# Application of MART Analysis to Infer Paleoseasonality in a Pleistocene Shallow Marine Benthic Environment

Matthew H. Dick[1,*], Masato Hirose[2], Reishi Takashima[3], Toyoho Ishimura[1], Hiroshi Nishi[1,4] and Shunsuke F. Mawatari[1,4]

[1]*COE for Neo-Science of Natural History, Faculty of Science, Hokkaido University, Sapporo 060-0810, Japan*
[2]*Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan*
[3]*School of Marine Science and Technology, Tokai University, 3-20-1 Shimizu-ku Orido, Shizuoka 424-8610, Japan*
[4]*Department of Natural History Sciences, Faculty of Science, Hokkaido University, Sapporo 060-0810, Japan*

## ABSTRACT

Zooids in bryozoan colonies show an ecophenotypic response in which zooid size varies inversely with temperature at the time of zooid growth. A technique called MART analysis allows estimation of the mean annual range of temperature (MART) in Recent or paleo- marine environments by measuring the mean coefficient of variation (CV) of zooid size in species of cheilostome bryozoans that lived in those environments. We conducted standard MART analyses of Recent specimens from nearshore shelf regions in Akkeshi Bay (Japan) and the western Aleutian Islands (Alaska) as controls on our application of the method, and of fossil specimens from a Pleistocene shallow benthic environment [Nakasato Congomerate Member, Utasai Section, lower Setana Formation (1.2~1.0 Ma), Kuromatsunai, Hokkaido, Japan] to examine paleoseasonality. In some cases, not enough material was available from fossil strata to conduct standard MART analyses. For these cases, we developed a modified technique that we call specimen-limited MART analysis, or SL-MART. We applied this technique to specimens from two stratigraphically sequential sediment samples from the Soebetsu Sandstone Member in the Soebetsu Section of the upper Setana Formation (1.0–0.6 Ma). Regardless of technique or age of the specimens, replicate samples in our analyses provided remarkably similar estimates of seasonality. The utility of the controls was questionable due to uncertainty about present-day temperature ranges in the localities sampled. A decrease in average MART value from the lower to upper Setana Formation (11.8°C and 8.6°C, respectively) indicates more pronounced seasonality in the lower than the upper Setana, perhaps suggesting a shift to colder conditions in the latter. However, the younger samples could also have lived at a greater depth, which would also reduce the MART. In addition, previous studies of marine mollusks indicate variability in paleoenvironment within both the upper and lower Setana Formation, perhaps related to the warm Tsushima current that flowed into the Sea of Japan during most interglacial periods from 1.71–0.8 Ma. Thus more than a few scattered MART estimates are necessary for reconstruction of paleoseasonality through the depositional interval of the Setana Formation.

**Keywords**: Bryozoa, Ecophenotypic response, Growth, MART, Paleoseasonality, SL-MART, Temperature

*Corresponding author, e-mail: mhdick@mail.sci.hokudai.ac.jp
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## INTRODUCTION

Zooids in bryozoan colonies show an ecophenotypic response in which zooid size, measured as length (L), width (W), or area (A = L x W), varies inversely with temperature at the time of zooid growth [1]. From this relationship, a technique was developed that allows estimation of the mean annual range of temperature (MART) in Recent or paleomarine paleoenvironments [2, 3]. This technique, referred to as MART analysis, measures the mean coefficient of variation (CV) of zooid size in species of cheilostome bryozoans taken from a particular environment. Colonies growing in relatively thermally uniform environments (e.g., tropics; polar regions; deep sea) show low variation in zooid size, and consequently a low CV; conversely, colonies growing in relatively thermally variable environments (e.g., shallow, cool-temperate habitats; tropical environments with upwelling) show high variation in zooid size, and consequently a high CV. The MART value is thus directly proportional to CV, and an empricially derived formula [2] can be used to convert CV to an estimate of MART. The MART technique has been shown to fairly accurately predict known annual temperature ranges in Recent bryozoans [4, 5]. In addition to MART analysis, which infers seasonality from an estimate of annual temperature range, the inverse relationship between temperature and zooid size can be used to directly detect annual growth cycles and thence colony growth rate and longevity [5, 6].

We have recently begun studies of bryozoans in Pleistocene nearshore marine deposits of the Setana Formation [7, 8] in the vicinity of Kuromatsunai, SW Hokkaido, Japan. Although the paleoclimate at the time of deposition has been inferred from the species composition of bivalve molluscs [9, 10] and of planktonic foraminifera and calcarous nanofossils [11], sources of error exist in this type of inference [2], and MART estimates can provide an independent assessment. In addition, changes in MART values in different sections can potentially indicate changes in climate. In this paper we present the results of preliminary MART analyses of species from modern shelf regions in Alaska and Japan (as controls on our performance of the method) and two sections of the Setana Formation at Kuromatsunai. The analyses are preliminary in the sense that they involved only two or three species per section or locality, and in one section involved a modified technique (SL-MART) whose reliability is unclear.

## METHODS

### Standard MART analyses

In practical terms, a significant amount of material is required in order to calculate an overall MART value for a particular locality or section. The estimated MART value is ideally the mean value from independent MART analyses of several species. In the development of the technique [2], at least 20 individual zooids were measured for each of a minimum of five colonies of each species analyzed; we refer to use of these sample sizes as "standard MART analysis." In addition, the particular species and colonies used in a MART analyses should fulfill a number of criteria [2] to ensure that as much as possible of the variation in zooid size will be due to temperature rather than other factors. Not all species from a particular locality will be suitable for MART analysis, nor will five suitable colonies always be available for species that are suitable. From the Setana Formation, we had sufficient material for standard MART analyses only from the Nakasato Congomerate Member in the Utasai Section (Kokemushi Paradise; lower Setana, 1.2~1.0 Ma). We conducted a standard MART analysis of two species (*Porella concinna* and *Escharoides hataii*) whose colonies were attached to the smooth interior surfaces of bivalve shells. In addition, we performed standard analyses on two species (*Porella acutirostris* and *Fenestrulina orientalis*) collected subtidally from Akkeshi Bay, Japan, with colonies also on the smooth inner surfaces of bivalve shells, and three species (*Tegella* sp. A, *Tegella* sp. B, and *Hayamiellina* sp. A) from a single sampling station (52° 54.742'N, 170°48.900'E) at 189 m depth in the western Aleutian Islands, Alaska, with the bryzoan colonies attached to the smooth, flat surface of the heavy plastic tunnel of a large crab pot.

To calculate a mean coefficient of variation (CV) of zooid area for each species, length (L) and width (W) were measured and area (A = L x W) calculated for 20 zooids in each of five colonies of the species; mean area ($A$) and standard deviation (SD) were calculated for each colony; the CV (= SD/$A$) was calculated for each colony; and the mean CV for the five colonies of the species was calculated. The mean intracolony CV ($b$) of zooidal area was used to calculate the MART value according to the formula MART (°C) = $-3 + 0.745\ (b)$ [2]. L and W measurements were taken to the nearest 1 ocular-micrometer unit (= 0.02564 mm) at 80X magnification on a Nikon SMZ-10 binocular stereoscopic microscope. Measurements in ocular-micrometer units were used directly in calculations without conversion to millimeters, since the calculated CV values were the same with or without conversion to millimeteres.

Theoretically, the 20 zooids measured in a colony should be selected randomly [2]. In practice this is difficult to do, and in any case the ultimate selection is not entirely random, because zooids that violate certain subjective criteria (e.g., they are ‘abnormal’ in size or shape as a result of physical damage or biotic interactions [2], or are unusually large zooids typically occurring at branch points in budded columns). Instead of random selection, we selected zooids haphazardly for measurement, as in the following example. Assume a circular colony with a zone of astogenetic repetition (ZAR) 20 zooids deep. With a marking pen, we drew four lines from the periphery of the colony to the center, dividing the colony into four approximately equal quadrants. We measured five zooids along each of these lines, within the ZAR. In the present example, with the ZAR 20 zooids deep, approximately every fourth zooid was measured starting at the periphery and working inward. If a zooid was obviously misshapen due to a local substrate irregularity or other factor, or was an unusually large zooid comprising a branch point in the column of zooids, another zooid in its vicinity was measured instead. While not random, this method ensures a sampling of the variation in zooid size that results from variable water temperature over the life of the colony (that is, from the colony periphery to the inner boundary of the ZAR).

**SL-MART analysis**

There was not enough material from stratigraphically sequential sediment samples from the Soebetsu Sandstone Member in the Soebetsu Section (upper Setana, 1.0~0.6 Ma) for standard MART analyses, so we conceived and employed a modified analytical technique, which we called «specimen-limited MART» (SL-MART). In principle, analysis of every suitable colony of every suitable species (that is, those fulfilling the general criteria for MART analysis [2]) that grew at a particular site under a particular mean annual temperature range attempts to estimate the same MART value. The average among-species MART value can thus be estimated by measuring the CV for several colonies from each of several species (whichever of the species and colonies collected meet the general criteria for MART). For SL-MART, we selected a standard of at least 10 colonies distributed among at least three species. The principle of SL-MART is illustrated in Fig. 1.

Relevant to the method of SL-MART, we conducted simulations using actual data from standard

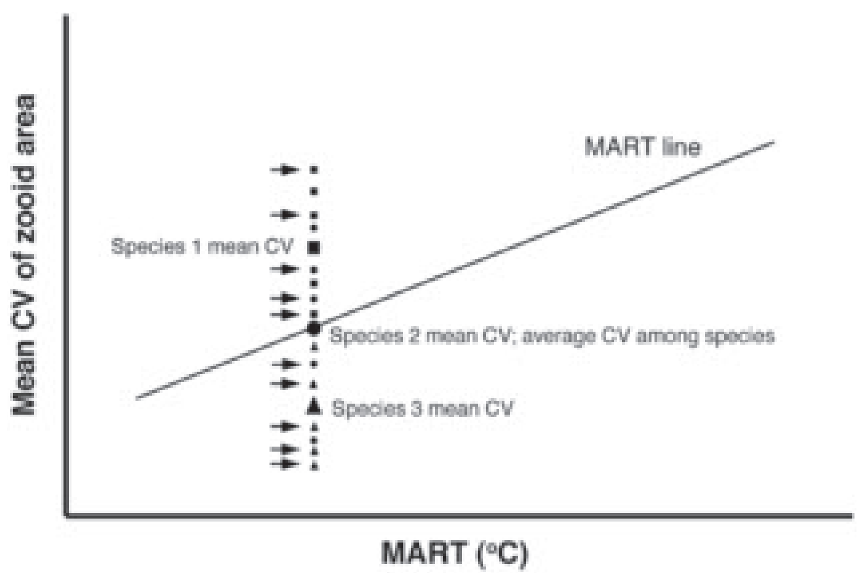


**Fig. 1** Principle of SL-MART. In this diagram, the mean CV of Species 2 (large circle) estimates the hypothetical true MART value, and is also the average of mean CV values of Species 1–3 analyzed (large square, circle, and triangle, respectively). Each mean CV value in turn derives from the CV values of five colonies (small squares, circles, triangles). In principle, measuring the CV for any 10 colonies among the three species [for example, the colonies indicated by arrows: three colonies of Species 1 (small squares), three colonies of Species 2 (small circles), and four colonies of Species 3 (small triangles)] will also estimate the mean CV of the total population of species and colonies at this site.

MART analyses of the three species from the western Aleutians (Table 1). Mean CVs were calculated for each of three species from a single trawl sample in the western Aleutian Islands, based on measurements of 20 zooids from each of five colonies per species in the standard manner. An average MART value = 6.4°C for the three species was determined by averaging the mean CVs. In each simulation, a sample of 10 intracolony CV values was randomly drawn (without replacement) from the 15 colonies measured in total among the three species. This was repeated 10 times (simulations 1–10 in Table 1), giving different combinations and numbers of colonies per species. The average CV and then the SL-MART value were determined in each case. MART values determined from the simulations ranged from 5.7 to 7.1°C. The simulations predicted a MART value of 6°C (rounded to nearest whole number) 60% of the time, and all values from the simulations fell within ± 0.7°C of the mean value of 6.4°C determined by standard MART analysis.

In the analysis of two sequentially collected samples from the Soebetsu Section, one to three colonies for each of six species were measured (Table 2) from each sample. The mean MART values of the two samples were quite similar (8.2 and 8.9°C), even though the variance among the values for the 10 colonies measured for each of the two samples was quite high (SD = 3.0–4.5°C).

## RESULTS AND DISCUSSION

Results of the various MART analyses outlined in Methods are presented in Table 3. In all cases, irrespective of whether the analysis involved fossil or Recent specimens, standard MART values calculated for the two or three species from a locality or section were very similar to one another; the largest difference was 1.1°C between the most divergent values (5.7 and 6.8°C) from the Aleutians. In the only application of SL-MART, values from different strata of the same member were very similar, despite high variance among colonies.

We analyzed Recent material as a control on our application of the method; however, the controls were not effective because we found that it was difficult to obtain accurate temperature data for the Recent sites. For example, we base the actual MART value of 1.5°C for the western Aleutian site on data from eastern Aleutian passes at similar depth [12]. The value of 6.4°C from the MART analysis appears to overestimate the actual MART by more than a factor of four; however, it could also be that the MART at around 200 m depth at the site sam-

**Table 1** Simulations (1–10) of specimen-limited MART (SL-MART) analyses using actual MART data for three species from the western Aleutian Islands, Alaska. See text for details. Values are MART values converted from CVs.

| | | | | SIMULATIONS (1–10) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Colony | MART | Mean | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| *Tegella* A | 1 | 4.74 | | 4.74 | 7.07 | 4.74 | 4.74 | 13.23 | 4.74 | 13.23 | 4.74 | 4.74 | 7.07 |
| | 2 | 13.23 | | 2.96 | 2.96 | 13.23 | 13.23 | 7.07 | 7.07 | 2.96 | 13.23 | 7.07 | 2.96 |
| | 3 | 7.07 | | 6.22 | 6.22 | 7.07 | 6.22 | 2.96 | 2.96 | 6.22 | 7.07 | 6.22 | 7.67 |
| | 4 | 2.96 | | 7.67 | 7.67 | 6.22 | 7.67 | 7.67 | 7.67 | 7.67 | 2.96 | 6.97 | 6.97 |
| | 5 | 6.22 | 5.7 | 6.97 | 6.97 | 7.67 | 5.34 | 6.97 | 6.97 | 6.97 | 7.67 | 5.34 | 5.34 |
| *Tegella* B | 1 | 7.67 | | 5.34 | 5.23 | 5.23 | 5.23 | 5.34 | 8.07 | 8.07 | 8.07 | 8.07 | 8.07 |
| | 2 | 6.97 | | 8.07 | 4.76 | 4.76 | 4.76 | 8.07 | 5.23 | 5.23 | 5.23 | 4.76 | 5.23 |
| | 3 | 5.34 | | 4.76 | 6.46 | 6.46 | 7.73 | 6.46 | 7.73 | 6.46 | 4.76 | 6.46 | 4.76 |
| | 4 | 8.07 | | 6.46 | 7.73 | 7.73 | 5.67 | 7.73 | 5.67 | 5.67 | 6.46 | 7.73 | 6.46 |
| | 5 | 5.23 | 6.7 | 4.04 | 4.04 | 5.67 | 4.04 | 5.67 | 4.04 | 4.04 | 5.67 | 5.67 | 4.04 |
| *Hayamiellina* | 1 | 4.76 | | | | | | | | | | | |
| | 2 | 6.46 | | | | | | | | | | | |
| | 3 | 7.73 | | | | | | | | | | | |
| | 4 | 5.67 | | | | | | | | | | | |
| | 5 | 4.04 | 6.8 | | | | | | | | | | |
| Average | | | 6.4 | | | | | | | | | | |
| Mean SL-MART | | | | 5.72 | 5.91 | 6.88 | 6.46 | 7.12 | 6.02 | 6.65 | 6.59 | 6.30 | 5.86 |

**Table 2** Taxa and MART values for each taxon in two strata of the Soebetsu River section. Each value associated with a species is the MART estimate for a single colony based on the intracolony CV.

| | Soebetsu River stratum: | |
|---|---|---|
| | SOE-017 | SOE-023 |
| *Cauloramphus* sp. A | 7.56 | 18.61 |
| | 8.39 | 6.08 |
| | 5.65 | – |
| *Cauloramphus ?disjunctus* | 10.13 | – |
| *Cauloramphus ?cryptoarmatus* | 8.12 | 9.92 |
| Cleidochasmatid sp. A | 9.41 | 7.22 |
| | 15.63 | 11.82 |
| | – | 4.44 |
| *Puellina* sp. A | 11.12 | – |
| *Schizoporella japonica* | 6.49 | 5.48 |
| | 6.17 | 7.86 |
| *Porella* sp. A | – | 8.18 |
| *Hayamiellina* sp. A | – | 2.38 |
| Average MART | 8.9 | 8.2 |
| S. D. | 3.0 | 4.5 |

**Table 3** Results of MART analyses of Pleistocene (upper part) and Recent (lower part) material. See text for details.

| Locality | Formation (Age) | MART Analysis | Actual MART (°C) | Calculated MART (°C) | Average MART (°C) |
|---|---|---|---|---|---|
| Soebetsu River | Upper Setana (1.0~0.6 Ma) | SL-MART | | | |
| Stratum SOE-017 | | | – | 8.9 | |
| Stratum SOE-023 | | | – | 8.2 | 8.6 |
| Kokemushi Paradise | Lower Setana (1.2~1.0 Ma) | Standard | | | |
| *Porella concinna* | | | – | 11.5 | |
| *Escharoides hataii* | | | – | 11.9 | 11.7 |
| Akkeshi Bay | Recent | Standard | 10.5 | | |
| *Porella acutirostris* | | | | 10.2 | |
| *Fenestrulina orientalis* | | | | 10.4 | 10.3 |
| Aleutian Islands, Alaska | Recent | Standard | 1.5 | | |
| *Tegella* sp. A | | | | 6.8 | |
| *Tegella* sp. B | | | | 6.7 | |
| *Hayamiellina* sp. A | | | | 5.7 | 6.4 |

pled actually differed from that at similar depth in the eastern Aleutians.

The average MART calculated from two species collected subtidally in Akkeshi Bay was 10.3°C. Actual MART values in Akkeshi Bay from the surface to 50 m depth range from 7~14°C (median ≈ 10.5°C) [13], depending on actual depth and site of measurement. The estimated MART value thus appears consistent with the actual MART in Akkeshi Bay, though again without actual measurements at the collecting site, this remains speculative.

Estimates by the SL-MART technique for two stratigraphically sequential sediment samples (SOE-017, SOE-023) from the Soebetsu Section are so similar to one another (8.2 and 8.9°C) as to provide no indication of a significant change in seasonality over the period spanning the two depositions. Interestingly, a difference in oxygen isotope values [14] between these two samples suggests in contrast that there was some sort of climatic change between the two times of depositions. The Soebetsu Sandstone Member in the Soebetsu Section lies in the upper Setana Formation (1.0–0.6 Ma) [7, 10, 11]. Molluscan faunal elements of this section suggest cool-temperate conditions of the sort characterized today by a sea-surface temperature of about 20–23°C in summer and 2–8°C in winter [9, 10], which in turn indicates a MART of ~16.5°C (based on the midpoint values of the winter and summer temperature ranges). Our estimated MART value of 8.2–8.9°C is considerably lower, and we can think of two explanations: 1) The previous estimate of paleoconditions reflected in sea-surface temperature [10] was correct, but the bryozoans lived deep enough that the MART they experienced was reduced compared to that at the sea surface. This could have been the case, as there is evidence that this section was deposited in an inner- to outer-shelf environment. 2) Seasonality was less pronounced than estimated by ref. [10] on the basis of the molluscan fossils. In this case, less seasonality should imply a colder regime than "cool temperate," rather than a warmer one, as the faunal composition of our samples (e.g., Table 2) is characteristic of the high boreal North Pacific today (for example, in the Recent fauna at Ketchikan, Alaska, several *Cauloramphus* species, a *Puellina*, *Schizoporella japonica*, and a *Porella* sp. very similar to that in SOE-023 were reported intertidally [15]). The fauna is very different from that in the present-day subtropical North Pacific [e.g., ref. 16].

The MART (11.7°C) we estimated for the lower Setana (1.2–1.0 Ma) Utasai Section (Kokemushi Paradise) was higher than that (8.6°C) of the upper Setana (1.0–0.6 Ma) Soebetsu Section. The molluscan faunal elements of the Utasai Section also suggest cool-temperate conditions [7, 9, 10], though there is evidence of subarctic conditions (sea-surface temperature about 12–20°C in summer and 0–2°C in winter [9]; MART ~15°C based on the midpoint values of these ranges) in the lower part of the section. The higher MART estimate from the lower Setana indicates more pronounced seasonality at the time of deposition compared to that from the upper Setana.

Interpretation of differences in our estimated MART values between members of the upper and lower Setana Formation is difficult. MART analysis of limited samples from either member will provide only a small part of the whole picture, especially as there is evidence of variability in sea-temperature ranges within members of the Setana Formation. For example, as mentioned above, molluscan fossils indicate that the Nakasato Conglomerate Member (lower Setana) varied from subarctic in the lower part to cool-temperate in the upper part. Likewise, occurrences of characteristic subtropical mollusks and a species of warm-water planktonic foraminiferan suggest there was a warming episode in the lower part and another in the middle part of the generally cool-temperate Soebetsu Sandstone Member (upper Setana).

Estimated MART values for the Setana Formation undoubtedly reflect the history of flow of the warm Tsushima Current into the Sea of Japan [17]. From 1.71–0.8 Ma, which spans two-thirds of the 1.2–0.6 Ma period of deposition of the Setana Formation, the Tsushima Current flowed into the Sea of Japan during almost every interglacial highstand, causing warming of the sea. During glacial intervals, cessation of flow due to shallowing of Tsushima Stait resulted in cooling of the Sea. These paleoenvironmental changes in the Sea of Japan mirrored global paleoclimatic cycles, but likely amplified the effects of the latter (i.e., during interglacial periods, the Sea of Japan along southwestern Hokkaido was likely warmer than the Pacific Ocean along southern and southeastern Hokkaido due to the effects of the Tsushima Current).

As the originators of MART analysis [2] pointed out, this technique offers a number of advantages for estimating paleoseasonality in shallow-water marine environments. However, the reliability of the technique needs investigation using colonies for which accurate, in-situ measurements of temperature range are available. Lack of measurements of actual MART regimes experienced by the specimens measured to obtain the original regression of mean CV against MART [Fig. 2C in ref. 2] might be a major source of the variation evident in the regression (i.e., considerable ranges in CV values for "known" MART values). Thus with more accurate data, the MART equation itself might be improved; in any case, it needs to be further checked. In addition, the sample sizes needed for MART analysis need to be better understood. Ref. [2], for example, gave no justification for measuring a sample of 20 zooids from each of a minimum of five colonies to obtain mean intracolony CV values. By the same token, our choice herein of a standard for SL-MART analysis of measuring 20 zooids from each of 10 colonies distributed among at least three species is arbitrary. At some point, the statistical bases of MART analyses will need to be better defined, and some studies have begun to lay the foundation for this [18]. What is remarkable about the MART technique is that, despite its not having yet been rigorously tested or widely applied, it has nonetheless provided remarkably consistent replicate estimates of the annual temperature regimes to which fossil or Recent populations of bryozons have been subjected. In some test cases [4, 5], it has also provided remarkably accurate estimates of known MARTs of Recent populations. We feel strongly that the technique, with further refinement, will provide an increasingly powerful tool in investigating paleoseasonality and climatic changes.

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