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260 Voyages Beneath the Sea: A global assessment of biodiversity and research effort at deep-sea hydrothermal vents

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For over forty years, hydrothermal vents and the communities that thrive on them have been a source of profound discovery for deep-sea ecologists. These ecosystems are found throughout the world on active plate margins as well as other geologically active features. In addition to their ecologic interest, hydrothermal vent fields are comprised of metallic ores, sparking a nascent industry that aims to mine these metal-rich deposits for their mineral wealth. Here we provide the first systematic assessment of biodiversity at hydrothermal vents normalized against research effort. Cruise reports from scientific expeditions as well as other primary literature were used to characterize the extent of exploration, determine the relative biodiversity of different biogeographic provinces, identify knowledge gaps related to the distribution of research effort, and prioritize targets for additional sampling to establish biodiversity baselines ahead of potential commercial exploitation. The Northwest Pacific, Southwest Pacific, and Southern Ocean biogeographic provinces were identified as high biodiversity using rarefaction of incidence data, whereas the North East Pacific Rise, Northern East Pacific, Mid-Atlantic Ridge, and Indian Ocean provinces had medium biodiversity, and the Mid-Cayman Spreading Center was identified as a province of relatively low biodiversity. A North/South divide in the extent of biological research and the targets of hydrothermal vent mining prospects was also identified. Finally, we provide an estimate of sampling completeness for each province to inform scientific and stewardship priorities.

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ABSTRACT

For over forty years, hydrothermal vents and the communities that thrive on them have been a source of profound discovery for deep-sea ecologists. These ecosystems are found throughout the world on active plate margins as well as other geologically active features. In addition to their ecologic interest, hydrothermal vent fields are comprised of metallic ores, sparking a nascent industry that aims to mine these metal-rich deposits for their mineral wealth. Here we provide the first systematic assessment of biodiversity at hydrothermal vents normalized against research effort. Cruise reports from scientific expeditions as well as other primary literature were used to characterize the extent of exploration, determine the relative biodiversity of different biogeographic provinces, identify knowledge gaps related to the distribution of research effort, and prioritize targets for additional sampling to establish biodiversity baselines ahead of potential commercial exploitation. The Northwest Pacific, Southwest Pacific, and Southern Ocean biogeographic provinces were identified as high biodiversity using rarefaction of incidence data, whereas the North East Pacific Rise, Northern East Pacific, Mid-Atlantic Ridge, and Indian Ocean provinces had medium biodiversity, and the Mid-Cayman Spreading Center was identified as a province of relatively low biodiversity. A North/South divide in the extent of biological research and the targets of hydrothermal vent mining prospects was also identified. Finally, we provide an estimate of sampling completeness for each province to inform scientific and stewardship priorities.

INTRODUCTION

As knowledge of plate tectonics and seafloor spreading advanced in the mid-twentieth century, geologists hypothesized the existence of hydrothermal vents—formations on the seafloor where superheated seawater emerged from the Earth's crust. Rock dredges across the Mid-Atlantic Ridge (Aumento et al., 1971) and heat flow measurements in the Galapagos Spreading Center (Williams et al., 1974), as well as other studies (e.g. Corliss, 1971), pointed to the necessity of these hot springs near spreading centers to account for thermal anomalies and unique geologic structures. Those early hypotheses also posited the presence of metal rich sulphide deposits on the sea floor (Emery and Skinner, 1977).

When the *RV Knorr* set sail for the Galapagos Rift in 1977, the geologists aboard eagerly anticipated observing a deep-sea hydrothermal vent field for the first time. What they did not expect to find was life—abundant and unlike anything ever seen before. A series of dives aboard the *HOV Alvin* during that expedition revealed not only deep-sea hydrothermal vents but fields of clams and the towering, bright red tubeworms that would become icons of the deep sea. So unexpected was the discovery of these vibrant ecosystems that the ship carried no biological preservatives. The first specimens from the vent field that would soon be named 'Garden of Eden' were fixed in vodka from the scientists' private reserves (Ballard, 2000).

Since that first discovery, deep-sea hydrothermal vents have been found throughout the world's oceans at mid-ocean ridges, volcanic arcs, and back-arc spreading centers (Beaulieu et al., 2013). As more geographic regions are explored, newly discovered vent fields present the potential for entirely new ecosystems as well as species. Just as "forest" can describe ecosystems ranging from boreal forests to tropical rain forest, "hydrothermal vent" describes a suite of deep-ocean ecosystems united by a shared dependence on chemosynthetically-derived primary production and above-ambient temperatures but diverse in their composition and connection to one another.

While the hydrothermal vent fields discovered in the Galapagos Spreading Center and East Pacific Rise are dominated by the deep-sea tubeworm, *Riftia pachyptila*, subsequent vent ecosystems are characterized by swarms of shrimp (*Rimicaris exoculata* on the Mid-Atlantic Ridge: Dover et al., 1988; *Rimicaris hybisae* on the Mid-Cayman Spreading Center: Plouviez et al., 2015), aggregations of large snails (*Alviniconcha* spp. and *Ifremeria hessleri* in northern and southern West Pacific back-arc basins: Desbruyères et al., 2006), and colonies of yeti crabs

77 (*Kiwa tyleri* in the Southern Ocean: Rogers et al., 2012).Many other biomass-dominant taxa have

78 been recorded at vents, including a variety of tubeworms, mussels, clams, crabs, shrimp, snails,

79 barnacles, and squat lobsters (Van Dover, 2000).

80   The discovery of large chemosynthetic communities around deep-sea hydrothermal vents

81 fundamentally altered our understanding of how life endures in extreme environments

82 (Rothschild and Mancinelli, 2001), the role of chemosynthesis in both exotic and mundane

83 ecosystems (Boston et al., 1992; Dubilier et al., 2008), the role of symbioses in biological

84 systems (Cavanaugh et al., 1981; Duperron et al., 2006), and has provided key insights into the

85 evolutionary origin of life on Earth (Martin et al., 2008). The discovery of other chemosynthetic

86 cognate communities in the deep sea (e.g. methane seeps, mud volcanoes, whale falls, and wood

87 falls: Van Dover, 2000) as well as terrestrial and shallow-water analogs (e.g. thermal springs:

88 Yang et al., 2011; and the anoxic sediments of salt marshes: Howarth, 1984) followed.

89   While the scientific and ecological value of hydrothermal vent ecosystems is difficult to

90 quantify (Thurber et al., 2014; Turner et al., 2019), the financial value of vent systems, and the

91 ores they contain, is increasingly driving exploration in the deep sea. Over the last five decades,

92 a new industry has emerged to explore the potential of mining Seafloor Massive Sulphides (or

93 Polymetallic Sulphides)—deep-sea hydrothermal vents that contain high concentrations of rare

94 and precious metals. Though industrial vent mining is in its infancy, multiple enterprises are

95 developing mining prospects that include both active and inactive deep-sea hydrothermal vent

96 fields.

97   Seafloor mineral resources in areas beyond national jurisdictions are managed by the

98 International Seabed Authority (ISA) who adopted Regulations on Prospecting and Exploration

99 for Polymetallic Sulphides in the Area in 2010. The ISA requires mining contractors to establish

100 environmental baselines and maintain an environmental monitoring program before, during, and

101 after operations(Bräger et al., 2018). Two international Codes of Conduct also apply to nations,

102 organizations, and institutions who have voluntarily elected to abide by them. The InterRidge

103 Statement of Commitment to Responsible Research Practices (Devey et al., 2007) relates

104 primarily to scientific research conducted at hydrothermal vents, including exploratory research

105 to assess ore deposits. The International Marine Minerals Society Code for Environmental

106 Management of Marine Mining establishes environmental principles and best practices for

107 marine mining as well as recognizes the value of both biological and mineral resources (Verlaan,

108 2011).

109   Within territorial waters, mining activities fall under national regulations, which vary

110 depending on the country in question. Currently, Papua New Guinea, New Zealand, the

111 Kingdom of Tonga, Japan, and Vanuatu have issued exploration permits to assess the value of

112 ore found at deep-sea hydrothermal vents within their territorial waters (Boschen et al., 2013). In

113 addition, Papua New Guinea has issued a single mining license for the resource-rich Solwara I

114 hydrothermal vent field (Hoagland et al., 2010). As scientists, managers, and conservationists

115 rush to establish best management practices ahead of proposed mining projects (Collins et al.,

116 2013; Van Dover, 2011, 2010), a major challenge lies in our relatively limited knowledge of

117 hydrothermal vent communities and our understanding of how these communities might respond

118 to catastrophic anthropogenic disturbance.

119   Among the most pernicious problems in establishing a global assessment of biodiversity

120 at deep-sea hydrothermal vents is the unequal distribution of research effort across the oceans.

121 Research has mostly focused on a few biogeographic provinces with multiple expeditions, long-

122 term time-series, and cabled observatories, while other provinces have only recently been

123 sampled or sparingly sampled on few expeditions. Managers, regulators, and mining companies

124 are working from incomplete data, with inferences about the consequences, as well as mitigation

125 and remediation practices, often drawn from studies of few vent ecosystems that are often

126 different from those in which the impacts are expected to occur. This is especially challenging as

127 biodiversity is frequently used as a proxy for resilience and as a metric for assessing biological

128 baselines (Sonter et al., 2018; Van Dover, 2010; Van Dover et al., 2017).

129   In order to better assess our current understanding of deep-sea hydrothermal vent

130 biodiversity, we undertook a survey of the last 40 years of vent research via cruise reports (post-

131 research cruise summary documents that provide a day-to-day narrative of work at sea, as well as

132 momentary sample logs and observations) from research expeditions that made biological

133 observations at hydrothermal vents. This allowed us to: assess and compare research effort

134 among different biogeographic provinces; determine the relative biodiversity of biogeographic

135 provinces when normalized against research effort; identify knowledge gaps related to the

136 unequal distribution of research effort; and prioritize targets for additional sampling in advance

137 of deep-sea mining.

METHODS

COMPILING CRUISE REPORTS

To estimate global biological research effort at deep-sea hydrothermal vents, reports from
discrete research expeditions were used as functional proxies for 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. For our purposes, "cruise reports" are considered any post-cruise primary literature
that directly summarizes the activities conducted at sea. This can include narrative reports,
observation logs from submersible or ROV surveys, or sample logs from shipboard sample
processing. Importantly, cruise reports do not include the results of post-cruise analyses such as
taxonomic studies or activities such as the publication of peer-reviewed manuscripts. This allows
us to treat individual cruises as discrete sampling events reflective of the state of knowledge at or
immediately after the time of sampling.

Cruise reports were acquired from institutional library archives, including those of
Scripps Institute of Oceanography (SIO), Woods Hole Oceanographic Institution (WHOI), Japan
Agency for Marine-Earth Science and Technology (JAMSTEC), French Research Institute for
Exploitation of the Sea (IFREMER), New Zealand National Institute of Water and Atmospheric
Research (NIWA), Korea Institute of Ocean Science and Technology (KIOST) and others;
regional databases, including rvdata.us and Natural Environment Research Council (NERC);
international collaborative databases, including InterRidge (Beaulieu et al., 2013) and
ChEssBase (Ramirez-Llodra et al., 2005); as well as direct queries to chief scientists, principle
investigators, and institutional archivists. Cruises were divided into 11 biogeographic provinces
based on assessments by Bachraty et al. (2009), Moalic et al. (2012), Rogers et al. (2012), and
Suzuki et al. (2018). Those provinces consisted of the Arctic Ocean, Indian Ocean,
Mediterranean Sea, Mid-Atlantic Ridge, Mid-Cayman Spreading Center, Northeast Pacific
(which we refer to throughout as the Juan de Fuca Ridge to avoid confusion with the Northern
East Pacific Rise, though other ridge axes are included in the assessment), Northern East Pacific
Rise (including Galapagos Spreading Center), Southern East Pacific Rise, Southern Ocean,
Northwest Pacific, and Southwest Pacific. Sampling effort was then assessed for each
biogeographic province.

169

DETERMINING SAMPLING EFFORT

171   A comprehensive survey of all available cruise reports for biological sampling records

172   from hydrothermal vent fields was undertaken. We define "biological sampling records" as

173   either observation or collection and identification of macrofauna and megafauna while at sea. In

174   cases where multiple ecosystems were observed or collected from during a single research

175   cruise, we relied on narrative description and location records to determine whether those

176   biological sampling records qualified as originating from a hydrothermal vent field. For

177   ambiguous cases, we excluded those records.

178   Every research cruise has different objectives and sampling regimes, which influence

179   how many and which taxa are sampled. To account for the high variability in sampling

180   methodology, we recorded incidence, rather than accumulation, data. We looked at macrofaunal

181   and megafaunal occurrences, rather than microbial and meiofaunal (which are often preserved

182   for post-cruise sorting and identification). We used identifications made at the time of sampling,

183   rather than post-cruise analyses. In cases where the identification was unambiguous, but the

184   taxonomic status of the organism has been revised since sampling (e.g. Siboglinidae,

185   Pogonophora, and Vestimentifera: Pleijel et al., 2009) or clear and distinct common names were

186   used prior to formal identification (e.g. the "Hoff Crab", *Kiwa tyleri*: Thatje et al., 2015 or

187   "Scaly-foot Gastropod", *Chrysomallon squamiferum*: Chen et al., 2015), the currently accepted

188   nomenclature, as established by the World Register of Marine Species (Costello et al., 2013) was

189   used. Organisms were documented to the lowest available taxonomic level reported as either

190   present or absent.

191

BIODIVERSITY ESTIMATES

193   To estimate biodiversity across a global, inconsistent, and incomplete data set, incidence

194   data was compiled at the taxonomic level of Family. Family richness has been shown to strongly

195   correlate with species and genus richness in macroinvertebrates, especially in regions with

196   relatively low species diversity (Heino and Soininen, 2007) and is useful in cases where sample

197   sizes are inconsistent (Raup, 1975). Each cruise report was treated as a discrete sample for the

198   purpose of this study.

199   The non-parametric asymptotic species richness estimator Chao2 (Chao et al., 2005) was

200   used to extrapolate family richness of incidence data compiled from each research cruise. Chao2

201   has been demonstrated to be among the most reliable richness estimators when tested against

202   simulated and real-world incomplete data sets where sampling effort is inconsistent (Walther and

203   Morand, 1998). The bias-corrected Chao2 formula was used except in cases where the

204   coefficient of variation for incidence distribution was greater than 0.5, in which case the classic

205   formula was used following recommendations of Chao et al., (2005). Rarefaction estimates were

206   extrapolated to twice the size reference sample, with 10,000 replicates randomized without

207   replacement. Rarefaction extrapolations were also projected out to asymptote. EstimateS (version

208   9.1.0) was used to calculate Chao2, extrapolate rarefaction curves, and generate 95% confidence

209   intervals (Colwell et al., 1994; Colwell and Elsensohn, 2014).

210   Family richness estimates were referenced against the ChEssBase taxonomic archive,

211   which contains self-reported identification of species from marine chemosynthetic ecosystems as

212   an imperfect control (Ramirez-Llodra et al., 2005). Though comprehensive at the time,

213   ChEssBase is no longer being updated and does not contain observations recorded after April

214   2006.

215   A secondary analysis was performed using methods outlined in Chao (2009) to estimate

216   how many additional samples were needed for each biogeographic province to reach 80%, 90%,

217   and 99% sampling completeness. This method can guide researchers and managers as to how

218   much additional sampling is necessary in order to account for rare species within a

219   biogeographic province and also inform management criteria in determining the proportion of

220   completeness that satisfies the need for adequate biodiversity baseline assessments.

221

222   **CAVEATS AND LIMITATIONS**

223   These samples are neither random nor even, but represent opportunistic sampling driven

224   by *a priori* scientific priorities. While a study of this nature should not be used to derive

225   fundamental ecologic principles, the use of opportunistic data within a management and

226   conservation framework is essential for assessing the state of the field, determining priorities for

227   future studies, and identifying knowledge gaps and data deficiencies. Rarefaction and

228   extrapolation based on opportunistic samples has been used to guide conservation decision-

229   making at local (Carvalheiro et al., 2013) and global scales (Maes et al., 2015).

230   Due to the variety of naming conventions, the incompleteness of the global research

231 record, and inconsistencies within and among institutions, it is likely impossible to account for

232 every research cruise that made biological observations at a deep-sea hydrothermal vent.

233 Research archives may, in some cases, be incomplete and the quality of documentation and

234 sample archiving at sea renders some cruise reports unsuitable for this study. In addition,

235 geopolitical forces often shape international collaboration, and many documents are not

236 necessarily available to the general public due to classified, proprietary, or privileged

237 information.

238   The variable quality and completeness of cruise reports means that this assessment

239 represents a minimum viable approximation of biodiversity and sampling effort at deep-sea

240 hydrothermal vents. Many deep-sea species are frequently undescribed at the time of sampling,

241 and samples from more well-studied regions are more likely to be fully characterized to the

242 species level, while samples from relatively understudied regions may be relegated to higher

243 taxonomic identifications or characterized as undescribed at the time of sampling. This provides

244 an additional challenge as rare species are far more frequently new-to-science and undescribed

245 while common species are much more thoroughly identified.

246   Finally, the ChEssBase database includes all chemosynthetic ecosystems and neighboring

247 ecosystems, as well as organisms sampled in the water column above a hydrothermal vent field,

248 but not directly connected to the vents. This may artificially inflate family counts from

249 ChEssBase.

250   Family incidence data and archive of cruise reports are provided as supplemental data.

251

RESULTS

SUMMARY OF CRUISE REPORTS

We identified a total of 260 research cruises representing 12 nations and one territory (Australia, Canada, France, Germany, Ireland, Japan, New Caledonia, New Zealand, Portugal, Russia or the Soviet Union, South Korea, the United Kingdom, and the United States) that collected biological samples or made biological observations at deep-sea hydrothermal vents spanning from 1977 to 2017. Of those, 122 had cruise reports of sufficient detail for biodiversity analysis (Figure 2).

Of the 841 research cruises recorded in the InterRidge archive, 88 contained sufficiently detailed biological sampling based on available cruise reports, while the remainder were geologic, geophysical, oceanographic, or exploration-related without a documented biological component or without detailed sample logs and dive narratives. 177 research cruises were identified through archive requests, primary literature, contributions from principle investigators and cruise participants, and other documentation (Table 1). 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 mining exploration, which are generally held as proprietary information. Research cruises from the late 1970s and early 1980s were less well documented and full cruise reports could not be located for several early research expeditions, particularly to the Galapagos Spreading Center.

Nearly a third of all available cruise reports were from research conducted in the Northwest Pacific ($n = 40$) due in no small part to the rigorous archiving conducted at JAMSTEC. The Mid-Atlantic Ridge ($n = 27$), Southwest Pacific ($n = 16$), and Juan de Fuca Ridge ($n = 14$) can also be considered extensively sampled systems. Surprisingly few cruise reports were available from the Northern East Pacific Rise ($n = 8$) despite a history of extensive sampling (we identified 31 biological research cruises to the Northern EPR). The Mid-Cayman Spreading Center, Indian, and Southern Ocean had the fewest available cruise reports ($n = 5, 7,$ and 5 respectively). No cruise reports containing biological sampling data of macrofauna were available from the Southern East Pacific Rise, Mediterranean Sea, or Arctic Ocean (Table 1). These three provinces were excluded from subsequent analyses.

Biological research at deep-sea hydrothermal vents has been historically concentrated in the northern hemisphere (Figure 2), while the majority of southern-hemisphere vents were only

283   discovered in last fifteen years with much fewer expeditions since (Beaulieu et al., 2013). Across

284   all known hydrothermal vent fields (those that have been either directly confirmed or inferred

285   based on chemical or geologic signals), a slight majority (275) occur in the southern hemisphere

286   compared with 260 from the northern hemisphere. While of the 255 visually-confirmed, active

287   hydrothermal vent sites, 152 occur in the northern hemisphere and 103 are found in the southern

288   hemisphere. More than three times as many biologic research cruises have been undertaken in

289   the northern hemisphere (171) than in the southern hemisphere (55). Of hydrothermal vent fields

290   that fall within established marine protected areas, all were found in the Northern Hemisphere

291   (31) while among vent fields that fall within exploratory or exploitation mining leases, a majority

292   were located in the Southern Hemisphere (5 in the Northern Hemisphere; 42 in the Southern

293   Hemisphere).

294   Comparisons between ChEssBase and raw cruise data were inconsistent. With the

295   exception of the Northwest Pacific, family counts on ChEssBase exceeded those compiled

296   directly from the cruise reports from well-sampled biogeographic provinces (those in which total

297   number of cruise reports available is eight or greater). For less well-sampled provinces, family

298   counts from cruise reports exceeded those of ChEssBase. This is in part due to some provinces

299   (such as the Mid-Cayman Spreading Center) only recently receiving more attention.

300

ESTIMATES OF FAMILY RICHNESS

302   Eight biogeographic provinces had sufficient data available for analysis and were

303   extrapolated out to twice the reference sample. Estimated family richness ranged from a high of

304   155.6 (Northwest Pacific; 95% confidence interval: 129.0.9 to 182.3) to a low of 17.1 (Mid-

305   Cayman Spreading Center; 95% confidence interval: 12.8 to 21.4). The Northwest Pacific and

306   Southwest Pacific (83.2; 95% confidence interval 63.4 to 102.6; Figure 3), while the Southern

307   Ocean (40.3; 95% confidence interval: 24.7 to 55.9) though it contained fewer samples, shared a

308   similar trajectory (Figure 4). The Northern East Pacific Rise (43.48; 95% confidence interval:

309   34.1 to 52.9) had greater family richness than the Juan de Fuca Ridge (23.0: 95% confidence

310   interval: 12.8 to 33.1) despite fewer available cruise reports (Figure 5). The Mid-Atlantic Ridge

311   (63.9: 95% confidence interval: 53.0 to 74.7) and Indian Ocean (42.6; 95% confidence interval:

312   32.1 to 53.2 shared a similar pattern with the Northern East Pacific Rise, while the Mid-Cayman

313   Spreading Center fell far below all other biogeographic provinces in family richness (Figure 5).

314   When ranked from highest to lowest biodiversity using extrapolation to asymptote for all

315   biogeographic provinces, the Northwest Pacific had the highest mean family richness, followed

316   by the Southwest Pacific, Southern Ocean, Mid-Atlantic Ridge, Indian Ocean, Northern East

317   Pacific Rise, and Juan de Fuca Ridge, with the Mid-Cayman Spreading Center coming in a

318   distant last (Figure 6). The wide confidence intervals for the Southern Ocean and Juan de Fuca

319   Ridge that intersect with null make any placement tenuous given the current data.

320

321   **ESTIMATES OF SAMPLE COMPLETENESS**

322   Using Chao's method for estimating sample completeness based on singletons,

323   doubletons, and observed families, we were able to generate rough estimates of how many

324   additional research cruises would be required to comprehensively sample each biogeographic

325   province. A few provinces required less than 10 additional research cruises in order to reach 90%

326   sample completeness, including the Indian Ocean (9) and Northern East Pacific Rise (9). Perhaps

327   not surprisingly, the Mid-Cayman Spreading Center was the closest to being comprehensively

328   sampled (86% complete with 11 additional cruises required to reach unity). Other provinces

329   required 10 to 100 additional research cruises, including the Mid-Atlantic Ridge (20), Juan de

330   Fuca Ridge (99), Southern Ocean (43), and Southwest Pacific (71) to reach 90% sampling

331   completeness. Despite being the most extensively sampled of all the biogeographic provinces,

332   the Northwest Pacific required an additional 216 research cruises to reach 90% completeness.

333   The three least sampled provinces with respect to their extrapolated biodiversity and estimates of

334   sample completeness were the Southern Ocean (22% complete), Northwest Pacific (37%

335   complete), and Southwest Pacific (38% complete).

336

DISCUSSION

Forty years after the discovery of deep-sea hydrothermal vents, these remote and inaccessible ecosystems continue to produce new insights and new discoveries. In the last decade, the number of known active vent fields has doubled and yet current estimates project that two thirds of all hydrothermal vent fields are still waiting to be discovered (Beaulieu et al., 2012). Since their discovery, two new species have been described, on average, each month from hydrothermal vents (Ramirez-Llodra et al., 2007). This rate of description is tempered by the fact that research effort has been, until recently, fairly narrowly focused on key biogeographic provinces in the northern hemisphere. Only a small fraction of all active ridge systems have been explored for hydrothermal activity (Baker and German, 2004).

The Global South is frequently underrepresented in both terrestrial and marine ecological studies (Ladle et al., 2015; Martin et al., 2012; Velasco et al., 2015). This pattern is reinforced byseveral 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) leading to a stark divide in the availability of comprehensive baseline surveys to make conservation and management decisions in at-risk ecosystems (Karlsson et al., 2007). It is clear that deep-sea research is not immune to this phenomenon.

Even with a severe bias in favor of research at hydrothermal vents in the northern hemisphere, biodiversity estimates did not correlate with research effort, and southern vent provinces demonstrated a pattern consistent with the geologic origin of hydrothermal venting. Biodiversity estimates clustered into three general overlapping groups. The biogeographic provinces with the highest estimated biodiversity, the North- and Southwest Pacific and the Southern Ocean, are back-arc basin spreading centers, while those with medium biodiversity, the Mid-Atlantic Ridge, Northern East Pacific Rise, Juan de Fuca Ridge, and Indian Ocean, all occur on mid-ocean ridges. The lowest biodiversity province, the Mid-Cayman Spreading Center, occurs along a transform fault on a relic spreading center. Multiple studies have highlighted that vent distribution on back-arc basins is geographically complex compared to the more linear mid-ocean ridges, leading to patchy connectivity among vent fields which can promote great biodiversity (Audzijonyte and Vrijenhoek, 2010; Vrijenhoek, 2010).

NORTHWEST AND SOUTHWEST PACIFIC

The highest extrapolated biodiversity among all biogeographic provinces was estimated in the Northwest Pacific, which also has the longest rising arc before reaching asymptote and the highest number of observed Families in the cruise reports (Figure 2). Due to its proximity to JAMSTEC, the Northwest Pacific was among the best studied biogeographic provinces based on available cruise reports, and yet it had among the lowest g-values (Table 2) for estimated sampling completeness, suggesting a vast, unsampled reservoir of family-level biodiversity still waiting to be discovered.

The Southwest Pacific followed a similar trend, with half the observed families and a lower mean family richness. Sampling effort was similar to that of the Northwest Pacific. Far fewer cruise reports are available from the Southwest Pacific, with sampling predominantly focused around the Kermadec Arc, where NIWA is situated. A number of additional research cruises are known to have been conducted in this province, in particular around Manus Basin in Papua New Guinea, as well as other Pacific Islands, by mining companies (Thaler, personal observation). Those cruise reports and sample logs are proprietary and not publicly available.

Of the seafloor massive sulphide mining prospects currently in development, the two closest to commercial production lie in the Northwestern Pacific off the coast of Japan (Okamoto et al., 2018) and in the Southwest Pacific in the territorial waters of Papua New Guinea (Coffey Natural Systems, 2008). Collectively, hydrothermal vent ecosystems of the West Pacific represent a region of exceptional biodiversity with tremendous potential for new discovery while simultaneously facing the most imminent threat from deep-sea mining of seafloor massive sulphides.

MID-ATLANTIC RIDGE AND INDIAN OCEAN

Despite dramatically different sampling regimes, the Mid-Atlantic Ridge and Indian Ocean biogeographic provinces shared many characteristics in terms of distribution and family abundance. With relatively direct access from both western Europe and the United States' east coast, and sustained attention from American and European research institutions, the hydrothermal vents on the Mid-Atlantic Ridge are the most well-studied of all the biogeographic provinces.

398   Meanwhile, hydrothermal vents in the Indian Ocean, likewise situated on a mid-ocean

399   ridge, exhibited a lower mean family richness within overlapping confidence intervals of roughly

400   the same extent as those of the Mid-Atlantic Ridge. Though there has historically been less

401   research focused on the Indian Ocean, this pattern, as well as a proliferation of novel species and

402   taxa (e.g. *Chrysomallon squamiferum*; Chen et al., 2015) and the growth of deep-sea research

403   institutions in India and China suggests that hydrothermal vents in the Indian Ocean could play

404   as significant a role in the exploration of the deep sea in this century as the Mid-Atlantic Ridge

405   played in the last.

406

407   **NORTHERN EAST PACIFIC RISE AND JUAN DE FUCA RIDGE**

408   The Northern East Pacific Rise and Juan de Fuca Ridge presented a challenging case to

409   assess, as there was a dearth of available cruise reports from these extensively studied regions.

410   The relatively low completeness of the Juan de Fuca Ridge in particular is likely an artifact of

411   these missing cruise reports, as ChEssBase lists many more taxonomic records than those

412   uncovered through sampling effort analysis (Table 1). Due to the way data is compiled and

413   queried in ChEssBase, this may represent an over-estimate, as ChEssBase includes all

414   chemosynthetic ecosystems, including methane seeps which are also found in close proximity to

415   hydrothermal vents in this region (Ramirez-Llodra et al., 2005).

416   The Northern East Pacific Rise biogeographic province followed the same pattern of

417   family accumulation and estimated family richness as other mid-ocean ridge systems, however,

418   though estimated family richness is comparable to the Juan de Fuca Ridge, the wide confidence

419   intervals of the Juan de Fuca Ridge are more in line with back-arc basin vent ecosystems (Figure

420   6). This furthers supports the interpretation that the region is undersampled, either practically or

421   as a result of the low availability of reports from known research cruises.

422

423   **SOUTHERN OCEAN AND MID-CAYMAN SPREADING CENTER**

424   Hydrothermal vent fields in the Mid-Cayman Spreading Center (Figure 4) and in the

425   Southern Ocean (Figure 2) along the East Scotia Ridge provided a useful illustration of the

426   variability within deep-sea vent communities. Both systems were only recently characterized—

427   hydrothermal vents in the Mid-Cayman Spreading Center were first sampled in 2010 (Plouviez

428   et al., 2015), while those of the East Scotia Ridge were first observed in 2009 (Rogers et al.,

429   2012). Both vent fields represent new, albeit small, biogeographic provinces. And, conveniently,

430   both vent systems were largely studied by the same personnel from the National Oceanography

431   Centre, Southampton, using similar sample designs deployed using the same equipment, with

432   many of the same taxonomists identifying taxa at sea (Thaler, personal observation). Five

433   separate research cruises made biological observations and provided extensive sample logs for

434   two discrete hydrothermal vent fields within each biogeographic province.

435   Despite nearly identical sampling effort, the Mid-Cayman Spreading Center exhibits the

436   lowest biodiversity of any known hydrothermal vent system, an observation that has been

437   anecdotally expressed by numerous hydrothermal vent ecologists (A. Glover, personal

438   communication; J. Copley, personal communication), while the Southern Ocean has among the

439   highest family richness (though the 95% confidence interval is quite wide). Completeness

440   estimates (Table 2) indicate that, while the Mid-Cayman Spreading Center is approaching unity

441   and is currently estimated to be among the best sampled hydrothermal vent systems in terms of

442   estimated family richness, the Southern Ocean is the poorest sampled biogeographic province.

443   This comparison is particularly valuable, as it demonstrates that family richness estimates

444   at deep-sea hydrothermal vents are not just an artifact of sampling effort but reflect real and

445   observable differences in biodiversity among hydrothermal-vent biogeographic provinces.

446

447   **ARCTIC OCEAN, MEDITERRANEAN SEA, AND SOUTHERN EAST PACIFIC RISE**

448   Three biogeographic provinces, the Arctic Ocean, Mediterranean Sea, and Southern East

449   Pacific Rise had too little data available to appropriately assess sampling effort. While there are

450   several know research cruises to the Arctic Ocean, in particular to the Loki's Castle vent field

451   along the Gakkel Ridge (Edmonds et al., 2003), the majority were conducted in conjunction with

452   commercial resource exploration and their subsequent reports are not publicly available. As

453   Loki's Castle shares vent fauna from both the Atlantic and Pacific and appears to be dominated

454   by an undescribed species of amphipod, as well as methane seep-associated tubeworms, it has

455   the potential to represent an intermediate province that connects Atlantic and Pacific vent

456   systems (Schander et al., 2010).

457   The Mediterranean Sea presents a much different story. Several recent expeditions have

458   sampled microbes from hydrothermal vent fields in the Mediterranean Sea, yet no vent-endemic

459   fauna were observed. It is likely that, due to their relatively shallow depth, Mediterranean

460   hydrothermal vent fields have not developed their own characteristic chemoautotrophic

461   macrofaunal communities (Biasi and Aliani, 2003; Dando et al., 1999; Danovaro et al., 2010).

462   Meanwhile, there are substantial biodiversity records from the Southern East Pacific Rise

463   available on ChEssBase, but few accessible cruise reports from the region. The current state of

464   knowledge suggests that the Southern East Pacific Rise allies closely with Northern East Pacific

465   Rise, with significant dispersal barriers for some, but not all, co-occurring taxa, and its

466   assignment as a separate biogeographic province may be premature (Jollivet et al., 2004;

467   Plouviez et al., 2010, 2009; Rybakova and Galkin, 2015; Won et al., 2003).

468

LIMITATIONS OF AVAILABLE DATA

470   While this study provides a rough initial estimate of global hydrothermal vent

471   biodiversity, it is necessarily incomplete. Despite over 250 documented research cruises

472   undertaken to investigate the biology, ecology, and evolution of macro- and megafauna at deep-

473   sea hydrothermal vents, we have barely begun to probe the surface of one of the world's most

474   remote and inaccessible ecosystems. Estimates of sample completeness are also derived from an

475   assumption of random sampling, of which these cruise reports are not, and while they serve as a

476   reasonable estimate for relative completeness within this dataset, they are not necessarily of

477   sufficient rigor for comparative analysis across datasets. While family-level richness studies have

478   been shown to be good proxies for species-level biodiversity, they do not account for regions of

479   exceptionally high diversification within lower-level taxonomic groupings.

480   Several known hydrothermal vents fields, particularly those associated with off-axis

481   volcanic arcs like the Hawai'ian archipelago (Karl et al., 1988), as well as shallow-water vents

482   fields (Tarasov et al., 2005), freshwater vent systems (Crane et al., 1991), and submerged

483   volcanoes like Kick'em Jenny in the Caribbean (Carey et al., 2016), are missing from this data

484   set. This is due to both relatively less research conducted in these regions as well as the general

485   unavailability of cruise reports. While these systems represent potential additional targets to

486   further fill knowledge gaps in the deep sea, we do not believe their exclusion substantively

487   impacts the results of our analysis.

488

IMPLICATIONS FOR DEEP-SEA MINING

490   The exploration, protection, and potential exploitation of deep-sea hydrothermal vents

491   mirrors a trend common in modern mineral extraction, where prospecting is heavily focused in

492   the Southern Hemisphere, while greater knowledge and understanding has led to more

493   protectionin the Northern Hemisphere (Gould et al., 2004). Baseline biodiversity data is critical

494   to effective management as it sets the context against which all potential impacts from

495   anthropogenic activities can be assessed. It is particularly concerning that biogeographic

496   provinces with the highest estimated biodiversity lie in the southern hemisphere, representing

497   tremendous potential for new discovery while simultaneously facing the most imminent threat

498   from deep-sea mining of seafloor massive sulphides.

499   Due to complex geological, chemical, and physical parameters, no hydrothermal vent

500   system is identical, leading to variation in community composition across vent fields.

501   Communities differ between ocean basins, within ocean basins, and even on much smaller scales

502   (e.g. within a few kilometers: Thaler et al., 2017). As a result, generalizations about

503   hydrothermal vents and their communities are tenuous and the disproportionate representation of

504   northern hemisphere hydrothermal vent ecosystems in the scientific literature could hinder

505   effective management and mitigation policies if used to inform management and mitigation at

506   southern hemisphere hydrothermal vent-derived ore deposits. For example, nearly all studies of

507   community recovery and succession following catastrophic disturbance at a deep-sea

508   hydrothermal vent, which could provide proxies for the impact of and recovery after deep-sea

509   mining, have been conducted at northerly vents on the East Pacific Rise and Juan de Fuca Ridge

510   (Marcus et al., 2009; Nees et al., 2008; Tunnicliffe et al., 1997), both of which are mid-ocean

511   ridges. This is problematic as the majority of proposed mining activities are located in the

512   Southwest Pacific back-arc basin, although one recent succession study is available from the

513   Eastern Lau Spreading Center in the Southwest Pacific (Sen et al., 2014). The dramatic

514   difference in biodiversity and abiotic factors such as hydrothermal vent fluid chemistry between

515   these two regions ensure that managers are unable to make direct comparisons between recovery

516   rates in the Eastern and Western Pacific.

517   This disparity can also have a substantial impact on the effectiveness of regional

518   environmental management plans and set asides (areas protected from mining and secondary

519   impacts that have the potential to act as refugia and larval sources for affected vent communities)

520   to preserve the biodiversity of hydrothermal vent systems (Boschen et al., 2016).Whether or not

521   a set aside will act as an effective buffer against catastrophic disturbance at nearby mining sites

522   depends on many factors, including the resilience of the overall region and the extent to which

523   vent communities are connected. This varies considerably between ocean basins but also within a

524   region. For example, in the Western Pacific, there is extensive regional variability in the ability

525   of vents to recover from disturbance on short time scales. In simulations, Northwest Pacific vent

526   ecosystems tend to have recovery time estimates in the range of 20 to 40+ years, while in the

527   Southwest Pacific, recovery times were much shorter, some vents were even predicted to recover

528   within 5 years of mining disturbance (Suzuki et al., 2018b).

529   At a broader perspective, ecosystems that have high biodiversity tend to be more resilient

530   to disturbance with shorter recovery times, while those with relatively low biodiversity are much

531   more vulnerable to disturbance and have longer recovery times, if at all (Oliver et al., 2015). This

532   phenomenon is largely circular, as frequent disturbance, up to a point, itself drives increased

533   diversification and produces more resilient communities, provided that disturbance is not so

534   great as to preclude the establishment of new communities. In the deep sea, this has been

535   demonstrated by simulating the impact of polymetallic nodule extraction, in which a relatively

536   undisturbed ecosystem has shown no significant signs of recovery after 40 years (Jones et al

537   2018). Hydrothermal vents, in contrast to the broader deep sea, do experience varying degrees of

538   local disturbance, which in turn may contribute to their resilience in the face of anthropogenic

539   insult.

540   Undoubtedly deep-sea mining has the potential for far-reaching impacts on our oceans,

541   both shallow and deep, that could reshape the seafloor for decades, centuries, or longer. Habitat

542   will be removed, sediment plumes will be created, and some biodiversity loss is inevitable (Van

543   Dover et al., 2017). A fundamental problem for predicting the impacts of deep-sea mining on

544   hydrothermal vents is our limited knowledge of these ecosystems in general (Gollner et al.,

545   2017). Hydrothermal vent biodiversity in most regions, especially in the global south, have not

546   been fully characterized. There is a lack of basic ecological information, especially for smaller

547   fauna, on population size, behavior, distribution, life history, growth rate, connectivity, and

548   function (Mullineaux et al., 2018). New species are discovered, and important ecological insights

549   emerge, on every expedition. Recent studies revealed that hydrothermal vent communities in the

550   EEZ of the Kingdom of Tonga are stable over long timescales (Du Preez and Fisher, 2018); that

551   hydrothermal vent ecosystems can act as nursery grounds for non-vent species (Salinas-de-León

552   et al., 2018); and that shallow-water hydrothermal vents may play a greater role in trophic

553   ecology than previously suspected (Chang et al., 2018). Given the advancement of the nascent

554   deep-sea mining industry, research must accelerate.

555

556

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569

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844

Biogeographic Province	Confirmed Vent Fields	Vent Fields in EEZs	Vent Fields in High Seas	Vent Fields in Mining Leases	Research Cruises	Available Cruise Reports	Families Sampled	ChEssBase Families
Arctic	8	8	0	0	2	0	-	1
Indian Ocean	13	3	10	10	16	7	33	6
Mediterranean	15	15	0	0	3	0	-	0
Mid-Atlantic Ridge	42	13	29	5	61	27	53	119
Mid-Cayman Spreading Center	2	2	0	0	8	5	16	0
Northeast Pacific (Juan de Fuca Ridge)	22	10	12	0	34	14	16	86
Northern East-Pacific Rise	48	19	29	0	31	8	36	104
Southern East-Pacific Rise	29	27	2	0	2	0	-	69
Southern Ocean	6	2	4	0	5	5	23	1
Northwest Pacific	58	56	2	0	54	40	106	55
Southwest Pacific	77	76	1	32	44	16	54	56

845 **Table 1.** Summary of distribution of hydrothermal vent field, research effort, and families identified from cruise reports and
846 databases by biogeographic province. Confirmed Vent Fields, Vent Fields in EEZs, Vent Fields in High Seas, and Vent
847 fields in Mining Leases from Beaulieu et al., (2013). ChEssBase accessed via Ocean Biogeographic Database System
848 Ramirez-Llodra et al., (2005).
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Biogeographic Province	T	Q_1	Q_2	t	F_{obs}	g	1.0	0.99	0.9	0.8
Indian Ocean	76	16	7	7	33	0.68	43	26	9	4
Mid-Atlantic Ridge	223	20	12	28	53	0.77	127	73	20	4
Mid-Cayman Spreading Center	32	6	6	5	15	0.86	11	7	1	-
Northeast Pacific (Juan de Fuca Ridge)	56	8	1	14	16	0.35	315	220	99	62
Northern East-Pacific Rise	102	12	5	8	36	0.74	49	29	9	3
Southern Ocean	28	20	2	5	23	0.22	150	90	43	28
Northwest Pacific	461	60	10	40	105	0.37	943	487	216	134
Southwest Pacific	117	36	7	16	54	0.38	286	162	71	44

851   **Table 2.** Chao estimates of sample completeness for hydrothermal vent ecosystems in eight biogeographic provinces. T is the
852   total number of presence records, Q_1 is the number of observed singletons, Q_2 is the number of observed doubletons, t is the
853   total number of samples, F_{obs} is the observed number of families, g is the proportion of completeness. 1.0, 0.99, 0.9, and 0.8
854   are the relative completeness proportions from which the number of additional samples needed was inferred (as these values
855   represent potential research cruises, they are rounded up to the nearest whole number).

856   **FIGURE CAPTIONS**

857   **Figure 1.** Global distribution of deep-sea hydrothermal vents (yellow domes), ISA-issued high

858   seas mining exploration leases (red circles; note, bounding area is exaggerated for clarity), and

859   mining exploration licenses issued within territorial waters (pink circles; note, bounding area is

860   exaggerated for clarity). Black boxes indicate the member nations sponsoring claims in the area.

861   White borders in inset represent exclusive economic zones. Large circles represent each

862   biogeographic province for which sufficient data was available for analysis, in descending order

863   of number of research cruises conducted in the region: 1. Mid-Atlantic Ridge, 2. Northwest

864   Pacific, 3. Southwest Pacific, 4. Juan de Fuca Ridge, 5. Northern East Pacific Rise, 6. Mid-

865   Cayman Spreading Center, 7. Indian Ocean, and 8. Southern Ocean. The Arctic, Mediterranean,

866   and Southern East Pacific Rise biogeographic provinces are not indicated. Map prepared by

867   Andrew Middleton.

868

869   **Figure 2.** Distribution of suspected and active hydrothermal vents, biological research cruises,

870   vent fields in protected areas, and vent fields that fall within mining leases across the equator.

871

872   **Figure 3.** Family richness in the Northwest Pacific, Southwest Pacific, and Mid-Atlantic Ridge.

873   Parametric interpolation (solid line terminating in black dot) and non-parametric asymptotic

874   extrapolation (dashed line) with 95% confidence intervals (colored bounding areas). Color-coded

875   guide bars on far right correspond to 95% confident intervals at twice the reference sample.

876

877   **Figure 4.** Family richness in the Southern Ocean, Indian Ocean, and Mid-Cayman Spreading

878   Center. Parametric interpolation (solid line terminating in black dot) and non-parametric

879   asymptotic extrapolation (dashed line) with 95% confidence intervals (colored bounding areas).

880   Color-coded guide bars on far right correspond to 95% confident intervals at twice the reference

881   sample.

882

883   **Figure 5.** Family richness on the Northern East Pacific Rise and Juan de Fuca Ridge. Parametric

884   interpolation (solid line terminating in black dot) and non-parametric asymptotic extrapolation

885   (dashed line) with 95% confidence intervals (colored bounding areas). Color-coded guide bars

886   on far right correspond to 95% confident intervals at twice the reference sample.
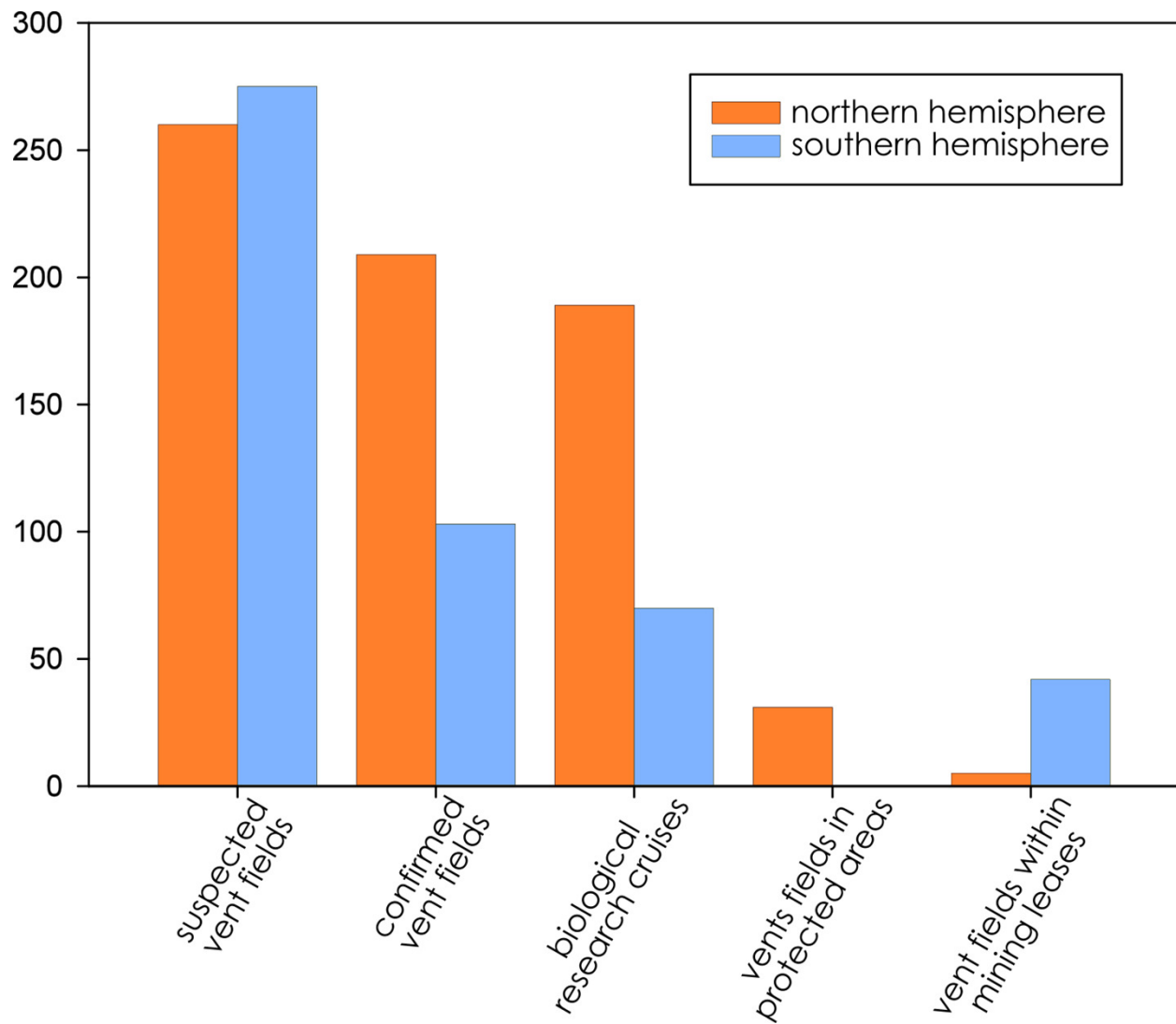
887

888 **Figure 6.** Family richness of all eight biogeographic provinces ranked by mean richness from

889 highest (left) to lowest) where all extrapolations reached asymptote. Bars represent extent of

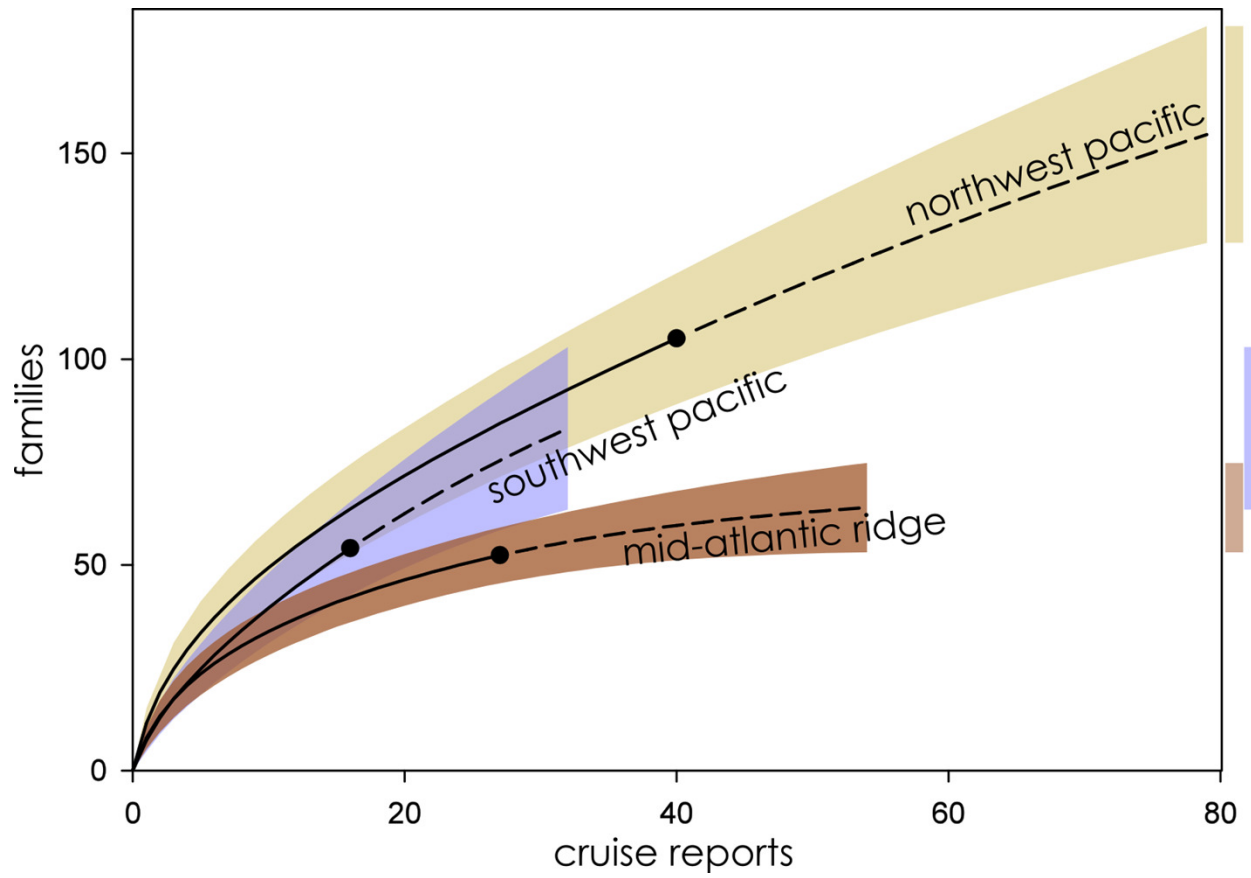890 95% confidence intervals.

891 **FIGURES**
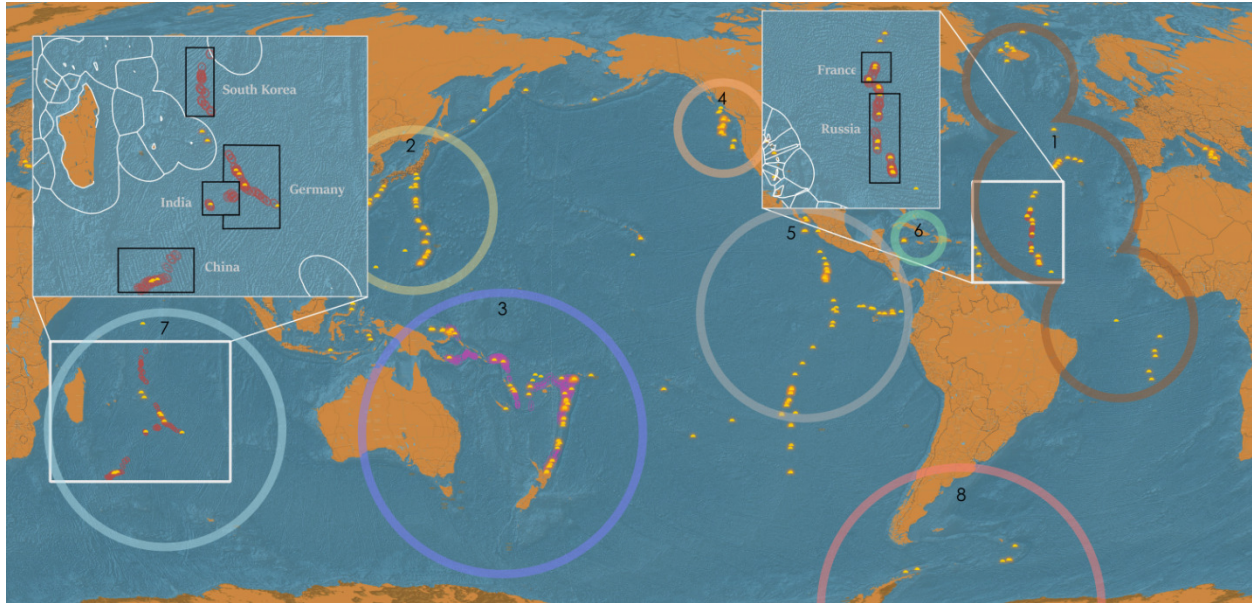
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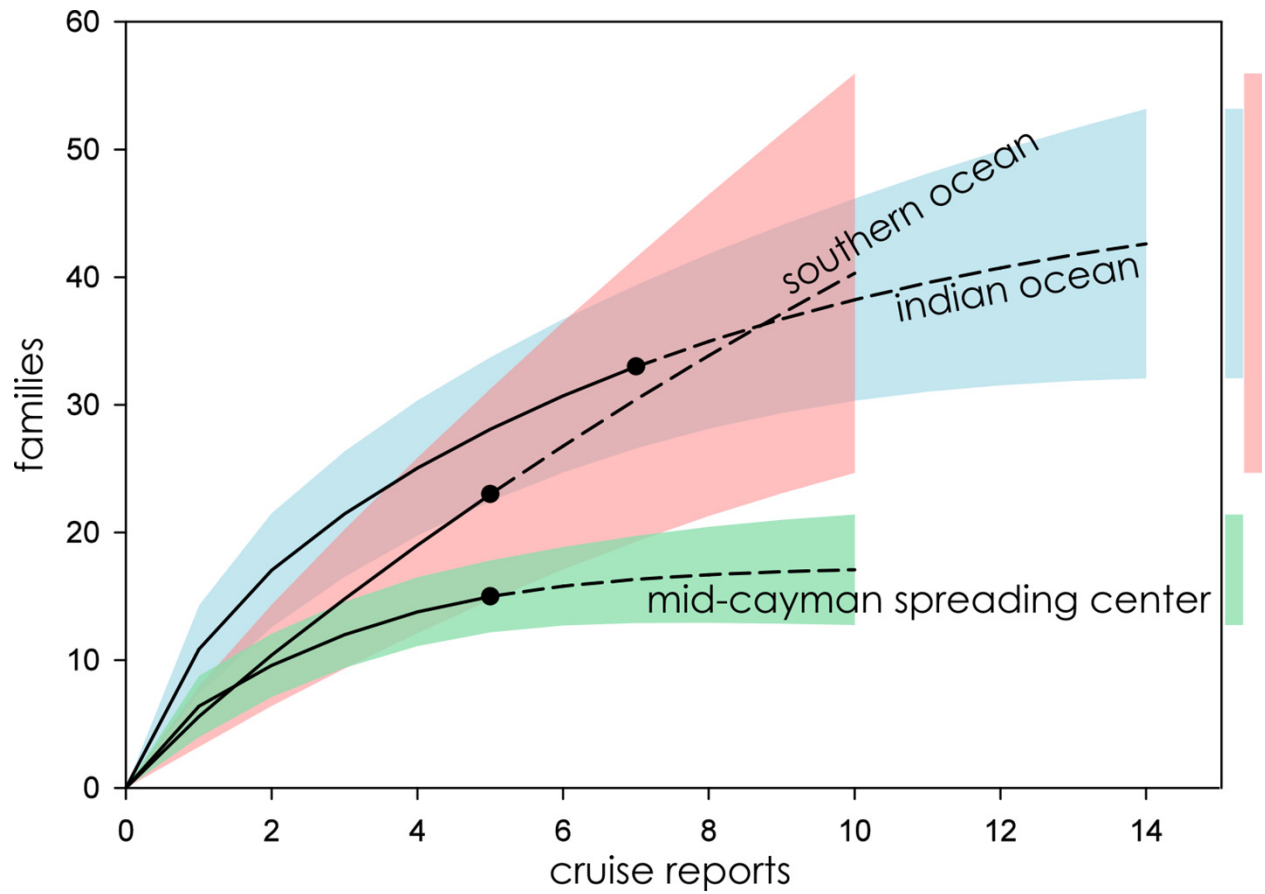893 **Figure 1.**
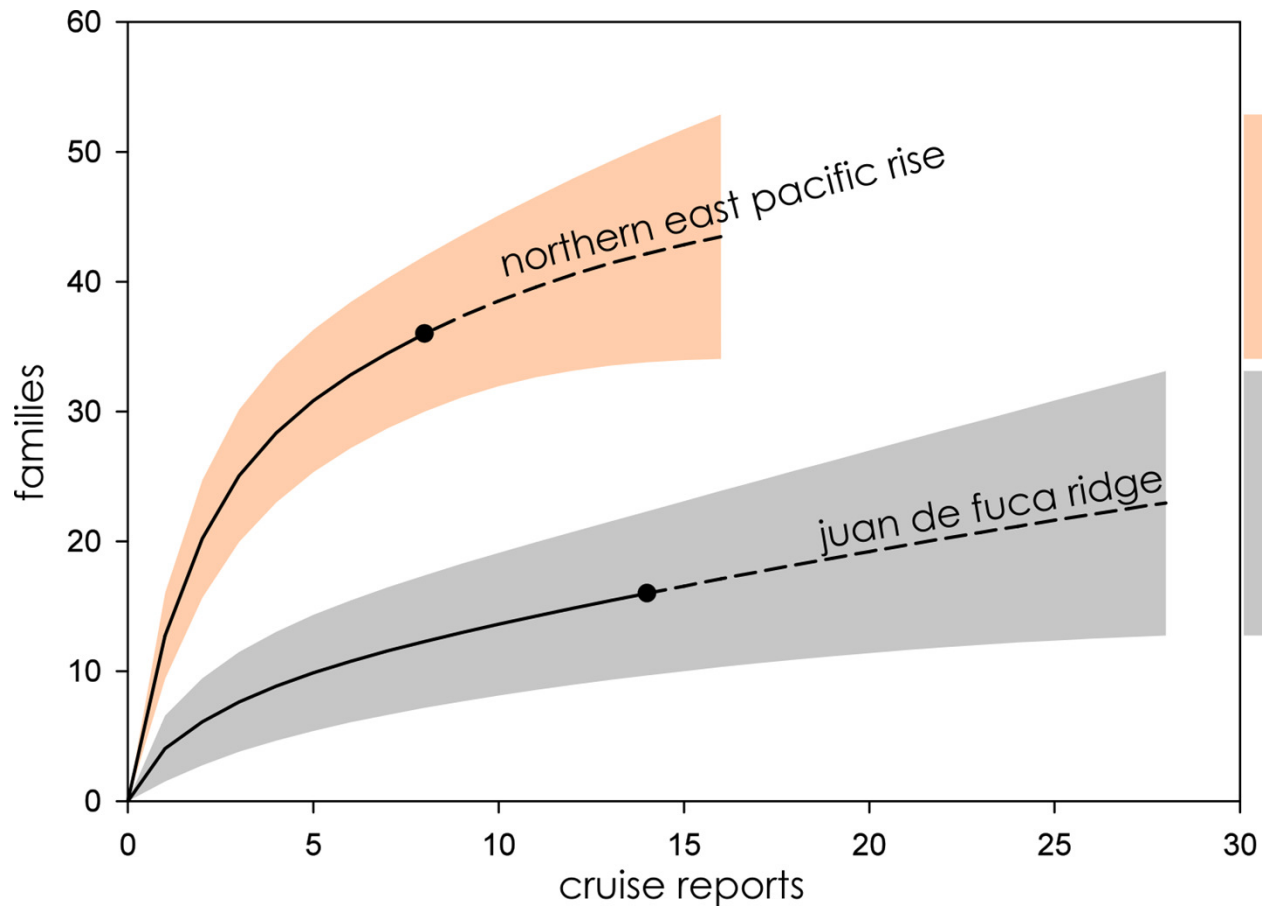
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896   **Figure 2.**

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901   **Figure 4.**

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904 **Figure 5.**

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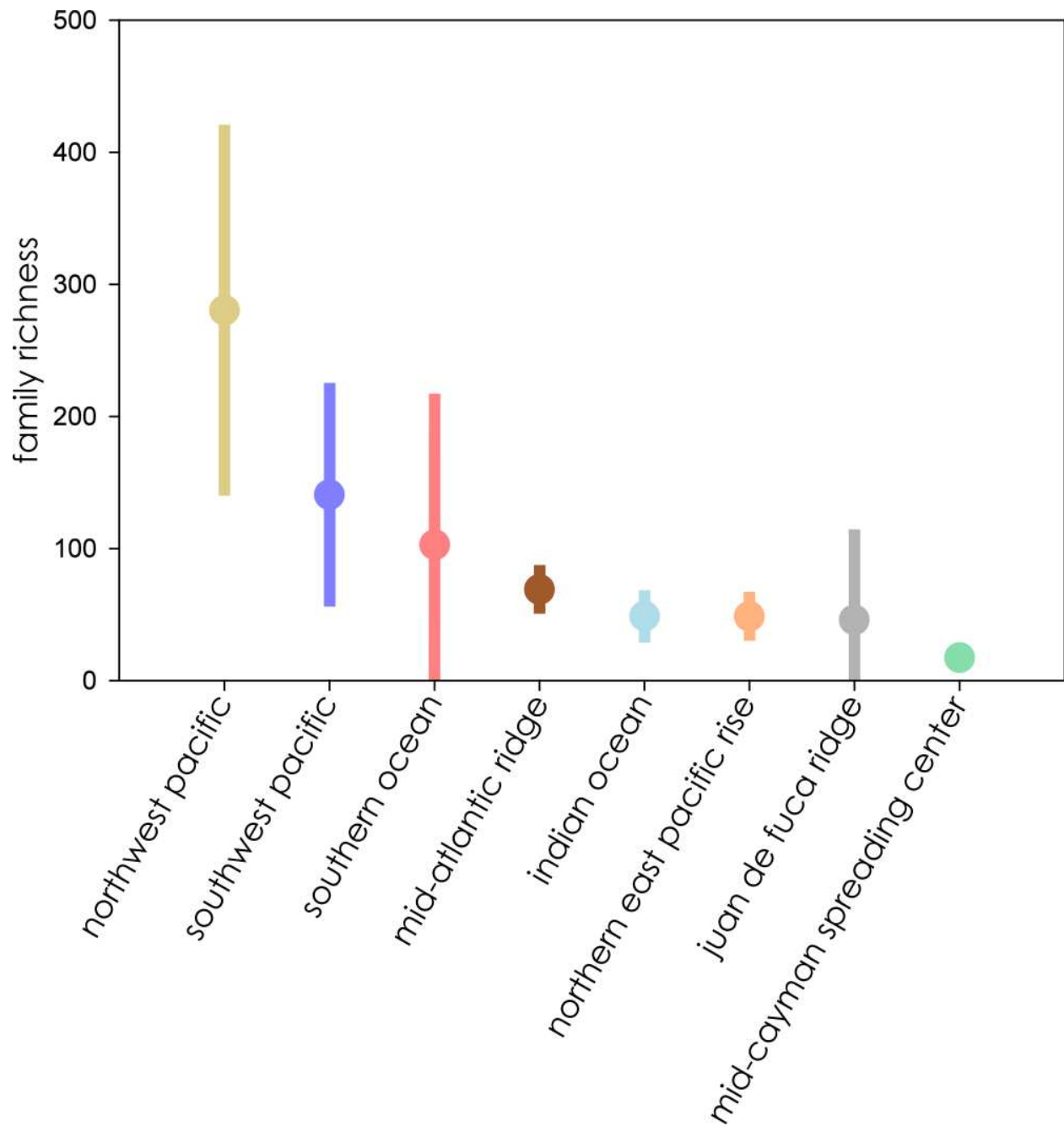
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907   **Figure 6.**

Figure 1

Global distribution of deep-sea hydrothermal vents, ISA-issued high seas mining exploration leases, and mining exploration licenses issued within territorial waters.

Global distribution of 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. MidCayman 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.
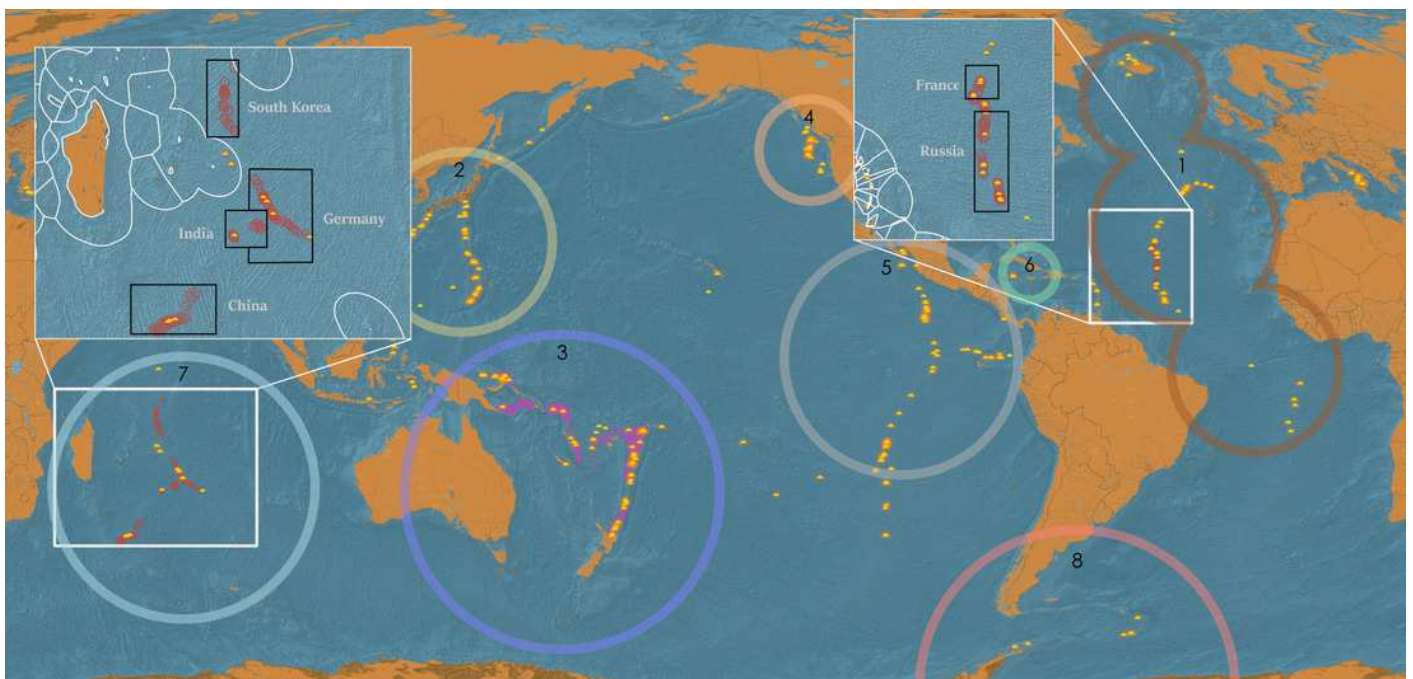
Figure 2

Distribution of suspected and active hydrothermal vents, biological research cruises, vent fields in protected areas, and vent fields that fall within mining leases across the equator.
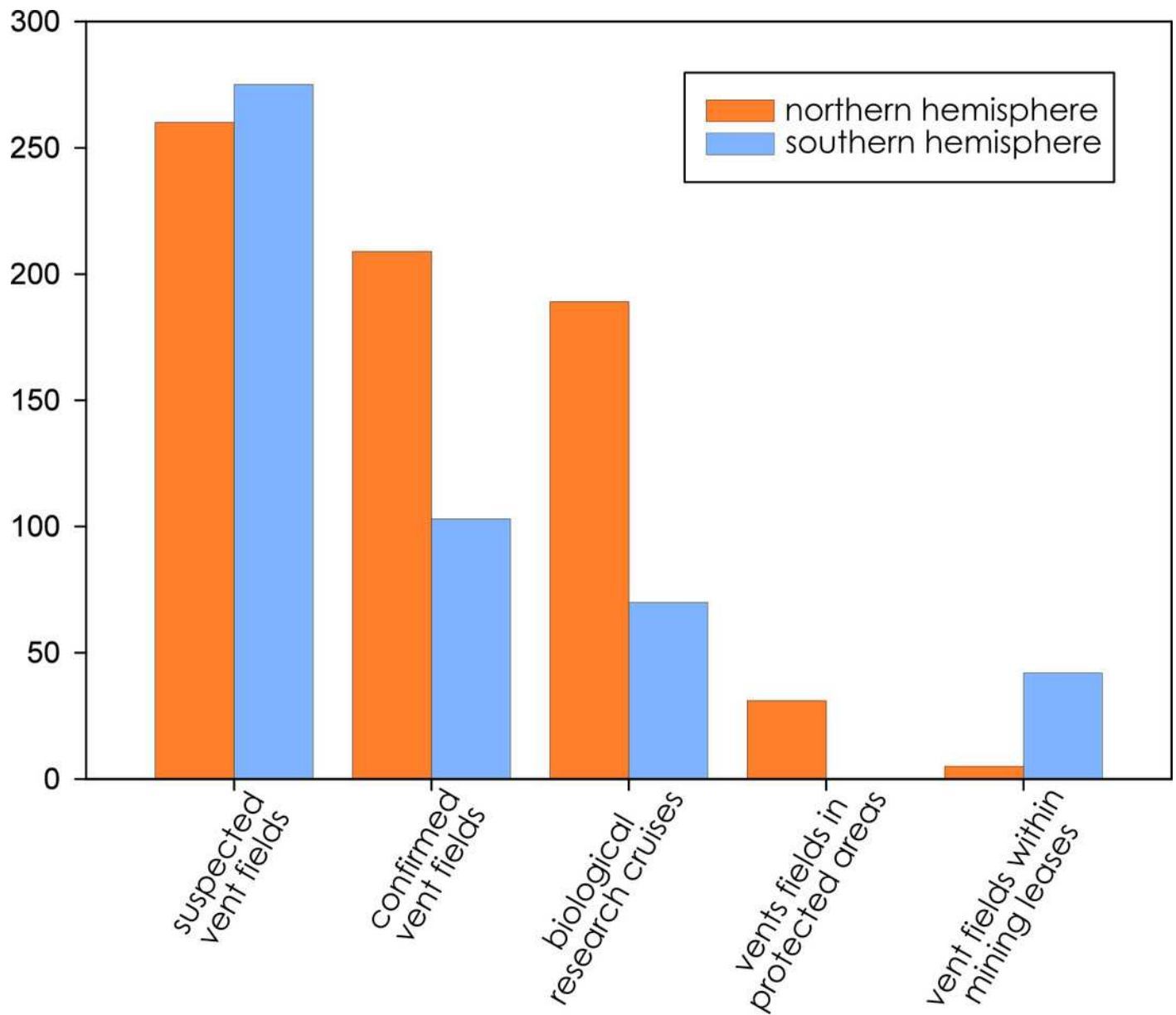
Figure 3

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
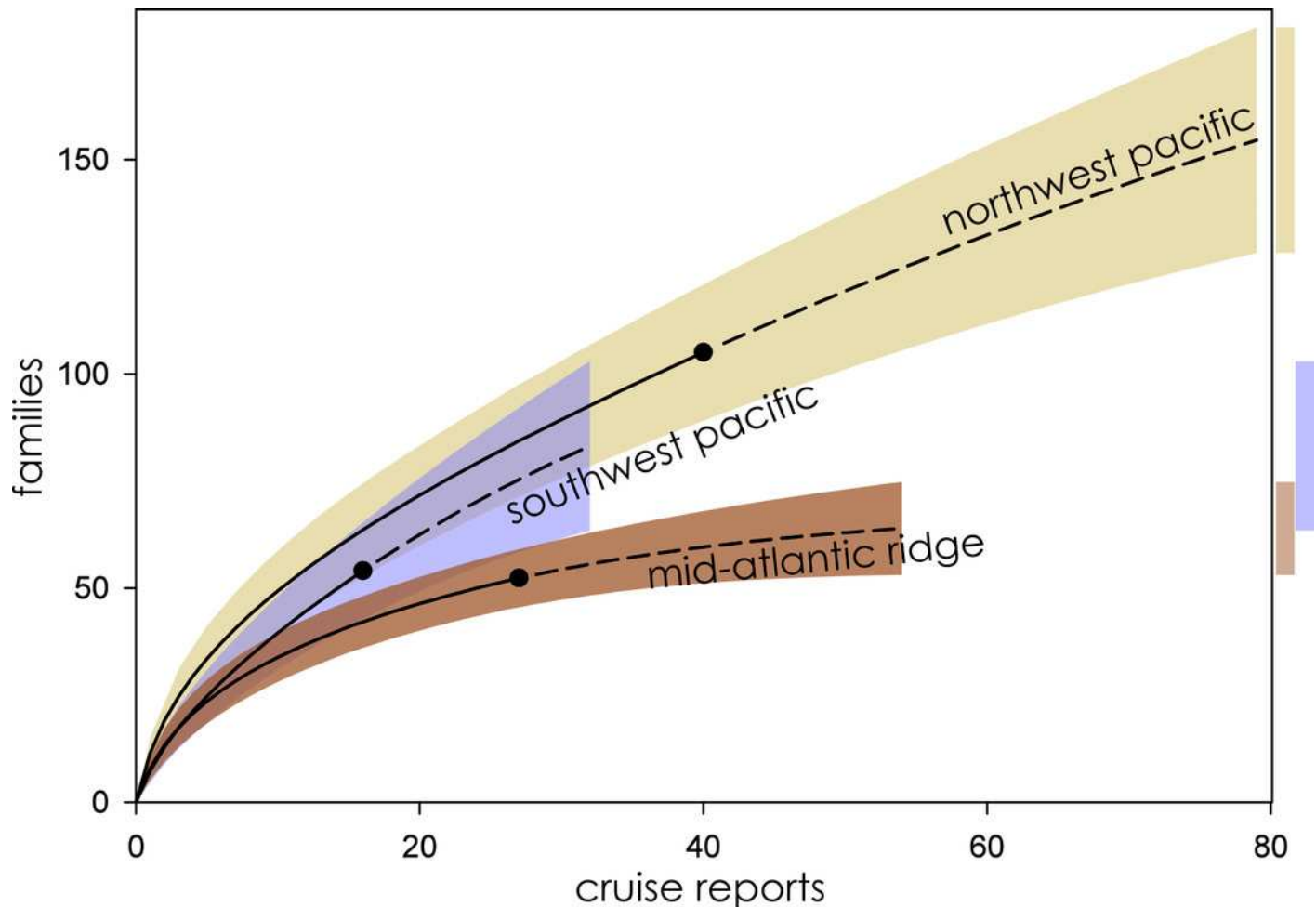
Figure 4

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
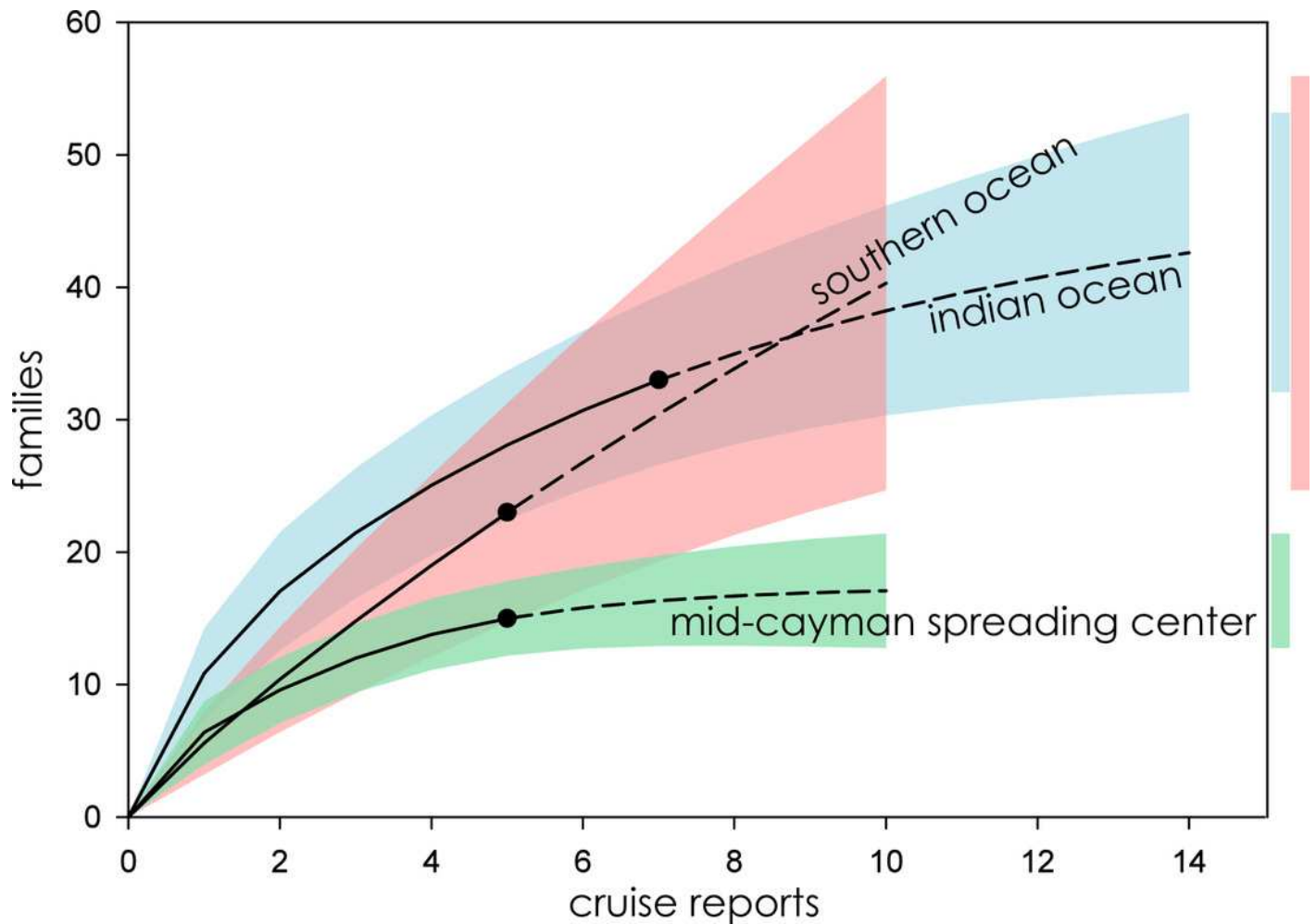sample.

Figure 5

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.
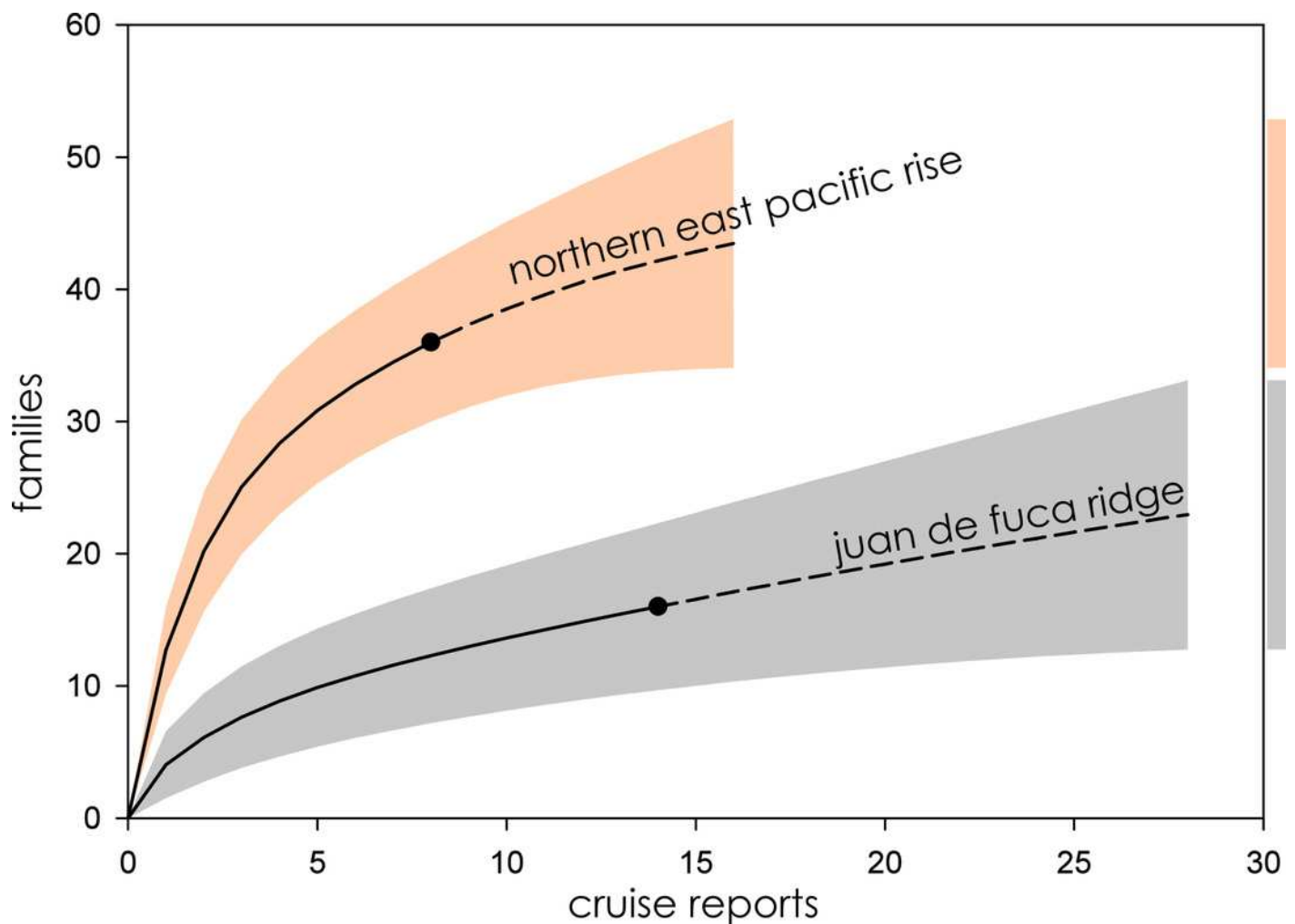
Figure 6

Family richness of all eight biogeographic provinces ranked by mean richness from highest (left) to lowest) where all extrapolations reached asymptote.

Bars represent extent of 95% confidence intervals.

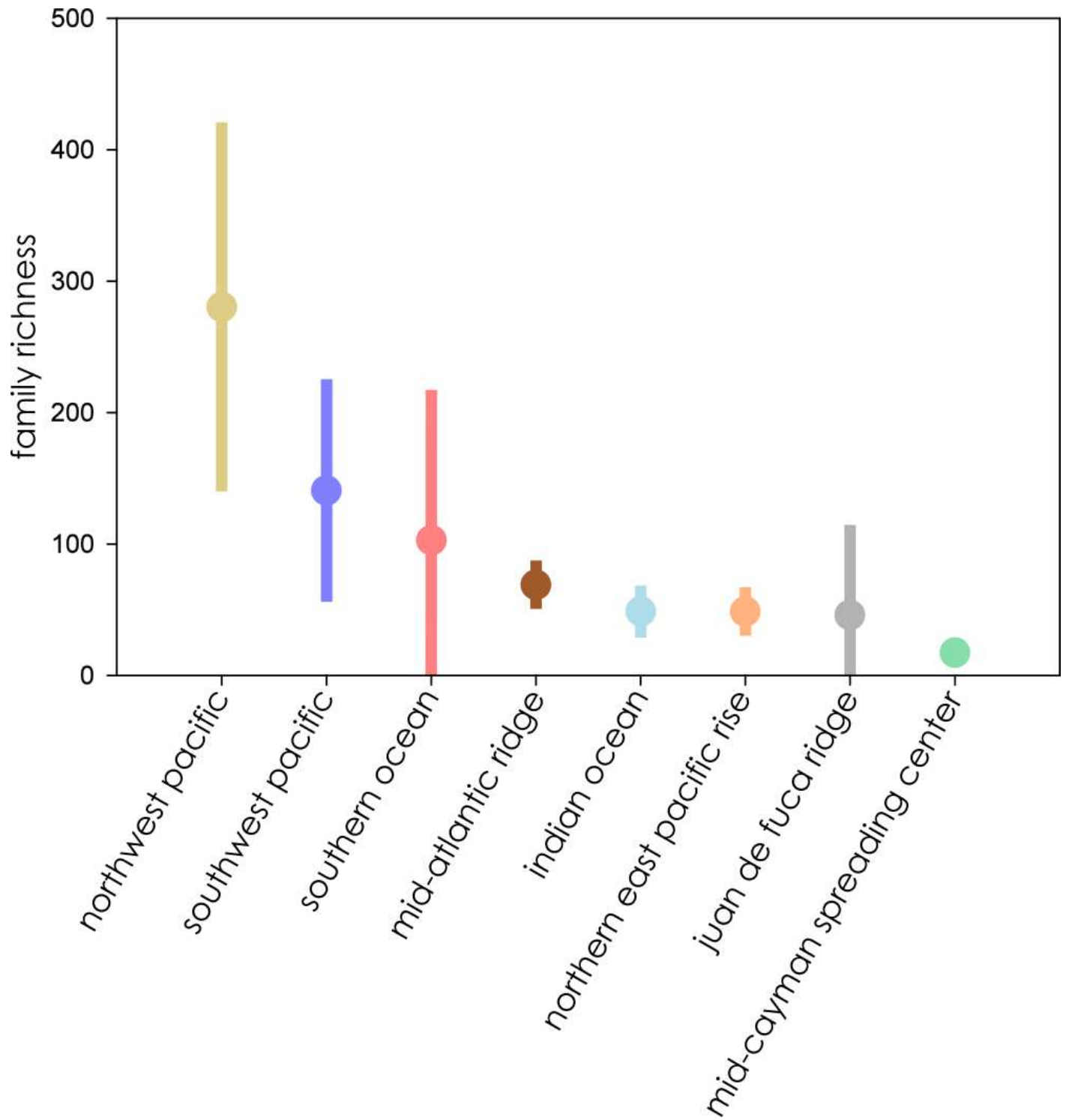# Table 1(on next page)

Summary of distribution of hydrothermal vent field, research effort, and families identified from cruise reports and databases by biogeographic province.

Confirmed Vent Fields, Vent Fields in EEZs, Vent Fields in High Seas, and Vent fields in Mining Leases from Beaulieu et al., (2013). ChEssBase accessed via Ocean Biogeographic Database System Ramirez-Llodra et al., (2005).

Biogeographic Province	Confirmed Vent Fields	Vent Fields in EEZs	Vent Fields in High Seas	Vent Fields in Mining Leases	Research Cruises	Available Cruise Reports	Families Sampled	ChEssBase Families
Arctic	8	8	0	0	2	0	-	1
Indian Ocean	13	3	10	10	16	7	33	6
Mediterranean	15	15	0	0	3	0	-	0
Mid-Atlantic Ridge	42	13	29	5	61	27	53	119
Mid-Cayman Spreading Center	2	2	0	0	8	5	16	0
Northeast Pacific (Juan de Fuca Ridge)	22	10	12	0	34	14	16	86
Northern East-Pacific Rise	48	19	29	0	31	8	36	104
Southern East-Pacific Rise	29	27	2	0	2	0	-	69
Southern Ocean	6	2	4	0	5	5	23	1
Northwest Pacific	58	56	2	0	54	40	106	55
Southwest Pacific	77	76	1	32	44	16	54	56

1   **Table 1.** Summary of distribution of hydrothermal vent field, research effort, and families identified from cruise reports and
2   databases by biogeographic province. Confirmed Vent Fields, Vent Fields in EEZs, Vent Fields in High Seas, and Vent
3   fields in Mining Leases from Beaulieu et al., (2013). ChEssBase accessed via Ocean Biogeographic Database System
4   Ramirez-Llodra et al., (2005).
5

Table 2(on next page)

Chao estimates of sample completeness for hydrothermal vent ecosystems in eight biogeographic provinces.

T is the total number of presence records, Q1 is the number of observed singletons, Q2 is the number of observed doubletons, t is the total number of samples, Fobs is the observed number of families, g is the proportion of completeness. 1.0, 0.99, 0.9, and 0.8 are the relative completeness proportions from which the number of additional samples needed was inferred (as these values represent potential research cruises, they are rounded up to the nearest whole number).

1

Biogeographic Province	T	Q_1	Q_2	t	F_{obs}	g	1.0	0.99	0.9	0.8
Indian Ocean	76	16	7	7	33	0.68	43	26	9	4
Mid-Atlantic Ridge	223	20	12	28	53	0.77	127	73	20	4
Mid-Cayman Spreading Center	32	6	6	5	15	0.86	11	7	1	-
Northeast Pacific (Juan de Fuca Ridge)	56	8	1	14	16	0.35	315	220	99	62
Northern East-Pacific Rise	102	12	5	8	36	0.74	49	29	9	3
Southern Ocean	28	20	2	5	23	0.22	150	90	43	28
Northwest Pacific	461	60	10	40	105	0.37	943	487	216	134
Southwest Pacific	117	36	7	16	54	0.38	286	162	71	44

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Table 2. Chao estimates of sample completeness for hydrothermal vent ecosystems in eight biogeographic provinces. T is the total number of presence records, Q_1 is the number of observed singletons, Q_2 is the number of observed doubletons, t is the total number of samples, F_{obs} is the observed number of families, g is the proportion of completeness. 1.0, 0.99, 0.9, and 0.8 are the relative completeness proportions from which the number of additional samples needed was inferred (as these values represent potential research cruises, they are rounded up to the nearest whole number).