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1 **Title** Highly structured populations of copepods at risk to deep-sea mining: integration
2 of genomic data with demogenetic and biophysical modelling

3

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25 **Abstract**

26

27 Copepoda is the most abundant taxon in deep-sea hydrothermal vents, where hard
28 substrate is available. Despite the increasing interest for seafloor massive sulphides
29 exploitation, there have been no population genomic studies conducted on vent
30 meiofauna, which are known to contribute over 50% to metazoan biodiversity at vents.
31 To bridge this knowledge gap, restriction site- associated DNA sequencing, specifically 2b-
32 RADseq, was used to retrieve thousands of genome-wide single nucleotide
33 polymorphisms (SNPs) from abundant populations of the vent-obligate copepod
34 *Stygiopontius lauensis* from the Lau Basin. SNPs were used to investigate population
35 structure, demographic histories, genotype-environment associations at a basin scale.
36 Genetic analyses also helped to evaluate the suitability of tailored larval dispersal models
37 and the parameterization of life history traits that better fit the population patterns
38 observed in the genomic dataset for the target organism. Highly structured populations
39 were observed on both spatial and temporal scales, with divergence of populations
40 between the north, mid and south of the basin estimated to have occurred after the
41 creation of the major transform fault dividing the Australian and the Niuafou'ou tectonic
42 plate (350 kya), with relatively recent secondary contact events (< 20 kya). Larval
43 dispersal models were able to predict the high levels of structure and the highly
44 asymmetric northward low-level gene flow observed in the genomic data. These results
45 differ from most studies conducted on megafauna in the region, elucidating the need to
46 incorporate smaller size when considering site-prospecting for deep-sea exploitation of
47 seafloor massive sulphides, and the creation of area-based management tools to protect
48 areas at risk of local extinction, should mining occur.

49 **Keywords:** Hydrothermal vents, copepods, connectivity, demography, larval dispersal
50 modelling, deep-sea mining

51

52 **Author Contributions:** **Coral Diaz-Recio Lorenzo:** design of the project, DNA
53 extractions, library preparation, data analyses, writing of draft manuscript; **Adrien Tran**
54 **Lu Y:** demographic modelling, contribution to draft manuscript; **Otis Brunner:** larval
55 dispersal modelling, contribution to draft manuscript, **Stefan Laurent:** supervision of
56 population genomic analysis, revision of draft manuscript, **Pedro Martinez Arbizu:**
57 providing resources (training and consumables) for library construction, revision of draft
58 manuscript, **Didier Jollivet:** providing of samples, revision of draft manuscript, **Sabine**
59 **Gollner:** design of the project, revision of draft manuscript.

60

61

62 **1. Introduction**

63 Genetic connectivity is essential in maintaining diversity and promoting the evolution of
64 marine organisms, and depends on factors such as dispersal ability, reproductive traits,
65 seafloor topology, and environmental conditions (De Wit et al., 2023; Blanchard and
66 Gollner, 2022; Virtanen et al., 2020; Brunner et al., 2023; Pereira et al., 2023; Portanier et
67 al., 2023; Yahagi et al., 2017; Ingels et al., 2023; Mouchi et al., 2023; Plouviez et al., 2013;
68 2019; Faria et al., 2021; Antich et al., 2022). High dispersal ability promotes gene flow
69 over long distances, while seafloor topology can create physical barriers that impede
70 movement and lead to allopatric speciation (Yahagi et al., 2017; Plouviez et al., 2013;
71 2019; Ingels et al., 2023). Additionally, environmental factors such as temperature,
72 salinity, and oxygen concentrations influence species distribution, potentially resulting in

73 local adaptation, and ultimately sympatric speciation (Virtanen et al., 2020; Faria et al.,
74 2021; Antich et al., 2022).

75

76 Deep-sea hydrothermal vents, found along Mid Ocean Ridges (MORs) and Back-Arc Basins
77 (BABs), support diverse meta-communities of mega-, macro-, and meiofauna (Mullineaux
78 et al., 2018) that exhibit deeply entwined interactions across organismal groups. The
79 community composition, succession, functional importance, and connectivity of
80 hydrothermal vent mega- and macrofauna has been explored since hydrothermal vents
81 were discovered in 1977. Recently, hydrothermal vent meiofauna has gained interest due
82 to their potentially important role in the food web (limen et al., 2007;2008; Nomaki et al.,
83 2023), broad horizontal range of vent-endemic genera (Gollner et al., 2011;2016) and the
84 ability of non-vent-endemic genera to adapt to an unprecedented range of hydrothermal
85 vent conditions (Nomaki et al., 2019; Nakasugi et al., 2021). Understanding the genetic
86 connectivity of smaller size classes in these habitats is crucial due to their ephemeral
87 nature and potential to create isolated populations at risk of local extinctions despite
88 observed gene flow among populations along fast and slow spreading MORs (Craddock et
89 al., 1995; Jollivet et al., 1995; Won et al., 2003; Hurtado et al., 2004; Mullineaux et al., 2010;
90 Bweedessee et al., 2013; Gollner et al., 2011; 2016; Breusing 2015, 2016; Teixeira et al.,
91 2011, 2012; Breusing et al., 2016; Yahagi et al., 2019; Yearsley et al., 2020; Perez et al.,
92 2021). The life history strategies of organisms in these environments are adapted to
93 volcanic eruptions, exhibiting R-strategist survival mechanisms characterized by rapid
94 growth, early maturation, high fecundity, and dispersal capabilities (Van Dover et al.,
95 2014). Recent studies have explored the demographic history of vent megafauna
96 populations in BABs, revealing contrasting dispersal strategies (Thaler et al., 2014;

97 Plouviez et al., 2019; Breusing et al., 2021; Tran Lu Y et al., 2021; Poitrimol et al., 2022).
98 However, there is currently no research on the genomic connectivity of the meiofauna
99 (animals between 32 μm and 1mm in size), in particular the Dirivultidae family of
100 copepods, which thrives on hard substrates and hydrothermal vents (Figure 1, inset).

101

102 The Dirivultidae (Siphonostomatoida) exist in the tens to hundreds of thousands of
103 individuals per vent wherever basalt rock, hard-shelled megafauna assemblages, or
104 patches of dead organisms creating landscapes of exoskeletons exist (Gollner et al.
105 2010;2016; Diaz-Recio Lorenzo et al., 2021). The Dirivultidae (Siphonostomatoida)
106 contains at least 80 described species that have adapted to vent environments,
107 dominating areas of high temperatures with high concentrations of hydrogen sulphide
108 and low oxygen levels where they feed predominantly on chemoautotrophic bacteria
109 (Gollner et al., 2016, Nomaki et al., 2019; 2023; Watanabe et al., 2021; Diaz-Recio Lorenzo
110 et al., 2021; Nakasugi et al., 2021). They have a lecithotrophic developmental mode and
111 likely disperse via hydrothermal plumes, settling as vent-obligate adults. Species of this
112 family exhibit large population sizes, high levels of mitochondrial gene diversity, and
113 demographic analysis of the latter has shown that the vast majority of Dirivultidae species
114 are undergoing population expansion (Gollner et al., 2016; Watanabe et al., 2021, Diaz-
115 Recio Lorenzo et al., 2023).

116

117 During the last decade, Next-Generation Sequencing technology significantly increased
118 the possibility of obtaining large genomic datasets. However, genome-scale population
119 genetic studies have focused mostly on flagship systems and organisms. Restriction-site
120 associated DNA sequencing (RAD-seq) has been widely applied as an alternative to obtain

121 meaningful genome-wide information in the form of Single Nucleotide Polymorphisms
122 (SNPs) and in particular, 2b-RAD (Wang et al., 2012) has the ability to target a large
123 number of markers throughout the genome of non-model organisms. This information
124 has now widely been applied to non-model organisms to address question about
125 contemporary population structure as well as how populations separated and
126 reconnected through time, by modeling the effect of migration and population growth on
127 genetic divergence (Gutenkunst et al., 2009; Excoffier et al., 2013; Rougeux et al., 2017;
128 De Jode et al., 2022).

129
130 The mining of polymetallic seafloor massive sulphides (SMS) poses the most significant
131 threat to hydrothermal vent communities, resulting in short- and long-term damage,
132 including changes in vent fluid strength and chemistry, toxic plumes, habitat removal,
133 fragmentation, and biodiversity loss (Blasiak et al., 2020; Drazen et al., 2020; Gollner et
134 al., 2017, 2021; Levin et al., 2020; Miller et al., 2018; Van Dover et al., 2018; Blanchard and
135 Gollner, 2022). The impacts of this damage may extend beyond the vent realm (Blanchard
136 and Gollner et al., 2022). Back-arc basins in the western Pacific contain high-grade SMS
137 deposits, with historical exploration tenement blocks issued by some island states
138 (Petersen et al., 2016; Du Preez and Fisher, 2018). However, certain Pacific Island states
139 have imposed a 10-year moratorium on mining activities to understand the
140 environmental and societal impacts better (Kakee, 2020). Advancing our understanding
141 of population connectivity across species size fractions, incorporating life-history traits,
142 evolutionary adaptations, larval dispersal modeling, and demographic modeling, can
143 contribute to defining the vent transition zone and determining the size and location of
144 Area-Based Management Tools (ABMTs) (Blachard and Gollner, 2022).

145

146 The resilience of hydrothermal vent meta-communities depends on the dispersal and
147 colonization abilities of organisms, which play a crucial role in their ability to adapt and
148 survive (Mullineaux et al., 2018). Previous studies have focused on modeling the dispersal
149 ability of a subset of vent fauna to identify isolated populations at risk of local extinction
150 from human disturbances (Mitarai et al., 2016; Breusing et al., 2021). However, these
151 models have primarily considered megafaunal dispersal behavior, which differs
152 inherently from the meiofauna due to variations in energy costs associated with their size
153 differences (Gollner et al., 2015). This study aims to investigate the demographic
154 connectivity of the copepod *Stygiopontius lauensis*, the most abundant deep-sea
155 hydrothermal vent animal in the Lau basin. By utilizing genomic markers across four vent
156 sites, we examine contemporary population structure, the relationship between genomic
157 variation and environmental factors, and the demographic history between populations.
158 Additionally, we assess the effectiveness of tailored larval dispersal models in predicting
159 connectivity between nearby and distant vents within the Lau basin. This multifaceted
160 approach allows for the identification of source and sink populations, and those most at
161 risk to the impacts of deep-sea mining.

162

163 **2. Materials and Methods**

164 ***2.1 Sampling***

165 Organisms were collected in 2016, and 2019 during the FK160407 aboard the R/V Falkor
166 (Charles and Peter, 2016: <https://doi.org/10.7284/906664>) and the Chubacarc
167 expedition aboard the R/V L'Atalante (Hourdez and Jollivet, 2019:
168 <https://doi.org/10.17600/18001111>) to the Southwest Pacific back-arc basin system.

169 During expedition FK160407 samples were collected using the remotely operated vehicle
170 (ROV) ROPOS, using scoops and slurp guns from *Alviniconcha* and *Ifremeria* megafaunal
171 assemblages at the vent fields Tui Malila, ABE, and Tahī Moana. During the Chubacarc
172 expedition aboard L'Atalante, samples were obtained using the ROV Victor 6000 using
173 slurp guns from *Alvinichoncha* megafaunal assemblages at the Tu'i Malila, ABE, and
174 Mangatolo vent sites (Figure 1, Table 1). Megafaunal collections were processed on board
175 of the ship as followed: Copepods were washed off from the megafauna and retained on a
176 32µm sieve. Copepods collected in 2016 were fixed in 96 % Ethanol, samples collected in
177 2019 were fixed in 99.9 % EtOH. Copepods were identified first to family level
178 (Dirivultidae), and then identified morphologically to species using taxonomic keys
179 described by Gollner et al. (2010). The most abundant species, namely *Stygiopontius*
180 *lauensis* was chosen for this study.

181

182 **2.2 Library preparation and sequencing**

183 All samples were given three consecutive ethanol baths to remove potential external
184 contaminants before DNA extraction. Extractions from whole specimens were carried out
185 using the E.Z.N.A.® Mollusc DNA Kit (omega BIO-TEK). 2µl of DNA extract were used to
186 amplify the cytochrome C oxidase, subunit I (COI) gene, using the universal Folmer
187 primers (Folmer et al., 1994) LCO1490 (5'GGTCAACAAATCATAAAGATATTGG'3), CO2198
188 (5'TAAACTTCAGGGTGACCAAAAAATCA'3), M13 tails M13F-pUC (-40)
189 (5'GTTTTCCAGTCACGAC'3), M13R-pUC (-40) (5'CAGGAAACAGCTATGAC'3). PCR cycle
190 conditions were initial denaturation for 3 minutes at 94°C followed by 40 cycles of
191 denaturation at 30 seconds for 94°C, annealing for 45 seconds at 45°C and extension for
192 45 seconds for 72°C and a final extension for 2 minutes at 72°C. Samples were sequenced

193 with Macrogen Europe. *Cox1* was chosen as a species delimiter due to its conserved nature
194 between species, and specimens that did not match at least 98% with *S. lauensis* when
195 blasting COI sequences against the NCBI database were not included in the library. Out of
196 168 specimens barcoded, 149 matched at least 98% with *S. lauensis* and were used to
197 construct the 2b-RAD libraries.

198

199 The library was constructed using a custom index array, and the enzyme *bgcl*. DNA
200 extraction and library preparation was conducted at the Senckenberg Institute/German
201 Center for Marine Biodiversity Research (DZMB). 2b-RAD was chosen due to the ability of
202 type IIb enzymes to find a large number of restriction sites across the genome that are not
203 error prone and the type IIb restriction enzyme *bgcl* was used due its simplistic
204 laboratory usage. DNA was digested, shearing DNA upstream and downstream of a
205 recognition site, resulting in fragments of a uniform size of 32 bp (Wang et al., 2012).
206 Population-specific and individual-specific barcodes were ligated to the fragments in
207 order to multiplex a large number of individuals, reducing the number of runs and
208 subsequent costs. Adapter-ligated fragments were then amplified using the Fusion2X
209 master mix, with 2X 20 cycles until 2 clear bands were visible, one containing non-ligated
210 adapter, and a second, longer (by 32 bp) fragment containing the RAD sequence with a
211 total fragment length of 182 bp. The longer fragments were cut from the gel and purified
212 using the Monarch® Genomic DNA Purification Kit (New England Biolabs). Paired-end
213 150-bp sequencing (400 million clusters) was conducted on an Illumina Nextseq500
214 platform at the University Medical Centre of Utrecht University (UMC) on samples from
215 2016. After processing samples from 2019, paired-end 150-bp sequencing (1 billion

216 clusters) was conducted on an Illumina Nextseq2000 platform at UMC. Samples were
217 demultiplexed by UMC.

218

219 ***2.3 De novo 2b-RAD-tag assembly, filtering, and SNP-calling***

220 The *STACKS2.6* software module *process_radtags* (Rochette et al., 2019) was used to
221 further demultiplex samples by the adapters used to delimit the populations, remove
222 inline barcodes, and remove PCR duplicates. All reads had a sequence length of 32bp, a
223 characteristic of 2b-RAD sequencing using the enzyme *bcgl*, that removes bias introduced
224 from having to truncate reads to a uniform length. A total of 149 samples were
225 successfully sequenced, with a mean coverage of 25 X. Samples with read depth of <5 and
226 >80 were removed. Initial exploration of the data was conducted to observe outliers, and
227 overall structure. This was done by comparing classic multivariate analyses that visualize
228 data under reduced dimensions such as Principal Component Analysis (PCA), non-metric
229 Multidimensional Scaling (nMDS) and Uniform Manifold Approximation and projection
230 (UMAP), combined with spectral clustering, to visualize population structure.

231

232 *S. lauensis* lives in vent environments containing a high abundance of chemoautotrophic
233 bacteria that they also feed on (Limen et al. 2007;2008; Nomaki et al. 2019). Due to the
234 small size of copepods, the entire specimen was used during the extraction to ensure
235 sufficient quantities of pure DNA for digestion and adapter ligation during library
236 preparation. It is therefore likely that some of the RAD tags retrieved may not belong to
237 the copepod genome. RADs created with 2b-RAD are too small to be blasted against
238 existing databases as a quality control method to eradicate non-copepod DNA. Although
239 still under debate, significant correlations have been found between GC content and

240 growth temperature in thermophilic prokaryotes (Hu et al. 2022). GC pairs have an
241 additional hydrogen bond than AT pairs, and GC-rich genomes are expected to provide
242 additional stability to the DNA double-helix under high temperatures. For this reason,
243 RADs belonging to those samples were filtered for GC content higher than 50 % as an
244 extra quality control step.

245

246 We used the SNP calling software *DiscoSnpRAD* (Gauthier et al. 2020) for SNP discovery
247 and genotyping for RAD-seq data, which uses a k-mer based approach, implementing the
248 construction of de Bruijn graphs to find bubbles of SNPs without the loss of too much data
249 and without the need for a reference genome. In *DiscoSnpRAD*, the variable parameter is
250 the length of the k-mer. This was tested with lengths between 5 and 31. An optimal k of
251 15 was chosen, as this resulted in a Variant Calling File (VCF) with the highest number of
252 called SNPs. SNPs were then clustered by loci using the provided post-processing scripts
253 from *DiscoSnpRAD*. Missing data is a common characteristic of RADseq data however
254 studies have highlighted that removing this data could lead to loss of valuable information
255 (Chattopadhyay et al., 2014; Eaton et al. 2016; Tripp et al. 2017; Crotti et al. 2018). Such
256 studies have also reported that setting too conservative parameters leads to detrimental
257 loss of information and that *de novo* SNP calling should be less stringent. Missing data
258 cutoffs were therefore set to 0.5. This method was compared to the classic SNP calling
259 *STACKS2* software and results are available in supplementary information (S1, figures 1
260 and 2).

261

262

263

264 **2.4 Outlier detection for structure analyses**

265 Loci under selection are expected to behave differently from neutral loci in terms of
266 population-related patterns of diversification and are thus typically removed from the
267 global dataset in population genomics studies for investigation of geographic structure
268 (Beaumont and Nichols, 1996; Luikart et al. 2003; Holderegger and Wagner, 2006; Foll
269 and Gaggiotti, 2008; Whitlock and Lotterhos, 2015; Benestan et al. 2016; François et al.
270 2016; Gagnaire and Gaggiotti, 2016; Dalongeville et al. 2018). However, some studies have
271 used outliers to investigate subtle geographic breaks in populations when local
272 adaptation is not overcome by migration (Milano et al., 2013; Araneda et al., 2016; Dorant
273 et al., 2022; Tran Lu Y et al., 2021). Outliers were identified using four different methods.
274 Firstly, the population based *Bayescan v.2.1* (Foll and Gaggiotti, 2008) was used to identify
275 markers deviating significantly from distributions of F_{st} values across all loci (alpha =
276 0.05) corrected for false positives using q -values (*qvalue v.2.3.0*, Storey et al. 2003).
277 Secondly, *Arlequin v.3.5.2.2* (Excoffier & Lischer, 2010), was used to identify outlier SNPs
278 based on F_{st} values calculated over all the loci, the p -values of which were significantly
279 different from the mean (alpha = 0.05). Thirdly, the individual based *PCAdapt v.4.3.3* (Luu
280 et al. 2017) was used to look for loci that are atypically (i.e., not geographically) related to
281 population structure as measured by latent factors also corrected for with q -value cutoffs.
282 A Venn diagram was created to visualize the intersection of outliers detected by all
283 methods software.

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2.5 Population structure and diversity

The *SNPRelate* package Zheng et al. (2012) in R v.4.2.3. was used to calculate the minor allele frequencies which were converted into distance matrices for use with dimension-reducing analysis as well as for calculating Identity by State (IBS). Non-metric Multidimensional Scaling (nMDS) was used to visualize the genomic structure of populations. This was compared to other methods to check whether structure was preserved across different dimension reducing techniques such as PCA and Uniform Manifold Approximation and Projection (UMAP), a non-linear dimension-reducing technique that preserves a global structure whilst revealing hidden or complex non-linear features in genomic data (Diaz-Papkovich et al. 2019; 2020). The latter was paired with Monte Carlo Reference-based Consensus Clustering (*MCRCC*) v.1.2.0 (John et al., 2020) to obtain statistics for the optimal number of genetic clusters (S2, figure 2). *ADMIXTURE* v.1.3.0 (Alexander and Lange, 2011) was used to assign ancestry to each individual based on cross validation error, where the lowest cross validation value denotes the optimal number of clusters. Analysis of Molecular Variance (*AMOVA*, Excoffier et al. 1992) was conducted in *Arlequin* v.3.5.2.2 (Excoffier & Lischer, 2010) to check for significant differences between and within populations (10,000 permutations, missing data cutoff = 20%), as well as to obtain statistics for pairwise fixation indices (F_{st}). Nucleotide diversity (π) was calculated with the population module of *STACKS2* using all sites from all 2b-RAD-tags (S1, table 1). Observed heterozygosity was calculated using the *vcfR* package (Knaus et al., 2017) in R.

312 **2.7 Demogenetic connectivity**

313 Population history reconstruction was conducted to investigate demogenetic
314 connectivity. This was done using a modified version of $\partial a\partial i$ that uses a dual annealing
315 optimization function in the diffuse approximation to simulate and optimize the joint
316 allele frequency of pairs of populations under different demogenetic scenarios (scripts
317 can be found at ([https://github.com/Atranluy/Scripts-
318 Ifremeria/tree/Main/Dadi_scripts](https://github.com/Atranluy/Scripts-Ifremeria/tree/Main/Dadi_scripts)). Modeling was performed using the observed folded
319 joint allele frequency spectrum (JAFS) on pairs of populations that had an F_{st} value equal
320 to or greater than 0.1. Twenty eight demographic models, described in Rougoux et al.
321 (2017), were simulated ranging from a low to a high complexity of population parameters
322 (S9, figure 9). The models include strict isolation (SI), isolation with migration (IM),
323 ancient migration (AM), and secondary contact (SC), derived from an ancestral population
324 of N_{anc} size that split into two daughter populations of sizes N_1 and N_2 with or without
325 demographic changes. The size of the ancestral populations is calculated as follows:

326

327
$$N_{anc} = \frac{\theta_{anc}}{4 * \mu * L}$$

328

329 Where μ , represents the mutation rate per site and generation and L represents the total
330 length of the DNA sequence used in $\partial a\partial i$:

331

332
$$L = \frac{z * y * 32}{x},$$

333

334 where x represents the initial total number of SNPs that were detected on y loci of 32
335 bp; and z represents the number of SNPs used in the $\partial a \partial i$ analyses (see Tran Lu Y et
336 al., 2022). Time (in years) of divergence (T_{div}) in the SC model was then calculated as:

337

$$338 \quad T_{div} = \frac{2N_{anc} (T_s + T_{sc})}{33},$$

339

340 where T_s represents the time (in generations: Time in coalescent units multiplied by
341 $2N_{anc}$) from the secondary contact to the initial split between the populations, T_{sc}
342 represents the time (in generations: : Time in coalescent units multiplied by $2N_{anc}$)
343 from present to the secondary contact, and 33 in the number of generations per year.
344 A mutation rate of 10^{-9} was used, based on updated reports of genomic substitution
345 rates vs mutation rates for the crustacea including the Copepoda (Thomas et al., 2020).
346 Statistics pertaining to each parameter were computed with each run, and those
347 computed for the best model are reported. The uncertainty of the parameters of the
348 best model computed by $\partial a \partial i$ was realized using the Fisher information matrix (FIM),
349 considering our markers independent. FIM uncertainty was achieved with an epsilon
350 = 0.001 from which all standard deviations and subsequent confidence intervals were
351 calculated. Effective Population Size (N_e) was calculated using the formula:

352

$$353 \quad N_e = Nu * b * N_{anc},$$

354

355

356 where Nu refers to the daughter population size and b represents the growth factor
357 during population size change. Migration rates (M_{ij} : number of migrants exchanged
358 per generation as calculated by $\partial a \partial i$ in coalescent units), were calculated as follows:

359

$$360 \quad M_{ij} = (Nu * b * m_{1 < -2})/2,$$

361

362 Where $m_{1 < -2}$, is the migration rate from population 2 to population 1.

363

364 ***2.8 Suitability of larval dispersal models in predicting empirical patterns of*** 365 ***gene flow in genomic datasets***

366 To investigate the direction and relative strength of migration between different
367 localities, we generated migration networks using the *divMigrate* function (Sundqvist et
368 al., 2016) from the R package *diveRsity* (Keenan et al., 2013) under the null hypothesis of
369 an n-islands model without demographic changes. We used the relative number of
370 migrants (Nm) to infer directional gene flow as an index between 0 and 1, where 0
371 indicates almost no migrants/generation, and 1 indicates one migrant/generation being
372 transported from population A to population B (Sundqvist et al., 2016). Significant
373 asymmetry was calculated by resampling with 1,000 bootstraps. Migration was calculated
374 as a relative value, by comparing either G_{st} of Joost's D estimates between pairs of
375 populations and a hypothetical pool of migrants, allowing for the identification of source
376 and sink populations.

377

378 Larval dispersal simulations, using Lagrangian particle tracking methods, were conducted
379 using Python version 3.10.2 (<http://www.python.org>) and PARCELS version 2.3.1
380 (Delandmeter and Sebillie, 2019). Lagrangian particle tracking, in this case, refers to the
381 advection and diffusion of simulated particles based on the velocity of currents within an
382 Ocean General Circulation Model (OGCM). The OGCM in question was 'MOI
383 GLORYS12_FREE' from MERCATOR, which has a 1/12th of a degree horizontal resolution
384 and daily temporal resolution at 50 depth bands from 0.5 to 5728m depth. Particles were
385 advected by the Northward and Eastward vertical velocities within the OGCM and effected
386 by horizontal diffusion (Smagorinsky, 1963) to approximate sub grid scale currents.
387 Particles were attributed a larval behaviour so that they would approximate the
388 planktonic nauplii of *S. lauensis*. The principal behaviour attributed to these particles was
389 a temperature dependent Larval Dispersal Duration (LDD). Each particle interacted with
390 OGCM temperature data via an equation to calculate LDD, adapted from O'Connor *et al.*
391 (2007) following the methods of Mitarai *et al.* (2016) and Breusing *et al.* (2021). For *S.*
392 *lauensis*, we assumed a generational turnover of 33 per year (LDD of 11 days) at 20°C and
393 10 per year (LDD of 36.5 days) at 10°C (Huntley *et al.*, 1991; Gollner *et al.*, 2016) to
394 calculate the magnitude of the relationship between LDD and temperature using the
395 equations of O'Connor *et al.* (2007). Particles were released at the location of the vent
396 fields 100m above the seabed to replicate the entrainment of larvae into vent plumes
397 (Ivanenko and Martinez Arbizu, 2007; Gollner *et al.*, 2015). One hundred particles were
398 simultaneously released from these locations every four hours for six years (2010 –
399 2016), resulting in a total of 876,000 particles released from each vent field. We used the
400 horizontal distribution of particles at the time they reached their LDD as a measure of
401 larval dispersal potential. We then extrapolated this distribution using a Lagrangian

402 Probability Density Function (PDF) to calculate the horizontal distribution of dispersal
403 probability. The probability densities can be interpreted as the likelihood that a particle
404 settles in a given location where the density values are proportional (Siegel et al., 2023),
405 smoothed across latitude and longitude using a Gaussian distribution. By extracting the
406 value of the PDF from each vent field at the location of all other vents, we determined the
407 probability of dispersal among all pairs of vent fields in both directions following the
408 methods of Mitarai *et al.* (2009; 2016). Where possible, we implemented the simulation
409 parameters recommended by the authors of PARCELS (Delandmeter and Sebillie, 2019),
410 and provide the detailed simulation parameters in supplementary information (S10, table
411 4).

412

413 ***2.9 Genotype-Environment Association Analysis (GEAA)***

414 The relationship between genotypes and environmental factors was investigated using
415 *Samβada*, a genome-environment association (GEA) software designed to search for
416 signatures of local adaptation (Duruz et al. 2019). In addition, a distance-based
417 redundancy analysis (db-RDA), combining regression and ordination was used to
418 investigate the relationship between environmental variables and genotypes as per
419 Benestan, Ferchaud, et al. (2016) and Benestan, Quinn, et al. (2016). A spatial
420 eigenfunction analysis was used to evaluate the relative contribution of geographic
421 distance and asymmetric processes driven by deep-water ocean current circulation to
422 genotype frequency variation in the genomic dataset. Firstly, a distance-based Moran's
423 eigenvector map (db-MEMs) (Legendre et al. 2013), was created to decompose the
424 Euclidean (geographic) distances between sites into vectors (db-MEMs) that can be used
425 for subsequent analysis based on a distance matrix. The matrix consists of Euclidean

426 distances calculated at a depth of 1800m, the average depth at which hydrothermal
427 plumes were found to travel in the Lau basin (Speer and Thurnherr, 2012), and therefore
428 the depth at which *S. lauensis* may disperse (Gollner et al. 2015). These additional
429 variables account for spatial autocorrelation and allow for the identification of non-
430 random structure. Further, Asymmetric Eigenvector Maps (AEMs) were generated by
431 translating the presence of a population connection in a larval dispersal probability
432 matrix (i.e., dispersal probability from the biophysical model > 0) between all pairs of sites
433 into a sites-by-edge matrix. We attributed a weight to each edge, which was based on the
434 probability of dispersal between each pair of sites derived from the biophysical model.
435 When connectivity between a given pair of sites was greater than zero in both directions,
436 we selected the direction with the highest probability of dispersal (Xuereb et al., 2018).
437 The db-MEMs therefore describe the geological and bathymetric setting, while the AEMs
438 describe dispersal based on oceanographic currents. For both db-MEMs and AEMs the
439 larger eigenvectors model broad-scale spatial structures such as topographic features
440 (transform faults, between the north and south or differences in the density of vents),
441 whereas the smaller eigenvectors model fine-scale spatial structures that could describe
442 other environmental parameters less related to geography (Dray et al., 2012). We used
443 the package *adespatial* v.0.0-8 (Dray et al., 2017) to generate db-MEMs both types of
444 spatial variables.

445

446 Samβada was then used to identify markers with a significant correlation to the
447 environmental variables (figure 3, S8, figure 8), based on several statistics: firstly, a G-
448 score compares the likelihood of modes with and without environmental parameters.
449 Secondly, the Wald-score checks whether the effect of the environmental parameters (β_2)

450 is different from zero, i.e., whether an environmental parameter is associated with a
451 significant change in genotype frequencies. Q-values were once again used to correct for
452 false positives. Markers retained after correction were added to the Venn diagram to
453 check if any markers were shared between outlier detection methods and genotype-
454 environment association methods. Lastly, a db-RDA was conducted on a dataset of
455 significant SNPs (vcf was filtered to only contain significant SNPs found by Samβada).
456 During the model selection in a db-RDA, an adjusted R^2 statistic is used to correct for the
457 number of explanatory variables. Akaike's Information Criterion (AIC) is then used to
458 select the best variables, and a permutation test of F (p -value) using Analysis of Variance
459 (AMOVA) is conducted. This allows for the testing of significance of the global model,
460 individual parameters as well as the individual RDA axis (S8, table 3).

461

462 **3. Results**

463

464 ***3.1 De novo assembly, filtering, and SNP-calling***

465 A pre-GC-filtered, *de novo* assembled dataset created using discoSnpRAD++ contained
466 149 individuals represented by 187,737 variant bubbles, and 104,009 SNPs. After filtering
467 for GC, a *de novo* assembled dataset contained 84,674 variant bubbles, and 18,672 SNPs
468 which were subsequently clustered into 9039 loci, using a k-mer length of 15 and a
469 maximum allowed indel size of zero. The dataset contained 28.4% missing data per SNP,
470 and 11 individuals were removed with missing data above 0.5. After filtering for
471 heterozygosity (cut off = 0.6) and 1 SNP per locus, a final SNP dataset of bi-allelic SNPs
472 contained 138 individuals and 5778 high quality SNPs (S4, table 2), with an average

473 heterozygosity of 0.2. Because high F_{st} SNPs may also be caused by drift alone (under
474 strong demographic changes), the fact that the target organism is non-model (no existing
475 genomic information), and the very low number of SNPs found across different outlier
476 methods (pointing to little evidence of selection), all SNPs were retained for the structure
477 and demogenetic analysis.

478

479 **3.2 Outlier Analysis**

480 Bayescan analysis did not identify any outliers, instead, only putatively balancing, and
481 neutral SNPs. In contrast, Arlequin and PCAdapt identified 123 and 81 outliers,
482 respectively, with 5 shared outliers. Samβada, which was used to explore the relationship
483 between genotype frequencies and environmental variables (db_MEMs and AEMs),
484 identified 671 SNPs that had a significant (alpha = 0.01) correlation with environmental
485 variables. Fifty-two of them were common between Samβada and PCAdapt, and 12
486 between Samβada and Arlequin, Due to the low number of SNPs identified as outliers
487 across two or more methods, no outliers were removed from the structure or
488 demogenetic analyses (figure 3).

489

490 **3.3 Population structure and diversity**

491 Non-metric Multidimensional Scaling identified four populations, three of which were
492 based on geographical location, and one was based on a temporal sub-structure within
493 the ABE hydrothermal field between sampling years 2016 and 2019 (figure 2A, S3, figure
494 4A, B, and C). Results were compared to PCA and UMAP with MRCC (S3, figure 4). All
495 methods captured the same structure, statistically supported by UMAP with MRCC that

496 was used to account for sample size and variance. The RCSI, entropy, and consensus index,
497 of the latter, suggest that the most significantly stable amount of genetically differentiated
498 groups within the basin is four (S2, figure 2C, E, and F). However, UMAP does not
499 represent genetic distances, and an nMDS approach was therefore chosen to best
500 represent the genetic distances concordantly throughout the paper.

501

502 *ADMIXTURE* found the most stable number of groups to be three but with almost
503 negligible difference between cross validation error values of 0.321, 0.319, and 0.322 for
504 values of $k=2$, $k=3$, and $k=4$ respectively (figure 2B and S5, figure 5B, C, and D). For $k=3$,
505 populations are highly structured across the basin from Mangatolo to Tu'i Malila with
506 some (albeit low) level of shared ancestry. We identified three distinct genetic clusters.
507 Cluster 1 corresponds to Tui' Malila, cluster 2 to ABE and Tahi Moana (from which we
508 conclude shared ancestry for the two populations, (which were therefore grouped for
509 downstream analysis) and cluster 3 to Mangatolo. These results were corroborated by
510 *STRUCTURE* analysis, where the additional testing for $K=4$ $K=5$ did not increase the
511 number of ancestral groups. Half of the individuals from Mangatolo, collected in 2019
512 have a low percentage of ancestry belonging to cluster 1, mostly represented by
513 individuals from Tu'i Malila as is the case for the ABE samples from 2019. indicating that
514 copepods sampled from Tu'i Malila in 2016 may have been a source to other populations
515 sampled in 2019. These ancestral pools were therefore termed south (Tu'i Malila), mid
516 (ABE and Tahi Moana), and north (Mangatolo).

517

518 Percentage variation was 17.7% among the populations and 82.3% within the
519 populations, with a global AMOVA F_{st} of 0.18 ($p = <0.001$). Pairwise F_{st} values were highest

520 between Mangatolo and ABE(2016) ($F_{st} = 0.26, p = <0.001$), followed by Tu'i Malila and
521 ABE(2016) ($F_{st} = 0.25, p = <0.001$), Tahī Moana and Mangatolo ($F_{st} = 0.24, p = <0.001$) and
522 Tahī Moana and Tu'i Malila ($F_{st} = 0.24, p = < 0.001$). F_{st} values between Tahī Moana and
523 ABE (2016) were almost zero ($F_{st} = -0.00084, p = 0.12$). The F_{st} value between Mangatolo
524 and Tu'i Malila was 0.12 ($p = <0.001$). Interestingly, F_{st} values between Mangatolo and
525 ABE(2019) decreased ($F_{st} = 0.05, p = <0.001$), as well as between Tu'i Malila and
526 ABE(2019) ($F_{st} = 0.08, p = <0.001$) and increased between Tahī Moana and ABE(2019) (F_{st}
527 = 0.11, $p = <0.001$), see table 2 for significance codes. Observed heterozygosity was 0.18,
528 0.12, 0.08, 0.12, and 0.24 for Tu'i Malila, ABE(2016), ABE(2019), Tahī Moana, and
529 Mangatolo, respectively.

530

531 **3.4 Demogenetic Connectivity**

532 The folded joint allele frequency spectra (JAFS) display the proportion of alleles shared
533 between the north and mid and the north and south populations for the observed data
534 (figure 4A and 5A, respectively) and the simulated spectra for the best model (figure 4B
535 and 5B, respectively). Secondary Contact (SC) appears to be the most appropriate model
536 in each instance and increasing the complexity with the addition of parameters 2N (linked
537 selection), 2m (heterogeneous migration rate across the genome) and G (population size
538 change) improved the AIC values (figure 4E and 5E, respectively). The time of divergence
539 between the north and mid using the best model (SC2N2mG) was calculated to be ~119
540 kya (UCI = 189 kya, LCI = 49 kya), with a more recent secondary contact event estimated
541 at ~4 kya (UCI = 4.5 kya, LCI = 3.5 kya) while the time of divergence between the north
542 and south populations using the best model (SC2N2mG) was estimated to be ~326 kya
543 (UCI = 795 kya, LCI = 239 kya), with a recent secondary contact event estimated at ~10

544 kya (UCI = 17 kya, LCI = 3.2 kya). However, absolute estimates are approximately the
545 same order of magnitude with an increase of 2.5 between them, potentially due to
546 uncertainty in the $\partial a \partial i$ simulations.

547

548 The proportion (1-P) of the genome that evolved under heterogeneous migration in
549 models with parameter $2m$, was 0.26, meaning that almost one third of the genome is
550 subject to constrained gene flow because of barrier loci. The effective population sizes of
551 the daughter populations Nu_1 and Nu_2 , indicate a severe bottleneck in the populations
552 (b_1 and $b_2 < 1$) since the time of population split. The local effect of selection at linked
553 sites seems to affect only 20% of loci ($Q = 0.17$) with a relatively large value of *hrf* (Hill-
554 Roberston factor = ~ 0.14) (Table 3). Meanwhile, the proportion of the genome that
555 evolved under heterogeneous migration in models with parameter $2m$ between north and
556 south, was 0.97, meaning that the majority of the genome is subject to constrained gene
557 flow because of barrier loci. The local effect of selection at linked sites seems to affect
558 almost half of the loci ($Q = 0.49$) with a relatively large value of *hrf* (Hill-Roberston factor
559 = ~ 0.11) (Table 3).

560

561 Both comparisons depict asymmetrical migration rate northward, with 5.97 (m_{21}) $>$ 0.68
562 (m_{12}) for Mid-North and 4.64 (m_{12}) $>$ 1.03 (m_{21}) for North-South (table 3). The number
563 of migrants (estimated by $(N_1 * b_1 * m_{12})/2$ and $(N_2 * b_2 * m_{21})/2$) between the north and
564 mid (1=mid & 2=north) is asymmetrical, and predominantly (albeit weakly) northward
565 oriented with ($Nm_{north \leftarrow mid} = 0.25$) than in the opposite direction ($Nm_{mid \leftarrow north} = 0.12$). Nme
566 was used to explain the orientation of gene flow between north and south as this
567 parameter was highly asymmetrical while Nm was very similar between the two

568 populations (Table 3). Gene flow was predominantly northward oriented between the
569 two populations as captured by N_{me} ($N_{me_{north<-south}} = 2.40$, $N_{me_{south<-north}} = 0.66$). In this
570 case, N_{me} does not represent true migrants, but rather the movement of introgressed
571 alleles that are not impacted by barrier loci.

572

573 ***3.6 Effective Population Size (N_e)***

574

575 Contemporary N_e estimates using parameters from $\partial a \partial i$ were high. When comparing the
576 north and mid populations, N_e was calculated as 299,738 and 202,206 for the north and
577 mid, respectively, showing a sharp decrease in N_e from an N_{anc} of 401,202 since the T_{div}
578 ~ 123 kya. When comparing the north and south, N_e was calculated as 701,645 and 865,
579 000 for the north and south, respectively, indicating an increase in N_e from a an N_{anc} of
580 677,263 since the $T_{div} \sim 335$ kya. Nevertheless, it remains complicated to distinguish the
581 differences between a decrease in the effective population size caused by a severe
582 bottleneck, as this signature in structured populations can also be caused by a reduction
583 of the gene flow over time, and these results are therefore interpreted with caution.

584

585 ***3.7 Suitability of larval dispersal models in predicting empirical patterns of*** 586 ***gene flow in genomic datasets***

587 ***3.7.1 Larval dispersal models***

588 Larval dispersal probability models were run with a passive vertical migration parameter,
589 a growth curve for copepods based on temperature response, and millions of particles
590 released daily from 2010-2016. Particles dispersed predominantly northward,
591 particularly in the case of the mid and south vent fields. Particles dispersing from the

592 north dispersed further east and west than the other sites. Larval dispersal from the south
593 and mid was constrained by the topography around the Peggy Ridge and the presence of
594 the Niuafou'ou plate. The lowest pairwise probability of dispersal among vent fields was
595 $7.25 \cdot 10^{-32}$ from ABE to Mangatolo (northward), while the highest was $3.26 \cdot 10^{-7}$ from Tui Malila
596 to ABE (northward) (figure 6A). Despite the low probability values, all vent fields were
597 connected to one another by very limited dispersal (values above 0) except the north
598 (figure 6B), and all vent fields displayed high levels of self-recruitment, highest so in the
599 mid and south. The average LDD of Lagrangian particles dispersing from all vent fields
600 was ~ 104 days (S10, figure 11).

601

602 **3.7.2 Migration inferred from genomic data**

603 Using empirical allele frequency data, *DivMigrate* identified significant, asymmetric,
604 northward migration from the southern and mid populations to the north (Figure 6A).
605 From the south to the north, Nm was 1.0 per generation, describing unidirectional gene
606 flow in purely northward orientation. From the mid to the north, Nm was 0.31 indicative
607 of a weaker, northward gene flow. From the mid to the south, Nm was 0.33, indicative of
608 a weak, southward gene flow (Figure 6A). These values were calculated under the strong
609 assumption of a n-islands model with no demographic changes, however, results from
610 *DivMigrate* are comparable to those from $\partial a \partial i$, with strong northward, asymmetric
611 geneflow, and approximately one third of each generation of migrants emigrating from
612 the mid to the north, and over twice the amount of migrants per generation emigrating
613 from the south to the north.

614

615 **3.8 Genotype-Environment Association Analysis**

616 A db-RDA conducted on a subset of 671 SNPs significantly associated with environmental
617 variables revealed that structural variables of intermediate scales (MEM4 and MEM5)
618 appeared to correlate significantly with differences between Tahiti and ABE on one hand,
619 and Tui Malila and Mangatolo, on the other hand (S8, figure 8, table 3). An AEM defining
620 high probabilities of dispersal (AEM1) also appeared to correlate significantly with
621 differences between these two groups of populations. The RDA had a global R^2 value of
622 0.84 (p -value <0.001). MEM5, MEM4, and AEM1 were highly significant with p -values of
623 <0.001 for all parameters. RDA1, explaining 83.78 % of the genomic variation was also
624 highly significant with a p -value of <0.001 , while RDA2 explained 3.21 % of the variation
625 (p -value = <0.001).

626

627 **4. Discussion**

628 This study examines population connectivity of the copepod *S. lauensis* in the Lau basin, a
629 hydrothermal vent habitat in the Southwest Pacific BABs. Using 5,778 SNPs, we confirmed
630 strong spatial and temporal structuring, with metapopulations originating from three
631 ancestral pools. Population separation likely occurred around ~119 kya (north-mid) and
632 ~326 kya (north-south), with secondary contacts at ~4 kya and ~10 kya, respectively.
633 Weak migration is observed from mid to north and south, while stronger northward
634 migration occurs from south to north. Bespoke larval dispersal patterns captured similar
635 directionality in the gene flow with the exception of gene flow from the mid to the south
636 and supported high levels of structure among all populations.

637

638 **4.1 Fine-scale population structure**

639 Previous studies have shown that within-basin structure is unlikely for megafaunal
640 species with planktonic larval dispersal, except for *Munidopsis lauensis* in the Manus basin
641 (Mitarai et al., 2016; Plouviez et al., 2019; Breusing et al., 2021; Tran Lu Y et al., 2021;
642 Poitrimol et al., 2022; Thaler et al., 2014). Although habitat preference and interspecific
643 dynamics are known to influence connectivity patterns (Micheli et al., 2002; Lenihan et
644 al., 2008; Beinart et al., 2012; Johnson et al., 2020), *S. lauensis* experiences high levels of
645 self-recruitment due to its short generation time, reducing the number of migrants being
646 exchanged between populations, thus allowing populations to diverge faster through
647 genetic drift in the absence of migration. Particularly in areas of diffuse hydrothermal
648 venting where *S. lauensis* dominates, nauplii will have less chance of being entrained in a
649 plume vortex and dispersed far into the water column as they are not in close proximity
650 to the vent source. Pronounced geographic structure was evident from ADMIXTURE, IBS,
651 and multiple dimension-reducing techniques within this study.

652

653 Temporal genetic structure has been reported for copepods in surface waters resulting
654 from demogenetic changes, due to variations in environmental conditions over time
655 (Tepper and Bradley, 1989; Posavi et al., 2014; Brennan et al., 2022). In the present study,
656 such temporal variations were also depicted at the ABE vent field, as seen in the IBS
657 analysis (S7, figure 7). Allelic introgression from Tu'i Malila (as observed from the
658 ADMIXTURE results in Figure 2B) point to Tu'i Malila having acted as a source for most
659 Lau basin populations after 2016. Furthermore, tectonic rearrangements occurred
660 between 2016 and 2019 with the extinction of the site Kilo Moana which was closer to
661 ABE than Tui' Malila is. However, as the effects of genetic drift act more strongly on small
662 populations due to founder effects, it is also possible that a disruption to the ABE field

663 caused a sporadic bottleneck. This is supported by the reduction in heterozygosity from
664 0.12 to 0.08 in samples from ABE from 2016 to 2019. A generation time of 33
665 generations/year, as reported by Gollner et al. (2016) for copepods at 20°C, was also used,
666 reflecting the r-strategy mechanisms displayed by hydrothermal vent fauna in response
667 to the environmental instability of the vent habitat (O'Connor et al., 2007; Tran Lu Y et al.,
668 2021). Drift acting on a population of reduced size would be especially non-negligible if
669 dirivultid copepods are undergoing 33 generations per year, allowing drift to act on a
670 turnover of almost 100 generations in three years. Bottlenecks also appear to have
671 occurred during the secondary contact event between the north and south, as shown by a
672 decrease in the b1 parameter from the $\partial a \partial i$ results (Table 3). Disruptions to the sea floor
673 of the Lau Basin are evident after the recent Tonga eruption blanketed a large proportion
674 of the Lau Basin, affecting vast areas of seafloor, including ABE (Seabrook et al., 2023).
675 There is evidence of catastrophic eruptions around the Tonga region throughout the last
676 thousand years (Monzier et al., 1994; Lavigne et al., 2021; Brenna et al., 2022), and this
677 activity has increased over the entire Tonga-Kermadec region within this period of time
678 (Watt et al., 2013), indicating that significant changes to the seafloor may have occurred,
679 giving rise to recurrent bottlenecks in populations of benthic organisms.

680

681

682 **4.2 Demogenetic history of *S. lauensis* within the Lau basin**

683 The demogenetic history of *S. lauensis* was investigated between the southern, mid, and
684 northern populations of the basin. A mutation rate of 1×10^{-9} , based on relatively recent
685 reports for crustaceans including copepods and amphipods (Thomas et al., 2020), was
686 used to estimate the time of divergence between the populations. This rate is lower than

687 the typical rate for mitochondrial DNA and aligns with evolutionary rates between
688 mitochondrial and nuclear genomes.

689

690 The commencement of spreading in the Mangatolo Triple Junction (MTJ) is estimated to
691 have occurred between 180 and 600 kya (Mensing et al., 2020, Steward et al., 2022), and
692 the birth of the major transform fault, Peggy Ridge, that separates the Australian plate and
693 the Niuafu'ou plate is estimated to be no older than 350 kya (Stewart et al. 2022). The
694 latter appears to act as a major barrier to dispersal at depths below 600 m, and
695 consistently, the time of split between metapopulations is estimated to have occurred
696 after the formation of this fault (327 kya and 119 kya for the north-mid and north-south,
697 respectively). Time of secondary contact events (~4 kya and 10 kya for the north-mid and
698 north-south, respectively) align with *Cox1* data from the same species and vents in the
699 region (Diaz-Recio Lorenzo et al., 2023), that point to an increase in effective population
700 size starting at 10 kya in the Lau basin. During this period, eruptions within the Tonga-
701 Kermadec arc went from making up 10 % of the global eruptions to 50 %, likely giving
702 rise to new vents across the region, and thus more stepping stone features along which
703 dispersal could have occurred (Watt et al., 2013). This would be consistent with the
704 occurrence of an SC event with sufficient genetic exchanges to cause a mixing of *cox1*
705 haplotypes from different geographic regions as reported by Diaz-Recio Lorenzo et al.
706 (2023), while genetic incompatibilities display a pronounced barrier with limited gene
707 flow over a non-negligible portion of the nuclear genome due to a long period of isolation.
708 Despite the rather high standard deviation values of theta for the north-mid (theta =
709 91.82, SD = 23.55) and the north-south (theta = 155.82, SD = 93.6), demogenetic
710 connectivity patterns appear to be roughly consistent with seabed changes over

711 geological timescales and the more nuanced events that recently contributed to the
712 complex geological setting of the Lau basin (Ruellan 2003; Martinez and Taylor, 2006;
713 Baker et al., 2019; Baxter et al., 2020). However, stochastic hydrodynamic events such as
714 deep-sea eddies (Speer and Thunher et al., 2012), which may modulate dispersal
715 sporadically alongside significant El Nino events, and modifications to regional surface
716 and deep ocean currents due to the onset of the Last Glacial Maximum, may also have
717 played a role (Hu and Piotrowski et al., 2020, Tran Lu Y et al., 2021). The values used in
718 this study are estimates and should therefore be interpreted cautiously. Assumptions
719 were made regarding generation turnover and non-overlapping generations and may not
720 have fully captured the complex reproductive and dispersal mode of *S. lauensis*. Further
721 research on female fecundity, ecology, and stressors is needed to validate these
722 assumptions for this specific species and the dirivultid family, in general.

723

724

725

726 ***4.2.1 Estimation of Effective Population Size (N_e)***

727 An overestimation of N_e can be expected when there is immigration from populations with
728 limited differentiation to the focal population, resulting in less drift due to the increase in
729 alleles introduced that are already present in the population (Nadachowska-Brzyska et
730 al., 2021). Conversely, we expect N_e to be underestimated when structured populations
731 exhibit migrants, introducing foreign alleles, leaving signatures in the genome that
732 resemble genetic drift, which could be the case for *S. lauensis*. Based on the structure
733 analysis it appears that individuals from ABE and Mangatolo from 2019 are admixed with
734 individuals from Tu'i Malila from 2016, which increase temporal variations in these two

735 populations and would add to the effect of drift in the structured populations, and yet the
736 estimates using $\partial a \partial i$ were high with values ranging from 192,576- 512,415. However, this
737 may also be a result of pooling the two temporal states with use in $\partial a \partial i$, and results of N_e
738 must therefore be interpreted with caution.

739

740 ***4.3 Suitability of larval dispersal models in predicting empirical patterns of*** 741 ***gene flow in genomic datasets***

742

743 Larval dispersal models tested two main hypotheses: depth restriction to the spatial
744 distribution of larvae and gene flow orientation across the Lau basin. The models
745 incorporated realistic scenarios of potential vertical movement and temperature-
746 dependent growth, considering the complex current dynamics within the Lau basin
747 (Speer and Thunherr, 2012; Simons et al., 2021) and the relationship between LDD and
748 temperature (O’Conner et al., 2007). The average larval dispersal duration was estimated
749 to be around 104 days, but potentially with a much shorter duration for self-recruiting
750 copepods in the local vent environment due to high temperatures.

751

752 The hypothesis that copepod nauplii travel over short distances with deep-water
753 hydrothermal plumes was confirmed by genetic differentiation of the *cox1* gene of
754 populations among basins (Diaz-Recio Lorenzo et al., 2023) and larval dispersal
755 simulations which showed that particles began leaving the Lau basin from each vent at
756 depths of 600 m and shallower. The simulations indicated highly structured populations,
757 even with a long larval dispersal duration of 104 days. Given the low level of gene flow
758 inferred from the genomic data, it appears that few migrants may be able to travel for a

759 prolonged period of time, likely in a state of delayed metamorphosis, acting as weak
760 connections between populations. Vertical passive movement allowed particles to cross
761 the transform fault separating the Australian plate and the Niuafu'ou plate, enabling low-
762 level gene flow. However, southward migration probabilities from the mid to the south
763 were zero, despite weak gene flow observed in genomic analyses. Nevertheless,
764 connections may also occur due to stepping-stones and ghost populations aided by the
765 many other vents that exist in the basin (denoted by the white triangles in figure 1) and
766 seafloor fissures forming potential connectivity corridors aided potentially by bottom
767 currents and sub-surface hydrothermal flow, elements not accounted for in the models.

768

769 This study identified the mid population, as a contemporary source in 2016, contributing
770 migrants to the north and south. Vents flanking the mid population, including Tow Cam
771 and Kilo Moana, form a cluster facilitating bidirectional gene flow. Tu'i Malila in the south
772 serves as an important source population for northward migration in 2019, however
773 historical changes in the distribution of source populations due to tectonic and volcanic
774 events may have influenced population structure through time. These findings emphasize
775 the significance of these populations in maintaining gene flow towards the north which
776 appears to act as a sink, and highlight the need to consider them in conservation
777 strategies, however they also highlight the need to incorporate time series data, as
778 populations may act as source or sinks depending on the sampling year. While
779 acknowledging the limitations of larval dispersal models, this study demonstrates their
780 value in understanding complex dispersal dynamics by incorporating organism-specific
781 traits.

782

783 The results of the GEAA analysis showed that intermediate-scale bathymetric structures
784 and fine-scale asymmetric dispersal played a role in structuring *S. lauensis* populations.
785 MEM4, MEM5 (intermediate scale db-MEMs associated with the spatial arrangement of
786 vents), and AEM1 (a fine scale asymmetric vector describing high probabilities of
787 dispersal predicted by Lagrangian simulations) correlated significantly with the observed
788 differences in genotypic frequencies between populations (S8, figure 8, table 3). The db-
789 MEMs used in the analysis likely captured geological features such as vent density,
790 transform faults, depth gradients, and axial ridges in the Lau basin. MEM5 was associated
791 mostly with values of depth, while MEM4 was associated with values of spreading rate.
792 Despite only having one value per vent for depth and spreading rate, these associations
793 appear meaningful, given the depth gradient between Tu'i Malila, ABE, and Tahī Moana
794 (1888 m, 2155 m, and 2273 m, respectively). Meanwhile, the AEM1 was associated with
795 high probabilities of dispersal, suggesting a higher probability of dispersal between the
796 north-south, compared to the mid-south and the mid-north. Depth may play an important
797 role in structuring vent populations, as nauplii from similarly deep vents, would need to
798 cross a smaller depth gradient in order to disperse (Breusing et al., 2021). Spreading rate
799 is an important factor governing both local extinction rate and the rugosity of the seabed
800 (faults and screes) at each vent location. The differences in spreading rates between the
801 north (38 mm/year⁻¹), mid (69mm/year⁻¹), and south (48 mm/year⁻¹) may result in
802 differences in local vent conditions and bacterial communities on which the copepods
803 feed, likely exerting differences among populations, via local adaptation and recurrent
804 bottlenecks. Furthermore, the frequency of vent occurrence is positively correlated with
805 magmatic supply (Baker and German, 2004), which increases with spreading rate (Olive
806 and Dublanchet et al., 2020) implying that fast spreading zones may harbor dense

807 aggregations of vent sites, providing stepping-stones for copepods to disperse, a theory
808 evaluated for megafauna of the Southwest Pacific vents (Breusing et al., 2021) and also
809 the East Pacific Rise (Jollivet et al., 1999; Vrijenhoek et al., 2010). To the north of ABE and
810 Tahiti Moana, spreading rates increase dramatically from 69 mm/ year⁻¹ to 120 mm/ year
811⁻¹ (Stewart et al., 2022), as do the number of confirmed vents along that gradient. The
812 aggregations can be seen in e.g., figure 1, where the white triangles denoting known vents
813 appear to form hotspots in the northeast, northwest, and mid/south of the basin. These
814 vents form two main stepping-stone corridors along which vent fauna are distributed, one
815 of which could explain preferential dispersal between north-south, but not between
816 north-mid.

817

818 ***4.4 Connectivity of hydrothermal vent meiofauna vs megafauna – implications for*** 819 ***resilience to deep-sea mining***

820

821 Relative migration inferred from empirical genetic data, agrees largely with that of
822 Breusing et al., (2021), who show that populations of *Alviniconcha* snails exhibit a
823 predominantly southward migration from Tahiti Moana to Tu'i Malila, and a predominantly
824 northward migration from both of those sites to the north. Plouviez et al., (2019) depicted
825 some population structure for the limpet *Lepetodrilus schrolli* using the *cox1* gene and
826 Poitrimol et al. (2022) showed that cryptic species also exist for a range of megafauna in
827 the Southwest Pacific including within the Lau basin based on *cox1*. However, Breusing et
828 al's study as well as other recent population genomics studies (Plouviez et al., 2019; Tran
829 Lu Y et al., 2021) and larval dispersal modelling of megafauna in the region (Mitarai et al.,
830 2016) have found little to no structure in the populations within the Lau basin when using

831 nuclear markers. Our results highlight that pattern of connectivity cannot be generalized
832 to all fauna in vent systems and that the different faunal groups need to be considered
833 when developing robust area-based management tools (ABMTs). The removal of these
834 abundant copepods from the vent environment through mining may have unprecedented
835 consequences for the ecosystem as a whole. Being the most abundant animal where hard
836 substrate is available, dirivultid copepods represent an unexplored but potentially
837 important functional group in these systems, feeding predominantly on
838 chemoautotrophic bacteria (Nomaki et al., 2023) and forming close associations with a
839 range of megafaunal species including *Rimicaris* shrimp (Gollner et al., 2016), the squat
840 lobster *Shinkai crosnieri* (Senokuchi et al., 2018), Bathymodiolin mussels (Gollner 2016),
841 *Ifremeria* and *Alviniconcha* snails (Gollner et al., 2016) and the vent polychaete
842 *Paralvinella sulfincola*, which was hypothesized to utilize the vent copepod *Stygiopontius*
843 *quadrispinosus* as a primary food source when densities of the copepod were high (1852
844 ind. per worm) (Limen et al., 2008). Copepods in the global oceans are hugely important
845 bioindicators, and the role of deep-sea copepods at hydrothermal vents as such is largely
846 unexplored. Further research is needed to investigate the trophic role of this family in the
847 vent environment and the potential risks to the ecosystem should populations of
848 abundant copepods suffer major bottlenecks as a result of anthropogenic disturbance.

849

850 **5. Conclusions**

851

852 This study reports the first data on population connectivity in the vent meiofauna,
853 specifically for the vent obligate copepod *Stygiopontius lauensis*. Limited gene flow
854 between north and south populations suggests a potential stepping-stone dispersal model

855 and recent secondary contact events associated with vent dynamics. Divergence between
856 populations likely occurred hundreds of thousands of years ago, with secondary contact
857 events occurring in recent geological history. Our results suggest that migration between
858 vents in the Lau basin is not sufficiently high to offset the effects of drift or local selection,
859 likely leaving populations at risk of local extinction, should mining occur. Larval dispersal
860 models incorporating temperature-dependent dispersal duration and passive vertical
861 movement accurately captured population isolation. However, they did not fully explain
862 the observed low-level southward gene flow from populations in the mid and south, and
863 further research is needed to address this discrepancy. We note that despite the
864 weaknesses in using any single analysis alone to draw conclusions about resilience of vent
865 communities, a multifaceted approach combining multiple complementary analyses
866 provides a much more robust picture of the consequences of anthropogenic activity in
867 these ecosystems. These results add much needed data to connectivity studies in the
868 region, informing dispersal models in the framework of understanding populations at risk
869 of extinction, and shed light on a majorly understudied subgroup of organisms in the
870 Southwest Pacific BAB system.

871

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888 **Data availability**

889 Raw sequence reads (Individual fasta files), individual genotype data (VCF) and metadata
890 are available on DataDryad (<https://doi.org/10.5061/dryad.zkh1893g2>). Scripts used in
891 this study (R, $\partial a \partial i$) are available on a public Github repositories:
892 <https://github.com/Atranluy/Scripts-Ifremeria>,
893 <https://github.com/otistwo/hydrothermal-thesis/blob/main/PARCELS/Copepod-PARC>
894 [ELS.ipynb](https://github.com/otistwo/hydrothermal-thesis/blob/main/PARCELS/Copepod-ELSA), and
895 [https://github.com/otistwo/hydrothermal-thesis/blob/main/PARCELS/Copepod-post](https://github.com/otistwo/hydrothermal-thesis/blob/main/PARCELS/Copepod-post-hoc.ipynb)
896 [hoc.ipynb](https://github.com/otistwo/hydrothermal-thesis/blob/main/PARCELS/Copepod-post-hoc.ipynb).

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899 **4. Bibliography**

900

901 Alexander, D.H., Lange, K., 2011a. Enhancements to the ADMIXTURE algorithm for
902 individual ancestry estimation. BMC Bioinformatics 12, 246.

903 <https://doi.org/10.1186/1471-2105-12-246>

904

905 Araneda, C., Larraín, M.A., Hecht, B. and Narum, S., 2016. Adaptive genetic variation
906 distinguishes Chilean blue mussels (*Mytilus chilensis*) from different marine
907 environments. Ecol Evol. 6: 3632-3644. <https://doi.org/10.1002/ece3.2110>

908

909 Baker, E.T., German, C.R., 2013. On the Global Distribution of Hydrothermal Vent Fields,
910 in: German, C.R., Lin, J., Parson, L.M. (Eds.), Geophysical Monograph Series.

911 American Geophysical Union, Washington, D. C., pp. 245–266.
912 <https://doi.org/10.1029/148GM10>
913

914 Baker, E.T., Walker, S.L., Massoth, G.J., Resing, J.A., 2019. The NE Lau Basin: Widespread
915 and Abundant Hydrothermal Venting in the Back-Arc Region Behind a Superfast
916 Subduction Zone. *Front. Mar. Sci.* 6, 382.
917 <https://doi.org/10.3389/fmars.2019.00382>
918

919 Bashevkin, S.M., Dibble, C.D., Dunn, R.P., Hollarsmith, J.A., Ng, G., Satterthwaite, E.V.,
920 Morgan, S.G., 2020. Larval dispersal in a changing ocean with an emphasis on
921 upwelling regions. *Ecosphere* 11. <https://doi.org/10.1002/ecs2.3015>
922

923 Beedessee, G., Watanabe, H., Ogura, T., Nemoto, S., Yahagi, T., Nakagawa, S., Nakamura,
924 K., Takai, K., Koonjul, M., Marie, D.E.P., 2013. High Connectivity of Animal
925 Populations in Deep-Sea Hydrothermal Vent Fields in the Central Indian Ridge
926 Relevant to Its Geological Setting. *PLoS ONE* 8, e81570.
927 <https://doi.org/10.1371/journal.pone.0081570>
928

929 Beinart, R.A., Sanders, J.G., Faure, B., Sylva, S.P., Lee, R.W., Becker, E.L., Gartman, A.,
930 Luther, G.W., Seewald, J.S., Fisher, C.R., Girguis, P.R., 2012. Evidence for the role
931 of endosymbionts in regional-scale habitat partitioning by hydrothermal vent
932 symbioses. *Proc. Natl. Acad. Sci. U.S.A.* 109.
933 <https://doi.org/10.1073/pnas.1202690109>
934

935 Benestan, L., Quinn, B.K., Maaroufi, H., Laporte, M., Clark, F.K., Greenwood, S.J., Rochette,
936 R., Bernatchez, L., 2016. Seascape genomics provides evidence for thermal
937 adaptation and current-mediated population structure in American lobster (*Homarus americanus*). *Mol Ecol* 25, 5073–5092.
938 <https://doi.org/10.1111/mec.13811>
939

940

941 Benestan, L.M., Ferchaud, A., Hohenlohe, P.A., Garner, B.A., Naylor, G.J.P., Baums, I.B.,
942 Schwartz, M.K., Kelley, J.L., Luikart, G., 2016. Conservation genomics of natural
943 and managed populations: building a conceptual and practical framework.
944 *Molecular Ecology* 25, 2967–2977. <https://doi.org/10.1111/mec.13647>
945

946 Benestan, L.M., Rougemont, Q., Senay, C., Normandeau, E., Parent, E., Rideout, R.,
947 Bernatchez, L., Lambert, Y., Audet, C., Parent, G.J., 2021. Population genomics
948 and history of speciation reveal fishery management gaps in two related redfish
949 species (*Sebastes mentella* and *Sebastes fasciatus*). *Evol Appl* 14, 588–606.
950 <https://doi.org/10.1111/eva.13143>
951

952 Bernatchez, S., Xuereb, A., Laporte, M., Benestan, L., Steeves, R., Laflamme, M.,
953 Bernatchez, L., Mallet, M.A., 2019. Seascape genomics of eastern oyster (*Crassostrea virginica*) along the Atlantic coast of Canada. *Evol Appl* 12, 587–
954 609. <https://doi.org/10.1111/eva.12741>
955
956
957

- 958 Blanchard, C., Gollner, S., 2022. Area-based management tools to protect unique
959 hydrothermal vents from harmful effects from deep-sea mining: A review of
960 ongoing developments. *Front. Polit. Sci.* 4, 1033251.
961 <https://doi.org/10.3389/fpos.2022.1033251>
962
- 963 Blasiak, R., Wynberg, R., Grorud-Colvert, K., Thambisetty, S., Bandarra, N.M., Canário,
964 A.V.M., Da Silva, J., Duarte, C.M., Jaspars, M., Rogers, A., Sink, K., Wabnitz, C.C.C.,
965 2020. The ocean genome and future prospects for conservation and equity. *Nat*
966 *Sustain* 3, 588–596. <https://doi.org/10.1038/s41893-020-0522-9>
967
- 968 Brenna, M., Cronin, S. J., Smith, I. E. M., Pntesilli, A., Tost, M., Barker, S. J., Tonga’onevai,
969 S., Kula, T., Vaiomounga R., 2022. Post-caldera volcanism reveals shallow
970 priming of an intra-ocean arc andesitic caldera: Hunga volcano, Tonga, SW
971 Pacific. *Lithos* 412-413. *Lithos* 412-413.
972 <https://doi.org/10.1016/j.lithos.2022.106614>
973
- 974 Brennan, R.S., deMayo, J.A., Dam, H.G., Finiguerra, M., Baumann, H., Buffalo, V., Pespeni,
975 M.H., 2022a. Experimental evolution reveals the synergistic genomic
976 mechanisms of adaptation to ocean warming and acidification in a marine
977 copepod. *Proc. Natl. Acad. Sci. U.S.A.* 119, e2201521119.
978 <https://doi.org/10.1073/pnas.2201521119>
979
- 980 Brennan, R.S., deMayo, J.A., Dam, H.G., Finiguerra, M., Baumann, H., Buffalo, V., Pespeni,
981 M.H., 2022b. Experimental evolution reveals the synergistic genomic
982 mechanisms of adaptation to ocean warming and acidification in a marine
983 copepod. *Proc. Natl. Acad. Sci. U.S.A.* 119, e2201521119.
984 <https://doi.org/10.1073/pnas.2201521119>
985
- 986 Breusing, C., Biastoch, A., Drews, A., Metaxas, A., Jollivet, D., Vrijenhoek, R.C., Bayer, T.,
987 Melzner, F., Sayavedra, L., Petersen, J.M., Dubilier, N., Schilhabel, M.B., Rosenstiel,
988 P., Reusch, T.B.H., 2016. Biophysical and Population Genetic Models Predict the
989 Presence of “Phantom” Stepping Stones Connecting Mid-Atlantic Ridge Vent
990 Ecosystems. *Current Biology* 26, 2257–2267.
991 <https://doi.org/10.1016/j.cub.2016.06.062>
992
- 993 Breusing, C., Johnson, S.B., Mitarai, S., Beinart, R.A., Tunnicliffe, V., 2023. Differential
994 patterns of connectivity in Western Pacific hydrothermal vent metapopulations:
995 A comparison of biophysical and genetic models. *Evolutionary Applications* 16,
996 22–35. <https://doi.org/10.1111/eva.13326>
997
- 998 Breusing, C., Johnson, S.B., Tunnicliffe, V., Vrijenhoek, R.C., 2015. Population structure
999 and connectivity in Indo-Pacific deep-sea mussels of the *Bathymodiolus*
1000 *septemdirum* complex. *Conserv Genet* 16, 1415–1430.
1001 <https://doi.org/10.1007/s10592-015-0750-0>
1002
- 1003 Brunner, O., Methou, P., Mitarai, S., 2023. The Role of Reproductive Periodicity in
1004 Dispersal Among Hydrothermal Vents and its Implications for Regional

1005 Connectivity and Conservation (preprint). Biophysics.
1006 <https://doi.org/10.1101/2023.03.07.531641>
1007

1008 Casanova, A., Maroso, F., Blanco, A., Hermida, M., Ríos, N., García, G., Manuzzi, A., Zane,
1009 L., Verissimo, A., García-Marín, J.-L., Bouza, C., Vera, M., Martínez, P., 2021. Low
1010 impact of different SNP panels from two building-loci pipelines on RAD-Seq
1011 population genomic metrics: case study on five diverse aquatic species. BMC
1012 Genomics 22, 150. <https://doi.org/10.1186/s12864-021-07465-w>
1013

1014 Fisher C. R., and Girguis P., 2016. cruise doi: <https://doi.org/10.7284/906664>
1015

1016 Chattopadhyay, B., Garg, K.M., Ramakrishnan, U., 2014. Effect of diversity and missing
1017 data on genetic assignment with RAD-Seq markers. BMC Res Notes 7, 841.
1018 <https://doi.org/10.1186/1756-0500-7-841>
1019

1020 Craddock, C., Hoeh, W.R., Gustafson, R.G., Lutz, R.A., Hashimoto, J., Vrijenhoek, R.J.,
1021 1995. Evolutionary relationships among deep-sea mytilids (Bivalvia: Mytilidae)
1022 from hydrothermal vents and cold-water methane/sulfide seeps. Marine
1023 Biology 121, 477–485. <https://doi.org/10.1007/BF00349456>
1024

1025 Crotti, M., Barratt, C.D., Loader, S.P., Gower, D.J., Streicher, J.W., 2019. Causes and
1026 analytical impacts of missing data in RADseq phylogenetics: Insights from an
1027 African frog (*Afrivalus*). Zool Scr 48, 157–167.
1028 <https://doi.org/10.1111/zsc.12335>
1029

1030 Dalongeville, A., Benestan, L., Mouillot, D., Lobreaux, S., Manel, S., 2018. Combining six
1031 genome scan methods to detect candidate genes to salinity in the
1032 Mediterranean striped red mullet (*Mullus surmuletus*). BMC Genomics 19, 217.
1033 <https://doi.org/10.1186/s12864-018-4579-z>
1034

1035 De Jode, A., Le Moan, A., Johannesson, K., Faria, R., Stankowski, S., Westram, A.M., Butlin,
1036 R.K., Rafajlović, M., Fraïsse, C., 2023. Ten years of demographic modelling of
1037 divergence and speciation in the sea. Evolutionary Applications 16, 542–559.
1038 <https://doi.org/10.1111/eva.13428>
1039

1040 De Wit, P., Faust, E., Green, L., Jahnke, M., Pereyra, R.T., Rafajlović, M., 2023. A decade of
1041 progress in marine evolutionary biology. Evolutionary Applications 16, 193–
1042 201. <https://doi.org/10.1111/eva.13523>
1043

1044 Delandmeter, P., Van Sebille, E., 2019. The Parcels v2.0 Lagrangian framework: new
1045 field interpolation schemes. Geosci. Model Dev. 12, 3571–3584.
1046 <https://doi.org/10.5194/gmd-12-3571-2019>
1047

1048 Diaz-Papkovich, A., Anderson-Trocmé, L., Ben-Eghan, C., Gravel, S., 2019. UMAP reveals
1049 cryptic population structure and phenotype heterogeneity in large genomic
1050 cohorts. PLoS Genet 15, e1008432.
1051 <https://doi.org/10.1371/journal.pgen.1008432>

1052
1053 Diaz-Papkovich, A., Anderson-Trocmé, L., Gravel, S., 2021. A review of UMAP in
1054 population genetics. *J Hum Genet* 66, 85–91. [https://doi.org/10.1038/s10038-](https://doi.org/10.1038/s10038-020-00851-4)
1055 [020-00851-4](https://doi.org/10.1038/s10038-020-00851-4)
1056
1057 Diaz-Recio Lorenzo, C., Bruggen, D.T., Luther, G.W., Gartman, A., Gollner, S., 2021a.
1058 Copepod assemblages along a hydrothermal stress gradient at diffuse flow
1059 habitats within the ABE vent site (Eastern Lau Spreading Center, Southwest
1060 Pacific). *Deep Sea Research Part I: Oceanographic Research Papers* 173,
1061 103532. <https://doi.org/10.1016/j.dsr.2021.103532>
1062
1063 Diaz-Recio Lorenzo, C., Patel, T., Arsenault-Pernet, E.-J., Poitrimol, C., Jollivet, D.,
1064 Martinez Arbizu., Gollner S., 2023. Highly structured populations of 42 deep-sea
1065 copepods associated with hydrothermal vents across the Southwest Pacific,
1066 despite contrasting life history traits. *PLoS ONE* 18(11): e0292525.
1067 <https://doi.org/10.1371/journal.pone.0292525>
1068
1069 Do, C., Waples, R.S., Peel, D., Macbeth, G.M., Tillett, B.J. and Ovenden, J.R., 2014.
1070 NeEstimator v2: re-implementation of software for the estimation of
1071 contemporary effective population size (Ne) from genetic data. *Mol Ecol Res.* 14:
1072 209-214. <https://doi.org/10.1111/1755-0998.12157>
1073
1074 Dorant, Y., Laporte, M., Rougemont, Q., Cayuela, H., Rochette, R., & Bernatchez, L.
1075 (2022). Landscape genomics of the American lobster (*Homarus americanus*).
1076 *Molecular Ecology*, 31, 5182– 5200. <https://doi.org/10.1111/mec.16653>
1077
1078 Dray, S., Péliissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P.R., Bellier, E.,
1079 Bivand, R., Blanchet, F.G., De Cáceres, M., Dufour, A.-B., Heegaard, E., Jombart, T.,
1080 Munoz, F., Oksanen, J., Thioulouse, J., Wagner, H.H., 2012. Community ecology in
1081 the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82,
1082 257–275. <https://doi.org/10.1890/11-1183.1>
1083
1084 Drazen, J.C., Smith, C.R., Gjerde, K.M., Haddock, S.H.D., Carter, G.S., Choy, C.A., Clark, M.R.,
1085 Dutrieux, P., Goetze, E., Hauton, C., Hatta, M., Koslow, J.A., Leitner, A.B., Pacini, A.,
1086 Perelman, J.N., Peacock, T., Sutton, T.T., Watling, L., Yamamoto, H., 2020.
1087 Midwater ecosystems must be considered when evaluating environmental risks
1088 of deep-sea mining. *Proc. Natl. Acad. Sci. U.S.A.* 117, 17455–17460.
1089 <https://doi.org/10.1073/pnas.2011914117>
1090
1091 Du Preez, C., Fisher, C.R., 2018. Long-Term Stability of Back-Arc Basin Hydrothermal
1092 Vents. *Front. Mar. Sci.* 5, 54. <https://doi.org/10.3389/fmars.2018.00054>
1093
1094 Duruz, S., Sevane, N., Selmoni, O., Vajana, E., Leempoel, K., Stucki, S., Orozco-terWengel,
1095 P., Rochat, E., Dunner, S., The NEXTGEN Consortium, The CLIMGEN Consortium,
1096 Bruford, M.W., Joost, S., 2019. Rapid identification and interpretation of gene-
1097 environment associations using the new R.SamBada landscape genomics

1098 pipeline. *Mol Ecol Resour* 19, 1355–1365. [https://doi.org/10.1111/1755-](https://doi.org/10.1111/1755-0998.13044)
1099 [0998.13044](https://doi.org/10.1111/1755-0998.13044)
1100

1101 Eaton, D.A.R., Spriggs, E.L., Park, B., Donoghue, M.J., 2016. Misconceptions on Missing
1102 Data in RAD-seq Phylogenetics with a Deep-scale Example from Flowering
1103 Plants. *Syst Biol* syw092. <https://doi.org/10.1093/sysbio/syw092>
1104

1105 Eldon, B., Riquet, F., Yearsley, J., Jollivet, D., Broquet, T., 2016. Current hypotheses to
1106 explain genetic chaos under the sea. *Curr Zool* 62, 551–566.
1107 <https://doi.org/10.1093/cz/zow094>
1108

1109 Pereira, E., Mateus, C.S., Alves, M. J., Almeida, R., Pereira, J., Quintella, B. R., Almeida, P.
1110 R., 2023. Connectivity patterns and gene flow among Chelon ramada
1111 populations. *Estuarine, Coastal and Shelf Science*. 281: 108209,ISSN 0272-7714.
1112 <https://doi.org/10.1016/j.ecss.2022.108209>
1113

1114 Beaumont M. A., Nichols R. A., 1996. Evaluating loci for use in the genetic analysis of
1115 population structure, 1996. . *Proc. R. Soc. Lond. B* 263, 1619–1626.
1116 <https://doi.org/10.1098/rspb.1996.0237>
1117

1118 Excoffier, L., Dupanloup, I., Huerta-Sánchez, E., Sousa, V.C., Foll, M., 2013. Robust
1119 Demographic Inference from Genomic and SNP Data. *PLoS Genet* 9, e1003905.
1120 <https://doi.org/10.1371/journal.pgen.1003905>
1121

1122 Excoffier, L., Lischer H. E. L., 2010. Arlequin suite ver 3.5: a new series of programs to
1123 perform population genetics analyses under Linux and Windows. *Mol. Ecol. Res.*
1124 10(3): 564-567. <https://doi.org/10.1111/j.1755-0998.2010.02847.x>
1125

1126 Faria, R., Johannesson, K., Stankowski, S., 2021. Speciation in marine environments:
1127 Diving under the surface. *J of Evolutionary Biology* 34, 4–15.
1128 <https://doi.org/10.1111/jeb.13756>
1129

1130 Ferrini, V.L., Tivey, M.K., Carbotte, S.M., Martinez, F., Roman, C., 2008. Variable
1131 morphologic expression of volcanic, tectonic, and hydrothermal processes at six
1132 hydrothermal vent fields in the Lau back-arc basin: Hydrothermal Processes in
1133 Lau Back-arc Basin. *Geochem. Geophys. Geosyst.* 9, n/a-n/a.
1134 <https://doi.org/10.1029/2008GC002047>
1135

1136 Foll, M., Gaggiotti, O., 2008. A Genome-Scan Method to Identify Selected Loci
1137 Appropriate for Both Dominant and Codominant Markers: A Bayesian
1138 Perspective. *Genetics* 180, 977–993.
1139 <https://doi.org/10.1534/genetics.108.092221>
1140

1141 Folmer, O., Black, M., Hoeh, W., Lutz, R., And Vrijenhoek, R., 1994. DNA primers for
1142 amplification of mitochondrial cytochrome c oxidase subunit I from diverse
1143 metazoan invertebrates. *Molecular Marine Biology and Biotechnology*. 3294-299.

- 1144 François, O., Martins, H., Caye, K., Schoville, S.D., 2016. Controlling false discoveries in
1145 genome scans for selection. *Mol Ecol* 25, 454–469.
1146 <https://doi.org/10.1111/mec.13513>
1147
- 1148 Gagnaire, P.-A., Gaggiotti, O.E., 2016. Detecting polygenic selection in marine
1149 populations by combining population genomics and quantitative genetics
1150 approaches. *Curr Zool* 62, 603–616. <https://doi.org/10.1093/cz/zow088>
1151
- 1152 Gartman, A., Yücel, M., Madison, A.S., Chu, D.W., Ma, S., Janzen, C.P., Becker, E.L., Beinart,
1153 R.A., Girguis, P.R., Luther, G.W., 2011. Sulfide Oxidation across Diffuse Flow
1154 Zones of Hydrothermal Vents. *Aquat Geochem* 17, 583–601.
1155 <https://doi.org/10.1007/s10498-011-9136-1>
1156
- 1157 Gauthier, J., Mouden, C., Suchan, T., Alvarez, N., Arrigo, N., Riou, C., Lemaitre, C.,
1158 Peterlongo, P., 2020. DiscoSnp-RAD: de novo detection of small variants for
1159 RAD-Seq population genomics. *PeerJ* 8, e9291.
1160 <https://doi.org/10.7717/peerj.9291>
1161
- 1162 Gautier, M., Foucaud, J., Gharbi, K., Cézard, T., Galan, M., Loiseau, A., Thomson, M., Pudlo,
1163 P., Kerdelhué, C., Estoup, A., 2013. Estimation of population allele frequencies
1164 from next-generation sequencing data: pool-versus individual-based
1165 genotyping. *Mol Ecol* 22, 3766–3779. <https://doi.org/10.1111/mec.12360>
1166
- 1167 Gollner, S., Fontaneto, D., Martínez Arbizu, P., 2011. Molecular taxonomy confirms
1168 morphological classification of deep-sea hydrothermal vent copepods
1169 (Dirivultidae) and suggests broad physiological tolerance of species and
1170 frequent dispersal along ridges. *Mar Biol* 158, 221–231.
1171 <https://doi.org/10.1007/s00227-010-1553-y>
1172
- 1173 Gollner, S., Govenar, B., Fisher, C., Bright, M., 2015. Size matters at deep-sea
1174 hydrothermal vents: different diversity and habitat fidelity patterns of meio-
1175 and macrofauna. *Mar. Ecol. Prog. Ser.* 520, 57–66.
1176 <https://doi.org/10.3354/meps11078>
1177
- 1178 Gollner, S., Govenar, B., Martinez Arbizu, P., Mullineaux, L.S., Mills, S., Le Bris, N.,
1179 Weinbauer, M., Shank, T.M., Bright, M., 2020. Animal Community Dynamics at
1180 Senescent and Active Vents at the 9°N East Pacific Rise After a Volcanic
1181 Eruption. *Front. Mar. Sci.* 6, 832. <https://doi.org/10.3389/fmars.2019.00832>
1182
- 1183 Gollner, S., Ivanenko, V.N., Arbizu, P.M., Bright, M., 2010. Advances in Taxonomy,
1184 Ecology, and Biogeography of Dirivultidae (Copepoda) Associated with
1185 Chemosynthetic Environments in the Deep Sea. *PLoS ONE* 5, e9801.
1186 <https://doi.org/10.1371/journal.pone.0009801>
1187
- 1188 Gollner, S., Kaiser, S., Menzel, L., Jones, D.O.B., Brown, A., Mestre, N.C., Van Oevelen, D.,
1189 Menot, L., Colaço, A., Canals, M., Cuvelier, D., Durden, J.M., Gebruk, A., Egho, G.A.,
1190 Haeckel, M., Marcon, Y., Mevenkamp, L., Morato, T., Pham, C.K., Purser, A.,

1191 Sanchez-Vidal, A., Vanreusel, A., Vink, A., Martinez Arbizu, P., 2017. Resilience of
1192 benthic deep-sea fauna to mining activities. *Marine Environmental Research*
1193 129, 76–101. <https://doi.org/10.1016/j.marenvres.2017.04.010>
1194

1195 Gollner, S., Stuckas, H., Kihara, T.C., Laurent, S., Kodami, S., Martinez Arbizu, P., 2016.
1196 Mitochondrial DNA Analyses Indicate High Diversity, Expansive Population
1197 Growth and High Genetic Connectivity of Vent Copepods (Dirivultidae) across
1198 Different Oceans. *PLoS ONE* 11, e0163776.
1199 <https://doi.org/10.1371/journal.pone.0163776>
1200

1201 Gutenkunst, R.N., Hernandez, R.D., Williamson, S.H., Bustamante, C.D., 2009. Inferring
1202 the Joint Demographic History of Multiple Populations from Multidimensional
1203 SNP Frequency Data. *PLoS Genet* 5, e1000695.
1204 <https://doi.org/10.1371/journal.pgen.1000695>
1205

1206 Hey, R.N., Massoth, G.J., Vrijenhoek, R.C., Rona, P.A., Lupton, J., Butterfield, D.A., 2006.
1207 Hydrothermal Vent Geology and Biology at Earth's Fastest Spreading Rates. *Mar*
1208 *Geophys Res* 27, 137–153. <https://doi.org/10.1007/s11001-005-1887-x>
1209

1210

1211 Holderegger, R., Wagner, H.H., 2006. A brief guide to Landscape Genetics. *Landscape*
1212 *Ecol* 21, 793–796. <https://doi.org/10.1007/s10980-005-6058-6>
1213

1214 Honza, E., 1995. Spreading mode of backarc basins in the western Pacific.
1215 *Tectonophysics* 251, 139–152. [https://doi.org/10.1016/0040-1951\(95\)00054-](https://doi.org/10.1016/0040-1951(95)00054-2)
1216 [2](https://doi.org/10.1016/0040-1951(95)00054-2)
1217

1218 Hourdez S. And Jollivet D (2019) CHUBACARC cruise, RV L'Atalante.
1219 <https://doi.org/10.17600/18001111>

1220 Hourdez, S., Jollivet, D., 2020. Metazoan adaptation to deep-sea hydrothermal vents, in:
1221 Di Prisco, G., Edwards, H.G.M., Elster, J., Huiskes, A.H.L. (Eds.), *Life in Extreme*
1222 *Environments*. Cambridge University Press, pp. 42–67.
1223 <https://doi.org/10.1017/9781108683319.004>
1224

1225 Hu, E.-Z., Lan, X.-R., Liu, Z.-L., Gao, J., Niu, D.-K., 2022. A positive correlation between GC
1226 content and growth temperature in prokaryotes. *BMC Genomics* 23, 110.
1227 <https://doi.org/10.1186/s12864-022-08353-7>
1228

1229 Hu, R., Piotrowski, A.M., 2018. Neodymium isotope evidence for glacial-interglacial
1230 variability of deepwater transit time in the Pacific Ocean. *Nat Commun* 9, 4709.
1231 <https://doi.org/10.1038/s41467-018-07079-z>
1232

1233 Hurtado, L.A., Lutz, R.A., Vrijenhoek, R.C., 2004. Distinct patterns of genetic
1234 differentiation among annelids of eastern Pacific hydrothermal vents. *Mol Ecol*
1235 13, 2603–2615. <https://doi.org/10.1111/j.1365-294X.2004.02287.x>
1236

- 1237 Ingels, J., Leduc, D., Zeppilli, D., Vanreusel, A., 2023. Deep-Sea Meiofauna—A World on
1238 Its Own or Deeply Connected? In: Giere, O., Schratzberger, M. (eds) New
1239 Horizons in Meiobenthos Research. Springer, Cham.
1240 https://doi.org/10.1007/978-3-031-21622-0_8
1241
- 1242 Ivanenko, V.N., Martínez Arbizu, P., Stecher, J., 2007. Lecithotrophic nauplius of the
1243 family Dirivultidae (Copepoda; Siphonostomatoida) hatched on board over the
1244 Mid-Atlantic Ridge (5°S): Nauplius of Dirivultidae (Copepoda). *Marine Ecology*
1245 28, 49–53. <https://doi.org/10.1111/j.1439-0485.2007.00142.x>
1246
- 1247 John, C.R., Watson, D., Russ, D., Goldmann, K., Ehrenstein, M., Pitzalis, C., Lewis, M.,
1248 Barnes, M., 2020. M3C: Monte Carlo reference-based consensus clustering. *Sci*
1249 *Rep* 10, 1816. <https://doi.org/10.1038/s41598-020-58766-1>
1250
- 1251 Johnson, S.B., Warén, A., Tunnicliffe, V., Dover, C.V., Wheat, C.G., Schultz, T.F.,
1252 Vrijenhoek, R.C., 2015. Molecular taxonomy and naming of five cryptic species
1253 of *Alviniconcha* snails (Gastropoda: Abysochrysoidea) from hydrothermal
1254 vents. *Systematics and Biodiversity* 13, 278–295.
1255 <https://doi.org/10.1080/14772000.2014.970673>
1256
- 1257 Jollivet, D., Chevaldonné, P., Planque, B., 1999. Polychaete dispersal in the eastern
1258 pacific. 2. A metapopulation model based on habitat shifts. *Evolution*. 53(4):
1259 1128–1141. <https://doi.org/10.1111/j.1558-5646.1999.tb04527.x>
1260
- 1261 Jollivet, D., Desbruyères, D., Bonhomme, F., Moraga, D., 1995. Genetic differentiation of
1262 deep-sea hydrothermal vent alvinellid populations (Annelida: Polychaeta) along
1263 the East Pacific Rise. *Heredity* 74, 376–391.
1264 <https://doi.org/10.1038/hdy.1995.56>
1265
- 1266 Kakee, T., 2020. Deep-sea mining legislation in Pacific Island countries: From the
1267 perspective of public participation in approval procedures. *Marine Policy* 117,
1268 103881. <https://doi.org/10.1016/j.marpol.2020.103881>
1269
- 1270 Keenan, K., McGinnity, P., Cross, T.F., Crozier, W.W., Prodöhl, P.A., 2013. *diveRsity* : An R
1271 package for the estimation and exploration of population genetics parameters
1272 and their associated errors. *Methods Ecol Evol* 4, 782–788.
1273 <https://doi.org/10.1111/2041-210X.12067>
1274
- 1275 Knaus, B.J., Grünwald, N.J., 2017. VCFR: a package to manipulate and visualize variant
1276 call format data in R. *Mol Ecol Res*, 17(1), 44–53. ISSN 757.
1277 <https://dx.doi.org/10.1111/1755-0998.12549>
1278
- 1279 Lavigne, F., Morin, J., Wassmer, P., Weller, O., Kula, T., Maea, A. V., Kelfoun, K., Mokadem,
1280 F., Paris, R., Malawani, M. N., Farai, A., Benbakkar, M., Saulnier-Copard, S., Vidal,
1281 C. M., Tu’afitu, T., Kitekei’aho, F., Trautmann, M., Gomez, C., 2021. Bridging
1282 Legends and Science: Field Evidence of a Large Tsunami that Affected the

1283 Kingdom of Tonga in the 15th Century. *Front. Earth. Sci.* 9:748755.
1284 <https://doi.org/10.3389/feart.2021.748755>
1285

1286 Leaché, A., Ogilvie, H.A., 2016. Bayes Factor Delimitation of Species (*with genomic
1287 data; BFD*): A Tutorial and Worked Example.
1288

1289 Legendre, P., Gauthier, O., 2014. Statistical methods for temporal and space-time
1290 analysis of community composition data <sup/>. *Proc. R. Soc. B.* 281, 20132728.
1291 <https://doi.org/10.1098/rspb.2013.2728>
1292

1293 Lelièvre, Y., Sarrazin, J., Marticorena, J., Schaal, G., Day, T., Legendre, P., Hourdez, S.,
1294 Matabos, M., 2018. Biodiversity and trophic ecology of hydrothermal vent fauna
1295 associated with tubeworm assemblages on the Juan de Fuca Ridge.
1296 *Biogeosciences* 15, 2629–2647. <https://doi.org/10.5194/bg-15-2629-2018>
1297

1298 Lenihan, H.S., Mills, S.W., Mullineaux, L.S., Peterson, C.H., Fisher, C.R., Micheli, F., 2008.
1299 Biotic interactions at hydrothermal vents: Recruitment inhibition by the mussel
1300 *Bathymodiolus thermophilus*. *Deep Sea Research Part I: Oceanographic*
1301 *Research Papers* 55, 1707–1717. <https://doi.org/10.1016/j.dsr.2008.07.007>
1302
1303

1304 Levin, L.A., Amon, D.J., Lily, H., 2020. Challenges to the sustainability of deep-seabed
1305 mining. *Nat Sustain* 3, 784–794. <https://doi.org/10.1038/s41893-020-0558-x>
1306

1307 Limén, H., Stevens, C., Bourass, Z., Juniper, S., 2008. Trophic ecology of
1308 siphonostomatoid copepods at deep-sea hydrothermal vents in the northeast
1309 Pacific. *Mar. Ecol. Prog. Ser.* 359, 161–170.
1310 <https://doi.org/10.3354/meps07344>
1311

1312 Lotterhos, K.E., Whitlock, M.C., 2015. The relative power of genome scans to detect
1313 local adaptation depends on sampling design and statistical method. *Mol Ecol*
1314 24, 1031–1046. <https://doi.org/10.1111/mec.13100>
1315

1316 Lowry, D.B., Hoban, S., Kelley, J.L., Lotterhos, K.E., Reed, L.K., Antolin, M.F., Storfer, A.,
1317 2017. Breaking RAD: an evaluation of the utility of restriction site-associated
1318 DNA sequencing for genome scans of adaptation. *Mol Ecol Resour* 17, 142–152.
1319 <https://doi.org/10.1111/1755-0998.12635>
1320

1321 Luikart, G., England, P.R., Tallmon, D., Jordan, S., Taberlet, P., 2003. The power and
1322 promise of population genomics: from genotyping to genome typing. *Nat Rev*
1323 *Genet* 4, 981–994. <https://doi.org/10.1038/nrg1226>
1324

1325 Luu, K., Bazin, E., Blum, M. G. B., 2017. pcadapt: an R package to perform genome scans
1326 for selection based on principal component analysis. *Mol. Ecol. Res.* 17(1): 67-77.
1327 <https://doi.org/10.1111/1755-0998.12592>
1328

- 1329 Mackenzie, C.L., Kent, F.E.A., Baxter, J.M., Gormley, K.S.G., Cassidy, A.J., Sanderson, W.G.,
1330 Porter, J.S., 2022. Genetic Connectivity and Diversity of a Protected, Habitat-
1331 Forming Species: Evidence Demonstrating the Need for Wider Environmental
1332 Protection and Integration of the Marine Protected Area Network. *Front. Mar.*
1333 *Sci.* 9, 772259. <https://doi.org/10.3389/fmars.2022.772259>
1334
- 1335 Martinez, F., Taylor, B., 2006. Modes of crustal accretion in back-arc basins: Inferences
1336 from the Lau Basin, in: Christie, D.M., Fisher, C.R., Lee, S.-M., Givens, S. (Eds.),
1337 Geophysical Monograph Series. American Geophysical Union, Washington, D. C.,
1338 pp. 5–30. <https://doi.org/10.1029/166GM03>
1339
- 1340 Mastretta-Yanes, A., Arrigo, N., Alvarez, N., Jorgensen, T.H., Piñero, D., Emerson, B.C.,
1341 2015. Restriction site-associated DNA sequencing, genotyping error estimation
1342 and *de novo* assembly optimization for population genetic inference. *Mol Ecol*
1343 *Resour* 15, 28–41. <https://doi.org/10.1111/1755-0998.12291>
1344
- 1345 Mees, J., Seys, J., 2023. Book of abstracts – VLIZ Marine Science Day, 1 March 2023,
1346 Bruges. Title : VLIZ Special Publication. Vlaams Instituut voor de Zee (VLIZ):
1347 Oostende. ISSN 1377-0950 Volume : 90 Issue : Pagination : vi + 112.
1348 <https://doi.org/10.48470/41>
1349
- 1350 Mensing, R., Stewart, M., Hannington, M., Baxter, A., and Mertmann, D., 2020. The
1351 tectonic and volcanic evolution of the Mangatolu Triple Junction, EGU General
1352 Assembly 2020, Online, 4–8 May 2020, EGU2020-19897.
1353 <https://doi.org/10.5194/egusphere-egu2020-19897>
1354
- 1355 Micheli, F., Peterson, C.H., Mullineaux, L.S., Fisher, C.R., Mills, S.W., Sancho, G., Johnson,
1356 G.A., Lenihan, H.S., 2002b. PREDATION STRUCTURES COMMUNITIES AT DEEP-
1357 SEA HYDROTHERMAL VENTS. *Ecological Monographs* 72, 365–382.
1358 [https://doi.org/10.1890/0012-9615\(2002\)072\[0365:PSCADS\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0365:PSCADS]2.0.CO;2)
1359
- 1360 Milano, I., Babbucci, M., Cariani, A., Atanassova, M., Bekkevold, D., Carvalho, G.R.,
1361 Espiñeira, M., Fiorentino, F., Garofalo, G., Geffen, A.J., Hansen, J.H., Helyar, S.J.,
1362 Nielsen, E.E., Ogden, R., Patarnello, T., Stagioni, M., , Tinti, F. and Bargelloni, L.,
1363 2014. Outlier SNP markers reveal fine-scale genetic structuring across European
1364 hake populations (*Merluccius merluccius*). *Mol Ecol.* 23: 118-135.
1365 <https://doi.org/10.1111/mec.12568>
1366
- 1367 Miller, K.A., Thompson, K.F., Johnston, P., Santillo, D., 2018. An Overview of Seabed
1368 Mining Including the Current State of Development, Environmental Impacts,
1369 and Knowledge Gaps. *Front. Mar. Sci.* 4, 418.
1370 <https://doi.org/10.3389/fmars.2017.00418>
1371
- 1372 Mitarai, S., Siegel, D.A., Watson, J.R., Dong, C., McWilliams, J.C., 2009. Quantifying
1373 connectivity in the coastal ocean with application to the Southern California
1374 Bight. *J. Geophys. Res.* 114, C10026. <https://doi.org/10.1029/2008JC005166>
1375

1376 Mitarai, S., Watanabe, H., Nakajima, Y., Shchepetkin, A.F., McWilliams, J.C., 2016.
1377 Quantifying dispersal from hydrothermal vent fields in the western Pacific
1378 Ocean. Proc. Natl. Acad. Sci. U.S.A. 113, 2976–2981.
1379 <https://doi.org/10.1073/pnas.1518395113>
1380

1381 Monzier, M., Robin, C., Eissen, J-P, 1994. Kuwae (\approx 1425 A.D.): the forgotten caldera. J.
1382 volcanol. Geotherm. Res. 59, 207-218. [https://doi.org/10.1016/0377-](https://doi.org/10.1016/0377-0273(94)90091-4)
1383 [0273\(94\)90091-4](https://doi.org/10.1016/0377-0273(94)90091-4)
1384

1385 Mouchi, V., Pecheyran, C., Claverie, F., Cathalot, C., Matabos, M., Germain, Y., Rouxel, O.,
1386 Jollivet, D., Broquet, T., Comtet, T., 2023. A step towards measuring connectivity
1387 in the deep-sea: elemental fingerprints of mollusk larval shells discriminate
1388 hydrothermal vent sites. Biogeosciences, 21, 145-160. BioRxiv.
1389 <https://doi.org/10.1101/2023.01.03.522618>
1390

1391 Mullineaux, L.S., Adams, D.K., Mills, S.W., Beaulieu, S.E., 2010. Larvae from afar colonize
1392 deep-sea hydrothermal vents after a catastrophic eruption. Proc. Natl. Acad. Sci.
1393 U.S.A. 107, 7829–7834. <https://doi.org/10.1073/pnas.0913187107>
1394

1395 Mullineaux, L.S., Metaxas, A., Beaulieu, S.E., Bright, M., Gollner, S., Grupe, B.M., Herrera,
1396 S., Kellner, J.B., Levin, L.A., Mitarai, S., Neubert, M.G., Thurnherr, A.M., Tunnicliffe,
1397 V., Watanabe, H.K., Won, Y.-J., 2018. Exploring the Ecology of Deep-Sea
1398 Hydrothermal Vents in a Metacommunity Framework. Front. Mar. Sci. 5, 49.
1399 <https://doi.org/10.3389/fmars.2018.00049>
1400

1401 Murdock, S.A., Tunnicliffe, V., Boschen-Rose, R.E., Juniper, S.K., 2021. Emergent “core
1402 communities” of microbes, meiofauna and macrofauna at hydrothermal vents.
1403 ISME COMMUN. 1, 27. <https://doi.org/10.1038/s43705-021-00031-1>
1404

1405 Nakasugi, F., Shimanaga, M., Nomaki, H., Watanabe, H.K., Kitahashi, T., Motomura, Y.,
1406 Iseda, K., 2021. Simple harpacticoid composition observed at deep
1407 hydrothermal vent sites on sea knoll calderas in the North-west Pacific. J. Mar.
1408 Biol. Ass. 101, 947–956. <https://doi.org/10.1017/S0025315421000874>
1409

1410 Nomaki, H., Kawatani, K., Motomura, Y., Tame, A., Uyeno, D., Ogawa, N.O., Ohkouchi, N.,
1411 Shimanaga, M., 2023. Bacterivory of the hydrothermal-vent-specific copepod
1412 *Stygiopontius senokuchiae* (Dirivultidae, Siphonostomatoida) from copepodite
1413 through adult stages. J. Mar. Biol. Ass. 103, e21.
1414 <https://doi.org/10.1017/S0025315423000139>
1415

1416 Nomaki, H., Uejima, Y., Ogawa, N., Yamane, M., Watanabe, H., Senokuchi, R., Bernhard, J.,
1417 Kitahashi, T., Miyairi, Y., Yokoyama, Y., Ohkouchi, N., Shimanaga, M., 2019.
1418 Nutritional sources of meio- and macrofauna at hydrothermal vents and
1419 adjacent areas: natural-abundance radiocarbon and stable isotope analyses.
1420 Mar. Ecol. Prog. Ser. 622, 49–65. <https://doi.org/10.3354/meps13053>
1421

- 1422 O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P., Weiss,
1423 J.M., 2007. Temperature control of larval dispersal and the implications for
1424 marine ecology, evolution, and conservation. *Proc. Natl. Acad. Sci. U.S.A.* 104,
1425 1266–1271. <https://doi.org/10.1073/pnas.0603422104>
1426
- 1427 Olive, J.-A., Dublanchet, P., 2020. Controls on the magmatic fraction of extension at mid-
1428 ocean ridges. *Earth and Planetary Science Letters* 549, 116541.
1429 <https://doi.org/10.1016/j.epsl.2020.116541>
1430
- 1431 Paris, J.R., Stevens, J.R., Catchen, J.M., 2017. Lost in parameter space: a road map for
1432 STACKS. *Methods Ecol Evol* 8, 1360–1373. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.12775)
1433 [210X.12775](https://doi.org/10.1111/2041-210X.12775)
- 1434 Perez, M., Sun, J., Xu, Q., Qian, P.-Y., 2021. Structure and Connectivity of Hydrothermal
1435 Vent Communities Along the Mid-Ocean Ridges in the West Indian Ocean: A
1436 Review. *Front. Mar. Sci.* 8, 744874.
1437 <https://doi.org/10.3389/fmars.2021.744874>
1438
- 1439 Petersen, S., Krätschell, A., Augustin, N., Jamieson, J., Hein, J.R., Hannington, M.D., 2016.
1440 News from the seabed – Geological characteristics and resource potential of
1441 deep-sea mineral resources. *Marine Policy* 70, 175–187.
1442 <https://doi.org/10.1016/j.marpol.2016.03.012>
1443
- 1444 Pineda, J., Porri, F., Starczak, V., Blythe, J., 2010. Causes of decoupling between larval
1445 supply and settlement and consequences for understanding recruitment and
1446 population connectivity. *Journal of Experimental Marine Biology and Ecology*
1447 392, 9–21. <https://doi.org/10.1016/j.jembe.2010.04.008>
1448
- 1449 Poitrimol C, Thiébaud É, Daguin-Thiébaud C, Le Port A-S, Ballenghien M, Tran Lu Y A,
1450 Jollivet D, Hourdez S, Matabos M. Contrasted phylogeographic patterns of
1451 hydrothermal vent gastropods along South West Pacific: Woodlark Basin, a
1452 possible contact zone and/or stepping-stone. *PLoS ONE.* 2022 Oct 5; 17(10):
1453 e0275638. <https://doi.org/10.1371/journal.pone.0275638>
1454
- 1455 Plouviez, S., LaBella, A.L., Weisrock, D.W., Von Meijenfildt, F.A.B., Ball, B., Neigel, J.E.,
1456 Van Dover, C.L., 2019. Amplicon sequencing of 42 nuclear loci supports
1457 directional gene flow between South Pacific populations of a hydrothermal vent
1458 limpet. *Ecol Evol* 9, 6568–6580. <https://doi.org/10.1002/ece3.5235>
1459
- 1460 Plouviez, S., Schultz, T.F., McGinnis, G., Minshall, H., Rudder, M., Van Dover, C.L., 2013.
1461 Genetic diversity of hydrothermal-vent barnacles in Manus Basin. *Deep Sea*
1462 *Research Part I: Oceanographic Research Papers* 82, 73–79.
1463 <https://doi.org/10.1016/j.dsr.2013.08.004>
1464
- 1465 Portanier, E., Nicolle, A., Rath, W., Monnet, L., Le Goff, G., Le Port, A.-S., Daguin-Thiébaud,
1466 C., Morrison, C.L., Cunha, M.R., Betters, M., Young, C.M., Van Dover, C.L., Biastoch,
1467 A., Thiébaud, E., Jollivet, D., 2023. Coupling large-spatial scale larval dispersal
1468 modelling with barcoding to refine the amphi-Atlantic connectivity hypothesis

1469 in deep-sea seep mussels. *Front. Mar. Sci.* 10, 1122124.
1470 <https://doi.org/10.3389/fmars.2023.1122124>
1471

1472 Posavi, M., Gelembiuk, G.W., Larget, B., Lee, C.E., 2014. Testing for beneficial reversal of
1473 dominance during salinity shifts in the invasive copepod *Eurytemora affinis*,
1474 and implications for the maintenance of genetic variation. *Evolution* 68, 3166–
1475 3183. <https://doi.org/10.1111/evo.12502>
1476

1477 Riginos, C., Crandall, E.D., Liggins, L., Bongaerts, P., Treml, E.A., 2016. Navigating the
1478 currents of seascape genomics: how spatial analyses can augment population
1479 genomic studies. *Curr Zool* 62, 581–601. <https://doi.org/10.1093/cz/zow067>
1480

1481 Rochette, N.C., Catchen, J.M., 2017. Deriving genotypes from RAD-seq short-read data
1482 using Stacks. *Nat Protoc* 12, 2640–2659.
1483 <https://doi.org/10.1038/nprot.2017.123>
1484

1485 Rochette, N.C., Rivera-Colón, A.G., Catchen, J.M., 2019. Stacks 2: Analytical methods for
1486 paired-end sequencing improve RADseq-based population genomics. *Mol Ecol*
1487 28, 4737–4754. <https://doi.org/10.1111/mec.15253>
1488

1489 Rougeux, C., Bernatchez, L., Gagnaire, P.-A., 2017. Modeling the Multiple Facets of
1490 Speciation-with-Gene flow toward Inferring the Divergence History of Lake
1491 Whitefish Species Pairs (*Coregonus clupeaformis*). *Genome Biology and*
1492 *Evolution* 9, 2057–2074. <https://doi.org/10.1093/gbe/evx150>
1493

1494 Ruellan, E., Delteil, J., Wright, I., Matsumoto, T., 2003. From rifting to active spreading in
1495 the Lau Basin - Havre Trough backarc system (SW Pacific): Locking/unlocking
1496 induced by seamount chain subduction: LAU BASIN-HAVRE TROUGH SYSTEM.
1497 *Geochem. Geophys. Geosyst.* 4, n/a-n/a.
1498 <https://doi.org/10.1029/2001GC000261>
1499

1500 Siberchicot, A., Julien-Laferrière, A., Dufour, A., Thioulouse, J., Dray, S., 2017.
1501 adegraphics: An S4 Lattice-Based Package for the Representation of
1502 Multivariate Data. *The R Journal.* 9 (2):198-212. <https://doi.org/10.32614/RJ-2017-042>
1503
1504

1505 Siegel, D.A., Kinlan, B.P., Gaylord, B. and Gaines, S.D., 2003. Lagrangian descriptions of
1506 marine larval dispersion. *Marine Ecology Progress Series*, 260, pp.83-96.
1507 <https://doi.org/10.3354/meps260083>
1508

1509 Simons, E., Speer, K., Thurnherr, A.M., 2019. Deep circulation in the Lau Basin and
1510 Havre Trough of the western South Pacific Ocean from floats and hydrography. *J*
1511 *mar res* 77, 353–374. <https://doi.org/10.1357/002224019833406150>
1512

1513 Smagorinsky, J., 1963. GENERAL CIRCULATION EXPERIMENTS WITH THE PRIMITIVE
1514 EQUATIONS: I. THE BASIC EXPERIMENT*. *Mon. Wea. Rev.* 91, 99–164.
1515 [https://doi.org/10.1175/1520-0493\(1963\)091<0099:GCEWTP>2.3.CO;2](https://doi.org/10.1175/1520-0493(1963)091<0099:GCEWTP>2.3.CO;2)

1516
1517 Speer, K., Thurnherr, A., 2012b. The Lau Basin Float Experiment (LAUB-FLEX). *oceanog*
1518 25, 284–285. <https://doi.org/10.5670/oceanog.2012.27>
1519
1520 Stewart, M.S., Hannington, M.D., Emberley, J., Baxter, A.T., Krätschell, A., Petersen, S.,
1521 Brandl, P.A., Anderson, M.O., Mercier-Langevin, P., Mensing, R., Breker, K.,
1522 Fassbender, M.L., 2022. A new geological map of the Lau Basin (southwestern
1523 Pacific Ocean) reveals crustal growth processes in arc-backarc systems.
1524 *Geosphere*. <https://doi.org/10.1130/GES02340.1>
1525
1526 Storey, J.D., 2003. The positive false discovery rate: a Bayesian interpretation and the
1527 q-value. *Ann. Statist.* 31. <https://doi.org/10.1214/aos/1074290335>
1528
1529 Sunde, J., Yildırım, Y., Tibblin, P., Forsman, A., 2020. Comparing the Performance of
1530 Microsatellites and RADseq in Population Genetic Studies: Analysis of Data for
1531 Pike (*Esox lucius*) and a Synthesis of Previous Studies. *Front. Genet.* 11, 218.
1532 <https://doi.org/10.3389/fgene.2020.00218>
1533
1534 Sundqvist, L., Keenan, K., Zackrisson, M., Prodöhl, P., Kleinhans, D., 2016. Directional
1535 genetic differentiation and relative migration. *Ecol Evol* 6, 3461–3475.
1536 <https://doi.org/10.1002/ece3.2096>
1537
1538 Teixeira, S., Cambon-Bonavita, M.-A., Serrão, E.A., Desbruyères, D., Arnaud-Haond, S.,
1539 2011. Recent population expansion and connectivity in the hydrothermal
1540 shrimp *Rimicaris exoculata* along the Mid-Atlantic Ridge: Genetic diversity of a
1541 hydrothermal vent shrimp. *Journal of Biogeography* 38, 564–574.
1542 <https://doi.org/10.1111/j.1365-2699.2010.02408.x>
1543
1544 Teixeira, S., Serrão, E.A., Arnaud-Haond, S., 2012. Panmixia in a Fragmented and
1545 Unstable Environment: The Hydrothermal Shrimp *Rimicaris exoculata*
1546 Disperses Extensively along the Mid-Atlantic Ridge. *PLoS ONE* 7, e38521.
1547 <https://doi.org/10.1371/journal.pone.0038521>
1548
1549 Tepper, B., Bradley, B.P., 1989. Temporal Changes in a Natural Population of Copepods.
1550 *The Biological Bulletin* 176, 32–40. <https://doi.org/10.2307/1541886>
1551
1552 Thaler, A.D., Plouviez, S., Saleu, W., Alei, F., Jacobson, A., Boyle, E.A., Schultz, T.F.,
1553 Carlsson, J., Van Dover, C.L., 2014. Comparative Population Structure of Two
1554 Deep-Sea Hydrothermal-Vent-Associated Decapods (*Chorocaris* sp. 2 and
1555 *Munidopsis lauensis*) from Southwestern Pacific Back-Arc Basins. *PLoS ONE* 9,
1556 e101345. <https://doi.org/10.1371/journal.pone.0101345>
1557
1558 Thomas, G.W.C., Dohmen, E., Hughes, D.S.T., Murali, S.C., Poelchau, M., Glastad, K.,
1559 Anstead, C.A., Ayoub, N.A., Batterham, P., Bellair, M., Binford, G.J., Chao, H., Chen,
1560 Y.H., Childers, C., Dinh, H., Doddapaneni, H.V., Duan, J.J., Dugan, S., Esposito, L.A.,
1561 Friedrich, M., Garb, J., Gasser, R.B., Goodisman, M.A.D., Gundersen-Rindal, D.E.,
1562 Han, Y., Handler, A.M., Hatakeyama, M., Hering, L., Hunter, W.B., Ioannidis, P.,

1563 Jayaseelan, J.C., Kalra, D., Khila, A., Korhonen, P.K., Lee, C.E., Lee, S.L., Li, Y.,
 1564 Lindsey, A.R.I., Mayer, G., McGregor, A.P., McKenna, D.D., Misof, B., Munidasa, M.,
 1565 Munoz-Torres, M., Muzny, D.M., Niehuis, O., Osuji-Lacy, N., Palli, S.R., Panfilio,
 1566 K.A., Pechmann, M., Perry, T., Peters, R.S., Poynton, H.C., Prpic, N.-M., Qu, J.,
 1567 Rotenberg, D., Schal, C., Schoville, S.D., Scully, E.D., Skinner, E., Sloan, D.B.,
 1568 Stouthamer, R., Strand, M.R., Szucsich, N.U., Wijeratne, A., Young, N.D., Zattara,
 1569 E.E., Benoit, J.B., Zdobnov, E.M., Pfrender, M.E., Hackett, K.J., Werren, J.H.,
 1570 Worley, K.C., Gibbs, R.A., Chipman, A.D., Waterhouse, R.M., Bornberg-Bauer, E.,
 1571 Hahn, M.W., Richards, S., 2020. Gene content evolution in the arthropods.
 1572 *Genome Biol* 21, 15. <https://doi.org/10.1186/s13059-019-1925-7>
 1573
 1574 Tran Lu Y, A., Ruault, S., Daguin-Thiébaud, C., Castel, J., Bierne, N., Broquet, T., Wincker,
 1575 P., Perdereau, A., Arnaud-Haond, S., Gagnaire, P., Jollivet, D., Hourdez, S.,
 1576 Bonhomme, F., 2022. Subtle limits to connectivity revealed by outlier loci within
 1577 two divergent metapopulations of the deep-sea hydrothermal gastropod
 1578 *Ifremeria nautili*. *Molecular Ecology* 31, 2796–2813.
 1579 <https://doi.org/10.1111/mec.16430>
 1580
 1581 Tripp, E.A., Tsai, Y.E., Zhuang, Y., Dexter, K.G., 2017. RAD seq dataset with 90% missing
 1582 data fully resolves recent radiation of *Petalidium* (Acanthaceae) in the ultra-arid
 1583 deserts of Namibia. *Ecol Evol* 7, 7920–7936.
 1584 <https://doi.org/10.1002/ece3.3274>
 1585
 1586 Tsurumi, M., De Graaf, R.C., Tunnicliffe, V., 2003. Distributional and Biological Aspects
 1587 of Copepods at Hydrothermal Vents on the Juan de Fuca Ridge, north-east
 1588 Pacific Ocean. *J. Mar. Biol. Ass.* 83, 469–477.
 1589 <https://doi.org/10.1017/S0025315403007367h>
 1590
 1591 Van Dover, C.L., 2014. Impacts of anthropogenic disturbances at deep-sea
 1592 hydrothermal vent ecosystems: A review. *Marine Environmental Research* 102,
 1593 59–72. <https://doi.org/10.1016/j.marenvres.2014.03.008>
 1594
 1595 Van Dover, C.L., Arnaud-Haond, S., Gianni, M., Helmreich, S., Huber, J.A., Jaeckel, A.L.,
 1596 Metaxas, A., Pendleton, L.H., Petersen, S., Ramirez-Llodra, E., Steinberg, P.E.,
 1597 Tunnicliffe, V., Yamamoto, H., 2018. Scientific rationale and international
 1598 obligations for protection of active hydrothermal vent ecosystems from deep-
 1599 sea mining. *Marine Policy* 90, 20–28.
 1600 <https://doi.org/10.1016/j.marpol.2018.01.020>
 1601
 1602 Virtanen, E.A., Moilanen, A., Viitasalo, M., 2020. Marine connectivity in spatial
 1603 conservation planning: analogues from the terrestrial realm. *Landscape Ecol* 35,
 1604 1021–1034. <https://doi.org/10.1007/s10980-020-00997-8>
 1605
 1606 Vrijenhoek, R. C., 2010. Genetic diversity and connectivity of deep-sea hydrothermal
 1607 vent metapopulations. *Mol. Ecol.* 19: 4391-
 1608 4411. <https://doi.org/10.1111/j.1365-294X.2010.04789.x>
 1609

- 1610 Wang, S., Meyer, E., McKay, J.K., Matz, M.V., 2012. 2b-RAD: a simple and flexible method
1611 for genome-wide genotyping. *Nat Methods* 9, 808–810.
1612 <https://doi.org/10.1038/nmeth.2023>
1613
1614
- 1615 Watanabe, H.K., Senokuchi, R., Nomaki, H., Kitahashi, T., Uyeno, D., Shimanaga, M., 2021.
1616 Distribution and Genetic Divergence of Deep-Sea Hydrothermal Vent Copepods
1617 (Dirivultidae: Siphonostomatoida: Copepoda) in the Northwestern Pacific.
1618 *Zoological Science* 38. <https://doi.org/10.2108/zs200153>
1619
1620
- 1621 Won, Y., Hallam, S.J., O’Mullan, G.D., Vrijenhoek, R.C., 2003. Cytonuclear disequilibrium
1622 in a hybrid zone involving deep-sea hydrothermal vent mussels of the genus
1623 *Bathymodiolus*. *Molecular Ecology* 12, 3185–3190.
1624 <https://doi.org/10.1046/j.1365-294X.2003.01974.x>
1625
- 1626 Xu, T., Wang, Y., Sun, J., Chen, C., Watanabe, H.K., Chen, J., Qian, P.-Y., Qiu, J.-W., 2021.
1627 Hidden Historical Habitat-Linked Population Divergence and Contemporary
1628 Gene Flow of a Deep-Sea Patellogastropod Limpet. *Molecular Biology and*
1629 *Evolution* 38, 5640–5654. <https://doi.org/10.1093/molbev/msab278>
1630
- 1631 Xuereb, A., Benestan, L., Normandeau, É., Daigle, R.M., Curtis, J.M.R., Bernatchez, L.,
1632 Fortin, M.-J., 2018. Asymmetric oceanographic processes mediate connectivity
1633 and population genetic structure, as revealed by RADseq, in a highly dispersive
1634 marine invertebrate (*Parastichopus californicus*). *Mol Ecol* 27, 2347–2364.
1635 <https://doi.org/10.1111/mec.14589>
1636
1637
- 1638 Yahagi, T., Fukumori, H., Warén, A., & Kano, Y., 2019. Population connectivity of
1639 hydrothermal-vent limpets along the northern Mid-Atlantic Ridge (Gastropoda:
1640 Neritimorpha: Phenacolepadidae). *Journal of the Marine Biological Association*
1641 *of the United Kingdom*, 99(1), 179-185.
1642 <https://doi.org/10.1017/S0025315417001898>
1643
- 1644 Yahagi, T., Kayama Watanabe, H., Kojima, S., Kano, Y., 2017. Do larvae from deep-sea
1645 hydrothermal vents disperse in surface waters? *Ecology* 98, 1524–1534.
1646 <https://doi.org/10.1002/ecy.1800>
1647
- 1648 Yahagi, T., Thaler, A.D., Van Dover, C.L., Kano, Y., 2020. Population connectivity of the
1649 hydrothermal-vent limpet *Shinkailepas tollmanni* in the Southwest Pacific
1650 (Gastropoda: Neritimorpha: Phenacolepadidae). *PLoS ONE* 15, e0239784.
1651 <https://doi.org/10.1371/journal.pone.0239784>
1652
- 1653 Yearsley, J.M., Salmanidou, D.M., Carlsson, J., Burns, D., Van Dover, C.L., 2020.
1654 Biophysical models of persistent connectivity and barriers on the northern Mid-
1655 Atlantic Ridge. *Deep Sea Research Part II: Topical Studies in Oceanography* 180,
1656 104819. <https://doi.org/10.1016/j.dsr2.2020.104819>

1657 Table 1: Location of sampling sites (latitude and longitude) with corresponding depth (m) at time of
 1658 sampling. Spreading rate values were taken from Stewart et al. (2022).
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Basin	Site	Latitude	Longitude	Depth (m)	Spreading Rate	Substrate	Sample size	Year sampled	References
ELSC	Tu'i Malila	-21.99	-176.57	1888	48	Basalt	24	2019	Hourdez and Jollivet (2019) Stewart et al. (2022)
ELSC	ABE	-20.76	-176.19	2155	69	Andesitic	24	2016	Beinart et al. (2018) Stewart et al. (2022)
ELSC	ABE	-20.77	-176.20	2153	69	Andesitic	11	2019	Hourdez and Jollivet (2019) Stewart et al. (2022)
ELSC	Tahi Moana	-20.05	-176.13	2273	69	Andesitic	15	2016	Beinart et al. (2018) Stewart et al. (2022)
ELSC	Mangatolo	-15.41	185.35	2039	37	Andesitic	64	2019	Hourdez and Jollivet (2019) Stewart et al. (2022)

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1664 Table 2: Analysis of Molecular Variance results of pairwise differences between populations, indicating the
 1665 pairs, the F_{st} value for each pair and the p -value associated with each F_{st} calculation. Significance codes:
 1666 (***) $p < 0.001$, (**) $p < 0.01$ (* $p < 0.05$). Observed heterozygosity for each population was calculated (H_{tobs}).
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Population	H_{tobs}	Tahi Moana	Mangatolo	Tui Malila	ABE (2016)	ABE (2019)
Tahi Moana	0.12	0				
Mangatolo	0.24	0.24*	0			
Tui Malila	0.18	0.24*	0.12*	0		
ABE (2016)	0.12	0.00	0.26*	0.25*	0	
ABE (2019)	0.08	0.11*	0.05*	0.08*	0.07*	0

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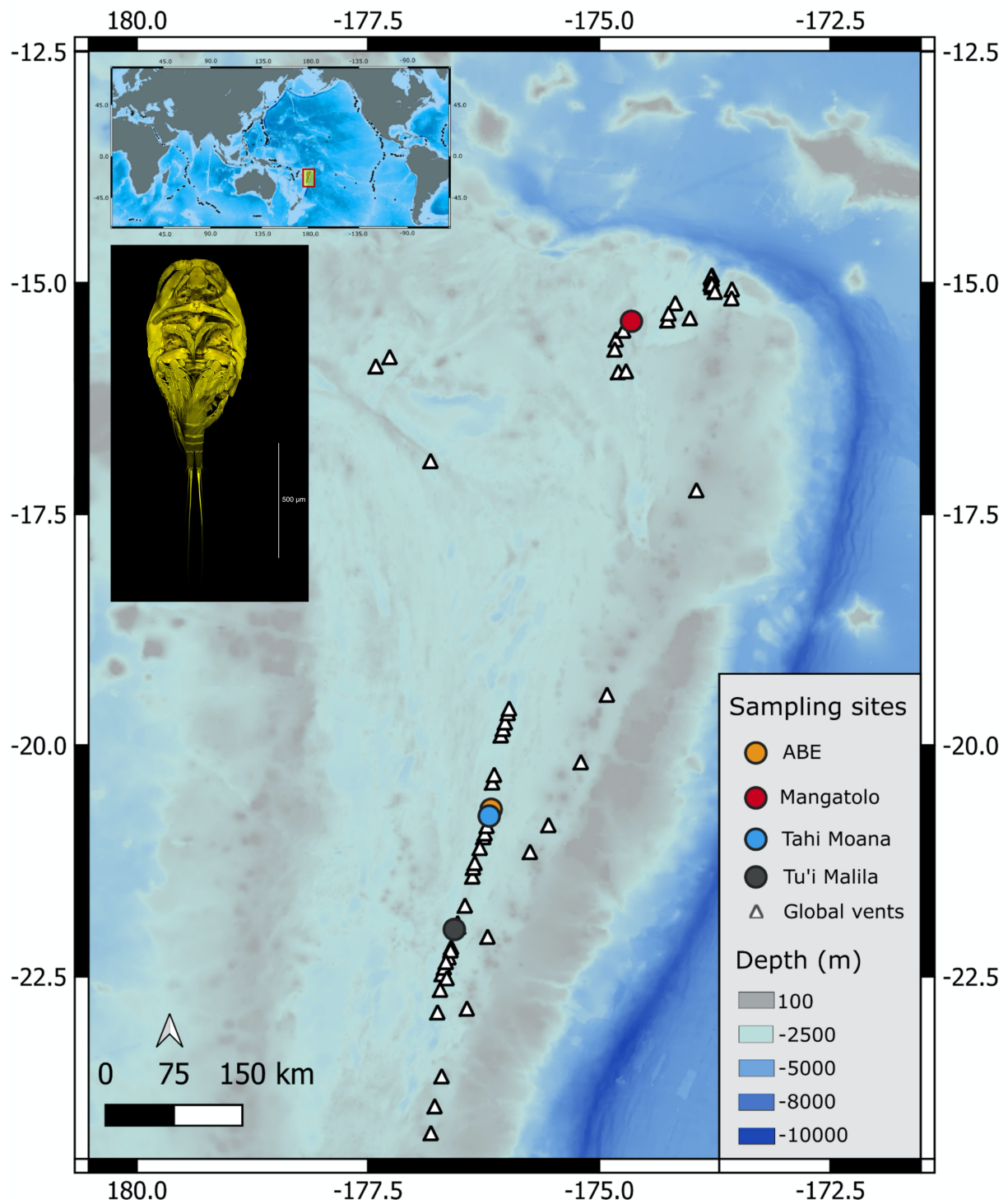
1678 Table 3: Parameters estimated from $\partial a \partial i$ for the best model (SC2N2mG) with their standard deviations (SD)
 1679 estimated using the Fisher Information Matrix (FIM), and with parameters describing effective population
 1680 size (2N), migration rate (2m), and population growth (G) between populations within the Lau basin.

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North-mid			North-south		
Parameter	Value	SD	Parameter	Value	SD
Nu1 (mid)	2.41	0.63	Nu1 (north)	1.40	0.76
Nu2 (north)	0.80	0.61	Nu2 (south)	1.24	1.16
b1	0.31	0.07	b1	0.74	0.21
b2	0.63	0.60	b2	1.03	0.19
hrf	0.14	0.07	hrf	0.11	0.06
T _s	4.91	1.47	T _s	7.92	5.80
T _{sc}	0.17	0.01	T _{sc}	0.26	0.07
m1<-2	0.68	0.10	m1<-2	5.24	1.16
m2<-1	5.97	0.40	m2<-1	6.24	2.35
me1<-2	0.98	0.09	me1<-2	4.64	1.39
me2<-1	0.51	0.13	me2<-1	1.03	0.64
P	0.74	0.04	P	0.03	0.23
Q	0.17	0.12	Q	0.49	0.28
Theta	91.82	23.55	Theta	155.82	93.60
Time to population split (years)	119,422	35,764	Time to the population split (years)	325,661	239,304
Time to secondary contact (years)	4,050	274	Time to the secondary contact (years)	10,762	3,231

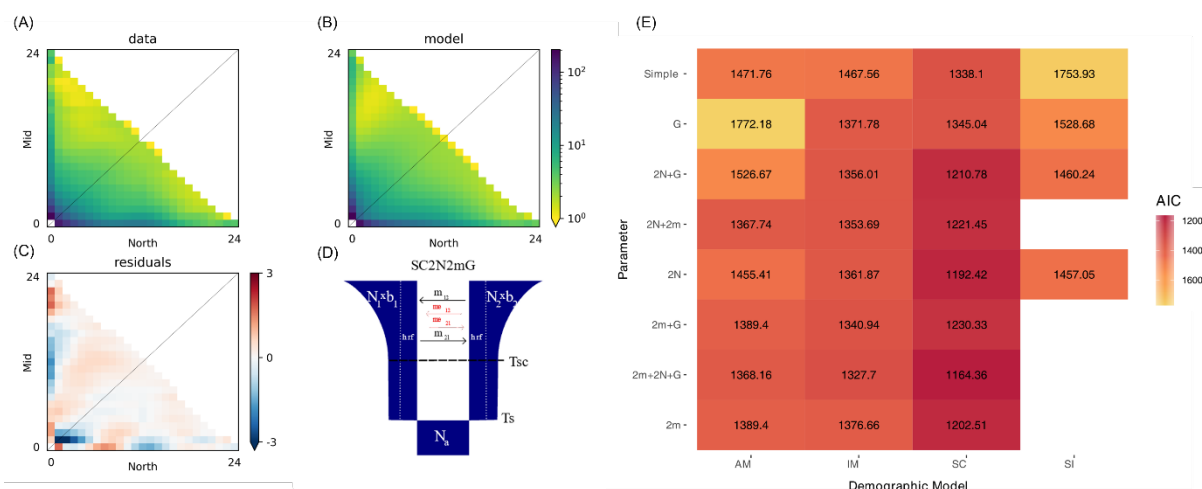
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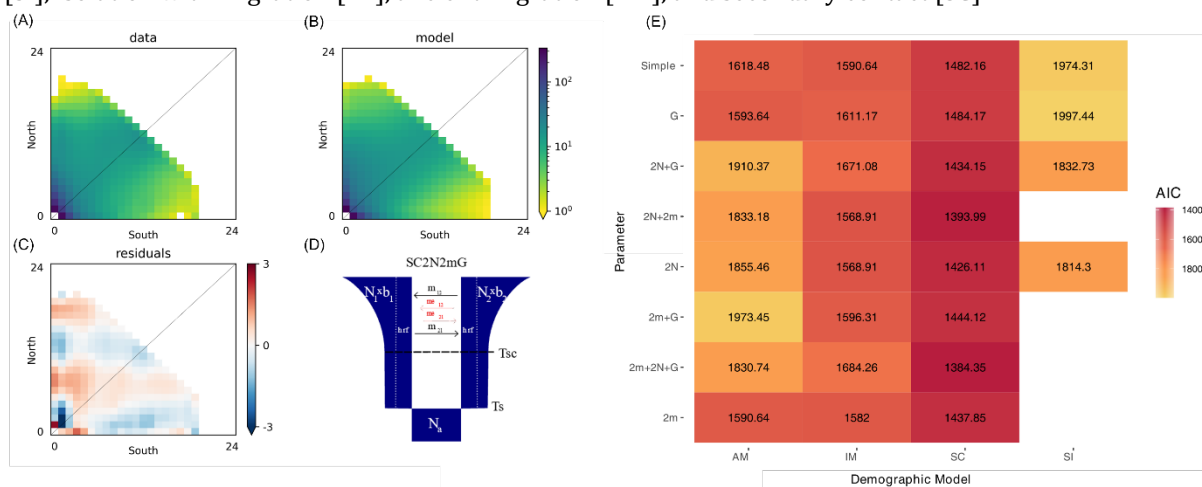
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1686 Figure 1: Map of sampling sites from 2016, and 2019 within the Lau Basin (Mangatolo, Tahi Moana, ABE,
1687 and Tu'i Malila). A dorsal confocal microscopic image of an *S. lauensis* female from the ABE hydrothermal
1688 vent field in the Lau Basin. Image taken at the German Center for Marine Biodiversity Research by Dr. Jimmy
1689 Bernot.
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1711 Figure 4: A) Joint allele frequency spectrum (JAFS) between North (Mangatolo) and Mid (pooled Tahī Moana
 1712 and ABE) vent sites within the Lau Basin. B) Simulated JAFS under the SC2N2mG model. The log scale
 1713 indicates the density of SNPs in each frequency class (shared between the mid and north). C) Residuals of
 1714 the fit of the simulated model on the data. D) Schematic of the fitted model (N , population size; b , population
 1715 growth factor; hrf , the Hill-Robertson factor, which simulates linked selection; m , unrestricted migration
 1716 rate; m_e , restricted migration rate, which simulates barrier loci). E) Heat-map of the best Akaike
 1717 information criterion (AIC) value for each parameter combination (population expansion or contraction [G],
 1718 effect of linked selection [$2N$] and heterogeneous migration [$2m$]) and demographic model (strict isolation
 1719 [SI], isolation with migration [IM], ancient migration [AM], and secondary contact [SC]).



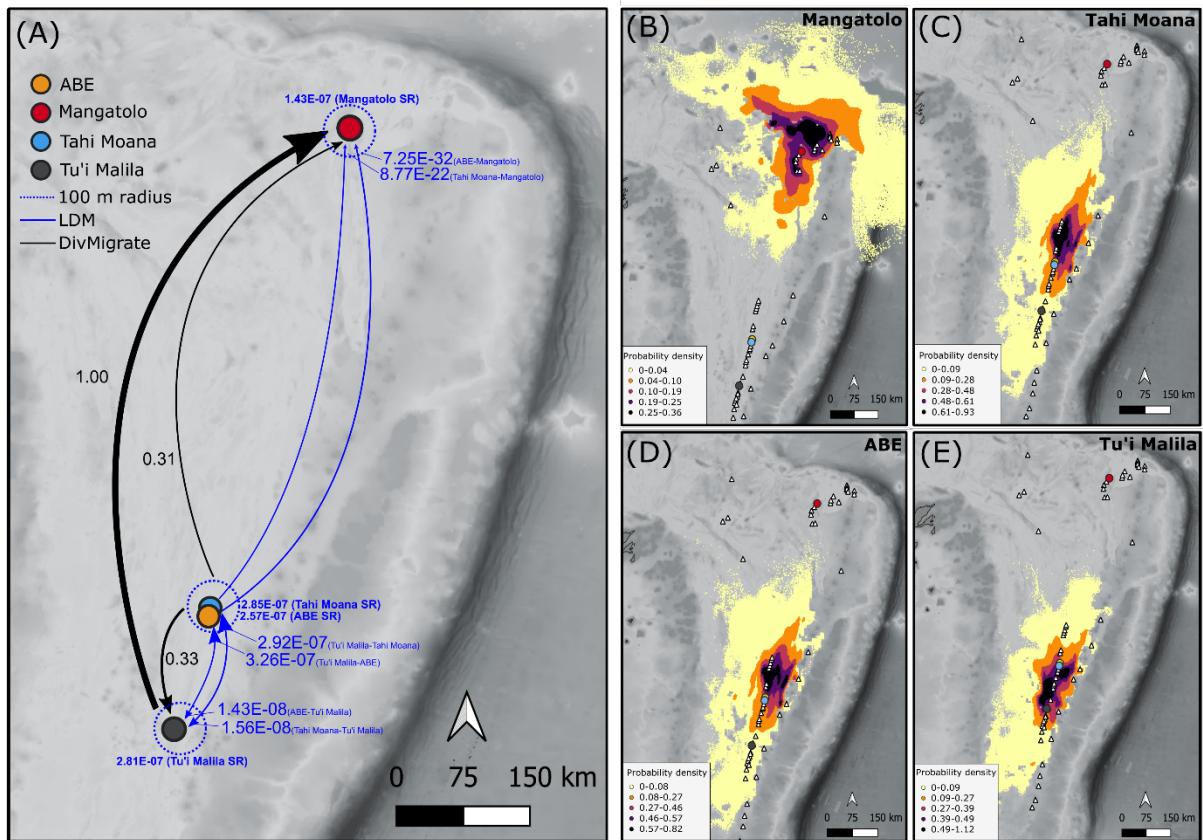
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1721 Figure 5: A) Joint allele frequency spectrum (JAFS) between North (Mangatolo) and South (Tu'i Malila)
 1722 vent sites within the Lau Basin. B) Simulated JAFS under the SC2N model. The log scale indicates the
 1723 density of SNPs in each frequency class. C) Residuals of the fit of the simulated model on the data.
 1724 D) Schematic of the fitted model (N , population size; b , population growth factor; hrf , the Hill-Robertson
 1725 factor, which simulates linked selection; m , unrestricted migration rate; m_e , restricted migration rate,
 1726 which simulates barrier loci). E) Heat-map of the best Akaike information criterion (AIC) value for
 1727 each parameter combination (population expansion or contraction [G], effect of linked selection [$2N$]
 1728 and heterogeneous migration [$2m$]) and demographic model (strict isolation [SI], isolation with
 1729 migration [IM], ancient migration [AM], and secondary contact [SC]).

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Figure 6: A) Significant relative migration (effective number of migrants, nM) calculated using the Nm statistic and 1000 bootstraps in *DivMigrate* (empirical data = black arrows), and larval dispersal model (LDM) simulations (blue arrows). Blue dashed line denotes a 100 m radius (not to scale around each vent). The thickness of the arrows and size of the arrow heads in each instance denotes the strength of directionality. SR = self-recruitment. Gaussian point distribution probabilities (probability density) for B) Mangatolo, C) Tahī Moana, D) ABE, and E) Tu'i Malila. Blue dashed white triangles denote existing (and possibly stepping stone) vents within the basin from which data was not collected.