Reproduction in deep-sea vent shrimps is shaped by diet and phylogeny, with rhythms unlinked to surface production

Authors and Affiliations

Pierre Methou[1,2,3]*, Chong Chen[3], Hiromi K. Watanabe[3], Marie-Anne Cambon-Bonavita[1], Florence Pradillon[2]**

[1]: Univ Brest, Ifremer, CNRS, Laboratoire de Microbiologie des Environnements Extrêmes, UMR6197, 29280 Plouzané, France

[2]: Ifremer, Centre Brest, Laboratoire Environnements Profonds (REM/EEP/LEP), 1625 route de Sainte Anne, 29280 Plouzané, France

[3]: X-STAR, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Yokosuka, 237-0061, Japan

*Contact author, email PM: pierre.methou@ifremer.fr; pmethou@jamstec.go.jp

**Corresponding author, emails FP: florence.pradillon@ifremer.fr

Running head: Reproductive strategies in *Rimicaris* vent shrimps

Abstract

Variations in offspring production according to feeding strategies or food supply have been recognized in many animals from various ecosystems. Despite an unusual trophic structure based on non-photosynthetic primary production, these relationships remain largely under-studied in chemosynthetic ecosystems. Here, we use *Rimicaris* shrimps from deep-sea hydrothermal vents as a study case to explore relations between reproduction, diets and food supply in these environments. For that, we compared reproductive outputs of three congeneric shrimps differing by their diets. They inhabit vents located under oligotrophic waters of tropical gyres with opposed latitudes, allowing us to also examine the prevalence of phylogenetic vs environmental drivers in their reproductive rhythms. For this we used both our original data and a compilation of published observations on the presence of ovigerous females covering various seasons over the past 35 years. We report distinct egg production trends between

Rimicaris species relying solely on chemosymbiosis – *R. exoculata* and *R. kairei* – and those relying on mixotrophy – *R. chacei* – where *R. chacei* produces broods with higher numbers of smaller eggs. Besides, our data and historical records suggest a reproductive period with substantial proportions of brooding females mostly between January and early April for all examined species whatever the region. Intriguingly, this periodicity does not correspond to seasonal variations in surface production with presence of brooding females during either boreal winter or austral summer. These observations contrast with the long-standing paradigm in deep-sea species for which periodic reproductive patterns have always been attributed to seasonal variations of photosynthetic production sinking from surface. Our results suggest the presence of intrinsic basis for biological rhythms in the deep sea, and bring to light the importance of having year-round observations in order to understand life history of vent animals.

Keywords

Biological rhythms, crustacean, deep sea, hydrothermal vent, reproduction, seasonality, trophic ecology

Introduction

Relationships between feeding strategies and offspring's production have been extensively studied for a number of animal phyla in various ecosystems (Pierotti and Annett 1990, Qian and Chia 1991, Broderick et al. 2003, Meiri et al. 2012, Sibly et al. 2012). Where no clear trends between trophic regime and reproductive outputs could be observed in lizards (Meiri et al. 2012), large variations of fecundity or reproductive outputs according to diets have been highlighted in others including birds (Pierotti and Annett 1990, Sibly et al. 2012), sea turtles (Broderick et al. 2003), annelids (Qian and Chia 1991), insects (Gutiérrez et al. 2020), or crustaceans (Lin and Shi 2002, Tziouveli et al. 2011, Almeida et al. 2018). All these studies are based on ecosystems where photosynthetic primary production is the sole basis of food webs. A number of ecosystems on Earth, such as deep-sea hydrothermal vents, cold seeps and organic falls, rely on another primary organic source: the chemosynthesis (German et al. 2011). In chemosynthetic-based ecosystems lush and dense faunal communities are supported by

57 microbial communities using chemical energy arising from geofluids to produce their organic
58 matter, and animals there often form intricate symbiotic associations with these
59 chemosynthetic bacteria for nutrition (Dubilier et al. 2008). From total reliance on symbiosis to
60 bacterivory to mixotrophy to carnivorous, these particular ecosystems display a variety of diets
61 in networks often differing strikingly from those found elsewhere (Govenar 2012). In this
62 context, these environments are natural laboratories to study relationships between
63 reproduction and trophic regimes. However, no study has yet explored these relationships
64 extensively in chemosynthetic-based ecosystems, with variations in the reproductive output
65 among or within animal groups being mostly attributed to phylogenetic constraints (Tyler and
66 Young 1999) or variations in female body size (Ramirez-Llodra et al. 2000, Copley and Young
67 2006, Nye et al. 2013, Marsh et al. 2015, Marticorena et al. 2020).

68 Although most species from deep-sea chemosynthetic-based ecosystems exhibit
69 continuous reproductive patterns (Jollivet et al. 2000, Faure et al. 2007, Tyler et al. 2008, Hilário
70 et al. 2009, Marticorena et al. 2020), seasonal cycles following variations in surface primary
71 production have been observed in many taxa such as bythograeid crabs, alvinocaridid shrimps,
72 and bathymodiolin mussels (Perovich et al. 2003, Dixon et al. 2006, Copley and Young 2006,
73 Tyler et al. 2007). In some groups, the surface production pattern is clearly linked to
74 reproductive patterns in the deep. For example, some vent crab species exhibit continuous
75 gametogenesis under the highly oligotrophic waters of the South Pacific Gyre, while others
76 living in more productive areas north of this gyre have seasonal reproduction (Perovich et al.
77 2003, Hilário et al. 2009). Such examples have led to the paradigm that rhythms of sinking
78 photosynthetic matter is the key time-synchronising cue for deep-water animals with seasonal
79 reproduction, signalling individuals to spawn at the same period of the year.

80 The symbiotic and sister-species shrimps *Rimicaris exoculata* and *R. kairei* are among the
81 most iconic hot-vent animals, with unique adaptations such as hosting symbiotic bacteria in
82 their enlarged head cavity and the fused "dorsal eye", a novel sensory system representing a
83 pinnacle of adaptation to vents (Zbinden and Cambon-Bonavita 2020). The entire family they
84 belong to, Alvinocarididae, is endemic to vents and seeps with different taxa exhibiting various
85 trophic regimes and various levels of reliance on symbiosis (Rieley et al. 1999, Gebruk et al.

86 2000, Apremont et al. 2018), constituting an ideal case for elucidating relationships between
87 reproduction and diet in chemosynthesis-based ecosystems. Species with different trophic
88 regimes often co-occur on same vent fields, for example *R. exoculata* which rely on symbiosis
89 and the mixotrophic *R. chacei*, allowing for a straight-forward comparison of species. The
90 symbiotrophic species such as *R. exoculata* and *R. kairei* exhibit greatly inflated cephalothorax
91 and live in large aggregations around the hot fluid flows (Rieley et al. 1999, Gebruk et al. 2000,
92 Van Dover 2002, Streit et al. 2015, Methou et al. 2020), whereas mixotrophic species such as *R.*
93 *chacei* (Gebruk et al. 2000, Apremont et al. 2018, Methou et al. 2020) lacks the inflated
94 cephalothorax and lives in small groups (Methou et al. 2021).

95 Attempts to understand the reproduction of *Rimicaris* shrimps have so far faced
96 contradicting evidences. While continuous reproduction was initially suggested from
97 examination of their reproductive tissues (Ramirez-Llodra et al. 2000, Copley et al. 2007) hardly
98 any ovigerous individuals could be collected in over 35 years of seagoing expeditions, despite a
99 relatively focused and repeated sampling effort (Williams and Rona 1986, Vereshchaka 1997,
100 Shank et al. 1998, Ramirez-Llodra et al. 2000, Copley et al. 2007, Komai and Segonzac 2008).
101 Brooding females were only found in large numbers in 2014 (Methou et al. 2019, Hernández-
102 Ávila et al. 2021) and to a lesser extent in 2007 (Guri et al. 2012), around a restricted period
103 between January and March. These females were living within dense aggregations close to vent
104 orifices (Hernández-Ávila et al. 2021), refuting previous hypothesis that brooding females
105 would migrate to vent periphery to protect their eggs from vent fluid, as observed for
106 bythograeid crabs (Perovich et al. 2003) as well as *Kiwa* squat lobsters (Marsh et al. 2015).
107 Taken together, these recent findings suggest a seasonal reproductive cycle possibly linked to
108 surface primary production, as shown in vent crabs, bathymodiolin mussels and some other
109 alvinocaridid shrimps (Dixon et al. 2006, Copley and Young 2006, Tyler et al. 2007). However,
110 the low primary productivity of oligotrophic surface waters and the overall low export to the
111 deep-sea compartment within the region where these shrimps have been collected (-3500 m
112 depth) (Pabortsava et al. 2017, Harms et al. 2021) challenges the possibility of such a link.

113 Here, we compare reproductive outputs – i.e., fecundities and egg volumes – of three
114 congeneric vent shrimps with contrasting diets, using two species with a full nutritional

dependence on their chemosymbiosis (i.e., *R. exoculata* and *R. kairei*) and one with a mixotrophic diet combining symbiosis, bacterivory, and scavenging (i.e., *R. chacei*) to find out if links between diets and reproduction are also present in chemosynthetic based ecosystems. Distribution of these species in two different hemispheres (Northern Atlantic and Southern Indian Ocean) with similar levels of, but seasonally opposed, surface production allows us to evaluate if their brooding periods are in synchrony with patterns of surface primary productivity.

Materials & Methods

Field sampling

Shrimps were collected from three hydrothermal vent fields (figure 1): TAG (26°08'12.12''N, 44°49'36.12''W, 3620 m depth) and Snake Pit (23°22'5.88''N 44°57'0''W, 3470 m depth) on the Mid Atlantic Ridge (MAR) between March and April in 2017 (HERMINE (doi:10.17600 /17000200)) and between February and March in 2018 (BICOSE2 (doi:10.17600/18000004)) for *R. exoculata* and *R. chacei*, and Kairei (25°19'10.2''S, 70°2'24''E, 2415 m depth) on the Central Indian Ridge (CIR) between February and March both in 2002 and 2016, as well as in November 2009 for *R. kairei*. Shrimps were sampled using suction samplers of the human-occupied vehicle (HOV) *Nautile* or the HOV *Shinkai 6500*. Upon recovery on-board, ovigerous females of *R. exoculata* and *R. chacei* were identified and individually sorted from the rest of the population. An additional published dataset for *Rimicaris exoculata* collected at TAG and Snake Pit in January-February 2014 is also included in our analyses and available in the Ifremer SEANOE (SEA scieNtific Open data Edition) database at: https://doi.org/10.17882/84112.

Ovigerous females include both brooding females and females that have just released their larvae but still retained modified pleopods, characteristic of a recent brooding status, following Nye at al. 2013 (Nye et al. 2013). For *R. kairei*, ovigerous females were identified and sorted from the rest of the population in the laboratory after the cruise. Egg stages in broods were identified on-board during the BICOSE2 expedition before being fixed in 10% neutral buffered formalin for 24h and then rinsed and stored in 80% EtOH. For other expeditions,

143 ovigerous females were fixed and stored in 10% formalin on-board and identification of egg
144 stages was conducted in shore-based laboratory.

145 **Shrimps and Eggs Measurements**

146 Carapace length (CL) of each female was measured with Vernier callipers from the
147 posterior margin of the ocular shield (or eye socket) to mid-point of the posterior margin of the
148 carapace, with an estimated precision of 0.1 mm. For each brood, total number of eggs was
149 manually counted. Ten eggs were selected randomly to measure maximum and minimum
150 diameters. Volume of embryos was estimated following the same method as (Hernández-Ávila
151 et al. 2021), considering a spheroid volume $v= (4/3).\pi.r1.r2^2$, where r1 and r2 are half of
152 maximum and minimum axis of each egg, respectively. Eggs in broods were classified in three
153 developmental stages (early, mid, and late), following the classification used in (Methou et al.
154 2019). Some ovigerous females harboured damaged or aborted broods and were thus
155 discarded from our fecundity analysis. Furthermore, we also compiled data for the presence of
156 ovigerous female shrimps from the literature and using dive videos from cruises over the last 35
157 years, in order to assess the reproductive seasonality. Proportions of ovigerous females within
158 samples were calculated against the number of sexually mature females (See supplementary
159 material). Dataset compiling size, reproductive status, fecundities, egg developmental stages,
160 and egg diameters of each shrimp individual is available in the Ifremer SEANOE (SEA scieNtific
161 Open data Edition) database at: https://doi.org/10.17882/84195.

162 **Statistical analysis**

163 Brooding females were grouped according to sampling year, species and vent field.
164 Visual examination of our dataset and Shapiro-Wilk normality tests revealed that size, egg
165 number, and egg volume of *Rimicaris* brooding females deviated from normal distribution.
166 Therefore, non-parametric tests were used for intergroup comparison, with a Kruskal-Wallis
167 test followed by post-hoc Dunn tests when three or more groups were compared. Spearman
168 rank-order correlation were used to assess relationship between $\log_e$-transformed realized
169 fecundity and $\log_e$-transformed carapace length of the different shrimp groups. Egg stage

170 proportions between groups were compared using χ^2 test with Yate's correction. All analyses
171 were performed in R v. 4.0.3 (R Core Team 2020).

172 ## Results

173 ### Interannual variation of *R. exoculata* reproduction

174 Realized fecundity of *Rimicaris exoculata* correlated positively with carapace length in
175 both 2014 (Spearman correlation r= 0.67, p < 0.0001) and 2018 (Spearman correlation r= 0.73,
176 p < 0.0001) (figure 2a). Moreover, slopes of the relationship between $\log_e$-transformed realized
177 fecundity and $\log_e$-transformed carapace length did not differ significantly between these two
178 sampling years (F= 1.175, p = 0.28) or between TAG and Snake Pit in 2018 (F= 0.004, p= 0.95).
179 Although no correlation was found in 2017 (Spearman correlation r= 0.38, p= 0.16), probably
180 due to the lower sampling effort, realized fecundity in 2017 still fell within the range of the
181 other sampling years (figure 2a).

182 Overall, size-specific fecundity ranged from 19 to 95 eggs mm^{-1} in 2014, from 15 to 80
183 eggs mm^{-1} in 2017 and from 10 to 134 eggs mm^{-1} in 2018 (figure 2b). Limited differences in size-
184 specific fecundities were observed between different sampling years (Kruskal-Wallis, H= 65.025
185 p < 0.05) with significant variations between 2014 and 2018 at TAG only (2014: 37.3 ± 11.4;
186 2018: 49.4 ± 12.9; Dunn's Multiple Comparison Test, p < 0.05). Differences in size-specific
187 fecundity were also observed between the two vent fields both in 2014 and in 2018, (Dunn's
188 Multiple Comparison Tests, p < 0.05). Carapace length of brooding females from TAG were
189 indeed larger in 2018 than in 2014 (Dunn's Multiple Comparison Test, p < 0.05) suggesting that
190 size-specific fecundity increase was attributable to this larger body size in 2018. Similarly,
191 carapace lengths of brooding females were always larger at Snake Pit compared to TAG both in
192 2014 and in 2018 (Dunn's Multiple Comparison Tests, p < 0.05).

193 Variations were also observed in egg volumes between different sampling years
194 (Kruskal-Wallis, H= 87.434, p < 0.05) (figure 2c). Larger egg volumes were found in 2014
195 compared to other years of sampling for both vent fields and across all developmental stages
196 (Dunn's Multiple Comparison Tests, p < 0.05). We note that the 2014 dataset was produced

197 separately in a previous study (See supplementary material) and may be biased by an observer
198 effect.

199 **Variations in reproductive patterns between *Rimicaris* species**

200 Like *R. exoculata*, the realized fecundity of *R. kairei* and *R. chacei* correlated positively
201 with carapace length (Spearman's correlation: *R. kairei*: r= 0.40, p= 0.0044; *R. chacei*: r= 0.70, p=
202 0.00066) (figure 3a). Moreover, the slopes of the relationship between $\log_e$-transformed
203 realized fecundity and $\log_e$-transformed carapace length did not significantly differ between *R.*
204 *exoculata* and its sister species *R. kairei* (F= 1.6168, p= 0.2054). However, they significantly
205 differed between *R. exoculata* and its co-occurring congener *R. chacei* (F= 6.6376, $p < 0.05$).

206 Overall, size-specific fecundity ranged from 23 to 112 eggs mm^{-1} for *R. kairei* and from
207 26 to 255 eggs mm^{-1} for *R. chacei* (figure 3b). Large differences in size-specific fecundity were
208 observed between *R. exoculata* and other *Rimicaris* species (Kruskal-Wallis H= 68.836, $p < 0.05$).
209 Size-specific fecundity of *R. chacei* was always significantly greater compared to *R. exoculata*
210 both at TAG (*R. exoculata*: 49 ± 13; *R. chacei*: 129 ± 59; Dunn's Multiple Comparison Test, $p <$
211 0.05) and Snake Pit (*R. exoculata*: 69 ± 31; *R. chacei*: 148 ± 87; Dunn's Multiple Comparison
212 Test, $p < 0.05$). These differences were independent of size variations between the two species
213 with *R. chacei* brooding females being either of similar size at TAG (Dunn's Multiple Comparison
214 Test, $p > 0.05$) or even smaller at Snake Pit (Dunn's Multiple Comparison Test, $p < 0.05$). Less
215 differences in size-specific fecundities were observed between *R. exoculata* and *R. kairei* with
216 only a higher size-specific fecundity for *R. kairei* (72 ± 20) from Kairei compared to *R. exoculata*
217 from TAG (49 ± 13; Dunn's Multiple Comparison Test, $p < 0.05$). Such variations may be linked
218 to differences in body size of brooding females, as *R. exoculata* from TAG were smaller in
219 average than *R. kairei* from Kairei (Dunn's Multiple Comparison Test, $p < 0.05$).

220 Large differences were also observed in egg volumes between the three *Rimicaris*
221 species (Kruskal-Wallis H= 49.80, $p < 0.05$) (figure 3c,d). Thus, egg volumes of *R. chacei* were
222 significantly smaller than those of *R. exoculata* at any stage across all vents (Dunn's Multiple
223 Comparison Test, $p < 0.05$) (figure 3c). In contrast, differences in egg volumes were more
224 limited between *R. exoculata* and *R. kairei* with significantly larger eggs for *R. kairei* from Kairei

225 compared to *R. exoculata* from TAG for mid stages only (figure 3d). Surprisingly, we did not find
226 gradual increase of egg volumes between successive developmental stages of *R. chacei* as was
227 observed in the two other *Rimicaris* species, either at TAG (Kruskal-Wallis H= 2.57, $p > 0.05$) or
228 at Snake Pit (Kruskal-Wallis H= 0.61, $p > 0.05$). Of note, we did not observe ready-to-hatch or
229 hatched egg broods in *R. chacei* as was seen in the other shrimps.

230 **Temporal variations in the presence of *Rimicaris* ovigerous females**

231 A large number of ovigerous females of *R. exoculata* and *R. chacei* were retrieved in
232 February 2018 at both MAR vent fields (figure 4a). Indeed, 55.4% and 18.2% of sexually mature
233 *R. exoculata* females collected from TAG and Snake Pit respectively, were ovigerous females,
234 while these account for 70.6% and 32.3% of sexually mature *R. chacei* females from TAG and
235 Snake Pit, respectively. Ovigerous females of *R. exoculata* were also present between late
236 March and April 2017 although in a relatively lower proportion, constituting 25.7% and 4% of
237 sexually mature females collected at TAG and Snake Pit, respectively (figure 4a). The majority of
238 *R. exoculata* ovigerous females were collected in dense aggregations close to vent orifices with
239 only two ovigerous females taken outside these assemblages. On the other hand, ovigerous
240 females of *R. chacei* were collected either in hidden aggregations where large populations of
241 their adults have been retrieved (Methou et al. 2021) or within dense aggregations of *R.*
242 *exoculata*. As highlighted previously (Hernández-Ávila et al. 2021), ovigerous females of *R.*
243 *exoculata* were almost absent from samples collected outside this period of the year – i.e.,
244 January to April – despite more than 35 years of sampling efforts along the MAR (figure 4a).
245 Similarly, ovigerous females of *R. chacei* were almost absent from other sampling reports with
246 only two ovigerous females collected in January 2014 at Snake Pit and one in June 1994 at
247 Lucky Strike (figure 4b)

248 Large numbers of ovigerous *R. kairei* were also retrieved in February 2002 and 2016 at
249 Kairei on the CIR (figure 4c), constituting respectively 16.3% and 19.2% of sexually mature
250 females collected at this vent field. Conversely, ovigerous females were completely absent from
251 samples collected in November 2009 (figure 4c). Like *R. exoculata*, all of these ovigerous
252 females were collected in dense aggregations of shrimps next to hot fluid emissions.

253 # Discussion

254 ## Distinct reproductive strategies in *Rimicaris* shrimps with evidence of diet influence

255 *Rimicaris exoculata* and *Rimicaris chacei* exhibit distinct reproductive traits unlikely to
256 simply result from differences in mean body sizes. *Rimicaris kairei* is similar to its sister species
257 *R. exoculata*, in terms of size-specific fecundity or mean egg size. Our results indicate that the
258 two lineages (*R. exoculata* and *R. kairei*, vs *R. chacei*) are situated at two ends of the trade-off
259 between size-specific fecundity and egg sizes currently observed within alvinocaridids (Ramirez-
260 Llodra et al. 2000, Ramirez-Llodra and Segonzac 2006, Copley and Young 2006, Nye et al. 2013).
261 On one hand, *R. chacei* brooding females display one of the highest size-specific fecundity and
262 one of the smallest mean egg volumes among alvinocaridids, whereas *R. exoculata/R. kairei*
263 brooding females present a rather low size-specific fecundity and a large mean egg volume for
264 this family.

265 These variations mirror differences observed in benthic post-settlement stages of these
266 two lineages, with significantly smaller body size for settled juveniles, as well as much larger
267 relative proportions of juveniles in populations of *R. chacei* (Methou et al. 2020, 2021). Higher
268 egg numbers per brood in *R. chacei* might thus contribute to its high supply of settlers despite
269 an apparently lower breeding population size than *R. exoculata* in northern MAR vent fields.
270 Previous work has hypothesized distinct larval life histories between these two species based
271 on distinct stable isotope ratios (Methou et al. 2020). Given we did not observe ready-to-hatch
272 or hatched egg broods for *R. chacei*, it is unclear if observed differences in mean egg size
273 between the two species would ultimately lead to distinct larval sizes at hatching. No size
274 variation was found among first zoeal larval stages of four phylogenetically distinct
275 alvinocaridids (Hernández-Ávila et al. 2015). Although *R. chacei* zoea have not been observed so
276 far, it is unlikely that hatching size difference only, if it exists, explains the large size difference
277 at recruitment between *R. exoculata* and *R. chacei*, which also probably results from differences
278 in their pelagic lives during their dispersal phase.

279 The sister species of *R. chacei* is *R. hybisae* from vents on the Mid Cayman Spreading
280 Centre, but interestingly size-specific fecundity of *R. hybisae* is more similar to *R. exoculata/R.*

281 *kairei* rather than *R. chacei* (Nye et al. 2013). *Rimicaris hybisae* share with *R. exoculata/R. kairei*
282 both a comparable ecological context, living in dense aggregations close to vent fluids
283 emissions, and a comparable gross morphology, with an enlarged cephalothorax (Zbinden and
284 Cambon-Bonavita 2020), characters lacking in *R. chacei*. These are linked to distinct feeding
285 strategies between the two groups of shrimps, with a mixotrophic diet for *R. chacei* (Gebruk et
286 al. 2000, Apremont et al. 2018, Methou et al. 2020) and dependency on chemosynthetic
287 symbionts for others including *R. hybisae* (Rieley et al. 1999, Gebruk et al. 2000, Van Dover
288 2002, Streit et al. 2015, Methou et al. 2020). Variations in fecundity according to feeding
289 strategies have been widely recognized in marine animals such as between carnivorous and
290 herbivorous sea turtles (Broderick et al. 2003), among seabirds with different feeding habits
291 (Pierotti and Annett 1990) or between *Capitella* worms fed with different food sources in
292 laboratory (Qian and Chia 1991). Reduced or increased fecundities have also been observed
293 experimentally in several shrimp species according to their diets (Lin and Shi 2002, Tziouveli et
294 al. 2011, Almeida et al. 2018). We therefore posit that the differences we observe between
295 fecundities in our three *Rimicaris* shrimps should be linked to their feeding ecology, rather than
296 being constrained by their phylogeny.

297 Despite these variations in average egg number, mean egg sizes of *R. hybisae* and *R.*
298 *chacei* were in contrary comparable with similar maximum and minimum egg diameters (Nye et
299 al. 2013). As *R. exoculata* and *R. kairei* also exhibit similar egg volumes, phylogenetic constraints
300 are possibly exerted on mean egg sizes for these shrimps. Further work on more alvinocaridid
301 shrimps with different feeding strategies should help to elucidate these questions.

302 **<u>The intriguing reproductive cycles of *Rimicaris* shrimps</u>**

303 We report here a much-increased presence of ovigerous *R. exoculata* in February 2018
304 and to a lower extent in late March-April 2017, compared to other year periods. Combined with
305 previous data from the literature (summarized in figure 4A), these results support the existence
306 of a brooding period for *R. exoculata* mostly during boreal winter, starting in January/February
307 and ending around March/April. Moreover, we did not observe any variability in reproductive
308 features of *R. exoculata*, either in terms of fecundity or proportions of reproductive females,

309 between different sampling years – indicating a relative inter-annual stability of these traits
310 (figure 2). Since gamete production can be sustained continuously in species depending on local
311 chemosynthesis for their diet, mechanisms driving periodicity in shrimp life cycles are more
312 likely to act on their planktotrophic larval phase through seasonality in availability of
313 photosynthetically derived food. The few previous studies looking at a limited number of
314 samples indeed reported asynchronous ovarian development for *R. exoculata* suggesting
315 continuous egg production (Ramirez-Llodra et al. 2000, Copley et al. 2007). However, the
316 oocyte maximum size appeared to be lower in individuals collected summer than in those
317 collected in autumn, regardless of the vent site origin [16, 34], which may also point at a
318 gradual accumulation of mature oocytes in ovaries, culminating in winter, prior to an increase
319 in females spawning activity. Additional observations of intraovarian development through the
320 year are clearly needed to better characterize rhythms in oocyte production, which may also
321 well be decorrelated from spawning activity as seen in some deep-sea corals from the MAR
322 (Rakka et al. 2021). Large proportions of *R. chacei* ovigerous females were also retrieved in
323 February 2018 at the two vent fields, in contrast to historical sampling at other periods along
324 the MAR (figure 4B). Hence, a similar periodicity in reproduction likely exists for both *Rimicaris*
325 shrimps at MAR. Ovigerous *R. chacei* females were however scarce in other expeditions both
326 during and outside this period (figure 4B), which could be due to difficulties in sampling this
327 rather fast swimming species, thus preventing so far, a full appreciation of its reproductive
328 activity.

329 We also found large proportions of *Rimicaris kairei* ovigerous females during austral
330 summer in February 2002 and 2016, while they were absent from collections in August 2000
331 and November 2009 (figure 4c). Spawning in *R. kairei* thus appears to follow the same timing as
332 *R. exoculata* and *R. chacei*. Such pattern was unexpected given their distribution in different
333 hemispheres, at vent fields with opposite latitudes (figure 1). Reproductive periodicity in deep-
334 sea animals has often been related to seasonal variations in surface photosynthetic production
335 [26]-[28], and *Rimicaris* shrimps from the two hemispheres are expected to experience
336 opposite trends in terms of surface primary production along the year (Pabortsava et al. 2017,
337 Harms et al. 2021), driving opposite reproductive timing. Although our dataset for *R. kairei* is

338 more limited than for *R. exoculata*, these sister species thus appear to share same periodic
339 brooding cycle, regardless of local seasonal variations in surface photosynthetic productivity.
340 *Rimicaris* species studied here provide a first example of reproductive periodicity in deep-sea
341 ecosystems apparently unlinked to seasonal variations of photosynthetic materials from the
342 surface.

343 Besides light and food supply, temperature has also been recognized as an important
344 external time-giving cue in marine organisms (Mat 2019). Compared to most of the deep sea
345 where temperature is relatively constant within regions, hydrothermal vents constitute heat
346 anomalies with steep and unpredictable gradients at small spatial scales, even within a same
347 animal aggregation (Schmidt et al. 2008). Thermal variability at an annual scale could perhaps
348 serve as a time-synchronising cue for these *Rimicaris* shrimps. So far, thermal variations in
349 these ecosystems at a year-round scale remain poorly documented. However, long-term
350 observatories deployed on two vent fields from the northern hemisphere have reported clear
351 tidal influence, although temperatures are relatively stable throughout the year (Barreyre et al.
352 2014, Cuvelier et al. 2017). Recently, it was revealed that bathymodiolin mussels inhabiting
353 vents on the MAR retain and express circadian clock genes following tidal cycles which may be
354 mediated by either tidal stimulus or internal clock (Mat et al. 2020). Possibly, *Rimicaris* shrimp
355 species studied herein also use a set of biological clocks to time their reproductive activity.
356 Though, not all alvinocaridid shrimps seem to exhibit periodicity in their reproductive patterns,
357 despite a gametogenesis phase being strongly constrained phylogenetically (Ramirez-Llodra et
358 al. 2000). For example, regular sampling of *Mirocaris fortunata* yielded ovigerous females
359 throughout the year (Ramirez-Llodra et al. 2000, Komai and Segonzac 2003, Methou 2019) and
360 similarly in *Rimicaris variabilis* (Komai and Tsuchida 2015, Komai et al. 2016). It therefore
361 appears unlikely that phylogenetic constraints alone have maintained a periodic brooding in
362 several alvinocaridid genera but not in others. Then again, other alvinocaridid species may also
363 indeed follow seasonality in surface production, like *Alvinocaris stactophila* with a brooding
364 period between November and March (Copley and Young 2006), and inhabiting relatively
365 shallow cold seeps under highly productive coastal waters. Hence, several synchronizing factors
366 may co-exist in vents and other deep-sea ecosystems, even within the same family of animals.

367 For example, our results here demonstrate that *R. exoculata* and *R. kairei* exhibit seasonality
368 decoupled from surface seasonality, but as the study areas have relatively low surface primary
369 productivity and export of particulate organic carbon (POC) to the deep (Pabortsava et al. 2017,
370 Harms et al. 2021) it is also possible that a higher POC export may begin to interfere with this
371 pattern. Taken together – primary surface production may be the key synchronising cue for
372 some deep-sea species as demonstrated in bathymodiolin mussels and vent crabs (Dixon et al.
373 2006, Tyler et al. 2007), but our results underscore that reproductive cycles and seasonality at
374 the deep is not as simple as it was thought to be.

375 A thorough understanding of reproductive ecology of the dominant species shaping the
376 ecosystem is key to assessing the resilience of deep-sea ecosystems, but little has been done so
377 far even for emblematic taxa like *Rimicaris*. With deep-sea mining for massive sulphides and
378 other resources being imminent (Van Dover et al. 2018), the habitat of these amazing animals
379 that can live nowhere else is being threatened. Elucidating the ecology of these inhabitants of
380 the deep is now more important than ever, and our data exemplifies the importance of time-
381 series studies. Research expeditions in a particular region tend to be conducted in similar
382 timings of the year due to seasonal variations in sea and weather conditions, but our results
383 show that communities need to be revisited at different times of the year.

384 **Ethics**

385 The animals used in this study were invertebrate carideans collected in the French contract
386 area for the exploration of polymetallic sulphur deposits (Mid-Atlantic Ridge) or International
387 Waters (Central Indian Ridge). Each individual was immediately preserved in ethanol after
388 recovery and no live experiments were carried out.

389 **Author's contributions**

390 P.M. collected and sorted specimens in 2018 on the MAR, carried out the identification and
391 measurement of specimens from all sampling cruises, lead the data analysis, participated in the
392 conception and design of the study and drafted the manuscript; C.C. carried out the collection
393 of specimens in 2016 on the CIR and helped draft the manuscript; H.K.W. carried out the
394 collection of specimens in 2009 and critically revised the manuscript; M-A.C-B. collected

specimens in 2017 on the MAR, coordinated the study and critically revised the manuscript; F.P. collected and sorted specimens in 2017 conceived and designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication and agreed to be held accountable for the work performed therein. The authors declare they have no competing interests.

Funding

This work was supported by the Ifremer REMIMA program and the Region Bretagne ARED funding. C.C. and H.K.W. were supported by a Japan Society for the Promotion of Science (JSPS) Grant-in-Aid for Scientific Research, grant code 18K06401. Travel of the first author from Ifremer to JAMSTEC was funded by Ifremer international mobility grant for PhD students.

Acknowledgements

The authors thank the captains and crews of R/V *Pourquoi pas*? and HOV *Nautile* submersible team for their efficiency, as well as the chief scientists and scientific parties of HERMINE (chief scientist: Yves Fouquet; http://dx.doi.org/10.17600/17000200) and BICOSE 2 cruise (chief scientist: Marie-Anne Cambon-Bonavita; http://dx.doi.org/10.17600/18000004). Further thanks also go to the captains and crews of R/V *Yokosuka*, and the HOV *Shinkai 6500* submersible team for their continuous support of the scientific activity at sea, as well as the chief scientists and scientific parties during the research cruises YK01-15 (chief scientist: Ken Takai), YK09-13 (chief scientists: Kentaro Nakamura, Satoshi Nakagawa) and YK16-E02 (chief scientist: Ken Takai). We also thanks Dr. Ivan Hernández-Ávila (Facultad de Ciencias Naturales, Universidad Autónoma del Carmen) for his help to sort the specimens on board and the analyses to determine sexual maturity of these shrimps.

Figure Captions

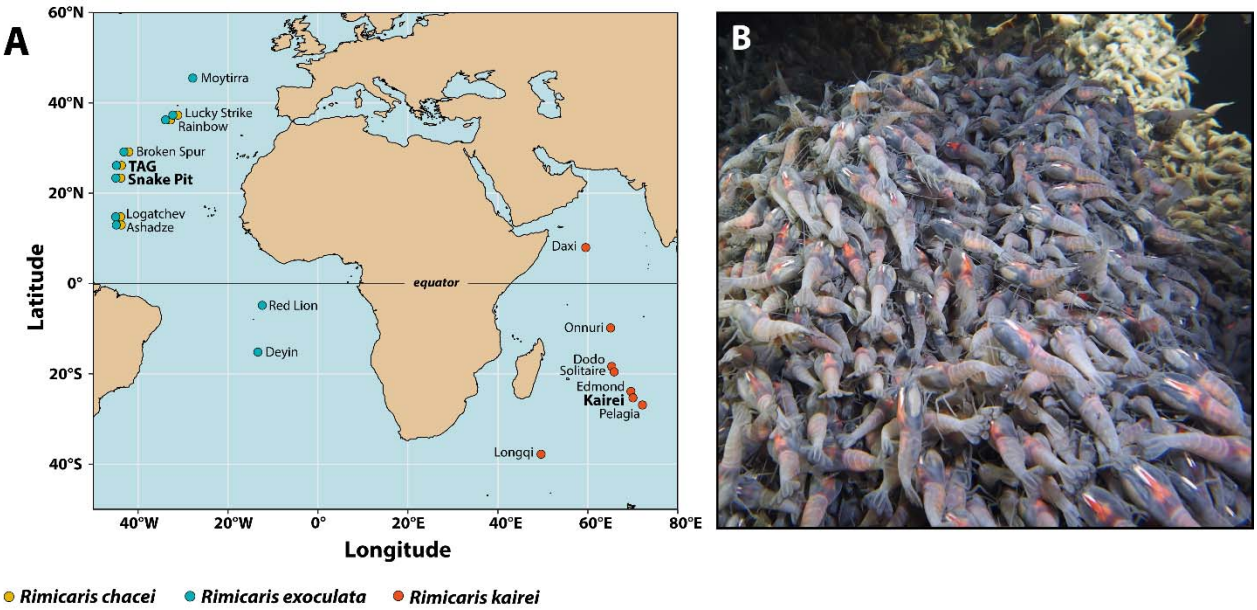
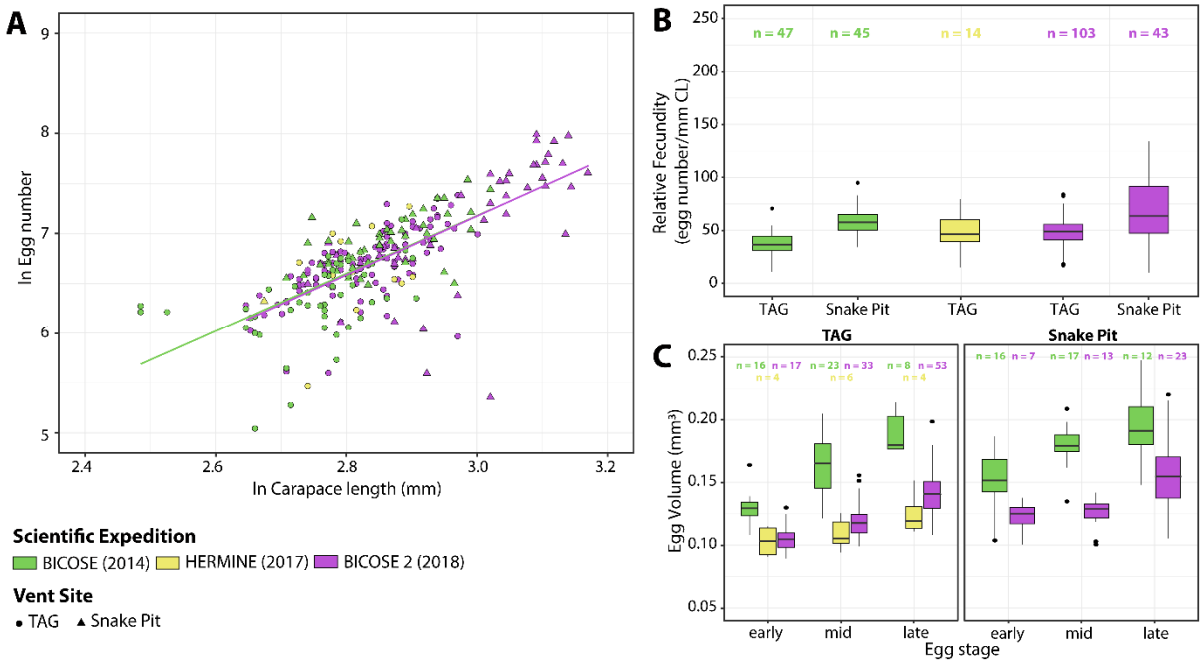


Figure 1. Context of the study. **a.** Current geographic distribution of the three *Rimicaris* species studied. **b.** Dense aggregations of *R. kairei* shrimps in February 2016 at the Kairei hydrothermal vent field.



431

432 **Figure 2.** Interannual comparison of reproductive features of *Rimicaris exoculata* collected
433 between 2014 and 2018. **n:** number of individuals for each condition. **a.** Variation of $\log_e$-
434 transformed minimum realized fecundity with $\log_e$-transformed carapace length. **b.** Fecundity
435 corrected for body size (carapace length) **c.** Egg volumes at different developmental stages.

436

437

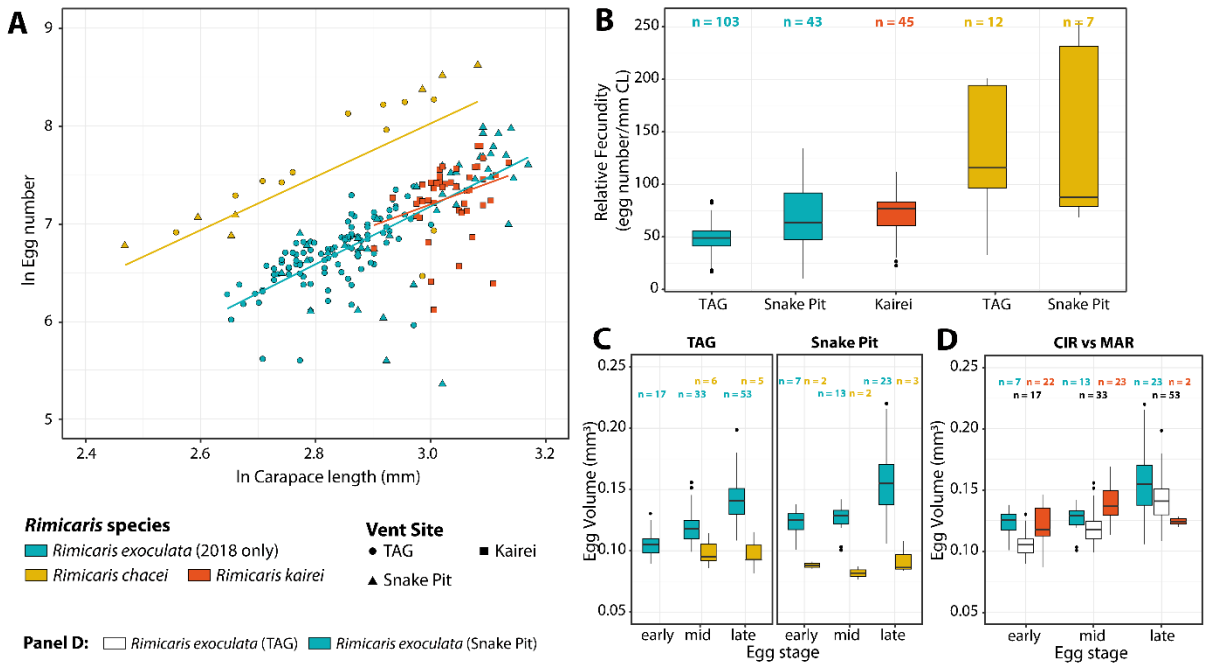
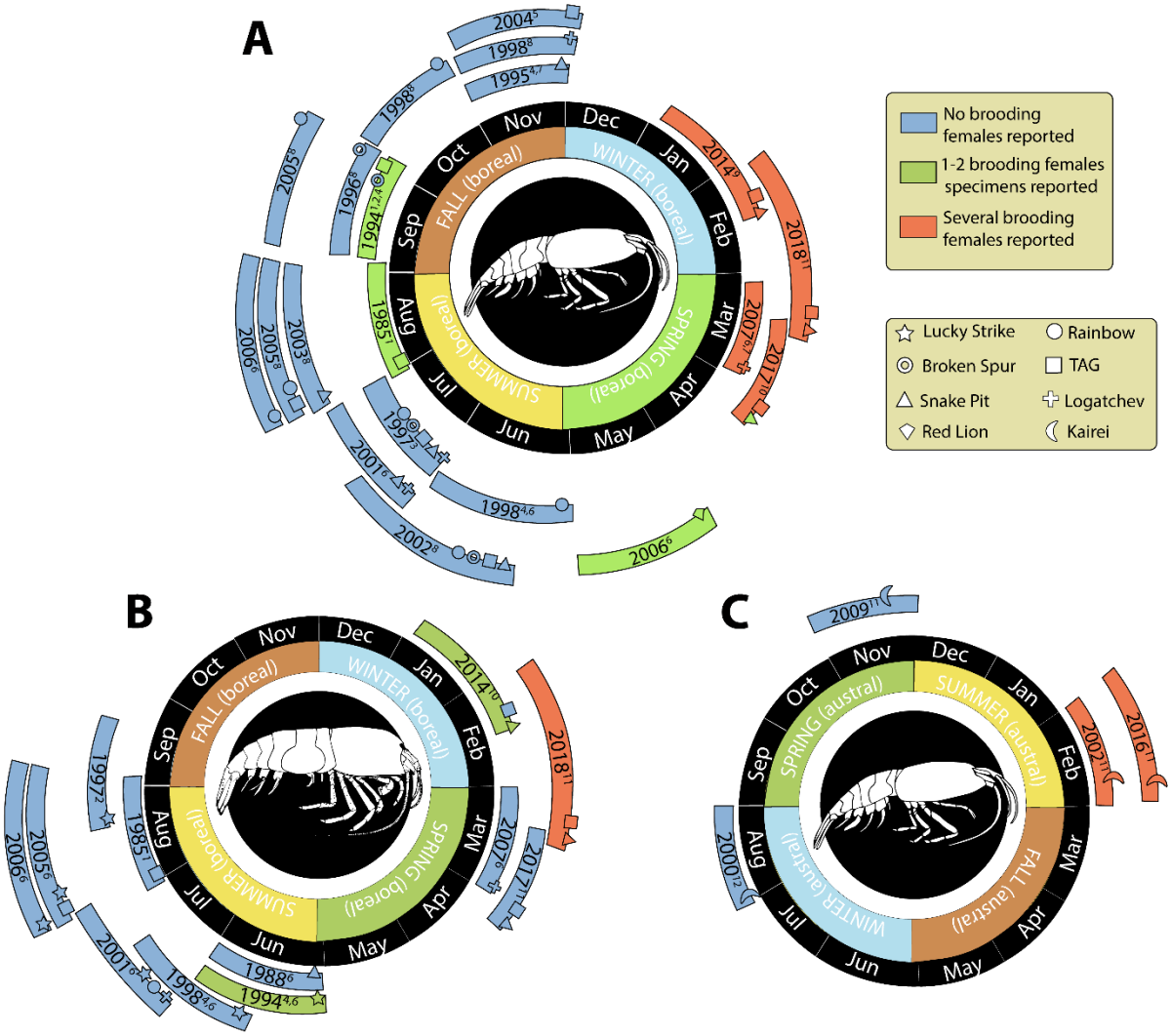


Figure 3. Comparison of reproductive features between *Rimicaris* species from the MAR and the CIR. **n:** number of individuals for each condition. **a.** Variation of $\log_e$-transformed minimum realized fecundity with $\log_e$-transformed carapace length. **b.** Fecundity corrected for body size (carapace length). **c.** Egg volumes at different developmental stages of *Rimicaris* shrimps from the MAR. **d.** Egg volumes at different developmental stages of *R. exoculata* and *R. kairei*.



[1]Williams and Rona (1986), [2]Vereshchaka (1997), [3]Shank et al. (1998), [4]Ramirez-Llodra et al. (2000), [5]Copley et al. (2007), [6]Komai and Segonzac (2008), [7]Guri et al. (2012) [8]Lunina and Vereshchaka (2014), [9]Methou et al. (2019) & Hernàndez-Avila et al. (2021), [10]Cruise Report BICOSE (2014), [11]This work, [12]Watabe & Hashimoto (2002)

Figure 4. Diagrams summarizing occurrence of reproductive stages of the studied *Rimicaris* shrimp species over different samplings realized between 1985 and 2018 according to the year period **a.** for *R. exoculata.* **b.** for *R. chacei.* **c.** for *R. kairei.*

453 **References**

454 Almeida, A. S. e, S. de Paiva Barros-Alves, G. L. Hirose, and D. F. R. Alves. 2018. Reproductive
455 output of the ornamental shrimp lysmata vittata (Stimpson, 1860) (decapoda: Caridea) in
456 wild populations and under different maturation diets. Invertebrate Reproduction and
457 Development 62:257–267.

458 Apremont, V., M.-A. Cambon-Bonavita, V. Cueff-Gauchard, D. François, F. Pradillon, L. Corbari,
459 and M. Zbinden. 2018. Gill chamber and gut microbial communities of the hydrothermal
460 shrimp Rimicaris chacei Williams and Rona 1986: A possible symbiosis. PLoS ONE
461 13:e0206084.

462 Barreyre, T., J. Escartin, R. A. Sohn, M. Cannat, V. Ballu, and W. C. Crawford. 2014. Temporal
463 variability and tidal modulation of hydrothermal exit-fluid temperatures at the Lucky Strike
464 deep-sea vent field, Mid-Atlantic Ridge. Journal of Geophysical Research: Solid Earth
465 119:2543–2566.

466 Broderick, A. C., F. Glen, B. J. Godley, and G. C. Hays. 2003. Variation in reproductive output of
467 marine turtles. Journal of Experimental Marine Biology and Ecology 288:95–109.

468 Copley, J. T. P., P. B. K. Jorgensen, and R. A. Sohn. 2007. Assessment of decadal-scale ecological
469 change at a deep Mid-Atlantic hydrothermal vent and reproductive time-series in the
470 shrimp Rimicaris exoculata. Journal of the Marine Biological Association 87:859–867.

471 Copley, J. T. P., and C. M. Young. 2006. Seasonality and zonation in the reproductive biology and
472 population structure of the shrimp Alvinocaris stactophila (Caridea: Alvinocarididae) at a
473 Louisiana Slope cold seep. Marine Ecology Progress Series 315:199–209.

474 Cuvelier, D., P. Legendre, A. Laës-Huon, P. M. Sarradin, and J. Sarrazin. 2017. Biological and
475 environmental rhythms in (dark) deep-sea hydrothermal ecosystems. Biogeosciences
476 14:2955–2977.

477 Dixon, D. R., D. M. Lowe, P. I. Miller, G. R. Villemin, A. Colaço, R. Serrão-Santos, and L. R. J.
478 Dixon. 2006. Evidence of seasonal reproduction in the Atlantic vent mussel Bathymodiolus

479 azoricus, and an apparent link with the timing of photosynthetic primary production.
480 Journal of the Marine Biological Association of the United Kingdom 86:1363–1371.

481 Van Dover, C. L. 2002. Trophic relationships among invertebrates at the Kairei hydrothermal
482 vent field (Central Indian Ridge). Marine Biology 141:761–772.

483 Van Dover, C. L., S. Arnaud-Haond, M. Gianni, S. Helmreich, J. A. Huber, A. L. Jaeckel, A.
484 Metaxas, L. H. Pendleton, S. Petersen, E. Ramirez-Llodra, P. E. Steinberg, V. Tunnicliffe, and
485 H. Yamamoto. 2018. Scientific Rationale and International Obligations for Protection of
486 Active Hydrothermal Vent Ecosystems From Deep-Sea Mining. Marine Policy 90:20–28.

487 Dubilier, N., C. Bergin, and C. Lott. 2008. Symbiotic diversity in marine animals: the art of
488 harnessing chemosynthesis. Nature Reviews Microbiology 6:725–40.

489 Faure, B., P. Chevaldonné, F. Pradillon, E. Thiébaut, and D. Jollivet. 2007. Spatial and temporal
490 dynamics of reproduction and settlement in the Pompeii worm Alvinella pompejana
491 (Polychaeta: Alvinellidae). Marine Ecology Progress Series 348:197–211.

492 Gebruk, A. V., E. C. Southward, H. Kennedy, and A. J. Southward. 2000. Food sources,
493 behaviour, and distribution of hydrothermal vent shrimps at the Mid-Atlantic Ridge.
494 Journal of the Marine Biological Association of the United Kingdom 80:485–499.

495 German, C. R., E. Ramirez-Llodra, M. C. Baker, P. A. Tyler, A. Baco-Taylor, A. Boetius, M. Bright,
496 L. C. de Siqueira, E. E. Cordes, D. Desbruyères, N. Dubilier, C. R. Fisher, Y. Fujiwara, F. Gaill,
497 A. Gebruk, K. Juniper, L. A. Levin, P. A. Lokabharathi, A. Metaxas, A. A. Rowden, R. S.
498 Santos, T. M. Shank, C. R. Smith, C. L. Van Dover, C. M. Young, and A. Warén. 2011. Deep-
499 water chemosynthetic ecosystem research during the census of marine life decade and
500 beyond: A proposed deep-ocean road map. PLoS ONE 6.

501 Govenar, B. 2012. Energy Transfer Through Food Webs at Hydrothermal Vents: Linking the
502 Lithosphere to the Biosphere. Oceanography 25:246–255.

503 Guri, M., L. Durand, V. Cueff-Gauchard, M. Zbinden, P. Crassous, B. Shillito, and M.-A. Cambon-
504 Bonavita. 2012. Acquisition of epibiotic bacteria along the life cycle of the hydrothermal

shrimp Rimicaris exoculata. The ISME journal 6:597–609.

Gutiérrez, Y., M. Fresch, D. Ott, J. Brockmeyer, and C. Scherber. 2020. Diet composition and social environment determine food consumption, phenotype and fecundity in an omnivorous insect. Royal Society Open Science 7.

Harms, N. C., N. Lahajnar, B. Gaye, T. Rixen, U. Schwarz-Schampera, and K. C. Emeis. 2021. Sediment trap-derived particulate matter fluxes in the oligotrophic subtropical gyre of the South Indian Ocean. Deep-Sea Research Part II: Topical Studies in Oceanography 183:104924.

Hernández-Ávila, I., M.-A. Cambon-Bonavita, J. Sarrazin, and F. Pradillon. 2021. Population structure and reproduction of the alvinocaridid shrimp Rimicaris exoculata on the Mid-Atlantic Ridge: variations between habitats and vent fields. bioRxiv:3–5.

Hernández-Ávila, I., M. A. Cambon-Bonavita, and F. Pradillon. 2015. Morphology of first zoeal stage of four genera of alvinocaridid shrimps from hydrothermal vents and cold seeps: Implications for ecology, larval biology and phylogeny. PLoS ONE 10:1–27.

Hilário, A., S. Vilar, M. R. Cunha, and P. Tyler. 2009. Reproductive aspects of two bythograeid crab species from hydrothermal vents in the Pacific-Antarctic Ridge. Marine Ecology Progress Series 378:153–160.

Jollivet, D., A. Empis, M. C. Baker, S. Hourdez, T. Comtet, D. Desbruyères, and P. A. Tyler. 2000. Reproductive biology, sexual dimorphism, and population structure of the deep sea hydrothermal vent scale-worm, Branchipolynoe seepensis (Polychaeta: Polynoidae). Journal of the Marine Biological Association of the United Kingdom 80:55–68.

Komai, T., L. Menot, and M. Segonzac. 2016. New records of caridean shrimp (Crustacea: Decapoda) from hydrothermally influenced fields off Futuna Island, Southwest Pacific, with description of a new species assigned to the genus Alvinocaridinides Komai & Chan, 2010. Zootaxa 4098:298–310.

Komai, T., and M. Segonzac. 2003. Review of the hydrothermal vent shrimp genus Mirocaris,

redescription of M. fortunata and reassessment of the taxonomic status of the family Alvinocarididae (Crustacea: Decapoda: Caridea). Cahiers de Biologie Marine 44:199–215.

Komai, T., and M. Segonzac. 2008. Taxonomic Review of the Hydrothermal Vent Shrimp Genera Rimicaris Williams & Rona and Chorocaris Martin & Hessler (Crustacea: Decapoda: Caridea: Alvinocarididae). Journal of Shellfish Research 27:21–41.

Komai, T., and S. Tsuchida. 2015. New records of Alvinocarididae (Crustacea: Decapoda: Caridea) from the southwestern Pacific hydrothermal vents, with descriptions of one new genus and three new species. Journal of Natural History:1–36.

Lin, J., and H. Shi. 2002. Effect of Broodstock Diet on Reproductive Performance of the Golden Banded Coral Shrimp Stenopus scutellatus. Journal of the World Aquaculture Society 33:383–386.

Marsh, L., J. T. Copley, P. A. Tyler, and S. Thatje. 2015. In hot and cold water: Differential life-history traits are key to success in contrasting thermal deep-sea environments. Journal of Animal Ecology 84:898–913.

Marticorena, J., M. Matabos, J. Sarrazin, and E. Ramirez-Llodra. 2020. Contrasting reproductive biology of two hydrothermal gastropods from the Mid-Atlantic Ridge: implications for resilience of vent communities. Marine Biology 167:1–19.

Mat, A. M. 2019. Chronobiology and the design of marine biology experiments. ICES Journal of Marine Science 76:60–65.

Mat, A. M., J. Sarrazin, G. V Markov, V. Apremont, C. Dubreuil, C. Eché, C. Fabioux, C. Klopp, P. M. Sarradin, A. Tanguy, A. Huvet, and M. Matabos. 2020. Biological rhythms in the deep-sea hydrothermal mussel Bathymodiolus azoricus. Nature Communications 11:1–12.

Meiri, S., J. H. Brown, and R. M. Sibly. 2012. The ecology of lizard reproductive output. Global Ecology and Biogeography 21:592–602.

Methou, P. 2019. Lifecycles of two hydrothermal vent shrimps from the Mid-Atlantic Ridge: Rimicaris exoculata and Rimicaris chacei.

Methou, P., I. Hernández-Ávila, J. Aube, V. Cueff-Gauchard, N. Gayet, L. Amand, B. Shillito, F. Pradillon, and M.-A. Cambon-Bonavita. 2019. Is It First the Egg or the Shrimp? – Diversity and Variation in Microbial Communities Colonizing Broods of the Vent Shrimp Rimicaris exoculata During Embryonic Development. Frontiers in Microbiology 10:1–19.

Methou, P., I. Hernández-Ávila, C. Cathalot, M.-A. Cambon-Bonavita, and F. Pradillon. 2021. Population structure and environmental niches of Rimicaris shrimps from the Mid Atlantic Ridge. bioRxiv.

Methou, P., L. N. Michel, M. Segonzac, M.-A. Cambon-Bonavita, and F. Pradillon. 2020. Integrative taxonomy revisits the ontogeny and trophic niches of Rimicaris vent shrimps. Royal Society Open Science 7:200837.

Nye, V., J. T. P. Copley, and P. A. Tyler. 2013. Spatial Variation in the Population Structure and Reproductive Biology of Rimicaris hybisae (Caridea: Alvinocarididae) at Hydrothermal Vents on the Mid-Cayman Spreading Centre. PLoS ONE 8.

Pabortsava, K., R. S. Lampitt, J. Benson, C. Crowe, R. McLachlan, F. A. C. Le Moigne, C. Mark Moore, C. Pebody, P. Provost, A. P. Rees, G. H. Tilstone, and E. M. S. Woodward. 2017. Carbon sequestration in the deep Atlantic enhanced by Saharan dust. Nature Geoscience 10:189–194.

Perovich, G. M., C. E. Epifanio, A. I. Dittel, and P. A. Tyler. 2003. Spatial and temporal patterns in development of eggs in the vent crab Bythograea thermydron. Marine Ecology Progress Series 251:211–220.

Pierotti, R., and C. a Annett. 1990. Diet and Reproductive Output in Seabirds. BioScience 40:568–574.

Qian, P. Y., and F. S. Chia. 1991. Fecundity and egg size are mediated by food quality in the polychaete worm Capitella sp. Journal of Experimental Marine Biology and Ecology 148:11–25.

R Core Team, . 2020. R: A language and environment for statistical computing. Vienna, Austria.

https://www.r-project.org.

Rakka, M., Í. Sampaio, A. Colaço, and M. Carreiro-Silva. 2021. Reproductive biology of two deep-sea octocorals in the Azores Archipelago. Deep-Sea Research Part I: Oceanographic Research Papers 175.

Ramirez-Llodra, E., and M. Segonzac. 2006. Reproductive biology of Alvinocaris muricola (Decapoda: Caridea: Alvinocarididae) from cold seeps in the Congo Basin. Journal of the Marine Biological Association of the United Kingdom 86:1347.

Ramirez-Llodra, E., P. A. Tyler, and J. T. P. Copley. 2000. Reproductive biology of three caridean shrimp, Rimicaris exoculata, Chorocaris chacei and Mirocaris fortunata. Journal of the Marine Biological Association of the United Kingdom 80:473–484.

Rieley, G., C. L. Van Dover, D. B. Hedrick, and G. Eglinton. 1999. Trophic ecology of Rimicaris exoculata: A combined lipid abundance/stable isotope approach. Marine Biology 133:495–499.

Schmidt, C., N. Le Bris, and F. Gaill. 2008. Interactions of Deep-Sea Vent Invertebrates with Their Environment: The Case of Rimicaris exoculata. Journal of Shellfish Research 27:79–90.

Shank, T. M., R. a Lutz, and R. C. Vrijenhoek. 1998. Molecular systematics of shrimp (Decapoda: Bresiliidae) from deep-sea hydrothermal vents, I: Enigmatic “small orange” shrimp from the Mid-Atlantic Ridge are juvenile Rimicaris exoculata. Molecular Marine Biology and Biotechnology 7:88–96.

Sibly, R. M., C. C. Witt, N. A. Wright, C. Venditti, W. Jetz, and J. H. Brown. 2012. Energetics, lifestyle, and reproduction in birds. Proceedings of the National Academy of Sciences of the United States of America 109:10937–10941.

Streit, K., S. A. Bennett, C. L. Van Dover, and M. Coleman. 2015. Sources of organic carbon for Rimicaris hybisae: Tracing individual fatty acids at two hydrothermal vent fields in the Mid-Cayman rise. Deep-Sea Research Part I: Oceanographic Research Papers 100:13–20.

Tyler, P. A., S. Pendlebury, S. W. Mills, L. Mullineaux, K. J. Eckelbarger, M. Baker, and C. M. Young. 2008. Reproduction of Gastropods from Vents on the East Pacific Rise and the Mid-Atlantic Ridge. Journal of Shellfish Research 27:107–118.

Tyler, P. A., and C. M. Young. 1999. Reproduction and dispersal at vents and cold seeps. Journal of the Marine Biological Association of the United Kingdom 79:193–208.

Tyler, P. A., C. M. Young, E. Dolan, S. M. Arellano, and S. D. Brooke. 2007. Gametogenic periodicity in the chemosynthetic cold-seep mussel ‘“ Bathymodiolus ”’ childressi. Marine Biology 150:829–840.

Tziouveli, V., M. Hall, and G. Smith. 2011. The Effect of Maturation Diets on the Reproductive Output of the White-striped Cleaner Shrimp, Lysmata amboinensis. Journal of the World Aquaculture Society 42:56–65.

Vereshchaka, A. L. 1997. Comparative morphological studies on four populations of the shrimp Rimicaris exoculata from the Mid-Atlantic Ridge. Deep-Sea Research Part I: Oceanographic Research Papers 44:1905–1921.

Williams, A. B., and P. A. Rona. 1986. Two New Caridean Shrimps from a Hydrothermal Field on the Mid Atlantic Ridge. Journal of Crustacean Biology 6:446–462.

Zbinden, M., and M. Cambon-Bonavita. 2020. Biology and ecology of Rimicaris exoculata, a symbiotic shrimp from deep-sea hydrothermal vents. Marine Ecology Progress Series 652:187–222.