Mining the Deep: A global assessment of biodiversity and research effort at deep-sea hydrothermal vents in relation to mining of seafloor massive sulphides

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EXECUTIVE SUMMARY

When the *RV Knorr* set sail for the Galapagos Rift in 1977, the scientists aboard expected to find deep-sea hydrothermal vents. What they did not expect to find was life—abundant and unlike anything ever seen before. Submersible dives revealed not only deep-sea hydrothermal vents but entire ecosystem surrounding them, including the towering bright red tubeworms that would become icons of the deep sea. This discovery was so unexpected that the ship carried no biological preservatives. These first specimens were fixed in vodka from the scientists' private reserves.

Since that first discovery, deep-sea hydrothermal vents have been found throughout the oceans. As more regions are explored, newly discovered vent fields present the potential for entirely species and ecosystems. Increasingly, however, it is not scientific discovery, but the financial value of vent fields, and the ores they contain, that is driving exploration in the deep sea. Over the last five decades, a new industry has emerged to explore the potential of mining Seafloor Massive Sulphides (deep-sea hydrothermal vents that contain high concentrations of rare and precious metals). Multiple enterprises are developing mining prospects that include both active and inactive deep-sea hydrothermal vent fields.

In order to understand the impacts of exploitation at deep-sea hydrothermal vents, scientists and miners must establish environmental baselines. Biodiversity is frequently used as a proxy for resilience and as a metric for assessing biological baselines but, since research effort is not distributed equally across the oceans, biodiversity estimates in the deep sea are rarely comprehensive. Studies have predominantly focused on a few key biogeographic provinces, while other regions have only been sampled sparingly. Managers, regulators, and mining companies are working from incomplete data, with inferences about the consequences, as well as mitigation and remediation practices, often drawn from studies of few vent ecosystems that are often different from those in which the impacts are expected to occur.

To better assess our current understanding of deep-sea hydrothermal vent biodiversity, we undertook a quantitative survey of the last 40 years of vent research. A stark north/south divide was detected, demonstrating that while research was disproportionately focused in the Northern Hemisphere, mining prospects were overwhelmingly positioned in the Southern Hemisphere. In addition, we provided a ranked assessment of biodiversity in eight major biogeographic provinces, identified knowledge gaps in the available deep-sea hydrothermal vent

exploration literature, and assessed sampling completeness to provide further guidance to regulators, managers, and contractors as they develop comprehensive environmental baseline assessments.

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INTRODUCTION

The deep sea, the Earth's "last great wilderness" (Ramirez-Llodra et al., 2011) is the largest unexplored ecosystem on the planet. Though the remoteness of the deep seafloor has buffered it from many of the activities impacting terrestrial, coastal, and shallow-water ecosystems, extractive industries are increasingly expanding into the deep sea. The seafloor, in particular, has faced continuous impacts from bottom trawling, offshore oil and gas exploration, and waste disposal. Less than 5% of the deep seafloor has been explored but the scars of exploitation are already apparent. Barely 13% of the ocean, including the deep sea, remains unspoiled marine wilderness (Jones et al., 2018). Among the emerging industries that threaten deep-sea ecosystems is deep-sea mining, the long-promised extraction of minerals from polymetallic nodule fields, cobalt-rich crusts, and hydrothermal vents (seafloor massive sulfides).

Deep-sea hydrothermal vents are formed when sea water percolates the crust and mantle under intense pressure. The contact with the mantle causes super-heated seawater to rise through stockworks in the Earth's crust while accumulating minerals and chemicals. As the chemical- and mineral-laden hydrothermal vent fluid meets the near-freezing water of the deep sea and erupts from the seafloor, it undergoes phase separation becoming a gaseous plume, which can reach temperatures in excess of 400°C (Schmidt et al., 2010). Minerals carried by this plume are deposited along the walls of the vent creating chimneys that grow and create large, exposed aggregations on the seafloor.

The geologists who launched the first expedition in 1977 were prepared to find, for the first time, a hydrothermal vent emerging from the seafloor. What they did not expect to find were the abundant, unique communities that thrive around hydrothermal vents and nowhere else. The discovery of these ecosystems was so unexpected that the scientists did not pack biological sampling equipment. The first specimens were preserved in vodka from the scientists' personal reserves (Ballard, 2000). Since that first discovery, deep-sea hydrothermal vents have been found throughout the world at mid-ocean ridges, back-arc spreading centers, and volcanic arcs (Beaulieu et al., 2013). Each newly discovered vent field comes with new species and, occasionally, entirely new communities forming novel biogeographic provinces.

Despite their global distribution, deep-sea hydrothermal vents are relatively rare ecosystems. Since their existence was first confirmed, only 345 hydrothermal vent fields have been observed, while an additional 356 have been inferred from chemical traces in the water column (InterRidge Vent Database version 3.4; Beaulieu et al., 2013).

Hydrothermal vents are found in all oceans and major seas, as well as some large inland lakes. Wherever tectonic plates converge under water, hydrothermal vents can be expected to occur (Van Dover, 2000). Where plates are moving away from each other, mid-ocean ridges form as the thinning crust at the spreading center exposes heat from the mantle, e.g. along the Mid-Atlantic Ridge stretching from the Arctic to the Antarctic. Where tectonic plates collide, fore-arc spreading centers form as the overriding plate is stretched thin, while the fractional melting of the subducting plate carries heat upwards, creating back-arc spreading centers, such as in the Pacific around the perimeter of the Ring of Fire, including the Lau, Fiji, and Manus Basins, the Kermadec Arc, and the Izu-Bonin-Mariana Arc. Because melting crust from the subducting plate intermingles with seawater being pulled down beneath the overriding plate, hydrothermal vent fluid from back-arc spreading centers is exceptionally metal-rich.

Relatively isolated hydrothermal vent fields also form at volcanic hot spots, as seen at the Hawai'i Hotspot, where mantle fluid is closer to the seafloor. Chemical processes, such as serpentinization, can also produce hydrothermal vent systems and freshwater hydrothermal vents exist in Russia's Lake Baikal, Yellowstone Lake in the USA, and Lake Tanganyika in East Africa.

ECOLOGY OF HYDROTHERMAL VENT ECOSYSTEMS

The deep sea is characterized by exceptionally high biodiversity, with some estimates rivalling even tropical rainforests for species richness, but, due to the energy-limited nature of the environment, exceptionally low biomass. Hydrothermal vents invert this deep-ocean paradigm, with ecosystems comprised of a few highly-specialized species that occur in incredibly high abundance (Van Dover, 2000).

At hydrothermal vents, geology drives diversity. Chemically-enriched hydrothermal vent fluid both excludes non-vent organisms from colonizing hydrothermal vents fields while also providing an energy source for the chemoautotrophic microbes that form the backbone of all

deep-sea hydrothermal vent ecosystems. In contrast to the generally stable and homogeneous deep background benthos, vents are characterized by extreme gradients: the chemical and thermal gradients of the hydrothermal vent plumes and surrounding mineral deposits, as well as the temporal gradients of the geologically dynamic energy source. To survive at a deep-sea hydrothermal vent, species evolved to deal with extremes of temperature, pressure, water chemistry, and the potential for catastrophic disturbance as the activity of the hydrothermal vent field waxes and wanes.

A typical deep-sea hydrothermal vent community is comprised of one or several foundational species that host chemoautotrophic endosymbionts—microbes capable of drawing chemical energy out of the vent fluid and converting it into biomass for the host species. These species provide, in many cases, both the bulk of the community's biomass as well as three-dimensional structure for other animals to colonize. Secondary species settle on or near large aggregations of foundational species, and though they often host chemoautotrophic microbes themselves, they have also adapted to opportunistically feed of the foundational species, graze microbes growing on the vent chimney, or filter food from the surrounding seawater. Often vent fields host several distinct species assemblages depending on the type of and proximity to hydrothermal venting. These assemblages are surrounded by a ring of opportunistic halo fauna that benefit from the physical topography of the vent system and the presence of elevated biomass.

Although this pattern of zonation is observed at many hydrothermal vent fields across the world, there is no “characteristic” vent habitat. Vent communities can be broadly separated into biogeographic provinces based on the species assemblages and especially the dominant species present. These can vary from low-temperature fields of mussels and clams, to gigantic plumes of vent-dependent shrimp, to even more novel systems dominated by yeti crabs, hairy-snails, or the iconic giant tube worm, *Riftia pachyptila*. Even within a biogeographic province, there may be stark differences between different vent ecosystems. Drawing conclusions about the potential resilience of a relatively understudied vent ecosystem based on an observation from a different biogeographic province may result in erroneous or incomplete assessments.

DEEP-SEA MINING AT HYDROTHERMAL VENTS

Deep-sea mining, the process of removing ore from the seafloor beyond the edge of the continental shelf, is an emerging industry that has, until recently, hovered just on the edge of science fiction. While shallow-water mining for sand, iron, and diamonds has been long established, the tremendous cost and technological challenges of extracting minerals from the deep sea has precluded commercial exploitation. Though the industry can trace its development back more than half a century, it is only in the last decade that deep-sea mining has made serious advancements towards economically sustainable extraction.

The development of deep-sea mining as an industry has a long and curious history. Polymetallic nodules (also called manganese concretions or manganese nodules) were discovered on the first *Challenger* Expedition, where both their mineral value and utter inaccessibility were noted (Murray, 1877). Mid-century geologists projected that just a fraction of the mineral wealth of the seafloor was enough to supply the world with precious metals for a millennium (Mero, 1965), though how to exploit those resources was a matter of speculation. As early as the 1970s, policymakers speculated that deep-sea mining could be a reality within a decade (Luard, 1977). As knowledge of the deep seafloor expanded, other potential mineral resources were added, including cobalt-rich crusts (Fuyuan et al., 2010), rare-earth-element enriched muds (Tlig and Steinberg, 1982), and seafloor massive sulfides (Herzig and Hannington MD, 1995), all of which remained financially and technologically inaccessible throughout the 20th century.

The first major exploratory endeavor to assess the value and potential of mineral ore on the deep-sea floor (in this case, polymetallic nodules) was the voyage of the USNS *Hughes Glomar Explorer*. Though this deep-sea drill ship did recover polymetallic nodules from the seafloor, the expedition was, in actuality, a CIA-sponsored front to locate and recover a Soviet submarine from 4900m depth (Redacted, 1978). Though the existence of Project Azorian became public only a few years after the operation, mining companies had already begun to negotiate access to mineral rights on the high seas, pointing to the CIA operation as proof that, with access to enough financial resources, recovering ore from the bottom of the ocean could be feasible (Bath, 1989; Larson, 1986). The nascent deep-sea mining industry was born.

Though some exploratory expeditions occurred in the 1970s, 1980s, and 1990s, it wasn't until the late 2000s that shifts in commodities markets, access to technology, and increasing

understanding of the seafloor would converge to make deep-sea mining feasible. In the interim, the discovery of deep-sea hydrothermal vents, referred to within the industry as seafloor massive sulfides or polymetallic sulfides, revealed a new mineral-rich ore that contained high densities of precious metals like gold, silver, copper, zinc, and nickel, as well as rare-earth elements (Hoagland et al., 2010).

Areas Beyond National Jurisdiction.

Seafloor mineral resources in areas beyond national jurisdictions are governed by the International Seabed Authority (ISA), which manages “The Area” under guidelines established through the United Nations Convention on the Law of the Sea. Any signatory nation or sponsored entity must apply directly to the ISA for exploration permits to assess the value of ore in a specified region or exploitation permits to extract valuable ores from the Area. The ISA Regulations on Prospecting and Exploration for Polymetallic Sulphides in the Area were adopted in 2010 and require that applicants establish environmental baselines in order to assess changes to hydrothermal vent communities and habitats, as well as maintain an environmental monitoring program before, during, and after operations. The ISA also requires areas of seafloor be set aside during extraction and provides recommendations for long-term seafloor protected areas.

The International Seabed Authority is currently in the process of developing draft regulations for the extraction of mineral resources from the Area by contractors.

Areas Within National Jurisdictions.

Within territorial waters, mining exploration and exploitation leases, as well as management and mitigation requirements, fall under national jurisdiction and vary depending on the regulations of the country in question. Currently, Papua New Guinea, New Zealand, the Kingdom of Tonga, and Vanuatu have issued exploration permits to assess the value of ore found at deep-sea hydrothermal vents within their territorial waters (Boschen et al., 2013). In addition, Papua New Guinea has issued a single mining license for the resource-rich Solwara I hydrothermal vent field (Hoagland et al., 2010).

In Papua New Guinea, mining hydrothermal-vent deposits falls under the 1992 Mining Act and the 2000 Environment Act, which establish that the government of PNG owns these mineral resources and requires anyone wishing to exploit them provide an environmental impact

statement. The Kingdom of Tonga was the first country to pass a law that directly addresses mining deep-sea mineral deposits. The 2014 Seabed Minerals Act requires a public comment period, environmental impact assessment, and ongoing monitoring for any seafloor mining project conducted either within Tongan waters or by Tongan-flagged vessels in international waters. Seafloor resources in New Zealand fall under the regulations of the 1991 Crown Minerals Act for resources found within 12-miles of the shore and the 2012 Exclusive Economic and Continental Shelf (Environmental Effects) Act, which regulates the environmental impacts of seafloor mining within New Zealand's Exclusive Economic Zone (EEZ). Vanuatu has no laws that directly address the mining of deposits associated with deep-sea hydrothermal vents, although several policies are currently under development.

Two international Codes of Conduct also apply to nations who have voluntarily elected to abide by them. The InterRidge Statement of Commitment to Responsible Research Practices (Devey et al., 2007) relates primarily to scientific research conducted at hydrothermal vents, including exploratory research to assess ore deposits. The International Marine Minerals Society Code for Environmental Management of Marine Mining establishes environmental principles and best practices for marine mining and recognizes the value of biological resources as well as mineral resources (Verlaan, 2011).

TRENDS IN GLOBAL RESEARCH EFFORT AT DEEP-SEA HYDROTHERMAL VENTS

Among the most pernicious problems in establishing a global assessment of biodiversity at deep-sea hydrothermal vents is that research effort is disproportionately distributed across the oceans. While some hydrothermal vent ecosystems, such as the Mid-Atlantic Ridge or East Pacific Rise, are well studied, with hundreds of research expeditions undertaken to study their geology, chemistry and biology, others, such as those of the Indian and Southern Oceans, have received a fraction of that attention, hosting only a handful of recent research expeditions. It is therefore difficult to assess knowledge gaps and make informed decisions about the management of relatively understudied hydrothermal vent systems threatened by deep-sea mining.

To address this issue, we used reports from individual research cruise as proxies for functional research effort. By assessing how many research cruises visited a particular region or

vent system, we can gain a better understanding of the extent of global research effort and how that corresponds with both assessments of biodiversity as well as gaps in our knowledge for vulnerable hydrothermal vent ecosystems. The methodology and results of this study are reported in detail in Thaler and Amon (2019a).

We compiled a total of 262 cruise reports representing 13 nations that collected biological samples or made biological observations at deep-sea hydrothermal vents spanning from 1966 to 2017. While there is no comprehensive archive of all deep-sea vent research cruises conducted globally, InterRidge maintains a substantive archive of known hydrothermal-vent research expeditions. Of the 841 cruises recorded in the InterRidge archive, 88 were confirmed to include biological sampling based on available cruise reports, subsequent publications, and cruise narratives, while the remainder were geologic, geophysical, oceanographic, or exploration-related without a documented biological component. For a complete description of the methodology, see Thaler and Amon (2019).

Notably absent were many Soviet-era cruises from the former USSR, the reports of which could not be located by colleagues, as well as cruises conducted by both national and corporate interests for the purposes of mineral exploration, which are generally held as proprietary information. Research cruises from the late 1970s and early 1980s were likewise less well documented and full cruise reports could not be located for several known early research expeditions, particularly to the Galapagos Rift.

Due to the incredible variety of naming conventions, the incompleteness of the global research record, and inconsistencies within and among institutions, it is likely impossible to account for every research cruise that has made biological observations at a deep-sea hydrothermal vent. We estimate that we have captured the majority of biological research expeditions to deep-sea hydrothermal vents (Figure 1) with a notable deficit in the Eastern Pacific.

Figure 1. Research cruises that made biological observations at deep-sea hydrothermal vent from 1966 to 2017.

Biological research at hydrothermal vents follows a weak decadal cycle, with peaks in research effort occurring in the early 1990s, early 2000s, and early 2010s. This is likely due to the volatility in academic funding cycles, the need to process and publish results from previous research cruises, and a tendency for major international efforts to be launched at the turn of the decade (i.e. Census of Marine Life from 2000 to 2010 and the upcoming UN Decade of Ocean Science from 2021 to 2030).

During the course of reviewing cruise reports, we located photographs from a 1966 cruise to the East Scotia Ridge aboard the *R/V Eltanin* which capture images of a Southern Ocean hydrothermal vent community (personal communications, J. Copley and L. Marsh) which predate the formal discovery of hydrothermal vents on the Galapagos Spreading Center in 1977.

Research cruises were heavily concentrated in 5 biogeographic provinces, the Mid-Atlantic Ridge, Northeast Pacific, Northern East-Pacific Rise, and North- and Southwest Pacific. Not surprisingly, these five provinces also contain the majority of confirmed hydrothermal vents, though the relatively unstudied Southern East-Pacific Rise also contains an abundance of confirmed hydrothermal vent fields. Prospective mining sites are currently only found in three biogeographic provinces, the Indian Ocean, Mid-Atlantic Ridge, and Southwest Pacific. Notably, all confirmed vents from areas beyond national jurisdiction in the Indian Ocean fall within an exploratory mining lease (Figure 2).

The pace of discovery at deep-sea hydrothermal vents is surprisingly brisk. On average two new species of hydrothermal vent-endemic fauna are described each month (Ramirez-Llodra et al., 2007). ChEssBase is a global, relational database of all species described from deep-sea

chemosynthetic ecosystems, including hydrothermal vents, methane seeps, and whale falls, that tracks individual records of species occurrences reported in the scientific literature. ChEssBase tracks over 640 species spread across more than 13,000 discrete records from 953 published scientific papers (Ramirez-Llodra et al., 2005). Though ChEssBase does not account for undescribed species, the data represent all known, described species that occur at deep-sea hydrothermal vents described before 2006. When complemented with sampling data from cruise reports that identify organisms to genus or family, we can create the most comprehensive possible picture of the current state of deep-sea hydrothermal vent richness and diversity.

Unsurprisingly, the best-studied biogeographic provinces also have the highest genus and species counts, though the Northeast Pacific is an outlier, with many more genera than putative

Figure 2. Distribution of active hydrothermal vent field, biological research cruises (subset used for biodiversity analysis in dark colors overlaid on all documented research cruises), vent fields in protected areas, and vent fields that fall within mining leases. Figure from Thaler and Amon (2019).

species. This is likely due to an overlap between vent and seep fauna found on and near the Juan de Fuca Ridge (see discussion in the following section). In several case, particularly the Arctic and Mid-Cayman Spreading Center, ChEssBase is out of date, and observations from more recent biological research cruises have not be archived in the database.

When research effort is compared across the equator, a stark contrast between the northern and southern hemispheres is apparent. Suspected vent fields are fairly evenly distributed between the northern and southern hemisphere. Despite that, twice as many vents have been confirmed in the northern hemisphere and almost three time as much research effort has been invested into studying northern vent ecosystems (Figure 2). InterRidge submitted draft recommendations for vent fields identified as targets for protection which are relatively evenly distributed across the Equator (Beaulieu et al., 2013).

The approximately one-hundred vent fields identified as being of particular ecologic importance which should be protected are roughly equally distributed across the equator, but among hydrothermal vents that actually fall within some form of marine protection, all occur in the northern hemisphere. In contrast, and with few exceptions, nearly every hydrothermal vent field that may be mined in the next decade lies in the southern hemisphere (Figure 3).

Figure 3. Global distribution of active, confirmed deep-sea hydrothermal vents (yellow domes), ISA-issued high seas mining exploration leases (red circles; note, bounding area is exaggerated for clarity), and mining exploration licenses issued within territorial waters (pink circles; note, bounding area is exaggerated for clarity). Black boxes indicate the member nations sponsoring claims in the area. White borders in inset represent exclusive economic zones. Large circles represent each biogeographic province for which sufficient data was available for analysis, in descending order of number of research cruises conducted in the region: 1. Mid-Atlantic Ridge, 2. Northwest Pacific, 3. Southwest Pacific, 4. Juan de Fuca Ridge, 5. Northern East Pacific Rise, 6. Mid-Cayman Spreading Center, 7. Indian Ocean, and 8. Southern Ocean. The Arctic, Mediterranean, and Southern East Pacific Rise biogeographic provinces are not indicated. Map prepared by Andrew Middleton.

BIOGEOGRAPHY OF DEEP-SEA HYDROTHERMAL VENTS

Deep-sea hydrothermal communities have been previously split into six biogeographic provinces: the Mid-Atlantic Ridge, Northern East Pacific Rise, Northeast Pacific, Western Pacific, Indian Ocean, and Southern East Pacific Rise (Bachraty et al., 2009; Moallic et al., 2012). However, newly discovered vent fields, as well as more extensive sampling throughout known regions, has led to several proposed further biogeographic provinces, including the Southern Ocean, Mid-Cayman Spreading Center, Arctic Ocean, and Mediterranean Sea (Moallic et al., 2012; Rogers et al., 2012; Van Dover et al., 2001). Currently, there is no universal consensus among the deep-sea hydrothermal-vent research community, however, these ten putative biogeographic provinces provide a useful delineation between different communities.

Hydrothermal vents also occur in shallow waters, often as part of the same geologic structures where deep-sea vents occur. Shallow-water hydrothermal vents tend to be dominated by common regional fauna with few vent-dependent species, and generally do not represent novel seafloor ecosystems (Dando, 2010; Tarasov et al., 2005). While shallow-water vent fields are considered as part of the global assessment of vent fields threatened by marine mining, they are dominated by non-vent regionally abundant macrofauna and are thus not factored into biogeographic assessments. Likewise, fresh water hydrothermal vents are known from some deep-water lake systems but are isolated and distinct from marine deep-sea hydrothermal vents (Crane et al., 1991).

Arctic

Loki's Castle: Arctic Ocean

Figure 5. Loki's Castle. Centre for Geobiology (University of Bergen, Norway). © by R.B. Pedersen.

Depth: 2,300m
Maximum Temperature: 317°C
Year Discovered: 2005

Loki's Castle is a complex of 5 active hydrothermal vent chimneys in the Arctic Ocean. It is the northernmost vent field and potentially among the largest seafloor massive sulphide deposits yet discovered.

Tube worms more commonly associated with methane seeps dominate Loki's Castle, occurring in dense fields around the sulphide mound. Small grazing gastropods, also common at deep-sea methane seeps, are found on the chimney walls. An undescribed species of endosymbiont-hosting amphipod is also abundant at this vent field and appears to fill the same ecologic niche as shrimp on the Mid-Atlantic Ridge. Along the vent periphery, species more commonly associated with the East Pacific Rise, including tube worms and stalked jellyfish, are found near cooler areas of diffuse flow.

Mid-ocean ridges in the Arctic Ocean are among the slowest-spreading ridge systems on the planet (Pedersen et al., 2010). Though there is significant evidence for hydrothermal venting along Arctic ridge axis, vents have so far only been identified on Gakkel Ridge and the Arctic Mid-Ocean Ridge (Edmonds et al., 2003; Pedersen et al., 2010). A single confirmed active vent is reported from Gakkel Ridge at a depth of 4100m. Six active vent fields and one inactive vent field are reported from the Arctic Mid-Ocean Ridge along the Mohn and Kolbeinsey Ridge segments, only one of which exceeds 1000m depth. One vent field occurs within the EEZ of Denmark's Greenland territory; four within Iceland's EEZ, and three fall within Norway's EEZ.

No known Arctic vent fields occur in areas beyond national jurisdiction.

The four vent fields that occur along Mohn Ridge that are relatively shallow are dominated by local, non-vent dependent species representative of regional bathyal diversity (Schander et al., 2010). Though biological samples have only been recovered from a single deep black smoker on the Arctic Mid-Ocean Ridge, Loki's Castle, the associated fauna have a shared affinity with fauna from Pacific vent fields, as well as from Atlantic seeps, suggesting that the Arctic Ocean represents a biogeographic province distinct from the hydrothermal vents that occur south of Iceland along the Mid-Atlantic Ridge. Loki's Castle is dominated by a seep-associated siboglinid tubeworm as well as an undescribed chemoautotroph-hosting amphipod found in crevices on the vent chimney (Pedersen et al., 2010). As of the most recent update to ChEssBase, no taxa are available from these vent fields (German et al., 2011; Ramirez-Llodra et

al., 2005). Six putative species were identified from a single research cruise to Loki's Castle (Pedersen et al., 2010).

Only 2 deep-sea research cruises were identified from InterRidge and other regional databases, both of which included biological observation or sampling of macrofaunal communities. No mining activity is currently proposed for hydrothermal vent fields in the Arctic, although both Norway and Denmark are actively exploring the potential for deep-sea mining within their EEZs. There is insufficient sampling data to adequately assess biodiversity in the Arctic.

Indian Ocean

Hydrothermal vents in the Indian Ocean are among the least studied vent ecosystems (Nakamura and Takai, 2015). This biogeographic province encompasses the entire ocean, however there is evidence that many populations are shared with the southwest Pacific, thereby representing a single larger province (Bachraty et al., 2009; Hashimoto et al., 2001; Moalic et al., 2012). While many species encountered at hydrothermal vents in the Indian Ocean share an affinity with southwest Pacific vent communities, one shrimp genus, *Mirocaris*, has so far only been found at Indian-Ocean and Mid-Atlantic-Ridge hydrothermal vents (Van Dover et al., 2001; Watanabe and Beedesse, 2015). The scaly-foot snail, *Chrysomallon squamiferum*, is among the few taxa that are considered endemic to Indian-Ocean hydrothermal vents and is representative of these vent fields (Chen et

Longqi: Indian Ocean

Figure 6. Squat lobsters, snails, and shrimp at the Longqi vent field.
University of Southampton.

Depth: 2,800m
Max Temperature: >300°C
Year Discovered: 2007

The Longqi vent field (also known as Dragon Horn or SWIR Area A) is a complex of 7 hydrothermal vent chimneys towards the south edge of the Southwest Indian Ridge.

A number of fauna unique to Indian Ocean vent systems dominate the Longqi vent field. On the chimneys nearest to vent effluent, scaly-footed gastropods, iconic to this region, as well as squat lobsters and alvinocarid shrimp are found in abundance. Mussels and barnacles frequent cooler areas further from the hydrothermal vent plume, with snails, stalked barnacles, and sea cucumbers occurring in lower abundance along the vent periphery. Many of the species found on Longqi are not yet reported from other locations, though other taxa are shared with other Indian Ocean vent fields along the Central Indian Ridge.

al., 2015; Watanabe and Beedessee, 2015). Vent fields in the southernmost region of the Southwest Indian Ridge host several unique species and display a species richness more akin to vent ecosystems along the Mid-Atlantic Ridge and East Pacific Rise (Copley et al., 2016).

There are 13 confirmed hydrothermal vent fields in the Indian Ocean, six of which are active and seven are dormant. Most known vent fields occur on the Central Indian Ridge (an intermediately fast spreading center; Hashimoto et al., 2001; Hellebrand et al., 2002), the Southeast Indian Ridge (an intermediate spreading center; Cochran and Sempéré, 1997), and the Southwest Indian Ridge (a slow or ultra-slow spreading center; Sauter et al., 2011) near the Central Indian Triple Junction, where the African, Indo-Australian, and Antarctic Plates meet. Two vent fields are also known from the Carlsberg Ridge, on the Central Indian Ridge north of the Triple Junction and one more active vent field is known from the Aden Ridge in the Gulf of Aden. Three of the known vent fields occur within national EEZs (two active vent fields in Mauritius and one active vent field in Djibouti) while the remainder occur in areas beyond national jurisdiction. The shallowest known vent fields occur at 1500m depth, the deepest are found at 5000m depth, while the average depth for known hydrothermal vent fields in the Indian Ocean is 3000m.

The difficulty in resolving biogeographic setting is likely due to the relatively low sampling effort within the region. A total of 45 deep-sea research cruises were available from InterRidge and other regional databases. Of those, 15 research cruises included biological observation or sampling of macrofaunal or megafaunal communities. Seven known hydrothermal vents fields (three active, four inactive) currently fall within ISA exploration contract areas (Beaulieu et al., 2013). As of the last update to ChEssBase, six taxa have been identified to the genus level from these vent fields (German et al., 2011; Ramirez-Llodra et al., 2005) but the literature indicates that at least 37 putative species have been reported from hydrothermal vent fields in the Indian Ocean (Copley et al., 2016; Watanabe and Beedessee, 2015).

Three additional vent fields are reported from the Southwest Indian Ridge but are not yet archived in the InterRidge Hydrothermal Vent Database (Tao et al., 2014). Eighteen new species were reported from that survey and connectivity analyses suggest that Indian Ocean vent communities may be intermediary between the Mid-Atlantic Ridge and East Scotia Ridge (Zhou et al., 2018). All three of these vent fields fall within exploration contract areas leased to China Ocean Mineral Resources Research and Development Association.

Kolumbo: Mediterranean Sea

Figure 7. Kolumbo high-temperature vent. © NOAA.

Depth: 500m
Maximum Temperature: 224°C
Year Discovered: 2006

The Kolumbo vent field sits at the base of the Kolumbo submarine volcano 8 kilometers northeast of Santorini. Hundreds of hydrothermal vents are scattered throughout the northern end of the volcano's crater forming large, metal-rich sulphide deposits.

The crater floor is covered in mats of reddish-brown bacteria characteristic of regions of hydrothermal venting. No vent-endemic macrofauna or megafauna have been documented from this formation.

Mediterranean

Deep-sea hydrothermal vents in the Mediterranean Sea are the least explored of any oceanographic region but it is presumed that conspicuous chemosynthetic communities are absent (Carey et al., 2011; Taviani, 2014). The majority of vents in the Mediterranean Sea are found in water less than 200m depth (Dando et al., 1999) and are dominated by fauna that are not endemic to hydrothermal-vent communities (Dando, 2010; Danovaro et al., 2010). Of the 15 known active vent fields, only five occur in waters deeper than 200m. Deep-sea vent fields are only known from volcanic craters on the Aegean and Tyrrhenian seamounts (Taviani, 2014). Siboglinid

tubeworms that are closely related to methane-seep species are found at these vent fields, but no vent-specific fauna have been observed (Taviani, 2014).

Only two research cruises that made biological observations of macrofaunal or megafaunal communities at deep-sea vents in the Mediterranean were found in either InterRidge or regional databases. The presence of these vent communities, however, does provide tantalizing support for investigations into the Lessepsian migration (the migration of marine species in and out of the Mediterranean via the Suez Canal) as cognate vents are found in the Gulf of Aden and are similarly understudied (Biasi and Aliani, 2003).

The Troodos ophiolite is a large fragment of seafloor that now forms portions of the island of Cyprus and contains metal-rich ore deposits produced from ancient venting. This terrestrial polymetallic massive sulfide has been mined for the last 6000 years and represents the oldest continuous mining operation in the world (Cann and Gillis, 2004). Despite this substantial

mineral wealth from uplifted seafloor massive sulphides, no mining activity is currently proposed for submerged hydrothermal vent fields in the Mediterranean Sea.

Mid-Atlantic Ridge

The Mid-Atlantic Ridge is the largest geologic structure on the planet. It stretches from the far north, where it intersects with the Gakkel Ridge in the Arctic, to the far south, where it intersects with the Antarctic plate. The Mid-Atlantic-Ridge biogeographic province stretches the entire length of the geologic feature. Connectivity studies suggest that dominant species are well-connected across vast distances that can be in excess of 7000km (Heijden et al., 2012; Teixeira et al., 2012, 2011). Despite this evidence for extensive connectivity along the ridge axis, very little is known about the southern Mid-Atlantic Ridge and how vent communities at higher southern latitudes relate to their northern counterparts (Perez et al., 2012). Deep hydrothermal vents throughout the Mid-Atlantic Ridge are largely dominated by the chemoautotroph-hosting shrimp *Rimicaris exoculata*, as well as *Mirocaris fortunata*, and *Chorocaris chacei* (Desbruyères et al., 2001; Van Dover, 1995), while shallower vents are frequented by mytilid mussels (Gebruk et al., 1997). There is substantial overlap, with the key factor determining community structure related to the metal content of the hydrothermal vent fluid rather than depth or latitude of the vent field (Desbruyères et al., 2000). Much like those in the Mediterranean, the shallowest vents, which occur in the photic zone, are dominated by common non-vent species and are not typical of vent-dependent communities (Fricke et al., 1989). From the literature, several hundred species are reported as endemic to hydrothermal vent fields along the Mid-Atlantic Ridge (Desbruyères et al., 2001; Gebruk et al., 1997). As of the last update to ChEssBase, 307 taxa have been identified to the genus level from these vent fields (German et al., 2011; Ramirez-Llodra et al., 2005).

In general, the Mid-Atlantic Ridge is a slow spreading center (Murton and Rona, 2015). Forty-two hydrothermal vent fields are reported from the Mid-Atlantic Ridge, 29 of which are found in areas beyond national jurisdiction. Nine vents fields are found within Portugal's EEZ, all of which fall within Portuguese Marine Protected Areas. An additional vent field, Rainbow, though located in areas beyond national jurisdiction, has also been accepted through international agreement for protection via the Convention for the Protection of the Marine Environment of the North-East Atlantic (Abecasis et al., 2015). Two vent fields occur within Iceland's EEZ and two more fall with the United Kingdom's EEZ. The average depth of Mid-Atlantic hydrothermal vent

fields is 2400m, with the shallowest occurring in less than 10m of water and the deepest at 4500m depth. Only six hydrothermal vent fields along the Mid-Atlantic Ridge have been confirmed in the south Atlantic, although there is substantial evidence that many more unexplored vents exist there (Beaulieu et al., 2013)

At least 120 deep-sea research cruises to the Mid-Atlantic Ridge were available from InterRidge and other regional databases. As the Mid-Atlantic Ridge is among the most heavily studied hydrothermal-vent regions, the number of research cruises to the Mid-Atlantic Ridge is likely much higher. Of those, at least 61 research cruises included biological observations or sampling of macrofaunal and megafaunal communities. Nine active hydrothermal vent fields fall within ISA exploration contract areas. An additional 13 confirmed active vent fields are recommended for protection by InterRidge, seven of which already have some form of marine protection (Beaulieu et al., 2013).

TAG: Mid-Atlantic Ridge

Figure 8. Shrimp and an ROV manipulator arm at TAG. Woods Hole Oceanographic Institution.

Depth: 3,500m
Max Temperature: 369°C
Year Discovered: 1985

The Trans-Atlantic Geotraverse (TAG) is an enormous complex of hydrothermal vents with an active area 250 meters wide and 50 meters tall. Seven active chimneys are found within TAG, including one low-temperature diffuse flow site. It was the first vent field discovered on the Mid-Atlantic Ridge and is among the best studied vent systems.

Like most vents on the Mid-Atlantic Ridge, TAG is dominated by the blind shrimp, *Rimicaris exoculata*, which are found close to the plumes of black smoker chimneys and farms chemoautotrophic microbes in their gills. Aggregations of *Rimicaris* can be dense enough to cover the entire chimney surface. Two other vent-dependent shrimp are also found at TAG, as well as crabs, squat lobsters, and snails. Unlike other Mid-Atlantic vents ecosystems, mussels and clams are not common at TAG.

Mid-Cayman Spreading Center

The age and location of the Mid-Cayman Spreading Center presents a tantalizing target for investigating the relationship between vent fields on the East Pacific Rise and Mid-Atlantic Ridge, with vents in the ancient Caribbean Sea acting as stepping stones prior to the closing of the isthmus of Panama (Tunnicliffe and Fowler, 1996; Van Dover et al., 2002). Vent fields within the Mid-Cayman Spreading Center are dominated by one endemic shrimp species, *Rimicaris hybisae*, which is closely related to shrimp found on the Mid-Atlantic Ridge (Nye et

al., 2013; Plouviez et al., 2015). Less abundant species are closely related to Pacific vent species—*Itheyaspira bathycodon* is most related to a snail from the Okinawa Trough and *Lebbeus virentova* to a shrimp from the East Pacific Rise (Plouviez et al., 2015). Several species more commonly associated with methane seeps in the Gulf of Mexico were also observed at the Von Damm vent field. The complex relationship between Pacific and Atlantic vents, as well as Gulf of Mexico methane seeps makes establishing a definitive biogeographic province challenging.

The Mid-Cayman Spreading Center is an ultraslow spreading ridge in the Caribbean Sea (Van Dover et al., 2002). Only two deep-sea hydrothermal vent fields are reported from the Mid-Cayman Spreading Center, the talc-dominated Von Damm vent field (Hodgkinson et al., 2015)

Von Damm: Mid-Cayman Spreading Center

Figure 9. Shrimp aggregations at Von Damm. © NOAA Okeanos Explorer. Office of Ocean Exploration and Research

Depth: 2,300m
Maximum Temperature: 215°C
Year Discovered: 2010

Von Damm is the shallower of the two hydrothermal vent fields known from the Mid-Cayman Spreading Center. Unique among known vents, Von Damm is predominately formed from precipitated talc.

Von Damm is overwhelmingly dominated by swarms of the vent shrimp *Rimicaris hybisae*, endemic to the Mid-Cayman Spreading Center. A close relative of shrimp found on the Mid-Atlantic Ridge, *Rimicaris hybisae*, a close relative of shrimp found on the Mid-Atlantic Ridge. Small snails and amphipods are also found around the vents chimney. Tube worms more commonly associated with Gulf of Mexico methane seeps are also found around the vent periphery. Though a mussel shell midden was observed near the Von Damm vent field, no living mussels have been observed on this geologic structure. Von Damm is notable for having relatively low biodiversity when compared with other vent ecosystems.

and the Beebe vent field, which currently holds the record for the world's deepest known hydrothermal system (Connelly et al., 2012). A third vent field has been hypothesized as a result of chemical signatures in the water column, but has not been confirmed (German et al., 2010). Both confirmed vent fields are found within the EEZ of the United Kingdom associated with the Cayman Island territory. The Von Damm vent field is found at 2400m depth, while the Beebe vent field is found at 5000m depth.

Despite extensive sampling in recent years, hydrothermal vent fields along the Mid-Cayman Spreading Center are still relatively poorly understood. As of 2015, a total of 32 vent-associated species from 23 families have been reported from the Beebe and Von Damm vent fields in the Mid-Cayman Spreading Center,

though only *Rimicaris hybisae* occurred in abundance at both vent fields (Plouviez et al., 2015). As of the most recent update to ChEssBase, no taxa are available from these vent fields (German et al., 2011; Ramirez-Llodra et al., 2005).

Despite its small size and few vent fields, the Mid-Cayman Spreading Center has been the focus of extensive research in recent years due to the uniqueness of the vent habitats and their relative accessibility. Eight research cruises were available from InterRidge and other regional databases, of which all involved some form of biological observation or sampling of macrofaunal communities. No mining activity is currently proposed for hydrothermal vent fields in the Mid-Cayman Spreading Center.

Endeavor: Northeast Pacific

Figure 10. Tube worms at the Endeavor vent field. Ocean Networks Canada.

Depth: 2,200
Max Temperature: 402°C
Year Discovered: 1984

The Endeavor vent field is a region of the Juan de Fuca Ridge 250 kilometers west of Vancouver. At least 16 active vent regions with over 100 discrete vent chimneys exist within the Endeavor vent field, which are contained within the Endeavor Hydrothermal Vents Marine Protected Area, Canada's first MPA.

Endeavor vent communities are dominated by the tube worm *Ridgeia piscesae*, which build large, complex habitats for other vent-dependent species, including snails, shrimp, worms, and anemones. The most heat tolerant organism yet discovered, a microbe which can survive temperatures up to 121°C is found along the Endeavor segment of the Juan de Fuca Ridge, though it has not yet been observed within the main Endeavor vent field.

Northeast Pacific

Hydrothermal vent fields along the Juan de Fuca Ridge are dominated by dense aggregations of *Ridgeia piscesae*, a vent-dependent tube worm that is the major foundational species in this biogeographic province (Tsurumi and Tunnicliffe, 2003). These tube worms create substantial habitat structure which allows niche partitioning within the vent ecosystem (Lelièvre et al., 2018).

Northeast Pacific hydrothermal vent fields occur predominantly along the Juan de Fuca Ridge, an intermediate spreading center on the border of the Pacific and Juan de Fuca plates (Normark et al., 1983). Twenty-two hydrothermal vent fields are reported from the Juan de Fuca Ridge, of which 10 occur within the EEZ of Canada while the remaining 12

occur in the high seas. Vent fields are relatively deep, occurring between 1500 and 23500m with an average depth of 2200m.

From the literature, approximately 60 vent-associated macrofaunal species have been identified from northern Pacific hydrothermal vent fields. As of the last update to ChEssBase, 262 taxa have been identified to the genus level from these vent fields, however some may be the result of overlap with nearby methane seeps (German et al., 2011; Ramirez-Llodra et al., 2005).

The Juan de Fuca Ridge was the site of eruption along the CoAxial Segment in the mid-1990s, which resulted in a complete extirpation of a hydrothermal vent field. Within two-years of the event, nearly one third of species known from the region had returned to the system, while several habitats had gone extinct (Tunnicliffe et al., 1997). A similar eruption occurred on Axial Volcano, where mature *Ridgeia piscesae* assemblages resembling pre-eruption communities were present after three years (Marcus et al., 2009). These eruptions, along with a series of two others along the Northern East Pacific Rise, are the only natural experiments in vent ecosystem extirpation and re-colonization following catastrophic disturbance and serve as the best natural proxy for potential succession and recovery following a mining event.

Due to its close proximity to shore and relative accessibility to US and Canadian research fleets, the Juan de Fuca Ridge and other northeast Pacific vent fields are among the most heavily studied hydrothermal vent systems. Over 100 research cruises are available from InterRidge and other regional databases, of which 34 involved some form of biological observation or sampling of macrofaunal communities. Though no mining activity is currently proposed for hydrothermal vent fields in the Northern East Pacific, six vent fields which occur within Canada's territorial waters already have some form of marine protection while InterRidge recommends an additional 5 high seas vent fields also be considered for protection (Beaulieu et al., 2013).

Northern East Pacific Rise

Hydrothermal vent fields along the Northern East Pacific Rise and Galapagos Rift are the most well-known by the public. They contain massive aggregations of the giant tube worm, *Riftia pachyptila*, with bright red plumes wafting through the roaring effluent of black smokers (Hessler and Smithey, 1983). These aggregations, along with mussels, limpets, shrimp, and anemones, occur close to actively venting chimneys, while distinct communities are observed in the vent periphery, including gastropods, worms, and barnacles (Van Dover et al., 1988).

The Northern East Pacific Rise biogeographic province comprises hydrothermal vent fields along the fast-spreading East Pacific Rise north of the equator as well as the Galapagos Rift and the Gulf of California (Haymon et al., 1991; Moalic et al., 2012). The first discovery of a deep-sea hydrothermal vent occurred along the Galapagos Rift in 1977, and since then forty-eight vent fields have been discovered within this province. Eight of these occur in the EEZ of Ecuador around the Galapagos Islands; eleven in the EEZ of Mexico; and the remainder occur in the area beyond national jurisdiction. The depths of hydrothermal vent fields in the Northern East Pacific Rise province range from 1600m to 5100m, with an average depth of 2500m.

From the literature, hundreds of species have been documented at hydrothermal vents in the Northern East Pacific Rise province. As of the last update to ChEssBase, 322 taxa have been identified to the genus level from these vent fields, although this is likely an underestimate (German et al., 2011; Ramirez-Llodra et al., 2005).

Like the North East Pacific, researchers working on the Northern East Pacific Rise had the opportunity to witness the aftermath of volcanic eruptions which extirpated entire vent fields. In one instance, the site had been surveyed just weeks before eruption, allowing an unparalleled opportunity to study the recovery of hydrothermal vent communities following catastrophic disturbance (Von Damm et al., 1995). In a second case, evidence of recent eruptions were observed on the seafloor and newly-formed hydrothermal vents were beginning to emerge (Shank et al., 1998). Sequential colonization by mobile vent fauna followed by growing aggregations of tubeworms and mussels over a 5 to 10-

Rose Garden: Northern East Pacific Rise

Figure 11. Giant tube worms and zoarcid fish at Rose Garden. Woods Hole Oceanographic Institute.

Depth: 2,500m

Max Temperature: 22°C

Year Discovered: 2010

Rose Garden is a field of at least eight low-temperature hydrothermal vent sites on the Galapagos Rift. These were the first deep-sea hydrothermal vents discovered on 1977. Though InterRidge classifies them together, in older literature Garden of Eden is considered a separate vent field.

Rose Garden is dominated by massive aggregations of the giant tube worm *Riftia pachyptila*. Their bright red plumes extract chemical energy from the surrounding vent effluent, which symbiotic microbes convert into food for the tube worm. Mussels, clams, other tube worms, crabs, and fish are also common at Rose Garden vents. As the first discovered and among the most visually stunning, these vents often serve as the archetype for hydrothermal vent ecosystems in the public conscious.

year recovery and recolonization period was observed, however, follow-up surveys over a decade later revealed a potential regime shift: while neighboring vent fields were tubeworm-dominated, the impacted field was mussel-dominated (Lutz et al., 2008). A third eruption was also observed at a vent site that had been relatively well studied pre-eruption and provided the best observations yet of community recovery following catastrophic disturbance (Nees et al., 2008). In this case, a mussel-dominated vent community showed reduced signs of mussel recovery, but high recruitment of tubeworms, two years post-eruption. These few case studies demonstrate that, even within a very narrow geographic range, the response to disturbance by hydrothermal vent communities can be highly variable.

The Northern East Pacific Rise is among the best studied biogeographic provinces. At least 126 research cruises are available from InterRidge and other regional databases, of which 31 involved some form of biological observation or sampling of macrofaunal or megafaunal communities. No mining activity is currently proposed for hydrothermal vent fields along the Northern East Pacific Rise, however five vent fields were recommended for protection (Beaulieu et al., 2013).

Southern East Pacific Rise

Hydrothermal-vent field communities along the Southern East Pacific Rise appear superficially similar to those of the Northern East Pacific Rise. They are dominated by several species of alvinellid tubeworms, in particular *Alvinella pompejana*, as well as less frequent aggregations of the giant tubeworm, *Riftia pachyptila* (Rybakova and Galkin, 2015). Swarms of *Chorocaris* shrimp are also common in these vent systems, as are other species common to the Western Pacific, such as the stalked barnacle *Neolepas* aff. *rapanui*, the barnacle *Eochionelasmus paquensis*, and several polychaete species (Jollivet et al., 2004). Vesicomylid clams and mytilid mussels are also frequent residents of Southern East Pacific Rise vent fields (Rybakova and Galkin, 2015).

The Southern East Pacific Rise is predominantly an ultra-fast spreading center and is among the fastest spreading centers in the world (Mahoney et al., 1994). Though formed from the intersection of the same geologic features, the Northern and Southern East Pacific Rise are physically bisected by the Galapagos Rift, Galapagos Plate, and Hess Deep, which may represent

Pito Seamount: Southern East Pacific Rise

Figure 12. Pito Seamount. © Woods Hole Oceanographic Institute.

Depth: 2,300m

Maximum Temperature: >300°C

Year Discovered: 1993

Pito Seamount is a hydrothermal vent field on the Southern East Pacific Rise northeast of the Easter Microplate. There is a small area of black smoker hydrothermal vents surrounded by a large number of inactive vent chimneys.

Pito Seamount has a relatively small hydrothermal vent community consisting of alvinellid worms, crabs, and alvinocaridid shrimp, though, notably, no tube worms. Vent communities on Pito Seamount share fauna with both Northern East Pacific Rise vent communities and those of the West Pacific. Mussel shell middens are found scattered throughout the inactive vents, suggesting the Pito Seamount hydrothermal vents may be in their waning stages in activity and the resulting in ecosystems are communities collapsing, as the remaining active vents slowly shut down.

physical barriers to dispersal, allowing these two regions to develop into separate biogeographic provinces (Bachraty et al., 2009; Plouviez et al., 2010, 2009).

Twenty-seven hydrothermal vent fields have been confirmed from the Southern East Pacific Rise and an additional two from the Pacific-Antarctic Ridge, the southernmost section of the East-Pacific Rise. The average depth of Southern East Pacific Rise vent fields is 2600m, with the shallowest known to occur at 2200m and the deepest at 3000m depth. As of the last update to ChEssBase, 97 taxa have been identified to the genus level from these vent fields (German et al., 2011; Ramirez-Llodra et al., 2005).

The Southern East Pacific Rise has received relatively less attention than its northern cousin. Only seven research cruises were available from InterRidge and

other regional databases, of which only three made biological observations of macrofaunal and megafaunal. No mining activity is currently proposed for hydrothermal vent fields on the Southern East Pacific Rise.

Southern Ocean

Discovered almost concurrently with vents on the Mid-Cayman Spreading Center, vent fields along the East Scotia Ridge and South Sandwich Arc comprise one of the most recently discovered biogeographic provinces (Rogers et al., 2012). Though relatively unsampled, the dominant taxa at these vents sites appear to be endemic to this region, particularly the newly-described squat lobster *Kiwa tyleri*, which occurs in incredible abundance around these vents (Roterman et al., 2013; Thatje et al., 2015; Zwirgmaier et al., 2015).

There are six confirmed active hydrothermal vent fields in the Southern Ocean. Two vent fields have been discovered on the East Scotia Ridge, an intermediate back-arc spreading ridge formed by the subduction of the South American plate beneath the South Sandwich plate (Thomas et al., 2003). Two other vent fields are found in the South Sandwich Arc in association with volcanic calderas. Two shallow sedimented vent systems are known from the Bransfield Strait but are largely colonized by non-vent dependent background species (Bell et al., 2016). Four vent fields occur within the United Kingdom's EEZ associated with the territories of South Georgia and the South Sandwich Islands. Two vent fields occur within the Antarctic Treaty Territory. The shallowest known vent fields occur at 100m depth while the deepest are found at 2600m. The average depth for known hydrothermal vent fields in the Southern Ocean is 1400m. From the literature, as of 2012, 27 putative species have been reported from hydrothermal vent fields in the Southern Ocean (Rogers et al., 2012). As of the last update to ChEssBase no taxa have been identified to the genus level from these vent fields (German et al., 2011; Ramirez-Llodra et al., 2005).

The Southern Ocean is among the least well-studied biogeographic provinces. A total of nine deep-sea research cruises were available from InterRidge and other regional databases. Of those, five research cruises included biological observation or sampling of macrofaunal communities. No mining activity is currently proposed for hydrothermal vent fields in the Southern Ocean.

E9: Southern Ocean

Figure 13. Squat lobsters and stalked barnacles at E9. University of Southampton.

Depth: 2,400m
Max Temperature: 380°C
Year Discovered: 2009

E9 is a field of six active hydrothermal vent chimney that occurs along the southern extreme of the East Scotia Ridge. The southernmost known black smoker is found in this vent field.

The hydrothermal vent community of E9 is dominated by *Kiwa tylerii*, a species of yeti crab so far only observed at East Scotia Ridge vent ecosystems and the only yeti crab known to occur in the Southern Ocean. This vent-dependent yeti crab can farm chemoautotrophic bacteria on specialized appendages and thrives in the warm waters immediately adjacent to vent effluent. As other yeti-crab species are found at cold-water chemosynthetic ecosystems, *Kiwa tylerii* could provide valuable insights into the evolution of vent ecosystems. Anemones, snails, and stalked barnacles also occur at E9 along the vent periphery.

West Pacific

The West Pacific represents the largest continuous biogeographic province among deep-sea hydrothermal vent ecosystems. It stretches from the Kermadec Arc southeast of New Zealand, to the Lau, Fiji, and Manus Basin spreading centers, the Solomon and New Hebrides Arcs, the Izu-Bonin-Mariana Arc, as well as the Okinawa Trough and numerous other geologic features associated with convergent plate boundaries along the western margins of the Pacific Ocean (Desbruyères et al., 2006; Mitarai et al., 2016). Spreading rates vary between basins and arcs, however, the active lifespan of west Pacific back-arc basin spreading centers exceeds those of east Pacific spreading centers by an order of magnitude, resulting in longer-lived vent fields with greater potential for migration and admixture among populations (Du Preez and Fisher, 2018; Mitarai et al., 2016).

The West Pacific has a complex history, with potential colonization from eastern Pacific hydrothermal vents occurring via now-extinct mid-ocean ridges spanning the Pacific (Tunnicliffe et al., 1998; Tunnicliffe and Fowler, 1996) while the Indian Ocean may have also acted as a stepping stone between Atlantic and Pacific vent ecosystems (Van Dover et al., 2001).

While there is strong evidence supporting the interpretation of the West Pacific as a single biogeographic province (Moalic et al., 2012), several species are not shared between the northern and southern hemispheres with evidence for limited dispersal across the equator (Mitarai et al., 2016; Vrijenhoek, 2010, 1997). Only a single species, the mytilid mussel *Bathymodiolus septemdierum*, is known to occur at all West Pacific back-arc basins spreading centers (Breusing et al., 2015). The longevity of west Pacific vents likely allows for immigration to occur over long timescales, creating the appearance of a single biogeographic province while sub-regions may be *de facto* isolated over ecologically relevant timescales. This points to the potential for numerous undiscovered vents that act as steppingstones between northern and southern vent systems and suggests that functionally, the northern and southern west Pacific, should be treated as separate provinces that are connected in deep time.

Northwest Pacific.

Deep-sea hydrothermal vent fields in the northern West Pacific are dominated by a complex of chemoautotroph-hosting snail species in the genus *Alviniconcha*, in which many cryptic species have recently been reported (Johnson et al., 2015). Sponges, worms, snails, limpets, clams, mytilid mussels, shrimp, crabs and squat lobsters (Hashimoto et al., 1995) as well as both fixed and stalked barnacles (Ohta and Kim, 2001) also frequent these vent systems. Notably, *Ifremeria nautiliei*, another chemoautotroph-hosting snail species, has so far not been found in West Pacific hydrothermal vent fields north of the equator. In southern West Pacific vents fields where *I. nautiliei* are found, they are known to outcompete *Alviniconcha* spp. for space on the vent chimney (Sen et al., 2014).

At least 58 active hydrothermal vent fields are confirmed from the southern West Pacific, ranging in depth from 1m to 5800m (with an average depth of 1200m). Only two vent fields are known from areas beyond national jurisdictions, with the remainder occurring within various nation's territorial waters, including Indonesia (4), Japan (27), Russia (3), Taiwan (2), and the United States in territories associated with Guam and the Commonwealth of the Northern Mariana Islands (20).

Southwest Pacific.

Deep-sea hydrothermal vents in the southern West Pacific are dominated by two taxa of chemoautotroph-hosting snails, *Ifremeria nautiliei* and *Alviniconcha* spp. as well as mytilid mussels (Desbruyères et al., 2006; Smith et al., 2004; Vrijenhoek, 2010). Notably, *Ifremeria nautiliei* is only known from Lau, Fiji, and Manus Basins, and are not present at other vent sites in the southern or northern West Pacific (Thaler et al., 2011). These habitat building species form the backbone for large communities of crabs, shrimp, limpets, snails, squat lobsters, worms, clams, and both fixed and stalked barnacles (Suzuki et al., 2009). Large halo fauna communities, some of which are supported by remnant chemosynthetic activity, occur at inactive hydrothermal vent fields (Erickson et al., 2009).

At least 77 active hydrothermal vent fields are confirmed from the southern West Pacific, ranging in depth from 2m to 3000m (with an average depth of 1500m). Only one vent field is known from areas beyond national jurisdiction, with the remainder occurring within various

nation's territorial waters, including Fiji (7), France (1), Indonesia (3), New Zealand (15), Papua New Guinea (17), the Solomon Islands (2), Kingdom of Tonga (28), and Vanuatu (3).

As of the last update to ChEssBase, 306 taxa have been identified to the genus level from hydrothermal vent fields in the West Pacific (German et al., 2011; Ramirez-Llodra et al., 2005). From the literature, species counts likely exceed 500 distinct species (Desbruyères et al., 2006; Vrijenhoek, 2010). At least 94 research cruises have made biological observations or recovered biological samples of macrofaunal and/or megafaunal communities from West Pacific hydrothermal vents with 54 occurring at vent fields in the Northern West Pacific and 44 in the southern West Pacific.

Unlike the Indian Ocean and Mid-Atlantic Ridge, mining leases for deep-sea hydrothermal-vent deposits occur exclusively within territorial waters. Thus, it is Pacific nations that have control over the issuance of deep-sea mining contracts. Thirty-one hydrothermal vent fields currently have mining exploration contracts issued, including New Zealand (1), Papua New Guinea (8), Kingdom of Tonga (20), and Vanuatu (2) (Beaulieu et al., 2013). In addition, Papua New Guinea has issued the first mining permit for a deep-sea hydrothermal vent, the Solwara I deposit (Coffey Natural Systems, 2008). InterRidge has identified 17 vent fields that would be appropriate for protection. All current mining exploration and exploitation leases are issued for hydrothermal vent fields south of the equator.

Mid-plate and Other Volcanically hosted Hydrothermal Vents

Hydrothermal vents may also occur in conjunction with volcanic island chains or seamounts such as Hawai'i, French Polynesia, or the Lesser Antilles Arc. Though these vents are important components of the deep ocean, they are often isolated from other vent systems, and, in many cases, do not host vent-endemic macrofauna or megafauna (Karl et al., 1988). These hydrothermal vents systems do not generally form metal-rich seafloor massive sulphides of substantial commercial value and are not currently considered feasible for deep-sea mining.

Solwara I: Western Pacific

Figure 14. Hydrothermal vent chimney covered in snails at Solwara I. © Nautilus Minerals.

Depth: 1,600m
Maximum Temperature: 332°C
Year Discovered: 1993

Solwara I (also known as North Su or Suzette Vent Field) is a massive hydrothermal vent field in Manus Basin, Papua New Guinea. Numerous active and inactive chimneys occur within the vent complex, ranging from black smokers to diffuse flow sites. Solwara I is 30 kilometers km from shore, making it a relatively easily accessed site, and is found along the northwest flank of the North Su submerged volcano. It is among the largest polymetallic- sulphide deposits and is rich in both gold and copper, as well as other commercially valuable minerals. A neighboring vent field, South Su, occurs 2.5km kilometers to the south and was often treated as part of Solwara I in early research expeditions.

Solwara I is dominated by a pair of large snails, the black snail *Ifremeria nautiliei* and the hairy snail, *Alviniconcha* spp. These two snails are found in a bullseye pattern around actively venting chimneys, with the hairy snail occurring close to the vent orifice and the black snail preferring slightly cooler waters nearby. This pattern makes it easy to locate sites of active venting. Neither snail has a functioning digestive system, instead depending on chemosynthetic microbes in their gills to extract energy from the vent fluid. The black snails' shells are frequently colonized by several species of limpets and worms. Small aggregations of vent-dependent shrimp also occur around the hydrothermal plume, while large aggregations of squat lobsters are found in the vent periphery. Solwara I vents also host both fixed and stalked barnacles, as well as crabs, octopuses, and zoarcid fish. While mytilid mussels are found at neighboring vent fields (including as South Su), mussels characteristic of Western Pacific vents have not been observed at Solwara I. Abundant halo fauna is found in the vent periphery and on inactive chimneys, include solitary tube worms, venus-flytrap anemones, sea cucumbers, and corals.

Though characteristic of other Western Pacific hydrothermal vent fields, vent ecosystems in Manus Basin appear to be genetically isolated from the rest of the biogeographic province, with limited gene flow among Manus Basin fauna and the same species that occur in neighboring basins, such as Lau and Fiji.

Solwara I is slated to become the first polymetallic massive sulphide prospect to be mined, with an active mining license issued by the government of Papua New Guinea and technological and maritime assets currently undergoing testing and sea trials.

RELATIVE BIODIVERSITY AND SAMPLING EFFORT

Eight biogeographic provinces had sufficient data for biodiversity estimates, including the Northwest Pacific, Southwest Pacific, Southern Ocean, Mid-Atlantic Ridge, Indian Ocean, Northern East Pacific Rise, Juan de Fuca Ridge, and Mid-Cayman Spreading Center (Figures 15 – 17). When ranked from highest to lowest biodiversity, the Northwest Pacific had the highest mean family richness, followed by the Southwest Pacific, Southern Ocean, Mid-Atlantic Ridge, Indian Ocean, Northern East Pacific Rise, and Juan de Fuca Ridge, with the Mid-Cayman Spreading Center coming in a distant last (Thaler and Amon, 2019).

Sampling completeness was highly variable. The Mid-Cayman Spreading Center was the closest to being comprehensively. A few provinces required less than 10 additional research cruises in order to reach 90% sample completeness, including the Indian Ocean (9) and Northern East Pacific Rise (9). Other provinces required 10 to 100 additional research cruises, including the Mid-Atlantic Ridge (20), Juan de Fuca Ridge (99), Southern Ocean (43), and Southwest Pacific (71). Despite being the most extensively sampled of all the biogeographic provinces, the Northwest Pacific required the most additional research cruises to reach 90% completeness. The three least sampled provinces were the Southern Ocean (22% complete), Northwest Pacific (37% complete), and Southwest Pacific (38% complete).

The highest estimated biodiversity was observed in the Northwest Pacific. The Northwest Pacific was among the best studied biogeographic provinces and yet it had among the lowest estimated sampling completeness, suggesting a vast reservoir of biodiversity waiting to be discovered. The Southwest Pacific followed a similar trend. Hydrothermal vents of the West Pacific represent exceptional biodiversity and potential for new discovery while facing the most imminent threat from deep-sea mining. Of the seafloor massive sulphide mining prospects currently in development, the two closest to commercial production lie off the coast of Japan in the Northwestern Pacific (Okamoto et al., 2018) and in the territorial waters of Papua New Guinea in the Southwest Pacific (Coffey Natural Systems, 2008).

The Mid-Atlantic Ridge and Indian Ocean biogeographic provinces share many characteristics. Hydrothermal vents in the Indian Ocean exhibit a family richness of similar extent as the Mid-Atlantic Ridge. Though there has historically been less research focused on the

Figure 15. Family richness in the Southern Ocean, Indian Ocean, and Mid-Cayman Spreading Center. Parametric interpolation (solid line terminating in black dot) and non-parametric asymptotic extrapolation (dashed line) with 95% confidence intervals (colored bounding areas). Color-coded guide bars on far right correspond to 95% confident intervals at twice the reference sample. Figure from Thaler and Amon (2019) and used with permission.

Indian Ocean, the growth of deep-sea research institutions in India and China highlight the role that hydrothermal vents in the Indian Ocean could play in the next century of deep-sea exploration.

The Northern East Pacific Rise and Juan de Fuca Ridge were difficult to assess. There was a dearth of available cruise reports from these regions. The low sampling completeness of the Juan de Fuca Ridge is probably an artifact of these missing cruise reports. The Northern East Pacific Rise biogeographic province followed the same pattern of biodiversity as other mid-ocean ridge systems. The wide confidence intervals of the Juan de Fuca Ridge are more in line with back-arc basin vent ecosystems. This supports an interpretation that the region is undersampled.

Figure 16. Family richness in the Northwest Pacific, Southwest Pacific, and Mid-Atlantic Ridge. Parametric interpolation (solid line terminating in black dot) and non-parametric asymptotic extrapolation (dashed line) with 95% confidence intervals (colored bounding areas). Color-coded guide bars on far right correspond to 95% confident intervals at twice the reference sample. Figure from Thaler and Amon (2019) and used with permission.

Hydrothermal vent fields in the Mid-Cayman Spreading Center and along the East Scotia Ridge in the Southern Ocean provided a useful illustration of the variability within deep-sea vent communities. Both systems are newly discovered—hydrothermal vents of the East Scotia Ridge were first observed in 2009 (Rogers et al., 2012) while those in the Mid-Cayman Spreading Center were first sampled in 2010 (Plouviez et al., 2015). Both vent fields represent new biogeographic provinces. Both vent systems were largely studied by the same personnel using similar sample designs deployed using the same equipment. Despite this, the Mid-Cayman Spreading Center exhibits the lowest biodiversity of any known hydrothermal vent biogeographic province while the Southern Ocean has among the highest.

This comparison is particularly valuable, as it demonstrates that biodiversity estimates at deep-sea hydrothermal vents are not just an artifact of sampling effects but reflect observable differences in biodiversity among biogeographic provinces.

Figure 17. Family richness on the Northern East Pacific Rise and Juan de Fuca Ridge. Parametric interpolation (solid line terminating in black dot) and non-parametric asymptotic extrapolation (dashed line) with 95% confidence intervals (colored bounding areas). Color-coded guide bars on far right correspond to 95% confident intervals at twice the reference sample. Figure from Thaler and Amon (2019) and used with permission.

CONNECTIVITY OF DEEP-SEA HYDROTHERMAL VENT ECOSYSTEMS

Understanding the diversity and connectivity of pre-disturbance vent communities essential for establishing environmental baselines at potential deep-sea mining prospects (Hoagland et al., 2010; Suzuki et al., 2018; Van Dover, 2010). The dynamic nature of some deep-sea hydrothermal vents may promote resistance to environmental disturbance and resilience following catastrophic disturbance, allowing vent-communities to recover after a mining event. In discrete ecosystems, genetic diversity increases with disturbance, up to a point, and genetically diverse communities tend to be more resistant to both natural and anthropogenic disturbance (Hughes et al., 2007). The International Union for the Conservation of Nature (IUCN) recognizes that the maintenance of diversity (genetic, species, and ecosystem) is essential for conserving biodiversity (McNeely et al., 1990) and connectivity among populations is a critical component in maintaining that diversity.

Deep-sea hydrothermal vents that occur at mid-ocean ridges are distributed along linear axes that function as dispersal corridors (Marsh et al., 2001; Thomson et al., 2003; Young et al., 2008). Geographic subdivision along these ridges are associated with geomorphological features, such as transform faults and microplates, though these patterns are not consistent across all species. *Bathymodiolus* mussels on the East Pacific Rise, for example, are divided into northern and southern populations across Easter Microplate (Won et al., 2003) while *Riftia pachyptila* and *Tevnia jerichonana* exhibit reduced gene flow (Hurtado et al., 2004). In contrast, *Alvinella pompejana* and *Branchiopolynoe symmytilida*, two similarly distributed polychaete species, are undifferentiated across the same feature. The Blanco Transform Fault is a 450-km long ridge offset that separates the Juan de Fuca and Gorda Ridges, *Lepetodrilus* limpet populations diverge across this boundary (Johnson et al., 2006) while populations of the tube worm, *Ridgeia piscesae*, are connected across this same boundary (Young et al., 2008).

Connectivity along the Mid-Atlantic Ridge is not as well characterized as the Eastern Pacific. Populations of *Rimicaris exoculate* are functionally identical, with no detectable differentiation, across over 7,100 kilometers (Teixeira et al., 2012, 2011) though there is some temporal variability within the population. *Bathymodiolus puteoserpentis*, a mussel, are similarly well-connected (Maas et al., 1999) but form a hybrid zone with *Bathymodiolus azoricus* along the northern Mid-Atlantic Ridge (O'Mullan et al., 2001). Meanwhile, populations of the

vesicomylid clam, *Abyssogena southwardae*, appear connected between northern and southern populations with a southward directional gene flow (Heijden et al., 2012).

Hydrothermal vents in Pacific back-arc basins are distributed in a non-linear pattern (Desbruyères et al., 2006). Western Pacific vents are geographically isolated from vents in the Eastern Pacific (Van Dover et al., 2002), with dramatically different faunal composition (Bachraty et al., 2009). In the Southern West Pacific, many species shared among Manus, North Fiji, and Lau Basin are distinct from related species in the Northern West Pacific, including the Okinawa and Marianna Troughs or the Izu-Ogasawara Arc (Desbruyères et al., 2006). Several species from the Southern West Pacific basins, such as the mussel *Bathymodiolus brevior* (Kyuno and Shintaku, 2009), are well connected across multiple basins, while other species, such as neoverrucid barnacles, are restricted to single basins (Watanabe et al., 2005). In models of larval dispersal, Western Pacific hydrothermal vent systems appear well-connected, with strong direction signals, and stark divides between northern and southern vents systems (Mitarai et al., 2016).

The complex picture of connectivity among hydrothermal vent systems is further complicated by a dearth of data from several putative biogeographic, including the Indian Ocean (though preliminary assessments of vent species in the Indian Ocean suggest a level of connectivity similar to that of other mid-ocean ridge systems; Beedessee et al., 2013), Southern Ocean, and Arctic, making any global assessment of hydrothermal vent connectivity premature. This picture is even further complicated by evolutionary links between hydrothermal vents, methane seeps, and whale falls, which may potentially, act as refuges for some vent-endemic species (Kiel, 2016).

KNOWLEDGE GAPS

Natural Variability and Regime Change

Among the most difficult problems to address when assessing the environmental and ecologic impacts of a deep-sea mining program is the extent to which natural variability shapes and re-shapes hydrothermal-vent communities within the timespan of a mining program. At slow and ultra-slow spreading centers, such as those which occur on the Southwest Indian Ridge, hydrothermal vent fields can persist from hundreds to thousands of years with minimal disturbance, while at ultra-fast spreading centers, such as in the Western Pacific, turnover at hydrothermal vents can occur in less than a decade.

Hydrothermal vent communities have evolved to cope with significant disruption. Where turnover at vents occurs quickly, natural processes can be catastrophically disruptive, with vent fields shutting down, fracturing, or being buried in lava flows or sediment. This can result in complete extirpation of the hydrothermal vent community, allowing new colonists to emerge in succession. Even in cases where disruption is wholly natural in origin, nascent vent communities emerging from a large-scale disturbance may not resemble the original assemblages of the pre-disturbance vent system.

Natural variability studies have been limited to a few discrete sites where the impacts of volcanic eruptions were serendipitously captured soon after the event. During several multi-year surveys, recovery times and patterns of succession were documented, providing a rough understanding of what happens to a hydrothermal vent following catastrophic disturbance. However, these studies are entirely restricted to the East Pacific Rise and Juan de Fuca Ridge, two biogeographic provinces that are currently not being considered for deep-sea mining. Within ISA contract areas and at prospective sites within territorial waters, natural-variability studies, and, in particular, studies investigating the consequences of complete extirpation of a single vent field, are almost completely lacking.

Complementary to the problem of observing and quantifying natural variability, is assessing what the ramifications are for management and mitigation protocols when regime changes occur. Regime changes are shifts in the composition of assemblages following disturbance as a result of natural and anthropogenic factors. When regime changes occur, emergent ecosystems can be drastically different from the original ecosystem. Because there are so few natural variability studies, there is minimal understanding of the extent and frequency of

regime changes in deep-sea hydrothermal vent ecosystems, either through succession and competition or through catastrophic disturbance followed by recolonization.

For non-catastrophic chronic disturbance, such as that which might be experienced from sustained mining operations, in the form of sedimentation from plumes, increased toxicity from mining tailings, as well as other non-acute stressors, almost no data is available (Weaver et al., 2018).

In order to comprehensively assess the environmental impacts of a deep-sea-mining program, a solid understanding of natural variability and succession at local and regional scales is essential. Without long-term observational studies of variability at hydrothermal vent sites, it is nearly impossible to extract the signal of deep-sea mining from the noise of natural turnover within these dynamic ecosystems, creating conditions where natural processes that shape the succession of hydrothermal vent systems following disturbance are attributed to mineral extraction within a deep-sea hydrothermal vent field.

Factors for good set asides

One critical component of a deep-sea hydrothermal vent mining regime is the establishment and enforcement of appropriate set asides during and after mining operations. Set asides are areas of the seabed that are protected from mining, either in perpetuity or from the time mining operations commence until acceptable recovery has been observed at the mining site, in order to protect and preserve local and regional biodiversity of hydrothermal vent systems (Boschen et al., 2016). These set asides should act as natural refuges for hydrothermal vent communities, providing habitat for mobile species affected by the disturbance caused by deep-sea mining as well as providing an ecologic repository for recruitment to disturbed sites after extraction concludes (Van Dover, 2011).

The challenge of determining a good set aside is highly dependent on the connectivity of local hydrothermal vent populations as well as the directionality of larval dispersal across sites. A set aside “downstream” of the mining site will not produce recruits to colonize the disturbed site, even if it is representative of the biodiversity of the mining site. If the objective of the set aside is simply to maintain the genetic diversity of a region and the hydrothermal vent community within the set aside is indistinguishable from that of the mining site, then it may still represent an adequate set aside if no other alternatives are available.

Whether or not a set aside will act as an effective buffer against catastrophic disturbance at nearby mining sites depends on the resilience of the overall region as well as the extent to which vent communities are connected. In the Western Pacific, there is extensive regional variability in the ability of vents to recover from disturbance on short time scales. In simulations, Northern West Pacific tended to have recovery time estimates in the range of 20 to 40+ years, while in the Southern West Pacific, recovery times were much shorter, some vents were even predicted to recover within 5 years of mining disturbance (Suzuki et al., 2018). The effectiveness and time horizon for an effective set aside is dependent on accurate estimates of local and regional resilience as well as the extent to which biological exchange happens within vent communities.

An Expanding Sphere of Influence

Though much effort has been spent understanding how vent ecosystems are connected within and across biogeographic provinces, relatively few studies have investigated how macrofaunal and megafaunal communities in hydrothermal vent ecosystems are connected to the generic deep-background fauna (Levin et al., 2016). The vertical impact of hydrothermal plumes can extend far upward into the water column, influencing ocean chemistry at local, regional, and global scales and forming the energetic basis of many deep-sea pelagic food webs which extend beyond the edge of the plume (Phillips, 2017). In water columns above vent plumes, bacterio- and zooplankton abundances have been observed up to four times higher than background abundance (Berg and Van Dover, 1987; Sorokin et al., 1998) while increased crustacean and zooplankton abundance has been observed 300m above hydrothermal vent fields (Burd and Thomson, 1995, 1994). The effects of this increased plankton abundance on higher trophic-level pelagic species, including those of commercially important fisheries, has not been adequately assessed. The influence of hydrothermal plumes on pelagic biology has so far been excluded from consideration in management decisions surrounding deep-sea mining at hydrothermal vents (Phillips, 2017).

Though vent-dependent species often have highly restrictive habitat requirements, the influence of hydrothermal processes can be observed far beyond the perimeter of an active hydrothermal vent field. Chemosynthetically-derived primary production from hydrothermal vents may account for ~3% of the total flux of organic carbon to the deep-sea floor (Van Dover,

2000). The margins of hydrothermal vent ecosystems represent transitional regions where background fauna interact with vent-dependent fauna, allowing chemosynthetically derived biomass to mobilize beyond the vent periphery. Opportunistic and vagrant species, such as squat lobsters, that are common in the deep background fauna, are often observed in large aggregations at or near both active and inactive vent sites (Thaler et al., 2014).

Hydrothermal vents are temporally dynamic ecosystems, with turnover at some ultra-fast spreading centers occurring on decadal time scales (Desbruyères, 1998). The transition from active to inactive vent, and ultimately to general deep background, also expands the influence of deep-sea hydrothermal vents beyond the periphery of an active vent field. As hydrothermal fluid wanes and the toxic conditions that make vents inhospitable to background fauna, rocky outcroppings produced by the process of hydrothermal venting provide hard substrate for many non-vent dependent species to colonize (Boschen et al., 2015). Biogenic substrate such as shells and worm tubes can provide substrate for settlement as well as a ready source of decomposing biomass for faunal recruitment (Marcus and Tunnicliffe, 2002). Active and inactive vents in regions like the Juan de Fuca Ridge both display the same extent of biodiversity, though inactive vent systems share much more in common with the deep background fauna (Tsurumi and Tunnicliffe, 2003).

Two notable studies recently drew attention to the possibility of hydrothermal vent ecosystems playing essential roles in the life cycles of otherwise non-vent associated species. In one instance, a Pacific deep-sea skate was observed using hydrothermal vents on the Galapagos Rift as nursery grounds and natural egg-case incubators, with the heat of active vents acting to accelerate embryonic development (Salinas-de-León et al., 2018). In another instance, a cluster of octopods utilized basalt outcrops near hydrothermal vents for egg brooding, although proximity to the vents was associated both with habitat availability and decreased reproductive success (Hartwell et al., 2018). Though there have now been several documented examples of non-vent fauna opportunistically utilizing hydrothermal vent ecosystems, there are no studies that look specifically at the dispersal of vent-dependent species to non-vent, non-chemosynthetic ecosystems (Levin et al., 2016).

Phylogenetic studies draw connections between chemosynthetic ecosystems—hydrothermal vents, methane seeps, and biomass falls, for example—showing patterns of colonization, diversification, and speciation (Johnson et al., 2006; Roterman et al., 2013; Rouse

et al., 2011; Vrijenhoek, 2013), however, the evolutionary relationships between vent-dependent species and sister clades that occur among the generic deep background fauna has not been well resolved. The lack of resolution surrounding the relationships among vent- and non-vent taxa represents a substantial knowledge gap that could inform management and mitigation decisions regarding human impacts in the deep sea.

Connectivity and Invasion via Anthropogenic Influences

Human activities are also progressively increasing the connectivity of the world's oceans, which could result in migration of non-native species into new deep-sea vent ecosystems. The closing of the isthmus of Panama is hypothesized to be a major biogeographic event that triggered the divergence of Atlantic and Pacific deep-sea vent ecosystems (Vrijenhoek, 2010). The opening of the Panama Canal may have created a bridge that allows vent species with planktonic larvae to cross between the Atlantic and Pacific. The Suez Canal may create a similar connection between communities in the Mediterranean and Gulf of Aden (Biasi and Aliani, 2003). Likewise, the opening of the Northwest Passage due to Arctic sea ice melting could result in a similar effect.

Increasingly, transport of species as stowaways on research and commercial equipment across biogeographic boundaries raises the possibility of invasive species in the deep sea (Thaler et al., 2015). Submersible assets working at deep-sea hydrothermal vents may act as vectors for marine invasions, carrying organisms from one vent field to another, potentially across vast distances or into new biogeographic provinces. In one extreme case, limpets found on the East Pacific Rise were transported 635km south between dives before being discovered upon vehicle recovery (Voight et al., 2012). In a separate and unconfirmed case, a novel fungal infection spreading across hydrothermal vent-dependent mussels in the western Pacific was hypothesized to be the result of transmission into the deep sea via deep submergence vehicles (Van Dover et al., 2007). These cases raise the possibility that, as activities related to mining and exploration increase in deep-sea vent ecosystems, and especially as mining companies look towards species translocation as a potential mitigation strategy, introduction of non-native species into distant vent ecosystems could result in species invasions similar to what are currently occurring in shallow waters.

This is a particularly pressing knowledge gap, as Arctic-Ocean hydrothermal vents are nearly completely uncategorized and biological homogenization driven by the decline in Arctic sea ice and subsequent range expansions and species invasions may overwrite the natural biodiversity of the region before comprehensive surveys can be conducted.

Hydrothermal-Vent Research and the Global South

The Global South has been significantly underrepresented in both terrestrial and marine ecological studies (Ladle et al., 2015; Martin et al., 2012; Velasco et al., 2015). This phenomenon has been ascribed to several factors including the modern concentration of financial and educational resources in the northern hemisphere, a history of colonization and post-colonial exploitation, and a lack of representation within the scientific community (Doi and Takahara, 2016; Wilson et al., 2016). This leads to a stark north/south divide in the quality of best-available-data to make conservation and management decisions in at-risk ecosystems (Karlsson et al., 2007).

Deep-sea research is not immune to this phenomenon. Global hydrothermal-vent research has historically focused on the northern hemisphere, with the majority of southern-hemisphere vent discoveries occurring in the last fifteen years (Beaulieu et al., 2013). Research effort for biological studies of deep-sea hydrothermal vents mirrors this trend, with almost three times as many research cruises undertaken in the northern hemisphere (189) than in the southern hemisphere (72). Of the 298 confirmed, active hydrothermal vent sites, 179 occur in the northern hemisphere, while 119 occur in the southern hemisphere. In contrast, when looking at all vents that have been either confirmed or inferred from chemical signatures, a slight majority (353) occur in the southern hemisphere compared with 300 from the northern hemisphere. Most concerning, the largest proportion of new vent discoveries in the southern hemisphere occurred in the southwest Pacific in conjunction with exploration for the purposes of identifying new mining prospects (Beaulieu et al., 2013).

Knowledge gaps derived from disproportionate representation of northern hemisphere ecologic research in the body of deep-sea hydrothermal vent literature may hinder effective management and mitigation policies. The policy implications of the North-South knowledge divide have been well documented (Karlsson et al., 2007). In an extreme example, during the 1960s, as the theory of plate tectonics was in its ascendancy, 52% of geologists whose research

was based in the northern hemisphere rejected the initial studies supporting plate tectonics, while more the 90% of geologists who had conducted any work in the southern hemisphere accepted the emerging theory (Martin et al., 2012; Solomon, 1992).

Of confirmed active hydrothermal vent fields, 45 fall within exploratory mining leases. Of those 45, only nine are found in the northern hemisphere, the remaining 36 are all south of the equator. Conversely, of the 31 confirmed active hydrothermal vent fields that currently fall within some form of marine protected area, all of them are found in the northern hemisphere. Of the hydrothermal vents recommended by InterRidge to the ISA for future targets of protection, a more equitable 52 are in the southern hemisphere and 50 are in the northern hemisphere. However, among those vent fields recommended for protection that fall within existing exploratory mining leases, 17 are in the southern hemisphere, while two are in the northern hemisphere, a phenomenon best explained by the relatively few vent fields in the northern hemisphere currently being explored for extraction in the northern hemisphere. The protection, management, and exploitation of deep-sea hydrothermal vents mirrors a trend common in modern mineral resource exploitation, where extraction is heavily focused in the Southern Hemisphere, while protection predominantly occurs in the Northern Hemisphere (Gould et al., 2004), both in the targeting of mining prospects and the protection of ecosystems.

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