.1$ are demographic rates that determine the host and parasite life span. In this model, the parasite has its own mortality rate, so the infectious period does not necessarily last the entire infected host life span, as is true for many macroparasites. These mortality rates were chosen because they are intermediate in the range of disturbance probabilities tested, allowing us to examine disturbances that occur more frequently than, equivalent to, or less frequently than the organism generation time. Since the cellular automaton model is stochastic, each set of parameters was run ten times on a randomly generated landscape. To test whether habitat configuration influences persistence and occupancy, two island configurations were tested: clustered and linear (Fig.5-3).

5.3.4 Adaptive dynamics

To test which combinations of parasite traits are adaptive across disturbance frequencies, the model was updated to include a resident parasite phenotype (State 2) and a mutant parasite phenotype (State 3), which compete to colonize hosts. Neither phenotype has priority colonizing a host; rather, the colonization probabilities are based on the relative density of hosts infected with the resident and mutant, and the traits of both strains. A trait is considered adaptive if the mutant phenotype has positive population growth from the amount at which it was introduced. Adaptive dynamics were incorporated into the patch occupancy and cellular automaton models by changing the system of equations governing transitions to include the mutant phenotype (Eq. 3) (Fig. 5-4):

$$
\begin{aligned}
x_0(t+1) &= (1-C_h)x_0(t) + \delta_s x_1(t) + \delta_{i1} x_2(t) + \delta_{i2} x_3(t) && \text{(3a)}\\
x_1(t+1) &= C_h x_0(t) + (1-\delta_s)[1 - C_{p2}(1-C_{p1}) - C_{p1}(1-C_{p2})]x_1(t) \\
&\quad + m_{p1}(1-\delta_{i1})x_2(t) + m_{p2}(1-\delta_{i2})x_3(t) && \text{(3b)}\\
x_2(t+1) &= C_{p1}(1-\delta_s)(1-C_{p2})x_1(t) + (1-\delta_{i1})(1-m_{p1})x_2(t) && \text{(3c)}\\
x_3(t+1) &= C_{p2}(1-\delta_s)(1-C_{p1})x_1(t) + (1-\delta_{i2})(1-m_{p2})x_3(t) && \text{(3d)}\\
x_4(t+1) &= x_4(t) && \text{(3e)}
\end{aligned}
$$

The colonization probabilities for the adaptive dynamics equations are:

$$
\begin{aligned}
C_h &= P\left[\text{at least 1 colonist arrives}\right] = 1 - e^{-(d_s x_1(t) + d_{i1} x_2(t) + d_{i2} x_3(t))} && \text{(4a)}\\
C_{p1} &= P\left[\text{at least 1 colonist arrives}\right] = 1 - e^{-d_{p1} x_2(t)} && \text{(4b)}\\
C_{p2} &= P\left[\text{at least 1 colonist arrives}\right] = 1 - e^{-d_{p2} x_3(t)} && \text{(4c)}
\end{aligned}
$$

It is theorized that parasites will evolve to minimize their harm to hosts in island-like habitats. However, as disturbance becomes more frequent, transmission becomes increasingly important to recolonize disturbed patches. I expect that island habitats will shift the adaptive

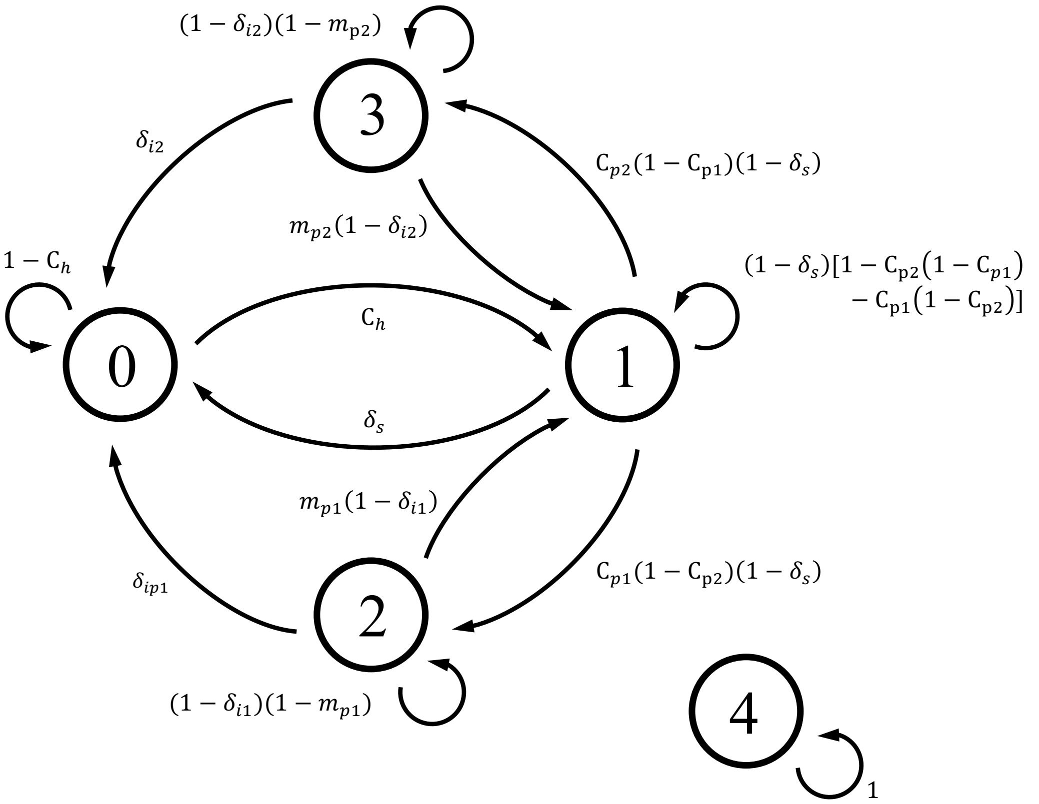


Figure 5-4: Transition diagram for adaptive dynamics with two competing parasite phenotypes. In this scenario, State 2 represents a resident parasite phenotype, State 3 represents a mutant phenotype with slight trait variations, and State 4 represents unsuitable habitat (equivalent to State 3 from the simpler, one-phenotype model).

advantage towards moderating harm to hosts relative to the patch occupancy model, but this relationship will not hold at high disturbance frequencies. To test this hypothesis, a small number of a mutant parasite phenotype (State 3) is introduced to a resident parasite phenotype (State 2) after it has reached equilibrium. Here, I define "adaptive" as a set of traits that allow a small number of a mutant phenotype to invade and become the dominant phenotype when introduced to a resident population at equilibrium (Doebeli, 2011). The trait I varied was the parasite colonization coefficient (d_p), which is related to virulence by the concave-down tradeoff function. First, I selected a "resident" parasite phenotype that is intermediate in the range of colonization coefficients explored ($d_{p(resident)} = 4.0$) and competed mutants with a deviation from the resident trait ranging from -2.0 to 2.0 over disturbance frequencies 0.0 to 0.3. Pairwise invasiblity plots were then used to identify evolutionary stable strategies (ESSs) and test whether disturbance frequency or island habitats change the ESS. An ESS signifies a local fitness optimum, where mutants with higher or lower values of the trait in question are unable to invade, and individuals with the optimal traits can invade all other trait values.

5.4 Results

5.4.1 Effects of disturbance on castrators versus mortality inducers in the patch occupancy model

Castrators reached higher occupancy at equilibrium (Fig. 5-5c) than mortality inducers (Fig. 5-5d) across all disturbance frequencies explored. Castrators also persisted under slightly higher disturbance frequencies than mortality inducers. Both castrators and mortality inducers reached the highest occupancy at low disturbance and intermediate colonization coefficients. Maximum occupancy occurred at a lower colonization coefficient for mortality inducers than for castrators ($d_p \sim 3.5$ and $d_p \sim 5$, respectively), indicating mortality inducers gain a greater advantage from doing less harm to hosts, as this increases their infective period.

Patterns in parasite prevalence (proportion of hosts infected) were similar to patterns in parasite occupancy, but the colonization coefficients that achieved the highest prevalence were greater than those that achieved the highest occupancy ($d_p \sim 4$ for mortality inducers and

$d_p \sim 8$ for castrators) (Figs. 5-5e&f). Castrators and mortality inducers had different effects on host occupancy (Figs. 5-5g&h). With low colonization coefficients, castrators decreased host occupancy less than mortality inducers. With high colonization coefficients, however, castrators decreased host occupancy much more than mortality inducers.

In undisturbed systems, mortality inducers required lower colonization coefficients than castrators to maximize occupancy (Fig. 5-6). As disturbance frequency increased, this relationship reversed, and mortality inducers required higher colonization coefficients than castrators to maximize occupancy. This pattern was robust across a broad range of colonization coefficients explored (Appendix J).

5.4.2 Effects of habitat structure and island configuration in the cellular automaton model

In the spatially explicit model, castrators and mortality inducers shared some similarities in their response to disturbance, but also had some key differences (Fig. 5-7). In undisturbed habitats, both castrating and mortality-inducing parasite species that were poorer colonizers reached higher occupancy than species that were more effective colonizers. At higher disturbance frequencies, this relationship inverted, and effective colonizers reached higher occupancy than poor colonizers. The strategies intersected at $D \sim 0.075$, representing disturbances that are less frequent than the species generation time.

Differences between castrators and mortality inducers became apparent when exploring the effects of spatial structure. As in the patch occupancy model, castrators reached higher occupancy than mortality inducers at nearly all disturbance frequencies explored. However, increasing disturbance frequencies had a larger negative impact on castrators, causing the occupancy of castrators and mortality inducers to converge at high disturbance frequencies (Fig. 5-7). For this reason, castrators persisted at only slightly higher disturbance frequencies than mortality inducers. This pattern was exacerbated by island habitats, particularly in the linear configuration (Fig. 5-8). Castrator occupancy was highest in the spatially implicit model, intermediate in clustered islands, and lowest in linear islands at moderate to high disturbance frequencies (Fig. 5-8, bottom two panels), which was the expected response. Mortality in-

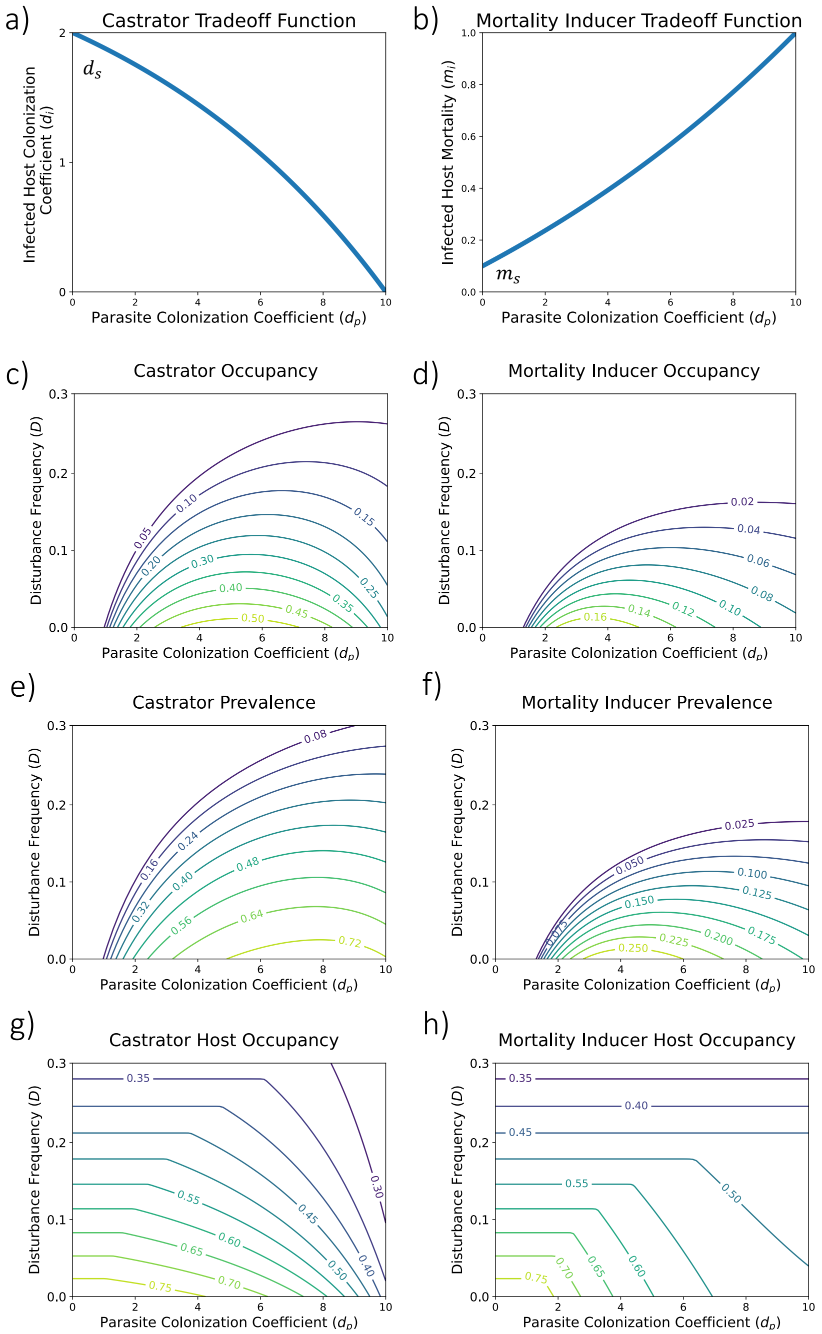


Figure 5-5: Schematic diagram of the shape of the virulence-colonization tradeoff for castrators (a) and mortality inducers (b). Contour plots showing the occupancy of castrators (c) and mortality inducers (d) across a range of colonization coefficients and disturbance frequencies. Occupancy is the fraction of habitable patches occupied by a parasite $x_2/(x_0+x_1+x_2)$. Prevalence of castrators (e) and mortality inducers (f), defined as the fraction of hosts occupied by a parasite $x_2/(x_1+x_2)$. Occupancy of hosts infected by castrators (g) and mortality inducers (h), defined as the fraction of habitable patches occupied by a host $(x_1+x_2)/(x_0+x_1+x_2)$. In all plots, occupancy at equilibrium was calculated by running the model for 500 time steps.

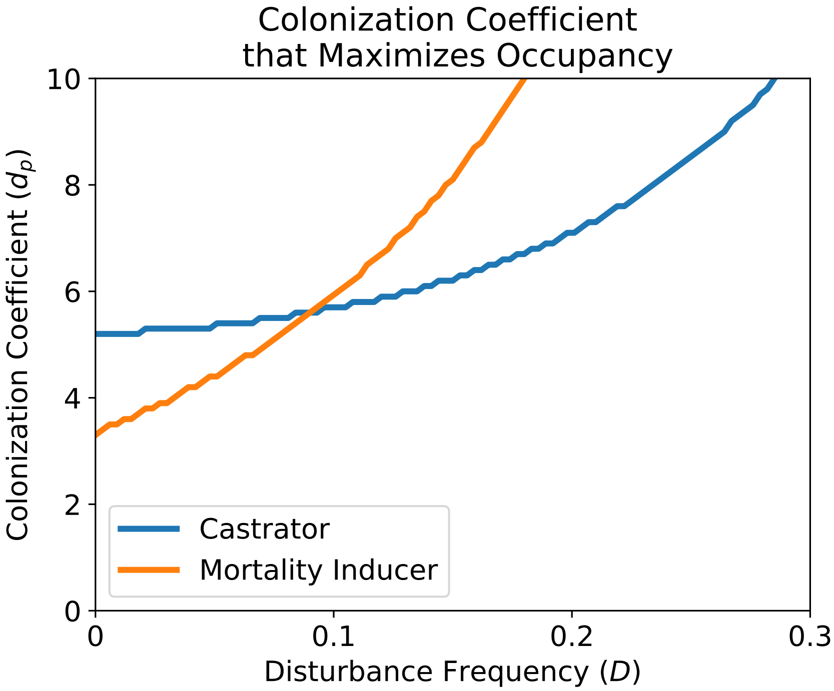


Figure 5-6: The colonization coefficient (d_p) that maximized occupancy over a range of disturbance frequencies (D) for castrators (blue line) and mortality inducers (orange line) in the patch occupancy model. As in other analyses, $d_p = 10$ was the maximum colonization coefficient explored and corresponded to the highest virulence.

ducers had an unexpected response to habitat structure. Their occupancy was not reduced in island habitats compared to the spatially implicit model under all disturbance scenarios, and they even achieved higher occupancy in clustered islands when disturbance was moderate (Fig. 5-8, second panel). The different dynamics in response to spatial structure implies castrators are limited by recolonization dynamics, since they delay host recolonization, whereas mortality inducers receive some benefit from spatial structure, likely an increase in neighboring uninfected hosts, that compensates for the higher likelihood of disturbance-induced extinction. For all parasite types explored, extinction was more likely in the spatially explicit, stochastic model than in the patch occupancy model (Fig. 5-8, bottom panel). This was expected, since time to recolonization becomes a limiting factor for persistence in the cellular automaton model, and stochastic extinctions are more likely in small populations.

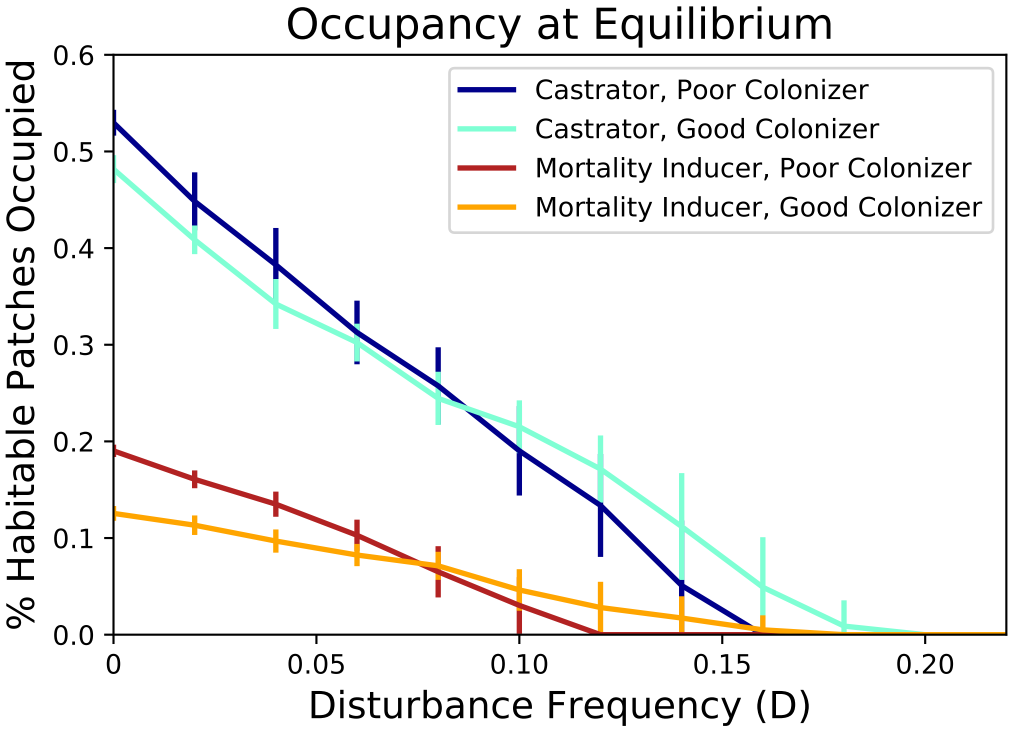


Figure 5-7: Occupancy over a range of disturbance frequencies for four different parasite strategies in cellular automaton simulations. The lines show the means (±SE) of ten model runs for randomly generated landscapes with islands arranged in clustered configuration. Poor colonizers were defined as $d_p = 4$ and good colonizers were defined as $d_p = 8$.

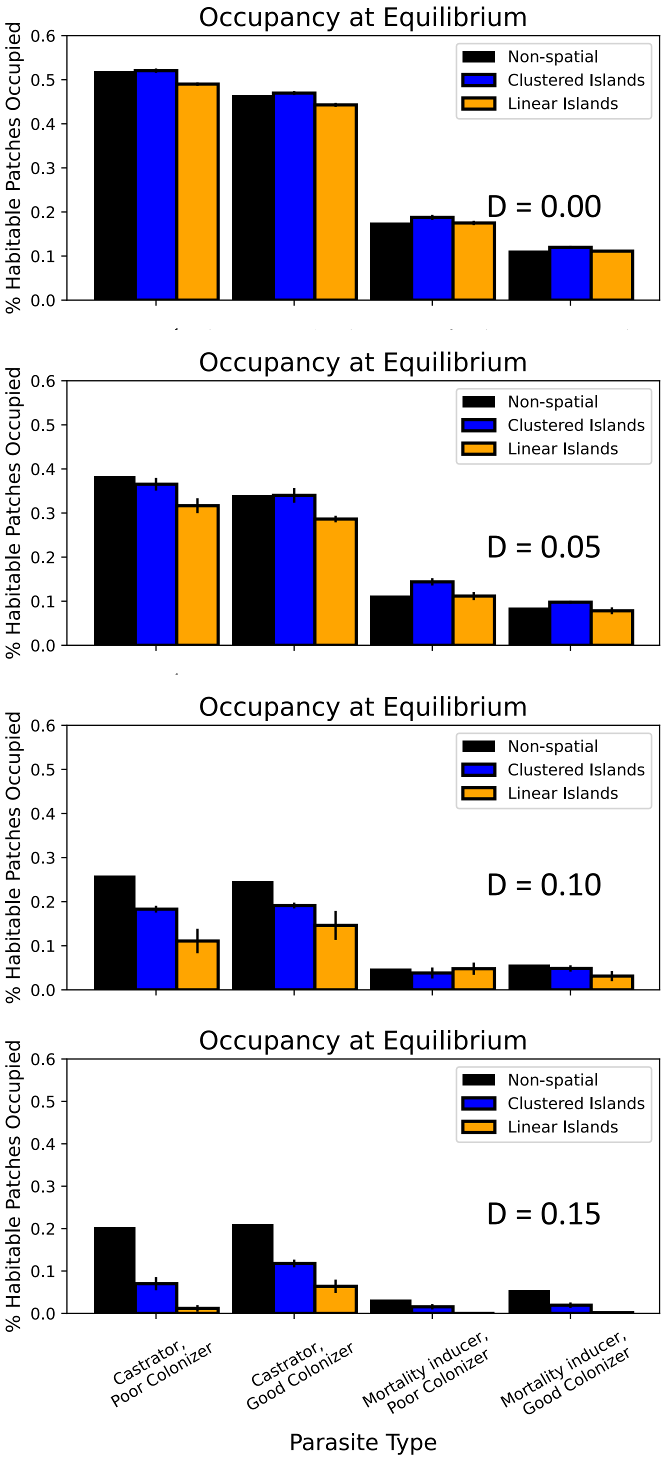


Figure 5-8: The influence of island-like habitat and island configuration (clustered versus linear) on parasite occupancy over a range of disturbance frequencies (top to bottom) compared to the patch occupancy model. For the spatially explicit model, bar height is the mean of ten model runs (±SE).

5.4.3 Effects of disturbance and isolation on adaptive dynamics

Usually, adaptive dynamics models result in a so-called evolutionarily stable strategy (ESS). An ESS signifies a local fitness optimum, where mutants with higher or lower values of the trait in question are unable to invade, and individuals with the optimal traits can invade all other trait values. The patch occupancy and cellular automaton parasite disturbance models did not result in an ESS. Rather, these models suggest evolution would always progress towards higher transmission. This result may be a feature of the model structure, since parasite colonization is a function of both the colonization coefficient d_p and infected host density x_2 (Eq. 4), or it could be due to the model being discrete-time. Despite the lack of an ESS in this model, the effect of disturbance on invasion of the mutant can still be compared. Disturbance had a pronounced influence on the invasion of mutant phenotypes by allowing mutants with smaller positive deviations in the colonization coefficient to invade (Fig. 5-9). At low disturbance frequencies, mutant phenotypes could only invade if the mutation severely enhanced colonization. In the spatially explicit, stochastic model, the point at which the mutant could invade shifted further right, towards higher positive mutations in colonization capacity. This is likely due to stochastic extinction of the mutant when it is at small population densities.

Pairwise invasibility plots (PIPs) do not reveal an evolutionarily stable strategy along the continuum of possible parasite colonization coefficients, but instead indicate that it is adaptive for the parasite to increase transmission regardless of the resident colonization coefficient in this model. As the colonization coefficient of the resident increased, mutant phenotypes required an increasingly large positive mutation in the colonization coefficient to invade. This relationship was more pronounced for mortality inducers than for castrators. Disturbance changed the slope of this relationship, making it possible for mutations of smaller degree to invade when the resident colonization coefficient was high.

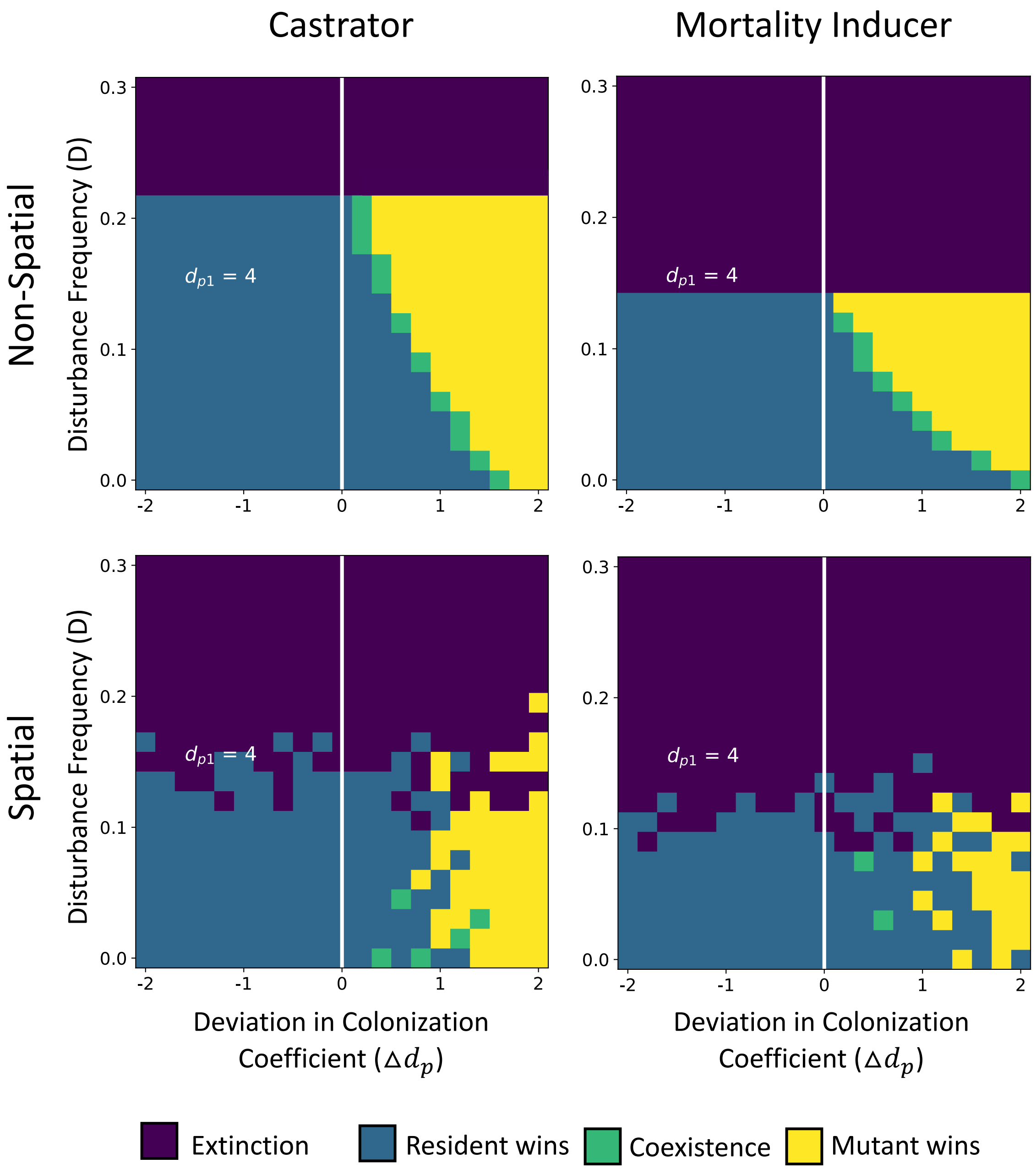


Figure 5-9: Phase diagrams showing whether a mutant parasite phenotype (yellow) can invade a population of the resident parasite phenotype at equilibrium (blue) under a range of disturbance frequencies (y-axis). Dark purple means the resident could not persist. The x-axis represents the magnitude of deviation of the mutant colonization coefficient d_{p2} from the resident colonization coefficient ($d_{p1} = 4$).

5.5 Discussion

5.5.1 Effects of disturbance and isolation on parasite occupancy and persistence

Parasites are important members of biological communities and are found in ecosystems worldwide, even in disturbed, isolated ones. I used spatially implicit and spatially explicit models to investigate how habitat disturbance and island-like structure influence the occupancy, persistence, and evolution of parasites with different strategies. I compare parasites with different colonization abilities and impacts on the host, specifically, parasites that decrease host reproduction (castrators) and parasites that shorten host life span (mortality inducers). Both these strategies are common in nature and occur across a broad range of taxa. Their distinct impacts on the host are expected to drive complex population dynamics that impact the parasite's persistence in disturbed systems. This study is intended to explore both ecological and evolutionary mechanisms that drive parasite species diversity.

Results of these models reveal differences in abundance and persistence between castrating and mortality-inducing parasites in disturbed environments. In these models, castrators reach higher occupancy (a proxy for population density) than mortality inducers overall (Fig. 5-5), but disturbance has a larger negative impact on castrators, causing the occupancy and persistence of both strategies to converge at high disturbance frequencies (Fig. 5-7). Recolonization dynamics likely play an important role in the relative responses of different parasite strategies to disturbance, as indicated by their distinct responses to habitat structure. Castrators are impacted more severely by disturbance in island habitats, particularly in linear islands (Fig. 5-8, Panels 3&4). In contrast, island-like habitat does not alter the occupancy and persistence of mortality inducers compared to the patch occupancy model. These results suggest strategies that decrease the production of new susceptible hosts are the most vulnerable to disturbance in isolated habitats, while strategies that increase the host loss rate seem to receive some benefit from spatial structure.

Castrators are likely effected the most in the disturbed, spatially explicit model because they slow host recolonization. Thus, the host is delayed in propagating across islands after dis-

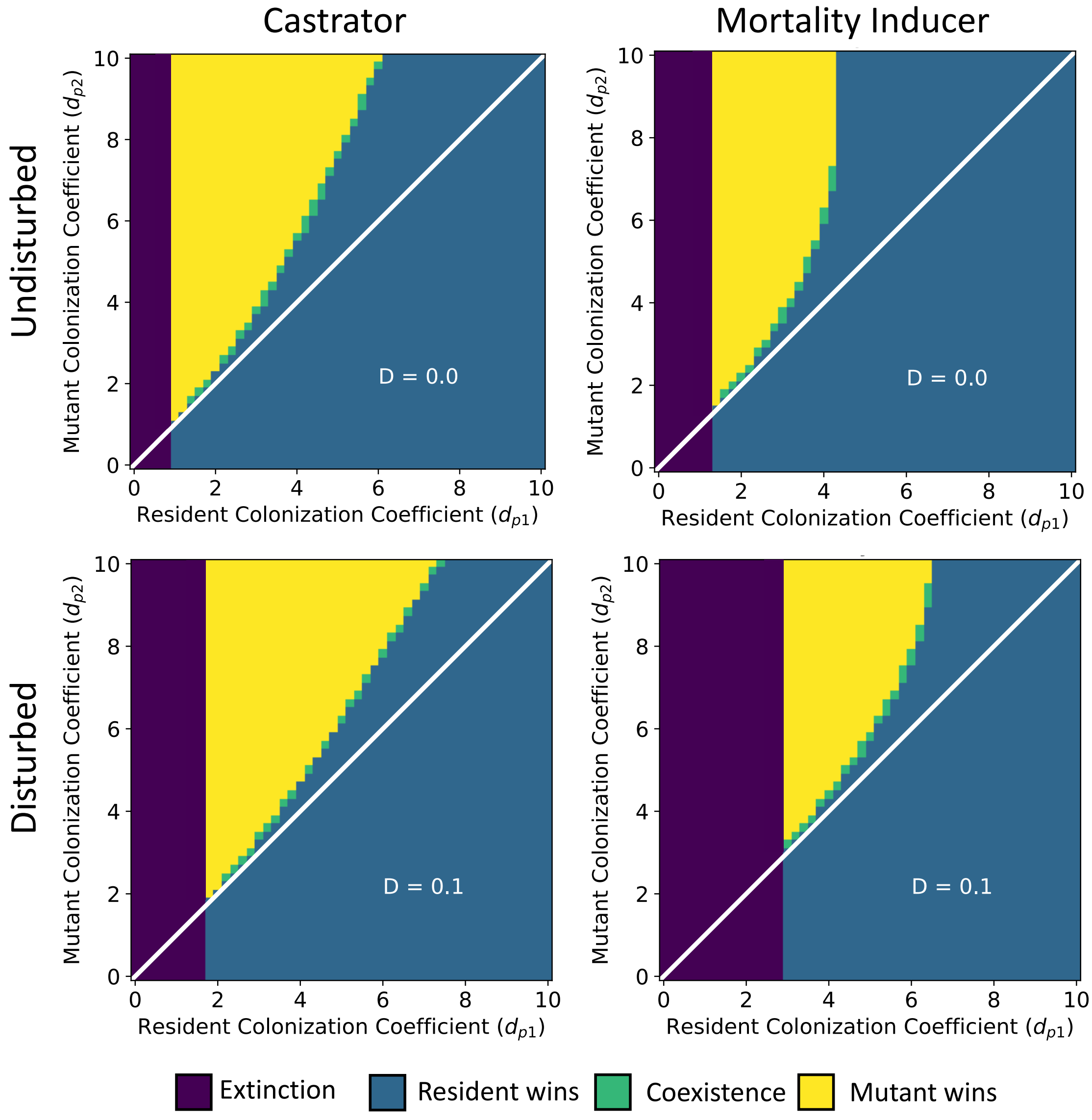


Figure 5-10: A pairwise invasibility plot showing which mutant colonization coefficients (d_{p2}) could invade resident colonization coefficients (d_{p1}) at equilibrium at two disturbance frequencies: $D = 0.0$ (top) and $D = 0.1$ (bottom). The white line shows the 1:1 relationship where the resident and mutant phenotypes are identical. Blue indicates the mutant was unable to invade the resident phenotype at equilibrium, green indicates coexistence, yellow indicates the mutant invaded and outcompeted the resident at equilibrium, and purple indicates neither could persist.

turbance, and the parasite is more quickly driven towards extinction. Castrators are known to decrease host densities in marine benthic invertebrates (Blower & Roughgarden, 1987; Ebert et al., 2000), but the role of castrating parasites in slowing host recolonization after disturbance has not yet been empirically tested to my knowledge. In field systems, the ability of castrators to reduce host density can be decoupled from local population dynamics if dispersal is distant and the larval pool is well-mixed (Blower & Roughgarden, 1987), or if the parasite has an indirect life cycle (Fong, 2016). The effects of castration on metapopulation connectivity may therefore be difficult to tease out in all but a few ideal model systems, but would be an interesting future research avenue.

In my model, mortality inducers are either unaffected by island-like habitats or receive some relative benefit from spatial structure that compensates for the increased challenges of colonization. By allowing some islands to be free from parasites, disturbance in isolated habitats may create refuges where hosts live longer and reach higher densities, providing rich pockets of host resource into which the parasite can later spread. In modeling studies, spatial structure with local dispersal is known to promote host persistence by creating refuge from parasites (Childs et al., 2004). The focus of these studies has mainly been on wildlife conservation (Hess, 1996; Dobson & Hudson, 1986), and so the influence of spatial structure on parasite occupancy is often not discussed. However, research has been directed towards understanding factors that increase the occupancy and persistence of parasitoids, since parasitoids are useful biological controls against insect pests on crops. In modeling studies of hosts and parasitoids in disturbed agricultural fields, disturbance mediated parasitoid-host coexistence but this effect depended upon the relative scale of disturbance and host and parasitoid dispersal (Childs et al., 2004). In experimental systems, metapopulation connectivity benefits both the host and parasite, by allowing the parasite to persist longer and reducing parasite burdens on the host (Tadiri et al., 2018). To my knowledge, studies have not explored the interaction of disturbance and island-like habitat structure in enhancing pathogen occupancy in the field.

This study also demonstrates that both castrators and mortality inducers can realize variable success in different disturbance regimes depending on where their traits fall on the tradeoff between colonization and virulence. In general, both strategies achieved higher occupancy by minimizing colonization (and harm to the host) at low disturbance frequencies, and by increasing colonization (and harming hosts more) at high disturbance frequencies. The colonization virulence tradeoff has mainly been examined in virus or microbial systems, and is beginning to be empirically demonstrated in macroparasites including species with indirect life cycles (Davies et al., 2001; Medica, 2002). Field studies should test the results of this model, for example, studying the reproductive traits in a group of closely related parasite species along a disturbance gradient to test whether the parasite species in the low-disturbance regions have lower reproductive output and/or virulence, and the species in the high-disturbance habitat have higher reproductive output and/or virulence. Sensitivity analyses also revealed that the shape of the tradeoff function could change these relationships. For example, under a sharper tradeoff curve, castrators that were good and poor colonizers realized similar occupancy (Appendix J, Fig. J-2).

A key observation in my model is that all the parasite strategies examined persist across a broad range of disturbance frequencies. These results are consistent with the observation that many different parasite taxa and life history strategies are found in frequently disturbed ecosystems. For example, deep-sea hydrothermal vents on the East Pacific Rise are extremely isolated ($\sim 3 - 10$ km apart) and frequently disturbed ($\sim 10 - 20$ years), and yet are home to many macroparasites, including castrators. Castrators at vents include a rhizocephalan and the sporocyst stage of trematode flatworms (Thesis Chapter 3). Non-castrating macroparasite taxa found at vents include acanthocephalans, copepods, nematodes, and the other trematode life stages (Thesis Chapter 3). Separate studies have confirmed the presence of fungal (Van Dover et al., 2007; Sapir et al., 2014), protozoan (Moreira & López-García, 2003), and bacterial (Powell et al., 1999; Terlizzi et al., 2004; Zielinski et al., 2009) pathogens in deep-sea chemosynthetic ecosystems. The impact of these parasites on host population dynamics at vents is unknown and should be explored. Since vents and other chemosyntheic systems have various degrees of disturbance and isolation, the influence of these environmental factors in regulating parasite diversity and abundance can only be untangled with additional data from more habitat types and regions. My model suggests mortality inducers that are poor colonizers would be the first species to go extinct as disturbance frequency increases, and castrators that are good colonizers would be the last. Therefore, we might expect to find fewer pathogens in disturbed, isolated habitats, but those that are present might be more virulent. Very few field studies analyze community-level parasite diversity data with the aim of comparing life strategies to investigate mechanisms (see Jean et al. 2016 for a good example), and the predictions of this model will be more directly testable with an increase in the number of data sets that focus on parasite life histories in a variety of ecosystems.

5.5.2 Effects of disturbance and isolation on adaptive dynamics

I hypothesized that disturbance would cause parasites to evolve towards greater virulence, while island-like habitats would cause them to evolve towards lower virulence (Nidelet et al., 2009; Lion & Boots, 2010). As expected, my results indicate that disturbance promotes the invasion of parasite mutant phenotypes with higher colonization capabilities. This pattern was apparent in both the spatially implicit and spatially explicit models (Fig. 5-9). In the context of natural ecosystems, this suggests parasites introduced to environments with frequent disturbance have the potential to evolve higher transmission and virulence to cope with the additional source of host mortality. We therefore might expect to find parasites with greater virulence and transmission in disturbed environments. This result agrees with other modeling studies that found parasites evolve higher virulence when host life span was shorter (Nidelet et al., 2009; Cressler et al., 2016). In some experimental systems, reducing host life span often leads to the evolution of higher virulence (Nidelet et al., 2009).

It is hypothesized that parasites would evolve to be less virulent in small host populations, such as on islands, because parasite-induced reductions in host populations might decrease transmission or drive the parasite extinct (Morand & Guégan, 2000). This outcome was not supported by the results of my model. There was no evidence that the cellular automaton model with island habitats selected for mutations of lower virulence compared to the spatially implicit model (Fig. 5-9). Instead, differences between the two models were sensitive to the size of the initial mutant population introduced, which is related to the chance of stochastic extinctions shortly after introduction when mutant populations are low (Appendix J, Fig. J-3). In laboratory studies, pathogens have been shown to evolve lower virulence when infections occur more locally (Boots & Mealor, 2007), but whether and how these results apply to larger geographic scales is still a question of debate. In a spatial model, Lion & Boots (2010) showed that parasites are more "prudent" (i.e., less virulent) when their dispersal radii are small, but evolve highest virulence at intermediate dispersal distances. Although I do not explicitly explore different dispersal radii with this study, this finding provides an interesting theoretical expectation to test with my model in the future. In my model, I set the dispersal radius such that the nearest neighboring islands could always be recolonized, effectively making it a metapopulation. It is possible that this dispersal radius was too large to result in the local adaptation detected in other modeling studies. Adaptive dynamics may play out differently if dispersal scale was reduced or if habitats were more isolated and could not be effectively recolonized from other patches.

The lack of an evolutionarily stable strategy (ESS) in this model is an intriguing open question that I am exploring further. I used the concave-down tradeoff function from Lion & Boots (2010) for simplicity and comparability. These authors always found an ESS with a concave-down tradeoff, but in my model, mutant parasites could only invade if they had higher colonization capabilities than the resident. The lack of an ESS has been observed in simple models with a linear tradeoff, in which case maximum transmission evolves (Lion & Boots, 2010), but this is usually solved by including a concave-down tradeoff. The differences with my model could arise because it is discrete in time, because the colonization function is density-dependent, or because results are sensitive to the precise tradeoff shape (Hal Caswell and André de Roos, pers comm).

Since the shape of contact-density functions in parasite-host modeling usually has an impact on outcomes (McCallum et al., 2001; Borremans et al., 2017), I performed preliminary analyses to test the effects of using steeper tradeoff curves on adaptive dynamics. With a sufficiently steep tradeoff, an area of parameter space arose for mortality inducers in which mutants could invade residents with higher colonization coefficients (Appendix J, Fig. J-4). Altering the steepness of the tradeoff curve had no impact on the dynamics of castrators (Appendix J, Fig. J-5). This implies that there are distinct selective gradients for parasites that reduce host reproduction and parasites that shorten host life span. This result agrees with prior studies and observations from natural systems. Other studies modeling the adaptive dynamics of castrators indicate evolution would progress towards ever higher virulence and transmission (O'Keefe & Antonovics, 2002; Hall et al., 2007), since host castration has no fitness cost to the parasite. In nature, castrators usually have the consequence of complete host sterilization (Lafferty & Kuris, 2009). There are other examples of overspecialization (when a trait is selectively advantageous for an individual, but is disadvantageous to the population) in parasites towards extremely high virulence and transmission. One prominent example is the parasitoid wasp, which has a suite of traits for effective host-finding and causes obligate host death (Kuris & Norton, 1985). These parasites are diverse and successful, despite having traits that are adaptive for the individual yet detrimental to the population (Kuris & Norton, 1985). An analysis of the effect of the tradeoff curve on parasite adaptation and occupancy in disturbed habitats is an intriguing next step, but at this stage remains preliminary. Despite a growing body of evidence empirically producing tradeoff curves for different parasite species (Ben-Ami, 2017), the shape of (and even the existence of) the tradeoff curve remains an assumption in most parasite-host systems (Ebert & Bull, 2003; Alizon et al., 2009).

5.6 Limitations and remaining questions

Several limitations in my model restrict its power to predict real-world systems. First, in nature, parasite responses to disturbance are mediated by interactive effects with other species, leading to complex and often divergent outcomes (Lafferty & Kuris, 2005; Turney et al., 2014). For example, disturbance might increase the densities of an intermediate host in an indirect life cycle, or change host behaviors in ways that favor transmission. In natural systems, many additional factors influence the diversity of mortality inducers. For example, in some plant pathogen systems, anthropogenic disturbance is correlated with higher pathogen diversity (Delavaux et al., 2021). However, disturbance is also known to decrease the prevalence of some wildlife diseases (Lehmer et al., 2008). This depends on the nature of the disturbance: for example, human activities increase connectivity and can introduce new pathogens (Jean et al., 2016), or alter the densities of other potential hosts (Turney et al., 2014).

Second, my model tracks a one-host, one-parasite system, which is the simplest example. Field evidence demonstrates that parasite taxa with indirect life cycles, such as trematodes, are successful in isolated, disturbed habitat. A model incorporating multiple host species and parasite life stages would be more complex and less tractable. However, my model does point towards some features of the trematode life cycle that might explain their success in disturbed habitat. Their first intermediate life stage is a castrator in the gastropod host, which asexually clones dispersive larvae for the duration of the host's life. Thus, this stage is a castrator and good colonizer, which was the life strategy that achieved the highest occupancy at the disturbance frequencies relevant deep-sea hydrothermal vents on the East Pacific Rise.

Third, my model focuses on hosts with limited adult mobility, for example, benthic invertebrates in aquatic systems. Therefore, this model is not necessarily appropriate for drawing conclusions about wide-ranging or migratory hosts as in Lion et al. (2006) and Peacock et al. (2020). I expect that allowing the parasite to arrive at a site with an infected mobile host would increase parasite persistence, as the parasite would be able to recolonize earlier after disturbance.

Finally, in natural systems, parasites and hosts coevolve (Anderson & May, 1982; May & Anderson, 1983). Feedback between parasite and host was omitted here for simplicity, however, the allowance of host evolution could lead to different model outcomes. For example, when parasites and hosts are allowed to coevolve, and the parasites can allocate harm to either mortality or reproduction, parasites always evolve to sterilize their host unless the host evolves tolerance (Best et al., 2010). Hosts can also allocate resources to moderate some of the negative impact of parasites: for example, populations subject to attack by castrators can evolve to reproduce earlier, and may grow to larger sizes in response to castration (Ebert et al., 2004). In my model, parasite species were fixed as either castrators or mortality inducers, without the option to exploit different host tissues. Updating the model to include energetic feedbacks between parasite and host would be an interesting next step.

5.7 Conclusions

Empirical tests for how habitat features drive parasite diversity and abundance are difficult to accomplish on large spatial and temporal scales. Computational modeling is a powerful tool for building predictions for the ecological and adaptive responses of different parasites to habitat isolation and disturbance. Comparison of parasites with different strategies (defined here by the nature of the impact on the host and colonization capability) suggests parasites that reduce host reproduction (castrators) will be more abundant under all disturbance regimes than parasites that reduce host life span (mortality inducers). However, since castrators are more vulnerable to disturbance in isolated habitats, they may be driven to extinction at a faster rate if habitats become farther apart, smaller in area, or less connected. Conversely, mortality-inducing parasites, such as pathogens and parasitoids, may receive some benefit from isolation and disturbance if these features generate spatial structure that promotes parasite-host coexistence. A key finding of my study, which is supported by field data from disturbed systems, is that parasites with a broad range of life history strategies can persist even under frequent disturbance. Variation between species in the traits that influence colonization success allows castrating and mortality-inducing parasite species to persist across a broad range of disturbance frequencies. Adaptation driven by disturbance further increases the potential for parasite species to persist. By focusing on processes that structure biodiversity – occupancy, persistence, and adaptation – this study suggests selective mechanisms that explain the diversity of parasite taxa and strategies observed in disturbed ecosystems.

5.8 Acknowledgements

The ideas in this chapter are the culmination of many discussions with my committee members Lauren Mullineaux, Mike Neubert, Serguei Saavedra, Carolyn Tepolt, and Armand Kuris. I thank these mentors for helping me work towards my ambitious goals of seamless (often in practice not-so-seamless) integration of parasite ecology, adaptive dynamics, metapopulation ecology, and virulence theory, all without prior training in computation. I thank Mike Neubert and Hal Caswell for introducing me to the fields of cellular automaton modeling and adaptive dynamics. Thanks to André de Roos for taking personal time to help with a sticky adaptive dynamics problem and Silke van Daalen for providing insight at many stages. I thank Lauren Mullineaux and Serguei Saavedra for challenging me to find the ecological relevance and broader significance of my work, and for pushing me out of old thought paradigms. I thank Armand Kuris for opening my mind to the diverse world of parasite consumer strategies, and teaching me how to think from the parasite's perspective. Finally, I must thank the MIT course 6.0001 Introduction to Computation and Programming Using Python. Through the mentorship of teachers and TAs at MIT, I progressed from never having encountered a programming

language (to be honest, a for-loop caused my brain to explode), to developing my own computational model for a thesis chapter. I have always had questions in my head that are too big in space and time to answer with field observations. Coding in Python and R have given me a language and skill set to explore these questions, opening many doors for my future career.

Chapter 6

Conclusion

In this thesis, I examined deep-sea hydrothermal vent ecosystems to understand how habitat isolation and disturbance shape parasite diversity. In Chapter 2, I found that the recovery of function at vents shows several distinct patterns compared to well-studied systems due to the unusual co-occurance of nutrients and environmental stressors at vents. Functional diversity recovered more slowly than species diversity and had not reached the pre-eruption state 11 years after a massive disturbance. In Chapter 3, I found that parasite diversity in vent host species is not significantly lower than in hosts from less isolated and less disturbed ecosystems, but the low number of vertebrate predator species limited parasite diversity in the vent community. Vents showed differences in their representation of major marine parasite taxa, but these differences were not explained by the number of hosts in the parasite life cycle. In Chapter 4, I demonstrated that parasites very likely complete indirect life cycles in the vent environment, and explored potential origins of trematode diversity at the EPR 9N hydrothermal vent field. In Chapter 5, I demonstrated that parasite strategies defined by their colonization capability and the nature of their impact on the host have some distinct ecological and adaptive responses to disturbance and island-like habitat, but overall a broad range of parasite strategies were able to persist. These chapters investigated several of the factors thought to structure parasite diversity in general, including habitat isolation and disturbance, parasite life strategies, host diversity and function, and the probability of introduction, establishment, and persistence. In this conclusion, I will discuss the extent to which the research projects in the thesis inform these themes, and present research gaps and future directions.

6.1 Contributions to parasite ecology and biogeography

Overall, the research in this thesis reveals a considerable scope for functional traits and adaptation to permit the invasion, establishment, and persistence of a broad diversity of parasite taxa in disturbed, isolated systems. The finding that parasite diversity in hosts from disturbed vents is not significantly lower than in well-connected and undisturbed marine ecosystems (Chapter 3) is surprising in light of expectations from disturbance ecology and biogeography. This provides yet another example of the ubiquity of parasites, even in a harsh environment. Differences in the composition of parasite taxa between systems was not explained by the number of hosts in the life cycle (direct versus indirect) (Chapter 3), but does point towards other potential mechanisms based on more nuanced traits related to dispersal and colonization. For example, monogeneans may be unable to persist in vent environments due to their ineffective dispersal capacity or sensitivity to the thermal or chemical environment. Trematodes may be particularly successful in disturbed environments because they maximize different strategies at different life history stages. The fish definitive host provides a vector for long-distance dispersal, while the castrating stage in the snail host asexually clones dispersive larvae, acting as an amplification step. Computational models reveal that castrating parasites reach higher occupancy than parasites that increase host mortality, and castrators with effective colonization, such as the sporocyst stage in the gastropod host, persist at the highest disturbance frequencies (Chapter 5). An exploration of the role of these nuanced traits as mechanisms driving parasite diversity and adaptation will become possible with greater research into the reproductive biology of vent parasites species.

Comparative analysis between ecosystems reveals the important role of host diversity as a driver of parasite diversity in the vent community. Although parasite diversity *within host species* was not significantly lower at vents, the low number of available vertebrate predator species limited parasite diversity in the *vent community* (Chapter 3). This may also explain differences in the representation of parasite taxa at vents compared to two coastal systems. The simple food web with few trophic links between top predators likely prevents some of the major marine ILC parasite taxa (nematodes and cestodes) from completing their life cycles at this vent field. The lack of intermediate parasite life stages in vent fishes (Chapter 3) is evidence

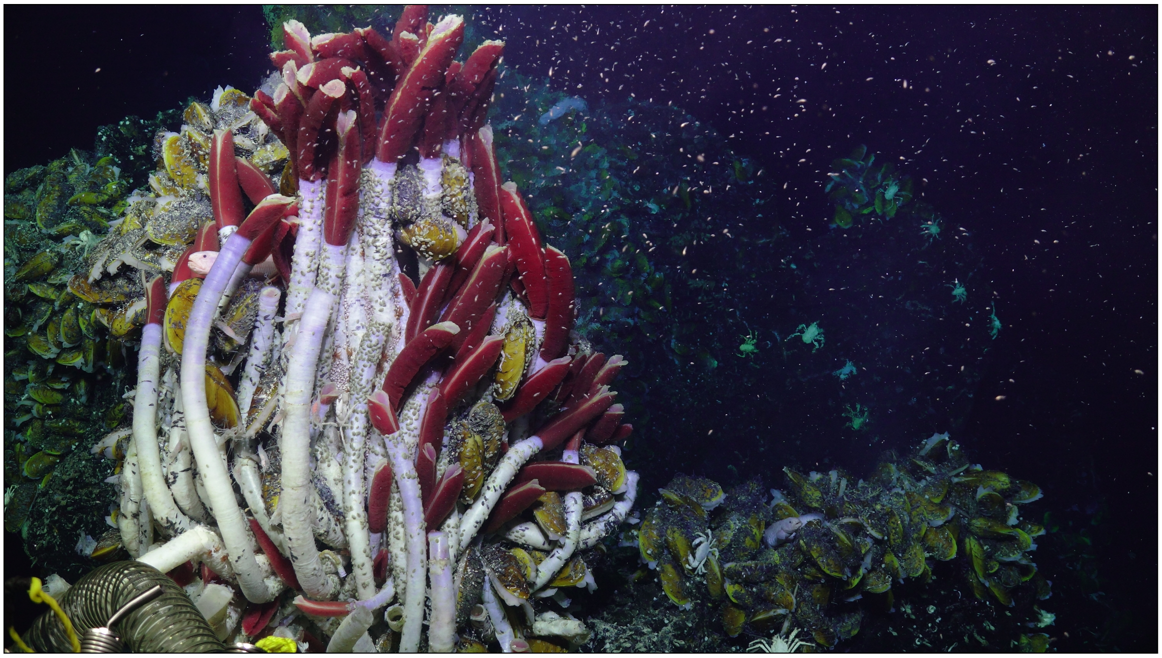


Figure 6-1: Tica vent from above, showing striking faunal densities and steep zonation in the community. Photo: Woods Hole Oceanographic Institution and National Deep Submergence Facility, ROV *Jason*, 2021).

that fish are the top predators at vents, and would be a dead-end as an intermediate host in a parasite life cycle. Many nematodes pass through multiple vertebrate hosts before maturing in the definitive host, and cestodes often mature in sharks. The number of links in the food web and the number of ILC parasite taxa in the ecosystem roughly correlates with the degree of connectivity with surrounding habitat types. In the kelp forest and atoll sandflat, many cestodes and nematodes complete their life cycles in birds, sharks, and marine mammals, which are key players in the food webs of the two coastal systems used as comparison ecosystems in this study. Vents are not only geographically isolated, but have distinct environmental conditions (low pH, high temperature, reduced sulfur, heavy metals) that discourage non-vent fauna from visiting and feeding. Taken together, these findings indicate that habitat isolation (both geographically and environmentally) plays a prominent *indirect* role in reducing parasite diversity by constraining host diversity and food web complexity. This indirect effect appears to be more influential than the *direct* impacts of isolation (i.e., challenges of introduction, dispersal, and colonization) on community-level parasite diversity.

Although simple food webs prevent the completion of some parasite life cycles, my research shows that ILC parasites that have the proper host requirements are able to establish and persist. The discovery of all life stages in the digenean life cycle at vents is novel. The high densities of some life stages in some hosts provides evidence that ILC parasites are efficiently reproducing in disturbed vent habitats. ILC parasites can only establish in new ecosystems if all their hosts establish first, or if they complete one or more host-switches. Thus, the study of multi-host life cycles can answer important questions in evolutionary biology, and in this case, provide preliminary information on possible routes of introduction into the vent environment. Genetic and morphological similarity of some digenean species at EPR 9N to described species at vents 3,000 km farther south indicates considerable connectivity along the East Pacific Rise over evolutionary timescales. It is possible that these clades are endemic to vents, and may be diversifying in vent ecosystems. Other vent trematodes use a limpet first intermediate host in a gastropod family that, to our knowledge, specializes entirely on chemosynthetic seafloor features. The distinct parasite communities in the two vent fish species is consistent with prior studies that show these fish have different diets and habitat preferences. Parasite composition is likely to reflect the distinct evolutionary history of these two fish species.

The persistence of species in networks of disturbed islands relies on effective recolonization from afar after disturbance. Analysis of the EPR 9N invertebrate community over 11 years of primary succession revealed a shifting mosaic of hosts available for parasites to use as habitat (Chapter 2). Some aspects of the recovery of functional traits and diversity in the free-living community agreed with successional theory and have important implications for parasite establishment. Specifically, species diversity, functional diversity, and the relative abundance of species at higher trophic levels increased over time after volcanic disturbance (Chapter 2). Parasite diversity is likely to also increase at later stages of recovery as more diverse hosts and trophic pathways become available. This remains speculative, because I was only able to collect parasitological data 13-15 years after the eruption when the community was at advanced stages of recovery. Intriguingly, the invertebrate species most heavily exploited by parasites in my samples (small gastropods and polychaetes in intermediate and peripheral zones) were only abundant in later stages in succession, and the vent species not found to host parasites (siboglinid tubeworms, thermally-tolerant limpets) were dominant in early stages (Chapter 2). The functional uniqueness of the early-successional species and the initial scarcity of preferred hosts may slow the recolonization and establishment of parasites at vents. Siboglinid tubeworms are the largest invertebrates in the EPR 9N vent field, which would normally imply more habitat for parasites. However, other unique aspects of tubeworm physiology remove usual routes of transmission: they have no mouth or gut, and their body is protected by a strong tube. Pairing data on host suitability with data on community assembly rates is necessary to understand parasite persistence in disturbed systems. Overall, the use of functional traits to test specific hypotheses provided insight into processes driving diversity patterns over succession and facilitated comparison between ecosystems. Examination of the full suite of small free-living colonists revealed slower recovery times than previously estimated by visual surveys. This is critical knowledge for conserving deep-sea chemosynthetic habitats, which are increasingly targeted for mining of rare earth minerals.

Species diversity at equilibrium is set by the relative rates of species introduction, establishment, persistence, and extinction. This thesis explores conditions that permit parasite establishment (Chapters 3 & 4) and persistence (Chapter 5), yet opportunities for introduction remain poorly understood. It is not possible with these data and methods to know which parasites were introduced and later went extinct, versus those that were never introduced. Data on parasite composition in hosts from ambient deep-sea habitat adjacent to vents would provide a baseline expectation for the parasite taxa that are likely to be introduced. Such a comparison could be used to indirectly estimate which parasite taxa might have been introduced to vents but were unable to persist, similar to the informal analysis in Dobson & May (1986). This thesis presents the largest sampling effort for parasites from a single vent community to my knowledge, but it is still a small sample size capturing a snapshot of diversity in a dynamic habitat. Therefore, when I present a parasite taxon as "absent" in this thesis, I merely mean absent from my samples. It remains a very realistic possibility that all marine parasite taxa will eventually be discovered at vents with greater sampling effort.

6.2 Future Directions

This thesis presents the field of vent parasite ecology and opens the field to further inquiry. Undoubtedly, any research increasing insight into parasite diversity at vents around the globe is critical. The first step in understanding "how" and "what" is knowing "who." Researchers undertaking biological sampling at vents, whether or not parasites are a focus, should be aware that parasites will likely be encountered. Samplers should be mindful to collect data that can be broadly useful in parasitology (Bush et al., 1997). This includes: 1) some metric of sampling effort, in most cases this will be the number of hosts sampled, in the best case it will include host densities, 2) data on prevalence, counts of parasites per host, and the tissue where the parasite was found, 3) the host species, length, and sex, and 4) the parasite life stage. Negative data are invaluable in parasite ecology, as it is just as important to ask why parasites are not in a place as to ask why they are. Without such metadata to contextualize samples, they will be of limited use for comparative parasite ecology.

Vents are a promising system for examining biogeographic questions related to connectivity, disturbance, and habitat spacing (Mullineaux et al., 2018). There is a seemingly limitless potential to explore these questions in vent parasite ecology going forward. In this thesis, I compared vents to two very different ecosystems because there is no other deep-sea ecosystem with comparable parasite data. Similar sampling efforts should be conducted at different vent fields with different disturbance frequencies, habitat spacing, fauna, and chemical environments. This would allow us to test more refined theories on the shape of diversity curves over an environmental gradient, such as disturbance frequency, while controlling for the other features that make chemosynthetic habitats unique. Expanding vent parasite ecology to different regions would also help resolve which features of parasite composition in this thesis were driven by disturbance and isolation, and which are signatures of the particular region. Future work should focus on further resolving the life cycles of vent parasites and using genetic techniques to inform the degree of dispersal and connectivity. Population genetic approaches comparing hosts and parasites along the East Pacific Rise would be particularly insightful.

Changes over time should be tracked following future seafloor eruptions to further resolve the role of dynamic colonization processes in parasite persistence and establishment. The deep sea is a challenging system in which to study parasite community assembly over time. However, data from remote, harsh systems are critical to test assumptions and theory that are usually built in easily accessible terrestrial or nearshore settings. Since my parasitological data were collected when the community was already at an advanced stage of recovery, parasite diversity in my study was likely high compared to earlier timepoints, and is probably more representative of parasite diversity in the vent field metacommunity. Information on rates of parasite species arrival and population growth after future eruptions, similar to the successional research in Chapter 2, would provide indirect estimates of parasite dispersal potential, resilience, and impacts on the community at different stages. This information would also allow us to test the hypothesis that parasites with direct life cycles will establish earlier in succession than parasites with indirect life cycles.

Quantitative comparison of vents to non-vent, deep-sea habitats remains an open and intriguing area of research. This will allow us to extend fundamental questions in deep-sea biology to parasitology, such as how concentrated food resources on the seafloor structure abundance and biodiversity. I expect that parasites in more general deep-sea habitat will be more diverse due to the higher richness and lower endemism of potential hosts, yet less prevalent due to lower abundances and encounter rates between hosts. Although vents tend to have a lower alpha diversity overall than the surrounding deep benthos, they also have higher biomass, and species interactions constrained to a tight space. I hypothesize that parasite transmission will be more efficient at vents, resulting in higher prevalence and intensities. Large organic food deposits in the deep sea, such as whale falls, may not have endemic parasite species since many of the free-living species that exploit these resources are generalist scavengers. However, I expect that the aggregations of scavengers drawn to organic falls will enhance parasite transmission at particular times and places.

The relationship between parasites and the steep chemical and thermal zonation at vents warrants further work. Potential physiological stressors at vents include high concentrations of reduced sulfur and heavy metals, low pH, and low dissolved oxygen, all of which could damage external parasite stages (Cross et al., 2001; Tobler et al., 2007; Tunnicliffe et al., 2008). My research did not focus on the small-scale thermal and chemical environment, yet several observations are worth mentioning. First, parasites were not found in species that live in the high-flux, high-temperature zones close to venting orifices (i.e., *Alvinella caudata*, *Alvinella pompejana*, *Cyathermia naticoides*, *Lepetodrilus elevatus*, *Paralvinella grasslei*, *Riftia pachyptila*). Rather, parasites were most diverse and prevalent in small (1-10mm) invertebrate species that live in the diffuse-flow and peripheral zones, and in mobile hosts (fish and crustaceans) that can move between zones and escape disturbance. These observations suggest the harsh chemical environment in high-temperature zones may provide a refuge from parasites for the species adapted to live there. On evolutionary timescales, refuge from parasites might reduce the maintenance of immune systems (Keogh et al., 2017), allowing allocation of more energy to growth and reproduction (Lochmiller & Deerenberg, 2000). Among species inhabiting the diffuse-flow zones of the vent field, however, parasite diversity and transmission appear to be high. My community-level data demonstrate the harsh chemical environment does not prevent parasites from persisting in vent communities, but it remains possible that it plays a role in structuring smaller-scale patterns within the habitat. Therefore, the thermal or chemical environment may provide a refuge from parasitism for certain host species, and might prevent the transmission of parasite taxa with sensitive transmission stages.

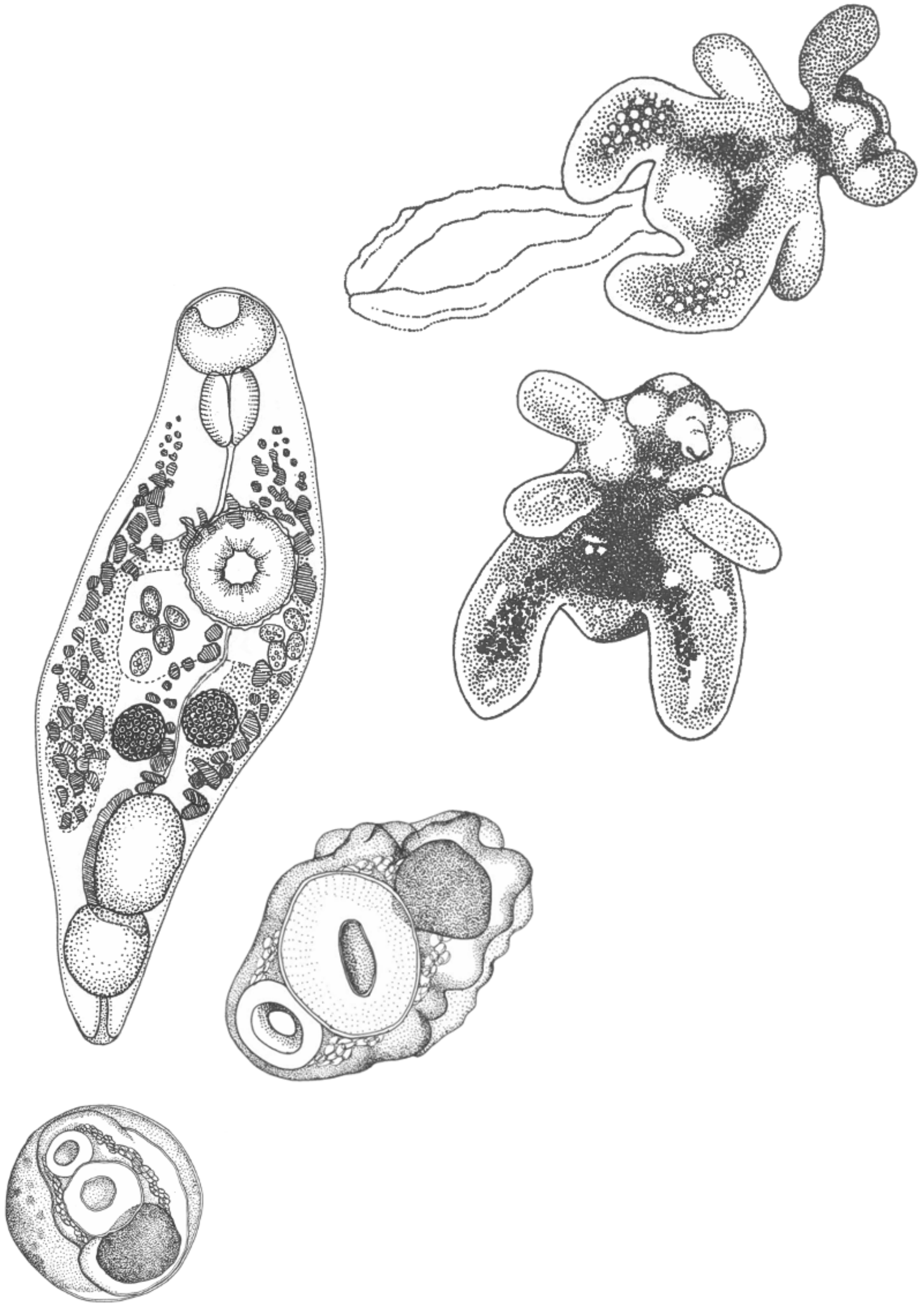
Finally, differences in the functional role of parasites between marine ecosystems remains largely unassessed. In this thesis, I take the "parasite's perspective" – focusing on parasites as marine invertebrates which, like any other, must colonize, persist, and make a living in a harsh and disturbed setting. My quantitative parasite data (Dykman et al., 2022), with an emphasis on consumer strategies and intermediate life stages, provides preliminary information on parasite species that are likely to play a significant functional role at EPR 9N. As the number of aquatic ecosystems with thorough, community-level data grows (McLaughlin et al., 2020), it is becoming possible to explore drivers of metazoan parasite diversity on a large geographic scale. The overall goal is to predict when and where parasites will be particularly important drivers of community dynamics. Further work examining parasite and host biomass would clarify the role of parasites in ecosystem energetics and relative impacts on host fitness. In some marine ecosystems, parasites can make up a substantial proportion of animal biomass (Kuris et al., 2008), yet this is likely not the case at vents, where the biomass-dominating species (tubeworms and mussels) were unparasitized. Finally, my research focuses on metazoan parasites, yet deep-sea chemosynthetic habitats are also home to fungal (Van Dover et al., 2007; Sapir et al., 2014), protozoan (Moreira & López-García, 2003), and bacterial (Powell et al., 1999; Terlizzi et al., 2004; Zielinski et al., 2009) pathogens. The impacts of these infectious agents on vent host populations and community function should be further explored.

6.3 Final thoughts

Human development in the past two hundred years has caused global change at an unprecedented rate. Habitat loss and anthropogenic disturbance are the leading causes of biodiversity loss worldwide. As disturbance intensifies, it is the specialist species and those with symbiotic relationships that often go extinct first (Tallamy, 2020). This includes many parasites (Dunn et al., 2009; Dharmarajan et al., 2021). Parasites are increasingly appreciated as sensitive consumers in food webs that could provide early indication of environmental degradation or tipping points. The use of parasites as indicators of ecosystem functioning relies on a detailed understanding of the hosts necessary to complete parasite life cycles, as well as explicit tests for how interactive environmental stressors impact parasite species differentially through their traits. The challenge of modern ecology is to predict how many threads we can remove from the fabric before the structure dissolves.

The deep sea is the largest continuous habitat on Earth. Since parasites are likely as diverse as free-living species, deep-sea parasites may be one of the most common consumer groups on the planet. And yet, deep-sea biodiversity in general remains poorly understood, with estimates of biodiversity ranging by orders of magnitude (Grassle & Maciolek, 1992; Lambshead & Boucher, 2003). In earliest days of exploration, the deep sea was thought to be relatively homogeneous and unstructured. This perception merely reflected limitations to exploration. Advances in seafloor mapping and deep submergence vehicle technology have facilitated an accelerating discovery of complex terrain and habitat types dotting the seafloor (Danovaro et al., 2014). All this complexity structures populations with discrete boundaries, separated from one another yet connected by dispersal. Vent communities were first discovered in 1977. We are still only beginning to grasp the diversity of island-like habitat types on the seafloor, each with the potential to support its own unique fauna.

Vent ecosystems have flourished for many millions of years before humans arrived on Earth (Martin et al., 2008; Dodd et al., 2017) and will likely persist long after we are gone. However, impacts of humans on the deep seabed are intensifying, with prospects of intensive mineral extraction now a near reality (Levin et al., 2020). Some species, especially those with strict habitat requirements, symbioses, or limited connectivity, may be unable to adapt to new sources of disturbance. Most terrestrial and shallow marine habitats on Earth have a shared history with humans (Kimmerer, 2013; Reid, 2015), but the history of human involvement in the deep sea is only just being written. When we meet new life, how will we respond? Will we rise to the responsibility of sharing our planet long-term? Will we consider also the small, the overlooked, the misunderstood life? Decisions for responsible action hinge upon good and plentiful data – not only on a few conspicuous species, but on all the varied actors. Our responsibility begins with knowing who we share our planet with. It must then be taken further, to understanding what they need for life and what they give to support life. The deep ocean still remains largely unknown. For better or for worse, it is now more within our reach than ever before.



Appendix A

Genetic barcoding of colonists from 9°50'N, East Pacific Rise

Individuals within the groups *Lepetodrilus* spp. and siboglinid spp. were too young to identify to species. Subsets of these individuals from months 9, 22, and 33 were sent to the Canadian Center for DNA Barcoding (CCDB) in July of 2018 for genetic sequencing. Sequencing targeted the mitochondrial cytochrome oxidase I (COI) gene, using the CCDB Next Generation Sequencing (NGS-FT) protocol. Specimen and sequence data were uploaded to the Barcode of Life DataSystems (BOLD) and queried against the BOLD COI full database. Of the 45 individuals of *Lepetodrilus* spp. sent for sequencing, all yielded sequences. Thirteen were matched to Barcode Index Numbers (BINs), which are operational taxonomic units, defined by widely used clustering algorithms. These closely correspond to species and reflect high levels of identification confidence. Of the specimens assigned to BINs, 11 were *Lepetodrilus tevnianus* and 2 were *Lepetodrilus elevatus*. Of the sequences not assigned a BIN, 19 were matched to *L. tevnianus*, 12 were matched to *L. elevatus*, and 1 was matched to *L. aff. galriftensis* (a conservative identification that has been grouped in the same BIN as *L. elevatus*) based on the BOLD COI full database. Individuals identified as *L. elevatus* were only present in the samples from 22 and 33 months, which agrees with observations that *L. elevatus* typically arrive later in succession than *L. tevnianus*. Of the 40 individuals of siboglinid spp. sent for sequencing, 38 yielded sequences. None were assigned BINs, but 35 were matched to *Tevnia jerichonana* and 3 were matched to *Oasisia alvinae* using the BOLD COI full database. *T. jerichonana* is the tubeworm species normally observed earliest in succession at the EPR. These data are publicly available using the project search "EPRBE" in: http://www.boldsystems.org/index.php/Public_BINSearch?searchtype=records.

Appendix B

Functional trait selection and modality assignments

Of the thirteen recommended traits in sFDvent (Chapman et al., 2019), we did not use: 1) gregariousness, 2) foundation species, 3) abundance, 4) chemosynthesis-obligate, 5) depth, 6) zonation from a vent, 7) nutritional source, and 8) substratum. Traits 1, 3, and 6 were omitted because we considered them "emergent" rather than "inherent" traits. In other words, these were seen as population-level patterns that arise due to the traits of species, not traits themselves (Garnier et al., 2016). Trait 2) was omitted because it was redundant with "habitat complexity," as foundation species by definition form structure. Traits 5) and 8) were omitted because our study took place at a single site with a depth of ∼2,500 meters and basalt substrate. Our trait "feeding method" (taken from the Biological Traits Information Catalogue (BIOTIC), MarLIN 2006) is similar to 7), however our modalities provide more detail as to the animal's feeding mechanism and are consistent with terminology used in other invertebrate trait studies. Terminology for this trait varies between studies; it is known as "functional feeding group" or "feeding guild" for freshwater invertebrates (Ding et al., 2017), "feeding position" in Veríssimo et al. (2017), "feeding mode" in Bolam et al. (2016), and "feeding type" in the online polychaete trait database Polytraits (Faulwetter et al., 2014). We used the "trophic mode" trait in sFDvent, however we added the modality "symbiont" to account for animals that have no mouths or guts and do not feed. We suggest that such species are technically not bacterivores, as they are categorized in sFDvent. For "relative adult mobility," we used the same modalities as in sFDvent, but assigned names to the numerical modalities based on other trait databases such as BIOTIC (MarLIN 2006). For example, mobility level "1" in sFDvent became "sessile," and mobility level "2" became "crawler."

Appendix C

Functional diversity indices

Diversity indices were calculated for species and functional guilds using Hill's diversity number of order 1 (Hill, 1973). Hill diversity (N_a) is a universal diversity equation that simplifies to relatives of three common diversity indices depending on the order a (Eq. 1):

$$N_a = (\sum_{i=1}^{S} p_i^a)^{1/(1-a)} \tag{1}$$

For this and all following equations, let S be the number of species in a sample and p_i be the proportion of species i in the sample. The three orders of Hill diversity differ in how they weigh species abundances: N_0 measures richness, so gives more weight to rare species; N_1 is related to the Shannon-Wiener index of diversity (Shannon, 1948) and weights species according to their abundance; N_2 is related to the Simpson dominance index (Simpson, 1949) and weights abundant species more heavily. We chose to focus on Hill of order 1 (Eq. 2) because it takes into account sample size and weights species according to their abundance. Note, N_a is undefined when $a = 1$, but by taking the limit as a approaches 1, the equation becomes the exponential of Shannon-Wiener diversity index (Eq. 3):

$$N_1 = exp(-\sum_{i=1}^{S} p_i ln p_i) \tag{2}$$

$$H' = -\sum_{i=1}^{S} p_i ln p_i \tag{3}$$

By taking the exponential of Shannon, Hill diversity converts the index into its "numbers equivalent." In other words, it scales the index to reflect the expected numbers of species in the sample. In addition to being more ecologically intuitive (unlike the raw diversity indices which lie on an arbitrary scale), numbers equivalents also maintain intuitive mathematical properties (Jost, 2006). For example, using Hill numbers, a community with equal numbers of five species will have half the diversity of a community containing equal numbers of ten species. Rao's quadratic entropy (RaoQ) is an index commonly used in biological trait analysis (Eq. 4). It considers both the abundance of species, and the average functional dissimilarity d_{ij} between two species i and j, without replacement (Rao, 1980).

$$RaoQ = \sum_{i=1}^{S} \sum_{i=1} d_{ij} p_i P_j \tag{4}$$

RaoQ accepts any dissimilarity metric where d_{ij} is a number between 0 and 1. When $d_{ij} = 1$ for all $i \neq j$ (meaning all species are functionally distinct) RaoQ simplifies to the Simpson diversity index (Eq. 5), which is the compliment of the Simpson dominance index (Botta-Dukát, 2005).

$$SD = 1 - \sum_{i=1}^{S} p_i^2 \tag{5}$$

Appendix D

Multinomial logistic regression

Results of multinomial logistic regression for functional guilds and traits. Deviance values and degrees of freedom "df" were calculated by the function multnom in the R (Version 3.4.3) package "nnet" (Ripley & Venables, 2011). Chi-squared values were calculated using the function lrtest in the package "lmtest" and comparing the observed multinomial model to a null model with no regressors. P values were calculated by producing 1,000 randomizations of the trait abundance data while holding the time identifier constant. Statistically significant values, indicated in bold with an asterisk (*), were determined at a cutoff of $p < 0.05$. This analysis was developed with Andrew R. Solow.

TRAIT	BASELINE	Deviance	df	Chisq	p
MAXIMUM ADULT BODY SIZE	Small ($\sim$ 1 mm)	1777	6	2322.5	0.427
HABITAT COMPLEXITY	Does not add complexity	646	9	3290.8	0.492
TROPHIC MODE	Symbiont	1132	12	9398.6	**0.003***
FEEDING METHOD	Non-feeding	1327	18	6536.9	**0.031***
RELATIVE ADULT MOBILITY	Sessile	2644	9	4914.2	0.166
EXTERNAL PROTECTION	Soft bodied	315	6	5219.0	**0.010***
LARVAL DEVELOPMENT	Lecithotrophic	554	9	1253.2	0.124
REPRODUCTIVE TYPE	Gonochoristic	129	6	102.3	0.512
FUNCTIONAL GUILD	A	1390	33	8489.6	**0.029***

Appendix E

Maps of sample sites for parasites at 9°50'N, East Pacific Rise

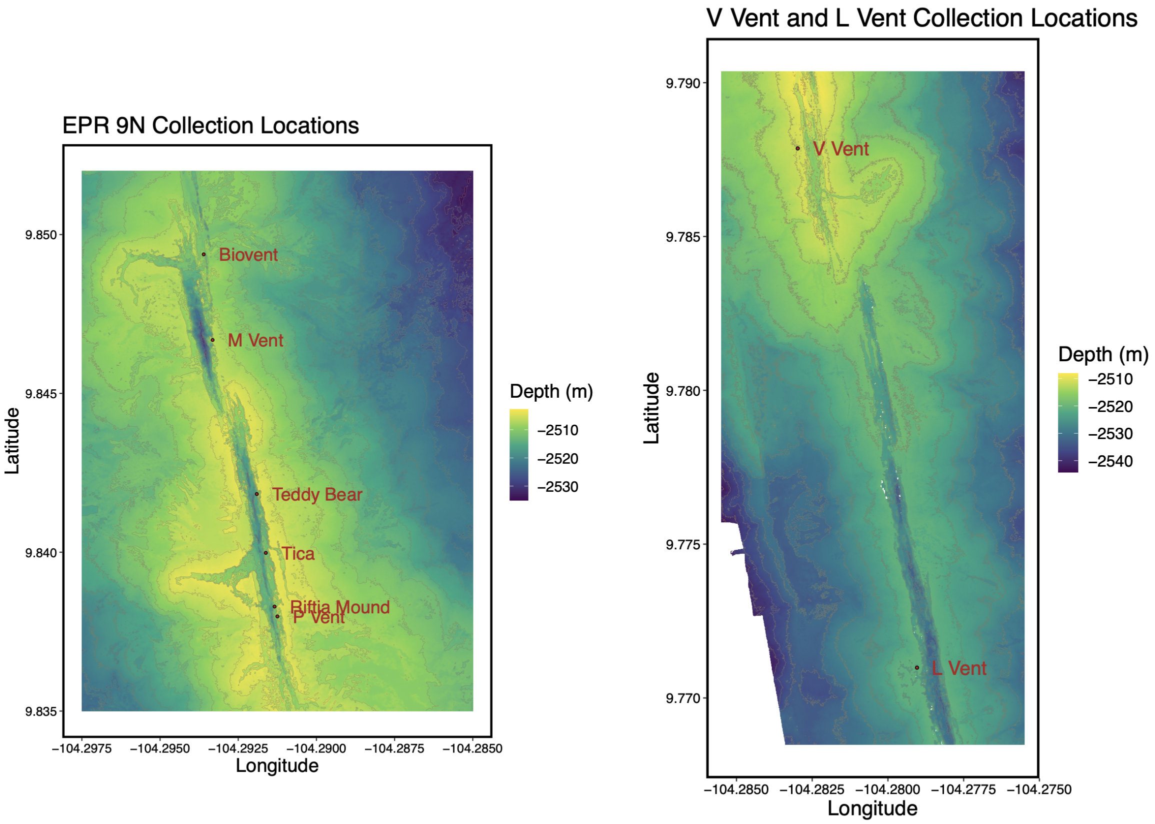


Figure E-1: Maps showing locations of faunal samples from vents in the 9°50'N vent field (left) and two vents ∼ 7 km farther south (right). High resolution bathymetry was taken by AUV *Sentry* in 2019 and 2021 (Wu et al., 2022). Precise latitude, longitude, and depth of the collection sites are available in Wu et al. (2022) and in BCO-DMO at https://www.bco-dmo.org/dataset/879118 (Dykman et al., 2022).

Appendix F

Detailed methods of dissections, data subsetting, and life cycle assignment for parasite species

Potential hosts were dissected fresh aboard the ship or frozen at -80°C immediately upon arrival at the surface. Hosts were identified to species using reference guides (Desbruyères et al., 2006) or COI barcoding with universal metazoan primers (Folmer et al., 1994). When species ID was uncertain, hosts were assigned a morphogroup ID or grouped at a higher taxonomic level (i.e., Family or Genus). Host length was measured along the maximum dimension following standard protocol for each taxon. Additional host information, such as weight, sex, gut contents, and condition, was recorded when possible. Each potential host was thoroughly examined following standard methods for detecting metazoan parasites (Kuris et al., 2008; McLaughlin, 2018; Morton et al., 2021). The exterior of each specimen and the wash from its storage bag or compartment were inspected for ectoparasites. Hosts were dissected, and parasites detected visually by pressing host tissues between two glass plates under a dissecting scope illuminated from beneath, and carefully scanning the slide in a grid pattern. For large animals, each organ was examined individually. Small animals were squashed and examined whole.

Metazoan parasites were assigned a species or morphogroup name and counted. When a species or morphogroup was first encountered or found in a new host species, several individuals were measured, photographed, and preserved in 80% ethanol and 95% ethanol for morphological and molecular description, respectively. If identification was uncertain, specialist taxonomists were consulted to ensure morphogroups were distinct to the species level. If a species or morphogroup was not known to be parasitic based on its taxonomic group (e.g., all trematodes are parasitic but copepods have both free-living and parasitic species), we decided a symbiont was parasitic based on three criteria: the species must be 1) found living in close association with a potential host and not elsewhere, 2) have specialized morphology for feeding or clinging, and 3) be embedded within host tissue, have evidence of feeding on host tissue, or show signs of localized damage to host tissue. All vent dissection data and associated metadata are available in BCO-DMO at https://www.bco-dmo.org/dataset/879118 (Dykman et al., 2022).

For all three data sets we generally retained all collection locations and time points for analysis. An exception was the removal of the California Channel Islands collection sites and three collection sites along the mainland coast from the Santa Barbara kelp forest data set. The Channel Islands have distinct oceanographic conditions and are separated from the mainland by the Santa Barbara Channel, so could be considered a separate ecosystem. The three most outlying mainland sites were omitted to reduce the geographic range of the kelp forest data and make it more comparable to the geographic range of the other data sets.

The three data sets were subset following a consistent protocol to facilitate comparison. Our analysis focuses on four host taxonomic groups: Crustaceans, Fish, Mollusks, and Polychaetes. Host species in other groups (e.g., Phoronida, Echinodermata, Anthozoa) were omitted from analysis because they were not represented in all three ecosystems. Host species with fewer than ten individuals were omitted to assure a sufficient sample size for each host species while retaining at least two species in each host group and ecosystem. Exceptions were the vent fishes *Thermarces cerberus* and *Thermichthys hollisi*, for which we were only able to collect nine and two fresh specimens, respectively. For these species, we supplemented our collections with specimens collected from the same sites during prior cruises: two whole frozen *Thermarces cerberus* collected in April of 2017 during cruise AT37-12 (dive A4897); and preserved gut contents of 22 *Thermichthys hollisi* collected in February of 2007 during cruise AT15-15 (dive A4317) (Buckman, 2009).

After subsetting, our comparative analyses included 2 crustacean, 12 fish, 12 mollusk, and 2 polychaete species from Santa Barbara kelp forests; 5 crustacean, 23 fish, 12 mollusk, and 4 polychaete species from Palmyra Atoll lagoon sandflats; and 6 crustacean, 2 fish, 10 mollusk, and 10 polychaete species from EPR 9N vents.

Each parasite species or morphogroup retained for comparative analyses was categorized as having a direct (single-host) or indirect (multi-host) life cycle based on direct observation or published literature. Life cycle assignments and references for each species used in analysis are available in BCO-DMO at https://www.bco-dmo.org/dataset/879253 (Dykman, 2022a). In some cases, parasite life cycles are conserved at a high taxonomic level, making assignment simple. For example, acanthocephalans, cestodes, and trematodes have indirect life cycles, while monogeneans and rhizocephalans have direct life cycles. If the life cycle of a parasite species or morphogroup was not known, the life cycle assignment was taken from the most closely related species for which a life cycle description was available. Some copepod and nematode morphogroups in the data set did not have taxonomic information. In these few cases, we assumed copepods have direct life cycles and nematodes have indirect life cycles, as these are the most common life cycle modes among species in these taxa.

Appendix G

A rank ANCOVA analysis for comparing parasite diversity between ecosystems

Let Y_{egj} be the Chao2 estimate of mean parasite richness of host species j $(j = 1, \ldots, n_{eg})$ in group g $(g = 1, \ldots, 4)$ and ecosystem e $(e = 1, \ldots, 3)$ and let R_{egj} be the rank among all the estimates of Y_{egj} with ties receiving the average rank. The systematic part of the rank analysis-of-covariance (ANCOVA) model can be written:

$$R_{egj} = \beta_e + \gamma_g + \delta L_{egj} \tag{1}$$

where β_e is the ecosystem effect, γ_g is the group effect, and δL_{egj} is the contribution of the rank mean host-species length L_{egj}. For identifiability:

$$\sum_{g=1}^{4} \gamma_g = 0 \tag{2}$$

Interest centers on testing the null hypothesis $H_0 : \beta_1 = \beta_2 = \beta_3 = 0$ of no ecosystem effect against the ordered alternative hypothesis $H_1 : \beta_1 > \beta_2 > \beta_3$ that the ecosystem effects follow the prediction of island biogeography theory. The alternative model can be fit by minimizing the residual sum of squares (RSS) subject to the order restrictions using, for example, the R routine qprog in the package 'coneproj' (Liao & Meyer, 2014). Significance can be assessed by repeatedly randomizing the ecosystem assignment of species within each host group, maintaining the observed numbers n_{eg}, and refitting the model. Importantly, mini-

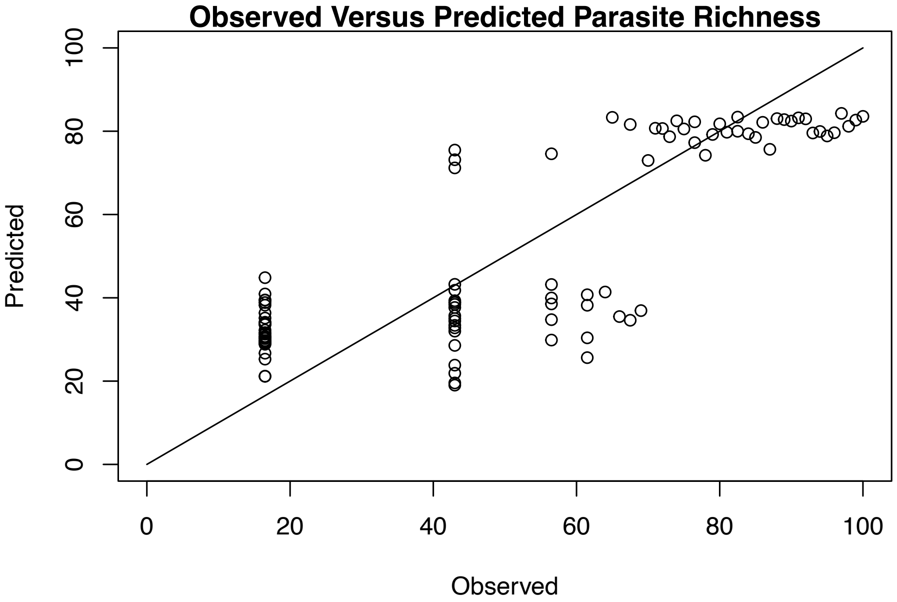


Figure G-1: Observed rank parasite richness per host species versus rank richness predicted by fitting the 2-way ANCOVA with ordered alternative (R-sq = 0.67, p = 0.39). The 1:1 line is shown for evaluation of fit.

mized RSS for the fitted null model is unaffected by this randomization. The observed significance level (or p value) is approximated by the proportion of randomized data sets for which the minimized RSS for the alternative model is less than its observed value.

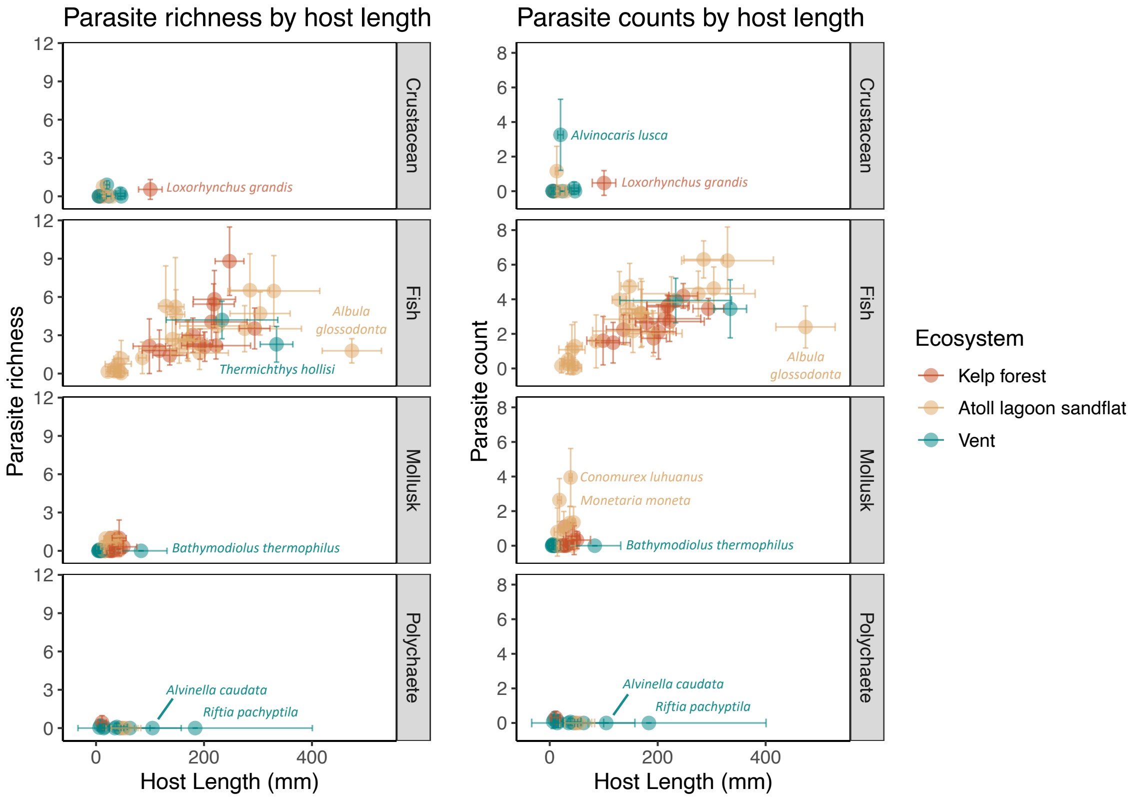


Figure G-2: Plot showing the mean (± SD) (vertical bars) parasite richness (left) and parasite counts (right) per host species by host length (horizontal bars). The y axis of parasite counts is on a log scale. Host species that were most distinct from the trend of the host group are labeled with their species name, which is color-coded by ecosystem.

Appendix H

Species richness curves

Accumulation curves for the estimated mean number of parasite species $\hat{p}$ contained in a random sample of h host species were calculated as in Solow & Smith (1991) and Smith & Grassle (1977) using the formula:

$$\hat{p} = \sum_{i=j}^{J} 1 - \frac{\binom{H-L_j}{h}}{\binom{H}{h}} \tag{1}$$

Here, J is the total number of parasite species, H is the total number of host species, and L_j is the number of host species containing parasite species j. This same equation was used to estimate the mean number of parasite species as a function of host individuals sampled in a given host species. In this case, h is a random sample of host individuals, H is the total number of host individuals sampled for a given host species, and L_j is the number of host individuals containing parasite species j.

Appendix I

A beta binomial test for comparing parasite prevalence between ecosystems

This analysis was developed with Andrew R. Solow, and the description in this appendix was translated directly from his notes. This analysis uses a beta binomial distribution to statistically fit presence/absence data of parasites on hosts (prevalence; Bush et al. 1997) in different ecosystems and host groups. Let n_{egj} be the number of individuals sampled in a host species and Y_{egj} be the observed number of individuals in that species that are infected by any parasite. Y_{egj} has a binomial distribution with n_{egj} trials and success probability π_{egj}:

$$Y_{egj}|\pi_{egj}\ Binomial(n_{egj}, \pi_{egj}) \tag{1}$$

The parasitization probability in an eg combination has a beta distribution with mean μ_{eg} and dispersion parameter θ_{eg}:

$$\pi_{egj}\ Beta(\mu_{eg}, \theta_{eg}) \tag{2}$$

The log likelihood for this model is given in Williams (1975):

$$logL = \sum_{e=1}^{3}\sum_{g=1}^{4}\sum_{j=1}^{n_{eg}}\left[\sum_{k=0}^{Y_{egj}-1} log(\mu_{eg} + k\theta_{eg}) + \sum_{k=0}^{n_{egj}-Y_{egj}-1} log(1-\mu_{eg} + k\theta_{eg}) - \sum_{k=0}^{n_{egj}-1} log(1 + k\theta_{eg})\right] \tag{3}$$

where e is the ecosystem, g is the group, and j is the species. In this study, there are three ecosystems (kelp forests, atoll lagoon, and vents) and four host groups (crustaceans, fish, mollusks, and polychaetes). The number of host species, j, and the number of individuals within a host, n_{egj}, varies between ecosystems and host groups. However, this variability is acceptable as long as there are at least two host species in each ecosystem group combination, which these data satisfy.

A simple ANOVA-type mean model is:

$$log\frac{\mu_{eg}}{1-\mu_{eg}} = \mu + \beta_e + \gamma_g \tag{4}$$

with inverse:

$$\mu_{eg} = \frac{exp(\mu + \beta_e + \gamma_g)}{1 + exp(\mu + \beta_e + \gamma_g)} \tag{5}$$

Here, μ is an overall effect, β_e is an environmental effect, and γ_g is a group effect. For identifiability, the following side conditions are imposed:

$$\sum_e \beta_e = \sum_g \gamma_g = 0 \tag{6}$$

The null model in this case is that there is no environmental effect, or in other words $\beta_e = 0$ for all e. In the alternative model, β_e is allowed to vary for all e. I used the function isres (Runarsson & Yao, 2000, 2005) in the R package *nloptr* (Ypma et al., 2018) to find the best fit set of parameters that minimized this log likelihood function. A minimized log likelihood was found for both the null constrained model ($logL_0$) and the alternate unconstrained model ($logL_a$). The test statistic was $-2(logL_a - logL_0)$.

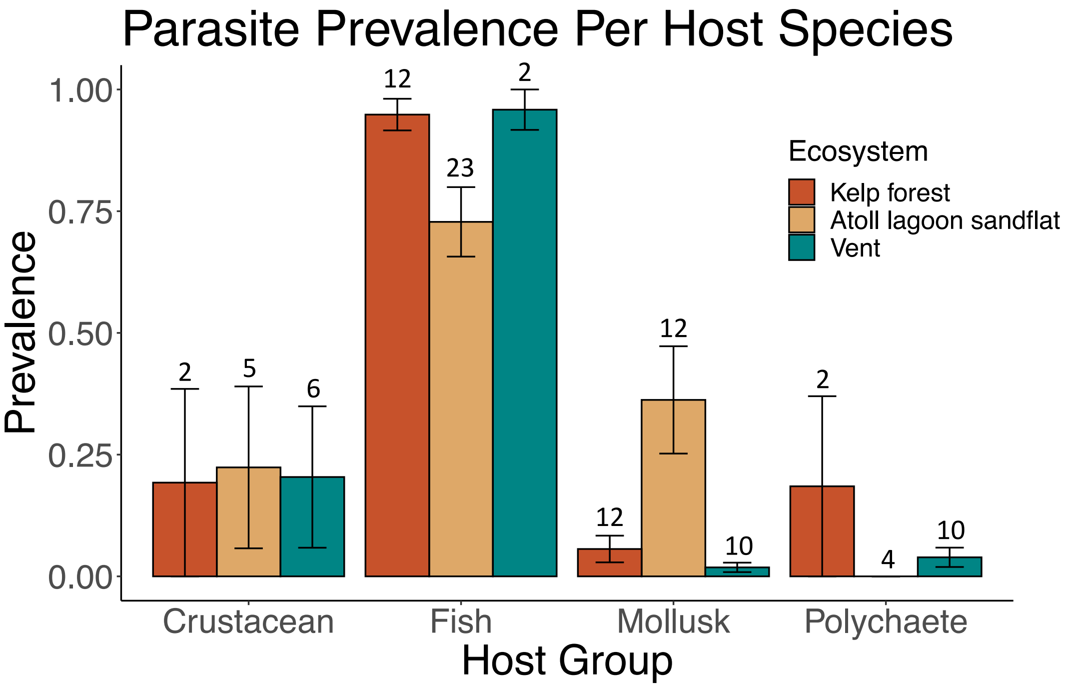


Figure I-1: Mean (± SE) parasite prevalence within host species in each ecosystem and host group. The number above the error bar is the number of host species included in the ecosystem and host group. Differences between ecosystems were not statistically significant based on a beta binomial statistical test ($p = 0.34$).

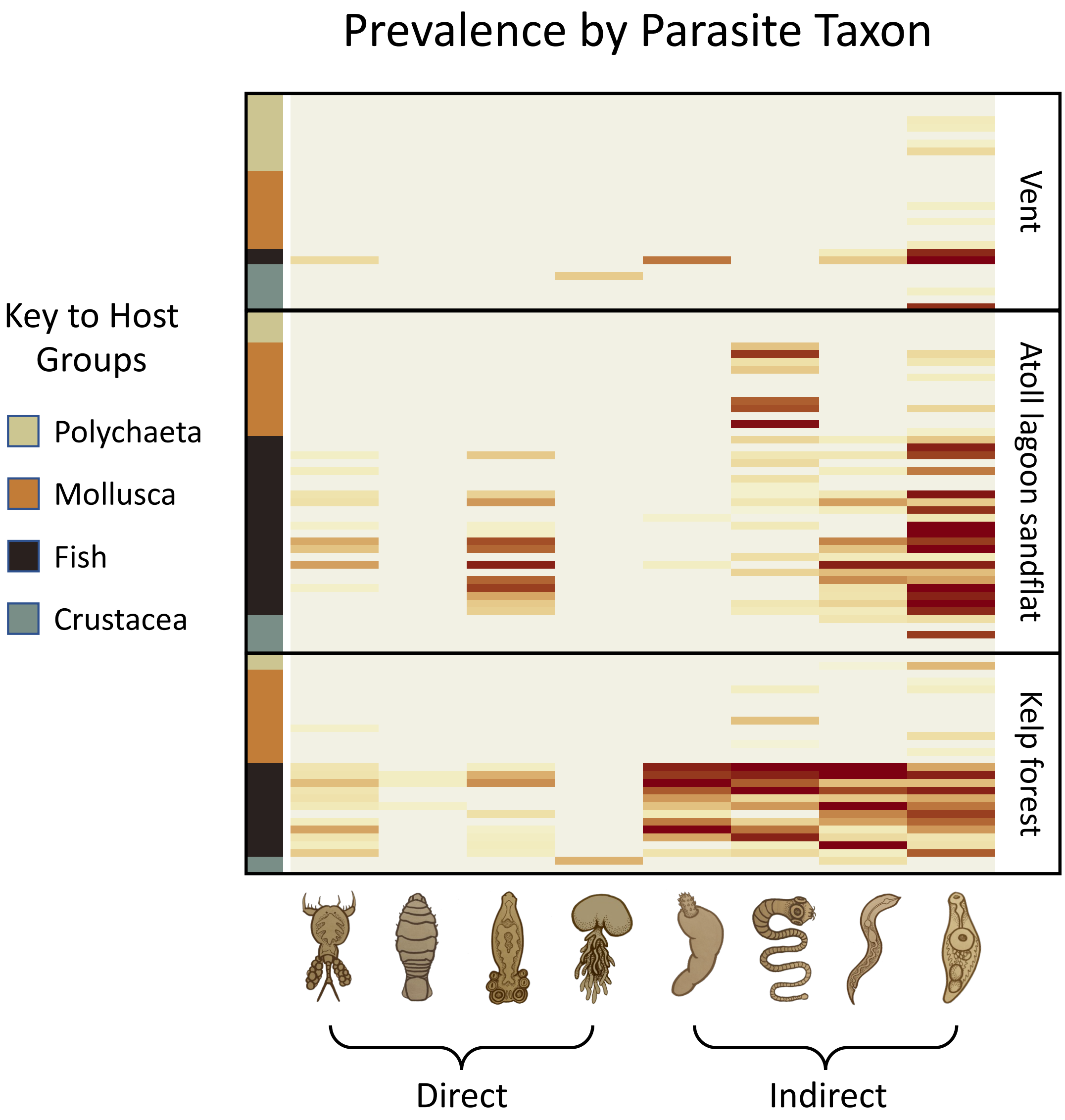


Figure I-2: Prevalence of each parasite taxonomic group in each host species included in analyses. Data are grouped by ecosystem and host group (color codes) on the y axis, and by parasite taxon on the x axis. Parasite taxa are grouped by whether they tend to have a Direct (Copepoda, Isopoda, Monogenea, Rhizocephala) or Indirect (Acanthocephala, Cestoda, Nematoda, Trematoda) life cycle. Darker colors indicate high prevalence, low colors indicate low prevalence.

Appendix J

Sensitivity analyses for influence of parameter choice on model outcomes

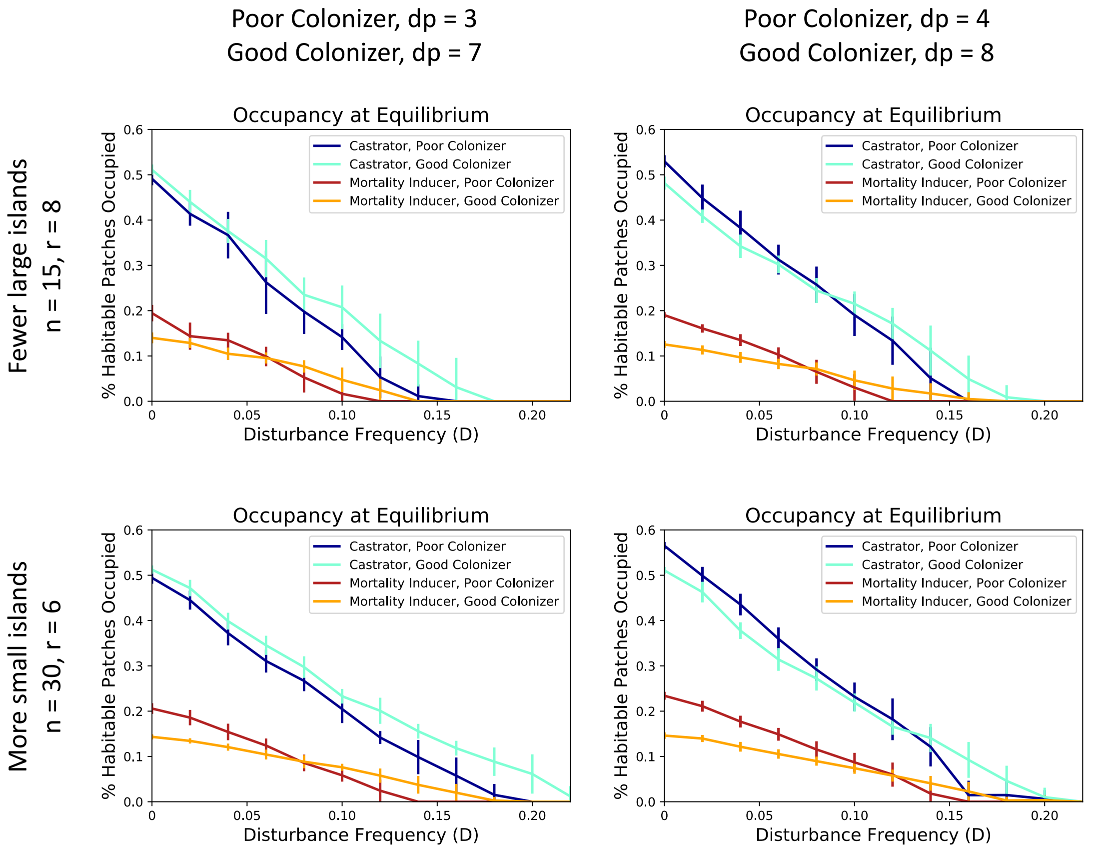
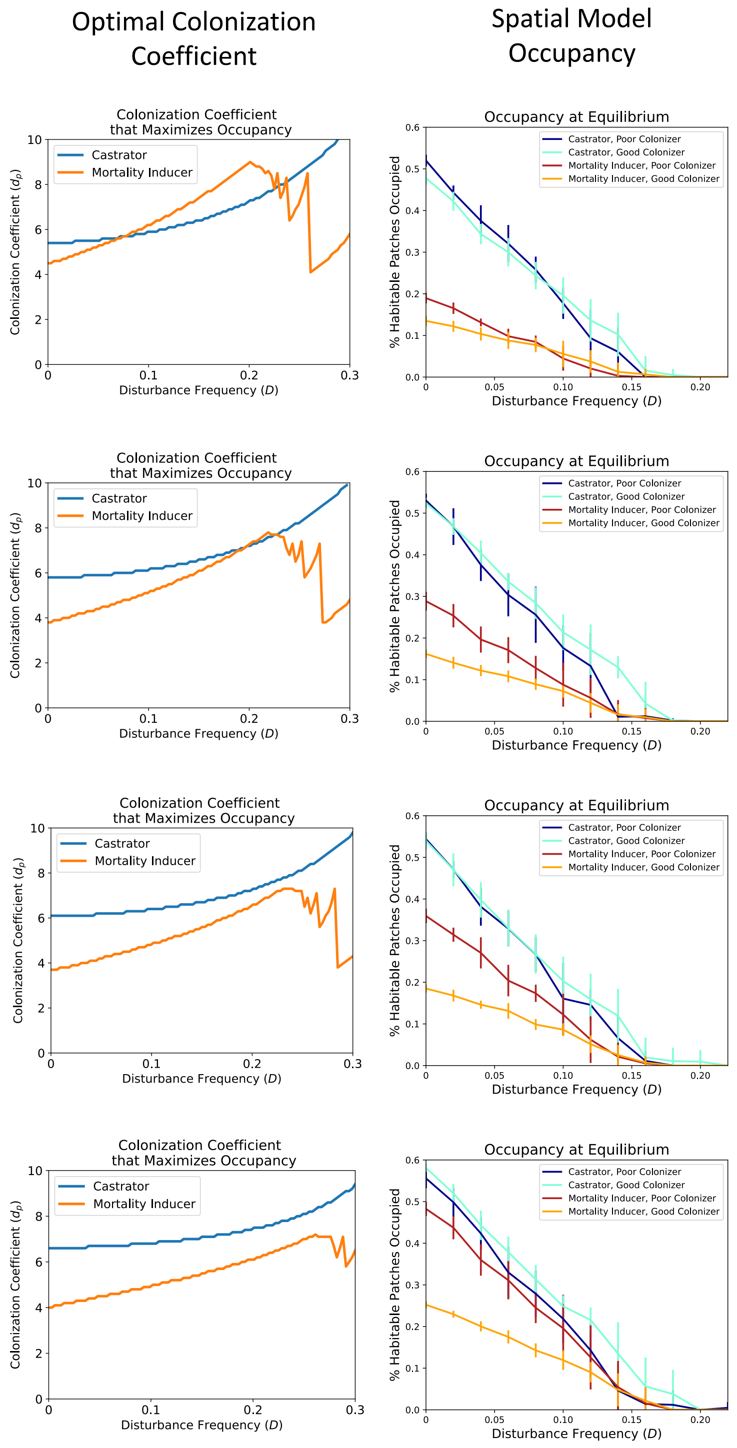


Figure J-1: The influence of different colonization coefficients, island size, and island number on the occupancy results for different parasite life strategies.



Castrator

$$d_i = d_s - \frac{1.2^{d_p}}{1.2^{0.62\, d_{pmax}}}$$

Mortality inducer

$$m_i = m_s + \frac{1.2^{d_p}}{1.2^{1.05\, d_{pmax}}}$$

Castrator

$$d_i = d_s - \frac{1.3^{d_p}}{1.3^{0.74\, d_{pmax}}}$$

Mortality inducer

$$m_i = m_s + \frac{1.3^{d_p}}{1.3^{1.045\, d_{pmax}}}$$

Castrator

$$d_i = d_s - \frac{1.4^{d_p}}{1.4^{0.80\, d_{pmax}}}$$

Mortality inducer

$$m_i = m_s + \frac{1.4^{d_p}}{1.4^{1.03\, d_{pmax}}}$$

Castrator

$$d_i = d_s - \frac{1.7^{d_p}}{1.7^{0.87\, d_{pmax}}}$$

Mortality inducer

$$m_i = m_s + \frac{1.7^{d_p}}{1.7^{1.01\, d_{pmax}}}$$

Figure J-2: The effect of different tradeoff curves on occupancy results for the spatial and non-spatial models. Tradeoff equations are shown to the left. In each case, the maximum colonization coefficient explored, $d_{pmax} = 10$. Coefficients are set such that no harm is caused to the host when $d_p = 0$ and maximum harm is caused to the host when $d_p = 10$.

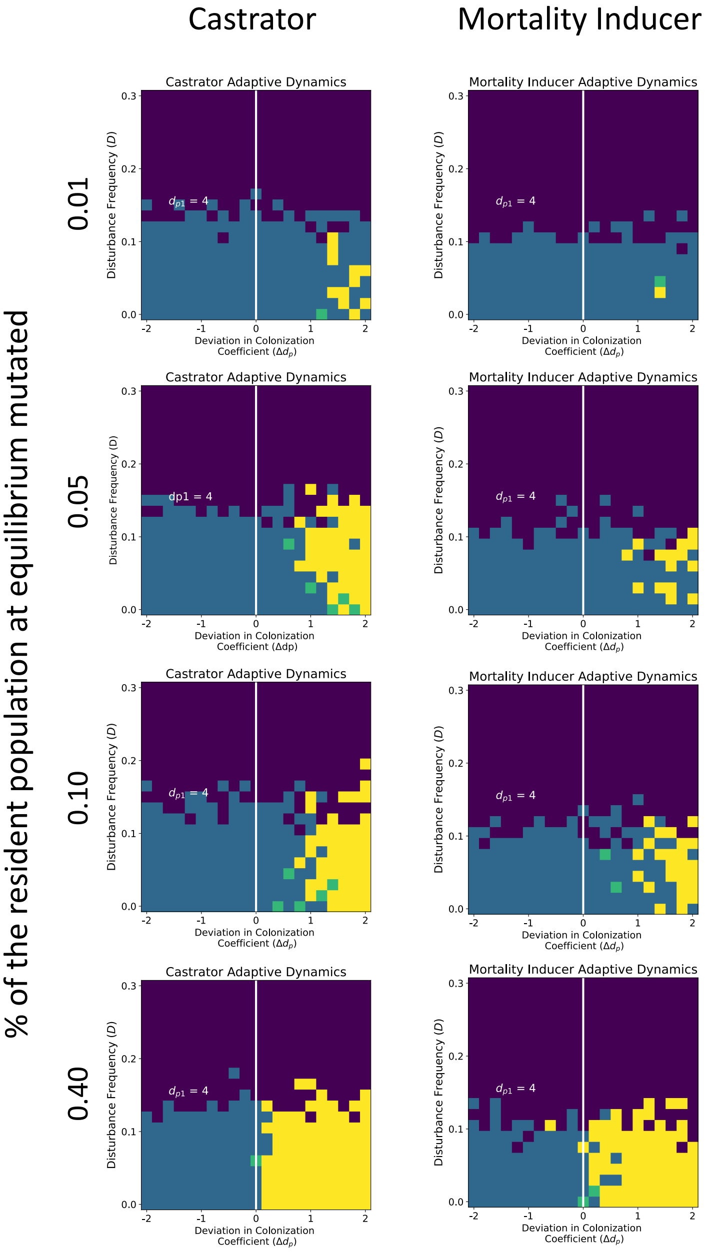


Figure J-3: Sensitivity analysis for the effect of the number of mutants introduced on the results of the spatial adaptive dynamics analysis. The numbers to the left indicate the proportion of the resident population at equilibrium that was mutated for adaptive dynamics analyses. Purple: extinction; Blue: resident persists; Green: coexistence; Yellow: mutant persists. The results presented in the main body of the thesis used mutation rates of 0.1.

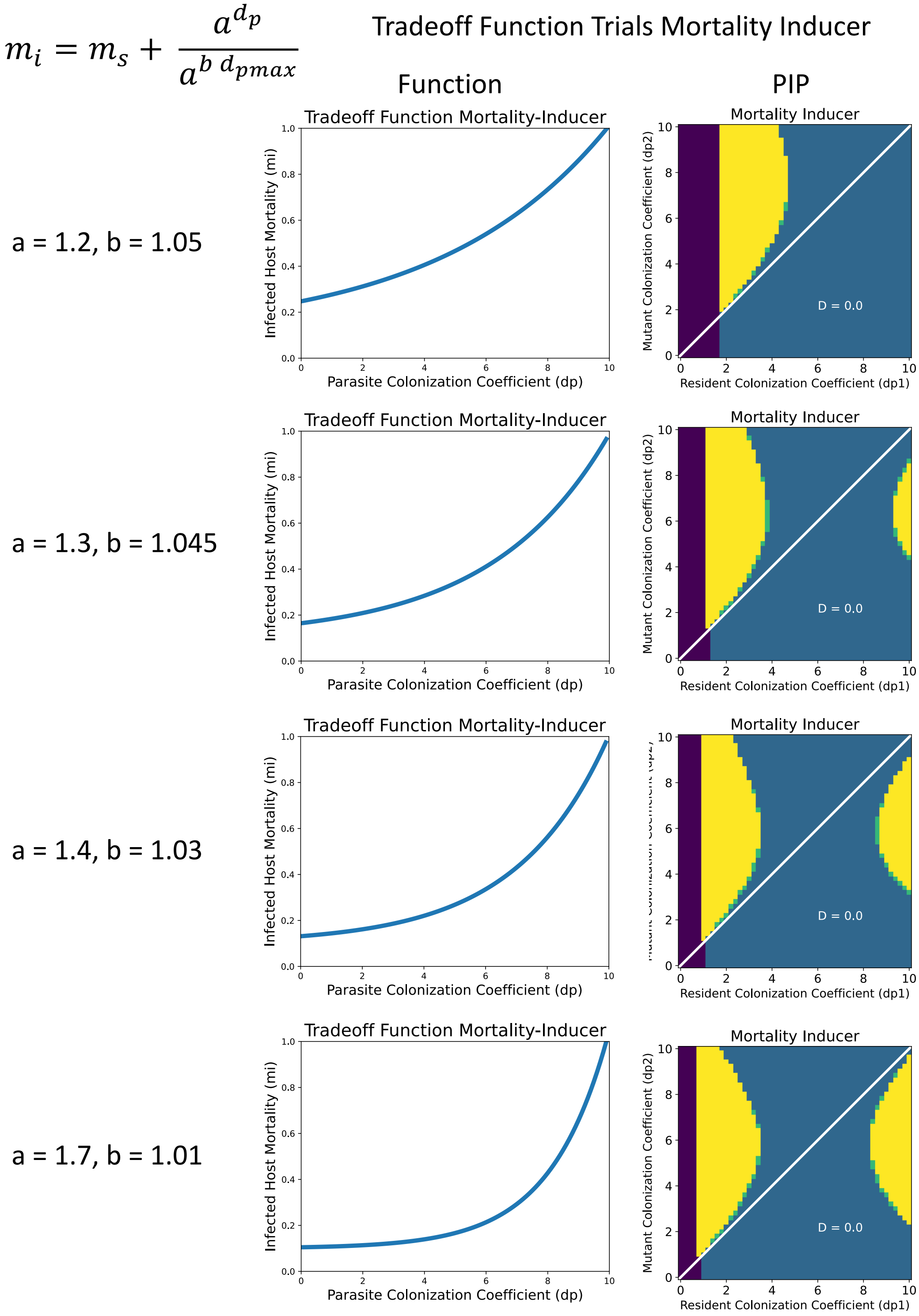


Figure J-4: The effect of different tradeoff functions on the pairwise invasibility plot for mortality inducer traits. Purple: extinction; Blue: resident persists; Green: coexistence; Yellow: mutant persists.

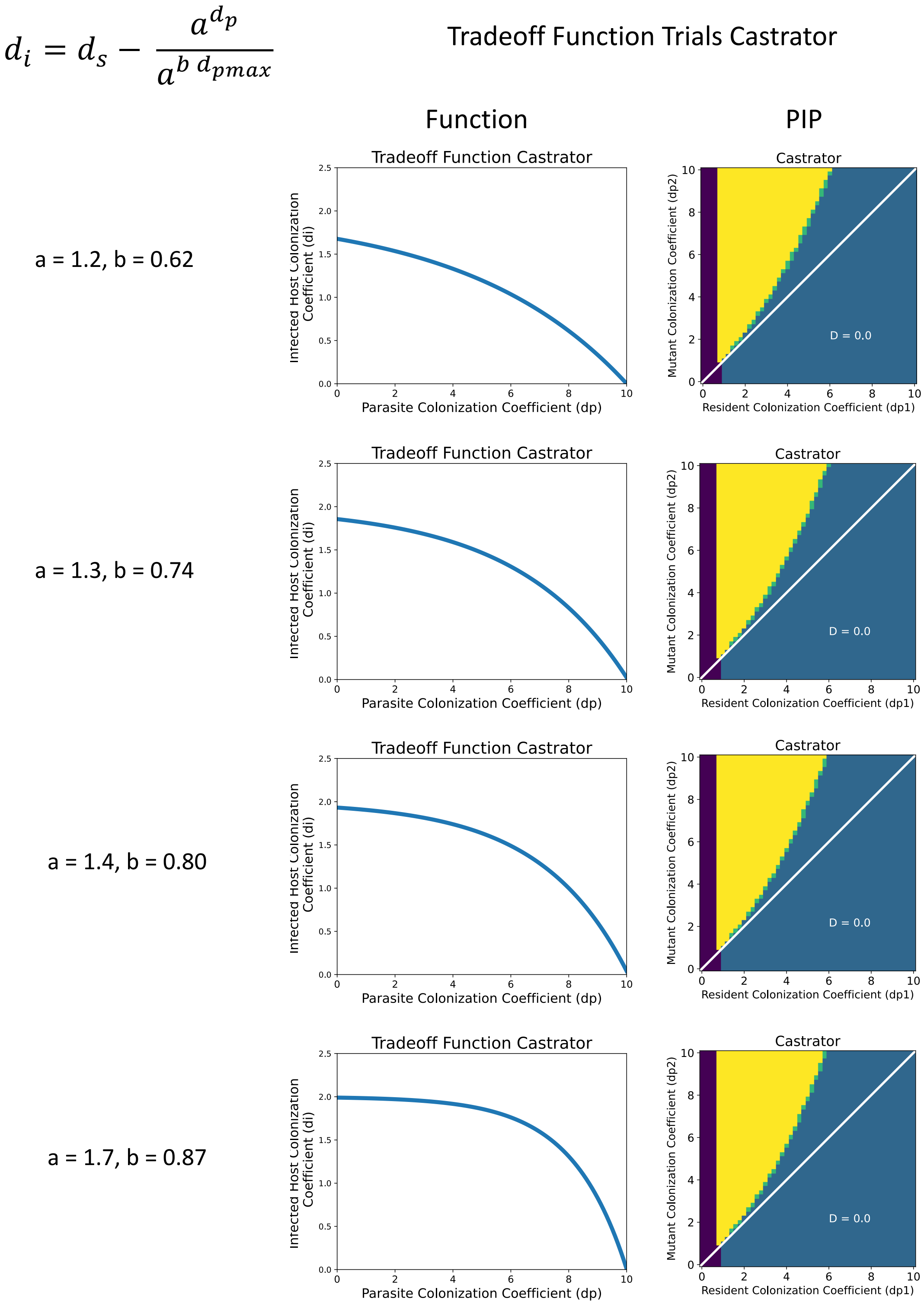


Figure J-5: The effect of different tradeoff functions on the pairwise invasibility plot for castrator traits. Purple: extinction; Blue: resident persists; Green: coexistence; Yellow: mutant persists.

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