Population History of a Hydrothermal Vent-Endemic Gastropod *Alviniconcha hessleri* in the Mariana Trough

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Abstract

Molecular evolutionary rate of the COI (cytochrome *c* oxidase subunit I) gene in the vent endemic genus *Alviniconcha* (Gastropoda: Provannidae) was estimated to be 0.69 % per million year based on GTR (General time-reversible) + G (Gamma) + I (Proportion Invariant) distances and hypothesized divergence dates of 59–64 Ma (million years ago) between *Alviniconcha* and its sister genus *Ifremeria*. The population history of *A. hessleri*, an endemic species to the Mariana Trough, the northwestern Pacific, was reconstructed by analyzing the nucleotide sequences of two fragments of mitochondrial DNA and an intron region of a nuclear gene for ATPS β (ATP Synthetase subunit β) and by extrapolating the estimated COI rate. Two genetically deviated *A. hessleri* groups with different patterns of geographical distribution were recognized in the analysis of the mitochondrial DNA and their age of divergence was estimated to be 0.91 Ma by the coalescent theory-based analysis of the nuclear gene data. The present geographical distributions of the two groups suggest that their ancestral populations were isolated in the central and southern Mariana Trough, respectively. Rapid expansion (increase of the population size) was suggested to have occurred in both groups at 0.26 and 0.17 Ma, respectively. Periodical changes of hydrothermal activity have apparently controlled the isolation and expansion of the local populations.

Keywords

Alviniconcha hessleri • ATP Synthetase subunit β • Hydrothermal vent • Intron • Mitochondrial DNA • Phylogeography

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26.1 Introduction

Since the discovery of the first deep-sea hydrothermal field in the late 1970s, many hydrothermal-vent endemic species have been reported from various vent fields over the world (Rogers et al. 2012). Hydrothermal vent fields are generally unstable environments; the activities sometimes rapidly abate, cease or increase to cause the catastrophic explosion and the longevity of a single vent is estimated to be no more than 10,000 years (Vrijenhoek 2010). Thus, species endemic to such environments are expected to have abilities to disperse and colonize other vent sites. Comparison of the population history of vent-endemic faunal groups would provide valuable information to understand mechanisms underlying the evolution of such animals. Recent development of phylogeographic analyses including the coalescent theory-based methodologies has enabled us to investigate population history in more detail (Kuhner 2008; Ho and Shapiro 2011). On the other hand, new geochemical analyses of hydrothermal sulfides and sulfate minerals, which reflect magmatic activities of their places of production, are also being developed to reconstruct the historical changes of hydrothermal activities more precisely (Ishibashi et al. 2009, Chap. 23). Results obtained from biological and geochemical evidences need to be integrated for more accurate understanding of history of hydrothermal ecosystems and for the improvement of each method (Kumagai et al. Chap. 5).

In this chapter, the population history of a hydrothermal vent-endemic snail *Alviniconcha hessleri* is reconstructed. *Alviniconcha* snails have highly specialized morphological and ecological characteristics to adapt the vent environments with chemoautosynthetic endosymbiotic gamma- or epsilon-proteobacteria (Suzuki et al. 2006). *Alviniconcha hessleri* dominates as an endemic species in hydrothermal areas in the Mariana Trough, the northwestern Pacific. This species was described based on specimens collected at the Alice Springs site (3,600 m depth) in the central Mariana Trough (Okutani and Ohta 1988). The second habitat of this species was discovered at the Forecast Vent site (1,470 m depth) in the southern Mariana Trough (Johnson et al. 1993). During the first decade of the twenty-first century, various hydrothermal vent fields have been discovered in the southernmost part of the Mariana Trough. Among them, *A. hessleri* has been reported from three sites, namely, the Snail (=Fryer), Archaean, and Pika sites. The Snail site (2,850 m depth) is situated on the South Mariana Backarc Spreading Center while the Archaean (2,990 m depth) and Pika (2,770 m depth) sites were discovered on off-axis seamounts (Wheat et al. 2003; Urabe et al. 2004; Kakegawa et al. 2008; Yoshikawa et al. 2012). These vent sites are distributed almost on a straight line from the ridge axis to the off-

ridge. Although the present hydrothermal activity of the Mariana Trough is estimated to have started about 7 Ma (Stern et al. 2003), detailed historical changes in the activity have been traced back only to 12,000 years ago by the geochemical approach (Stüben et al. 1994; Takamasa et al. 2013; Ishibashi et al., Chap. 23).

Johnson et al. (2010) estimated phylogenetic relationships and deviation dates among provannid gastropods including *Alviniconcha* snails, with the Bayesian evolutionary analysis on the basis of nucleotide sequences from the mitochondrial COI (cytochrome *c* oxidase subunit I), 12S and 16S ribosomal RNA (rRNA) genes and nuclear Histone H3 and 18S and 28S rRNA genes. They calibrated molecular clocks based on a hypothetical age of vicariance between the Pacific and Atlantic deep-sea faunas at 15–16 Ma in prior to the closure of the Isthmus of Panama, or fossil records that suggest the divergence between *Provanna* and *Desbruyeresia* at 93–100 Ma and two outgroup *Neptunea* species at 33–37 Ma. Using this clock, the population history of *A. hessleri* can be estimated. However, the intraspecific molecular evolutionary rate is expected to be higher than intergeneric rates, as the estimate of rate decrease with enlargement of time-scale investigated due to the saturation of genetic mutations, which results in the overestimation of ages. The present study attempted to decrease this problem by calculating rates based on genetic distances between congeneric species.

This chapter report population history of *A. hessleri* in the Mariana Trough from 1 to 0.2 Ma revealed by phylogeographic analyses using adequate molecular evolutionary rate mentioned above and discuss changes of the hydrothermal activity during this period, which might have greatly contributed to the population dynamics of vent-endemic species.

26.2 Materials and Methods

26.2.1 Evolutionary Rate of COI Gene in *Alviniconcha*

The molecular evolutionary rate of the COI gene in *Alviniconcha* was estimated by analyzing sequences from additional species of the genus and other provannids under the GTR (General time-reversible) + G (Gamma) + I (Proportion Invariant) distances model and by extrapolating suggested divergence dates between *Alviniconcha* and *Ifremeria* in Johnson et al. (2010). Seven COI sequences published in Suzuki et al. (2006) were incorporated with 18 representative sequences from Johnson et al. (2010) and 25 operational taxonomic units (OTUs) with the length of 530 base pair (bp) were used in the succeeding Bayesian phylogenetic analysis. The genus *Alviniconcha* was represented by all the five known species (Hidaka et al.

Table 26.1 List of samples used for population genetic analyses

No.	Site	Coordinates	Depth (m)	Dive#	Date	N ^a
1	Alice Springs	18°13' N, 144°43'E	3,600	6 K153	9 November 1992	20 ^b (18)
2	Forecast	13°24' N, 143°55'E	1,470	6 K186	22 October 1993	20 ^b (13)
3	Snail	12°57' N, 143°37'E	2,850	6 K1228	22 September 2010	20 (18)
4	Archaean	12°56' N, 143°38'E	2,990	6 K1224	9 September 2010	20 (14)
5	Pika	12°55'N, 143°39'E	2,770	6 K1225	10 September 2010	20 (18)

^aNumbers of specimens used for sequencing the ATP Synthetase subunit β gene are shown in parentheses

^bNucleotide sequences of mitochondrial DNA were reported in Hidaka et al. (2013)

2013) to better correct the genetic distances between these ingroup OTUs, while only three conspecific individuals were included for the monotypic *Ifremeria*.

Bayesian tree reconstruction was performed with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The shape, proportion of invariant sites, state frequency and substitution rate parameters were estimated for each codon position separately. Two parallel runs were made for 10,000,000 generations (with a sample frequency of 1,000), using the default value of four Markov chains. The first 5,000 trees for each run were discarded to ensure the four chains reached stationarity by referring to the average standard deviation of split frequencies (Ronquist and Huelsenbeck 2003). The consensus tree and posterior probabilities (PP) were computed from the remaining 10,000 trees (5,000 trees, 2 runs).

26.2.2 Population History of *Alviniconcha hessleri*

The specimens of *A. hessleri* used for population genetic analyses in this study were collected by the submersible *SHINKAI 6500* of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC; Table 26.1). Sampling at the Snail, Archaean, and Pika sites in the southernmost area of the Mariana Trough was conducted as a part of the TAIGA Project. Total genomic DNA was extracted from the foot tissue of sixty specimens from the three sites with a DNeasy Tissue Extraction Kit (Qiagen, Valencia, CA). DNA samples from a previous study (Kojima et al. 2001) were used for populations at the Alice Springs and Forecast sites. The extracted DNA was treated with GeneReleaser (BioVenture Inc., Murfreesboro, TN) to sequester the products of cell lysis that might have inhibited polymerase activity.

Three fragments were amplified for each of the newly collected specimens from the southernmost Mariana Trough by polymerase chain reaction (PCR) with the extracted DNA as a template and *Takara Ex Taq* Hot Start Version (Takara Bio Inc., Shiga, Japan). These included two mitochondrial DNA fragments for the cytochrome *c* oxidase subunits I (COI) and a region spanning from the tRNA^{Met} gene to the 12S rRNA gene,

as well as an intron region of a nuclear gene for ATP Synthetase subunit β (ATPS β). The COI fragment was amplified using primers LCO1490 (5'-GGTCAACAAATCATAAA-GATATTGG-3') (Folmer et al. 1994) and COI-6 (5'-GGRTARTCNSWRTANCGNCGNGGYAT-3') (Shimayama et al. 1990). The second fragment, which contains the tRNA^{Met}, tRNA^{Tyr}, tRNA^{Tyr}, tRNA^{Cys}, tRNA^{Gln}, tRNA^{Gly}, tRNA^{Glu}, and 12S rRNA genes and six non-coding regions, was amplified using a primer set AlifCOII-1 (5'-GGGCATCART-GATAYTGRAG-3') (Hidaka et al. 2013) and Alif12S-1R (5'-GTCTAAAGCACCGCCAAGCCC-3') (Hidaka et al. 2013) or another set AlifATP6-1 (5'-TATACAATTTTT-GARTTYGG-3') (Hidaka et al. 2013) and Alif12S-2R (5'-TATAYTTWYAAGTCAGAGCCAAGC-3') (Hidaka et al. 2013). This region has been shown to provide much more information about the genetic structure of *A. hessleri* than the COI gene does (Hidaka et al. 2013). PCR conditions for the two mitochondrial DNA fragments were as follows: incubation at 94 °C for 2 min, followed by 40 cycles of incubation at 92, 50, and 72 °C for 40 s, 1 min, and 90 s, respectively, and a final extension at 72 °C for 7 min. DNA fragments containing the intron region of the nuclear ATPS β gene were amplified using a primer ATPS β f1 (5'-CGTGAGGGNAA-Y-GATTTHTACCATGAGATGAT-3') (Jarman et al. 2002) in combination with either ATPS β r1 (5'-TACTTGCTTGNGGDCRCGGGCACGGGC-3') (Jarman et al. 2002) or ATPS β r2 (5'-ACACCTGCA-CAAATCACAC-3'; synthesized on the basis of determined sequences). PCR conditions for this fragment were as follows: incubation at 94 °C for 2 min, followed by 35 cycles of incubation at 94, 54, and 72 °C for 20 s, 1 min, and 1 min, respectively. For specimens from the Alice Springs and Forecast Vent sites, only the third fragment was newly amplified as nucleotide sequences of two mitochondrial DNA fragments have been determined and published elsewhere (Kojima et al. 2001; Hidaka et al. 2013).

Each PCR product was incubated with ExoSAP-IT (United States Biochemical, Cleveland, OH) at 37 °C for 15 min to digest the unused primers and nucleotides and at 80 °C for 15 min to deactivate ExoSAP, used in cycle sequencing reactions performed with a BigDye Terminator Cycle Sequencing Kit Version 3.0 (Applied Biosystems Inc., Foster City, CA), and sequenced on an automated sequencer

(ABI3130; Applied Biosystems) with the same primers as used in PCR. Low quality ends were trimmed from the obtained sequences and the final dataset comprised 491 bp and 631–633 bp for the COI gene and the region spanning from the tRNA^{Met} gene to the 12S rRNA gene, respectively. The ATPS β intron dataset was represented by nucleotide sequences of 194–226 bp from a limited number of individuals, where genotype could be determined through direct-sequencing; those yielded multiple amplicons with more than one substitutions and/or indels were excluded from the succeeding coalescence theory-based analyses. The nucleotide sequences determined in the current study were deposited in the DDBJ/EMBL/GenBank databases under the accession numbers AB874407–874415 (COI), AB874416–874443 (tRNA^{Met}–12SrRNA), and AB874444–874468 (ATPS β).

Haplotype networks were constructed on the basis of differences in the nucleotide sequences of the mitochondrial datasets with the median-joining method implemented in Network version 4.6.1.0 (Bandelt et al. 1999). Differences in the frequencies of haplotypes between populations were evaluated using the exact test of population differentiation (Raymond and Rousset 1995) in the Arlequin software package version 3.5.1.2 (Excoffier and Lischer 2010). This software package was also used to estimate the unbiased fixation index, F_{ST} (Weir and Cockerham 1984) and to test the significance of the F_{ST} values by nonparametric permutation with 10,000 runs.

The same mitochondrial datasets were also analyzed to infer the demographic history of the species based on the distribution of pairwise sequence differences. Historical population expansion (a rapid increase of population size) was assessed by performing mismatch distribution analysis (Rogers and Harpending 1992; Rogers 1995) in Arlequin. Whether or not a given population has recently experienced a sudden expansion was evaluated by testing the null hypothesis that the mismatch distribution expected under the sudden expansion model is different from the observed distribution. If the population was considered to have recently experienced a sudden expansion, the time from the expansion (t) was estimated according to the relationship $\tau = 2tu$, where τ is the mode of the distribution and u is the mutation rate of a sequence calculated as $u = \mu k$ (where μ is the mutation rate per nucleotide and k is the number of nucleotides) (Rogers and Harpending 1992). Moreover, Tajima's D test (Tajima 1983) and Fu's F_s test (Fu 1997) of neutrality were performed in Arlequin to further evaluate the possible events during population expansion. A population that has experienced expansion generally shows a significant negative Tajima's D value; F_s is also sensitive to population expansion, which generally leads to large negative F_s values (Fu 1997).

The distribution of the posterior probabilities for the deviation date between populations of *A. hessleri* were estimated using the ATPS β intron dataset and Bayesian coalescent inference (Hey and Wakeley 2001) implemented in the program IM (Hey and Nielsen 2007). The prior distributions of parameters were adjusted as a function of what was observed in the first run with the default settings according to the program documentation. Replicate runs with different seed numbers were conducted to ensure each run had approximately the same results. Ten million steps were sampled for each run after a burn-in of 1,000,000 steps. The converged ten runs with the complete posterior distributions of all parameters within the prior distributions were used for the final divergence time estimates.

The mutation rates of the tRNA^{Met}–12S rRNA and ATPS β intron regions were approximated by comparing Kimura-corrected average pairwise distances (Kimura 1980) for these regions and the COI gene among the individuals of *A. hessleri* and by extrapolating the estimated evolutionary rate for the latter gene in the entire *Alviniconcha* (see above).

26.3 Results

26.3.1 Evolutionary Rate of COI Gene in *Alviniconcha*

The Bayesian phylogenetic reconstruction under the GTR + G + I model estimated COI genetic distances between the six individuals of *Alviniconcha* and three of *Ifremeria nautilei* to be 0.8088–0.8514 with an average of 0.8264 (Fig. 26.1). The divergence date for the split between *Alviniconcha* and *Ifremeria* was estimated either at 64.4 Ma (31.4–98.9 Ma: 95 % highest probability density interval) or 59.2 Ma (18.8–74.5 Ma) using fossil calibration points or the hypothesized vicariance of deep-sea taxa across the Isthmus of Panama, respectively (Johnson et al. 2010). Assuming that reasonably well corrected distances were observed in the present Bayesian phylogram and the two lineages leading to *Alviniconcha* and *Ifremeria* evolved at an equal pace, the substitution rate of their COI gene was calculated to be 0.64 % per million years (My) (95 % confidence range: 0.42–1.32 %/My) with the fossil dates or 0.70 %/My (0.55–2.19 %/My) with the vicariance calibration. As the two estimates were similar to each other, the average value (0.67 %/My) was used in the following assessment of population history of *A. hessleri*. This average value roughly corresponded to the lower limit of the range of COI evolutionary rates for animal lineages (0.7–1.2 %/My) reviewed by Wilke (2003).

Fig. 26.1 Bayesian phylogram of 22 provannid and three outgroup gastropods, reconstructed from the 530-bp alignment of the cytochrome *c* oxidase subunit I gene. Numerals on branches indicate Bayesian posterior probabilities, shown as percentage for values above 50 %. See Johnson et al. (2010) and Hidaka et al. (2013) for the details of the study specimens

Table 26.2 The genetic diversity of five populations of *Alviniconcha hessleri* estimated from two mitochondrial regions

Region	Vent site	N	Haplotype	Gene diversity	Nucleotide diversity
COI	Alice Springs	20	10	0.85 ± 0.06	0.00322 ± 0.00223
	Forecast	20	10	0.91 ± 0.04	0.00398 ± 0.00263
	Snail	20	6	0.52 ± 0.13	0.00177 ± 0.00145
	Archaeon	20	9	0.80 ± 0.09	0.00268 ± 0.00195
	Pika	20	6	0.64 ± 0.12	0.00241 ± 0.00180
tRNA ^{Met} –12SrRNA	Alice Springs	20	11	0.76 ± 0.10	0.01385 ± 0.00894
	Forecast	20	12	0.92 ± 0.04	0.02729 ± 0.01576
	Snail	20	11	0.89 ± 0.05	0.01894 ± 0.01154
	Archaeon	20	13	0.91 ± 0.05	0.01891 ± 0.01152
	Pika	20	13	0.88 ± 0.07	0.01978 ± 0.01197

26.3.2 Population History of *Alviniconcha hessleri*

Twenty-five and 53 types of sequences (haplotypes) were identified among a hundred individuals of *A. hessleri* in the COI gene and the fragment spanning from the tRNA^{Met} gene to the 12S rRNA gene, respectively. The COI region contained 21 variable sites, eight of which were parsimoniously informative; the tRNA^{Met}–12S rRNA region had 50 variable and 26 parsimoniously-informative sites. The genetic diversity of populations of *Alviniconcha hessleri* at different five hydrothermal sites was estimated from two mitochondrial regions (Table 26.2). The unbiased *F*_{ST} and exact tests of population

differentiation for a combined dataset of the two mitochondrial regions showed no significant genetic difference among populations from the five vent sites (*p* > 0.05) except between the Snail and Pika sites in the latter test (*p* = 0.047).

The above comparison between the two gene regions showed that the tRNA^{Met}–12S rRNA fragment contained more informative signals than the COI gene as noted in a previous study (Hidaka et al. 2013). Indeed, genetically distinct groups were recognized only in the haplotype network of the former gene region: seven haplotypes construct a group (Group 2 in Fig. 26.2b), which is separated from another group constructed by 46 other haplotypes (Group 1 in Fig. 26.2b), by three substitutions. The two groups

Fig. 26.2 Median-joining networks connecting haplotypes found in the five populations of *Alviniconcha hessleri* for the cytochrome *c* oxidase subunit I gene (a) and the region spanning from the tRNA^{Met} gene to the 12S rRNA gene (b). Open circles denote missing

haplotypes. The areas of the colored circles are proportional to the frequency of each haplotype: the smallest ones represent single individuals. Two haplotype groups (separated by three missing haplotypes) were recognized in the network shown in (b)

Fig. 26.3 Mismatch distributions for two groups of *Alviniconcha hessleri*, the Group 1 (a) and Group 2 (b), based on combined nucleotide sequences of the gene for the cytochrome *c* oxidase subunits I and the region spanning from the tRNA^{Met} gene to the 12S rRNA gene. Lines: expected distribution for the sudden expansion model; bars: observed distribution

showed an apparent difference in geographic distribution. While the Group 1 was evenly distributed over the five study sites, the Group 2 was rare at the northernmost Alice Springs site. An average genetic distance of 0.015 (K2P) between the two haplotype groups was larger than the average distance between all pairs of individuals (0.007). By applying the average distance of 0.003 for the COI gene between the same pairs and its suggested rate of 0.67 %/My (see above), the evolutionary rate for the tRNA^{Met}–12S rRNA region was calculated to be 1.56 %/My and hence the divergence between the Groups 1 and 2 at 0.958 Ma.

The mismatch distribution analysis showed that the Group 1 (mismatch observed mean = 3.413, τ = 3.479, θ_0 = 0.040, θ_1 = 100.625, SSD = 0.0001, p = 0.980) and the Group 2 (mismatch observed mean = 2.250, τ = 2.270,

θ_0 = 0.004, θ_1 = 99,999.000, SSD = 0.0080, p = 0.480) have recently experienced sudden expansions in population size (Fig. 26.3). Using the calculated rates of the COI gene and the tRNA^{Met}–12S rRNA region, the expansions of the Group 1 and the Group 2 were estimated to have occurred at 0.264 and 0.172 Ma, respectively. Tajima's D (−2.071 and −1.700, respectively) and Fu's F_s (−27.34 and −3.446, respectively) were significantly negative for both groups (p < 0.05), also suggesting the recent expansions.

The average and standard deviation of mode values of the distributions of the posterior probabilities for the deviation date between the Groups 1 and 2 (i.e., the most probable estimates) among 10 runs was 5.23 ± 3.52 and seven of ten replicate runs showed the mode values around 5.0. The average genetic distance between all pairs of available

Fig. 26.4 Estimated population history of *Alviniconcha hessleri* in the Mariana Trough between 1 and 0.2 million years ago (Ma)

individuals was 0.011 for the ATPS β gene. Extrapolation of the average distance and substitution rate for the COI gene implied that this intron region has a rate of 2.46 %/My. The estimated age of divergence between the two groups, 0.937 Ma, agreed well with the result inferred from the average genetic distance for the tRNA^{Met}-12S rRNA region (0.958 Ma).

26.4 Discussion

The genetic distances estimated based on nucleotide sequences of the COI gene from the six individuals of *Alviniconcha* and three of *Ifremeria nautili*, were approximately 1.9 times larger than that based on a single species for each genus (0.44) (Johnson et al. 2010), which suggests the saturation of genetic distance due to multiple substitutions at the same sites since the split between *Alviniconcha* and *Ifremeria*. The molecular evolutionary rate calculated based on such a more reasonable estimation is expected to enable reconstruction of reliable population history of *Alviniconcha hessleri*.

Population dynamics of hydrothermal-vent endemic species such as *A. hessleri* are thought to be controlled primarily by fluctuating hydrothermal activity. A decline in the activity results in the reduction of population size which accelerates divergence between local populations. In contrast, recovery of the activity causes an expansion of population size, fusion of isolated populations, and

secondary contact between genetically differentiated individuals. Population divergence around 1 Ma and expansions around 0.3 and 0.2 Ma, which were estimated for *A. hessleri* in the present study, are also attributable to changes in the hydrothermal activity (Fig. 26.4). Hydrothermal activities in the Mariana Trough, which started around 7 Ma (Stern et al. 2003), are thought to have been more intense during its young stage than the present and therefore *A. hessleri* might have been distributed over a wider area in the trough. The present results showed genetic differentiation between populations in the central and southern parts of the Mariana Trough at around 1 Ma. The decline in hydrothermal activity might have resulted in the reduction of local populations of the species and loss of connectivity between them, which possibly represent the origin of the Groups 1 and 2.

The mismatch distribution analysis suggested that the Groups 1 and 2 expanded at 0.3 and 0.2 Ma, respectively. These expansion events might be attributable to the recovery of the local hydrothermal activity. In that case, the increase of the activity in the central Mariana Trough preceded that in the southern Mariana Trough and gene flow from expanding central population into southern ones might have predominated for about a 100,000 years and resulted in ubiquitous distribution of individuals of the Group 1. In contrast, the more recent increase of the population size in the southern Mariana Trough might have resulted in the uneven geographical distribution of individuals of the Group 2 (Fig. 26.3).

The snails of *Alviniconcha* are one of the representative animal groups in the hydrothermal vent fields of the Pacific and Indian Oceans. Due to their dominance and strict endemism to the hydrothermal vent environment, which means their local populations change reflecting hydrothermal activities clearly, they are expected to be useful model animals for the evaluation of effects of artificial or natural environmental change such as those by the hydrothermal deposit mining or volcanic eruption on this deep-sea ecosystem. The general biology and natural history of these species have been the subject of several studies. For example, their spatial distribution within a single vent field and species compositions at different fields have been reported in the Lau Basin in the southern Pacific (Podowski et al. 2009; Beinart et al. 2012). Similar studies have been conducted for the closely related *Ifremeria nautilei* in the Manus Basin (Thaler et al. 2011). Information about the effects of the past environmental changes on the populations of such model species will be very useful for the interpretation of results of monitoring their genetic characteristics after the environmental change.

The history of hydrothermal ecosystems can be better reconstructed by comparing and integrating estimates of past environmental changes from biological and geochemical methodologies. Such studies are expected to contribute to more accurate reconstruction of history of hydrothermal ecosystems. Unfortunately, the present results cannot be compared with geochemical evidence. The historical fluctuation in the hydrothermal activity of the Mariana Trough have been traced back only to 12,000 years ago by the geochemical approach (Stüben et al. 1994; Takamasa et al. 2013; Ishibashi et al., Chap. 23), while our results suggested environmental changes between 1 to 0.2 Ma. Future progress in both methodologies will enable us to further explore the hypothesis that historical changes in hydrothermal activity promote genetic structuring of hydrothermal vent-endemic species.

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