

Floral Response of Coccolithophores to Progressive Oligotrophication in the South Equatorial Current, Pacific Ocean

Kyoko HAGINO and Hisatake OKADA

*Division of Earth and Planetary Sciences, Graduate School of Science,
Hokkaido University, N10 W8, Sapporo 060-0810, Japan*

Abstract. Horizontal distributions of living coccolithophores were investigated over a wide area in the equatorial and subequatorial Pacific Ocean between 20°N and 20°S. Based on the results of Q-mode Cluster Analysis and the floral composition, three main coccolithophore assemblages were identified, including one neritic and six pelagic subassemblages. Pelagic subassemblages displayed zonal distribution with the most eutrophic flora as a center, and a floral composition controlled by water temperature and nutrient concentration. The observed floral zoning was a response to the westward, as well as latitudinal, water oligotrophication associated with a transition from upwelled (Equatorial Divergence Zone) to more stratified waters (Western Pacific Warm Pool and the North and South Pacific Central Waters).

Keywords: coccolithophores, coccolith, biogeography, Equatorial Pacific Ocean

1. INTRODUCTION

Coccolithophores, marine unicellular haptophytes, produce tiny calcite scales called coccoliths. These coccoliths surround the living cell of the coccolithophore, forming an outer covering called a coccosphere. Coccolithophores are distributed throughout the entire photic zone of all oceans except in polar waters (Jordan and Chamberlain, 1997). Extensive studies of coccolithophore biogeography have shown that five and four latitudinal floral zones exist in the Atlantic (McIntyre and Bé, 1967) and Pacific Oceans (Okada and Honjo, 1973a), respectively. However, floral data are still scarce in the central part of all oceans.

Regional studies have clarified the environmental controls on the coccolithophore flora. The horizontal and vertical distributions of coccolithophores are controlled by water masses (e.g., Friedinger and Winter, 1987) and water stratification (e.g., Hagino *et al.*, 2000), respectively. Floral composition varies seasonally (e.g., Okada and McIntyre, 1979), and is affected by the change in nutrient level that accompanies water turbulence (Giraudeau and Bailey, 1995). However, mega-scale floral response to hydrographic change within an individual current has not been studied extensively.

The surface water of the equatorial Pacific is dominated by the South

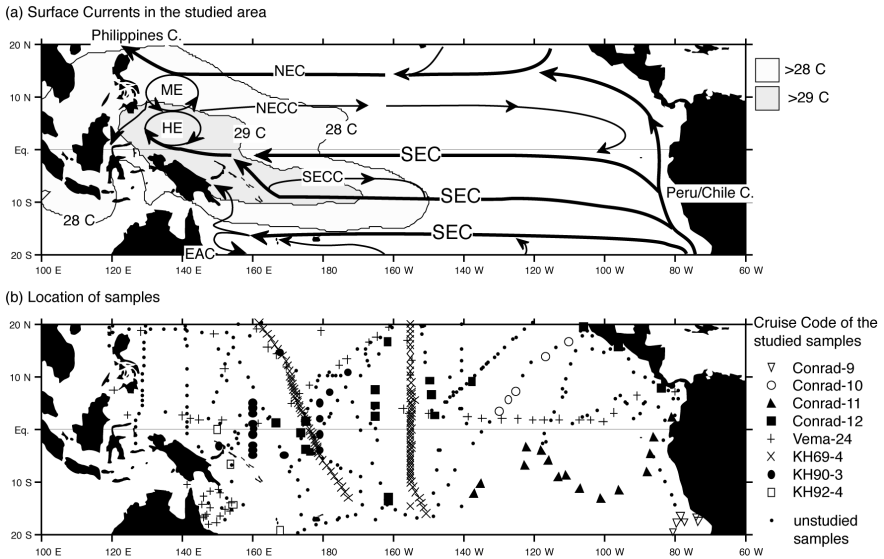


Fig. 1. (a) Distribution of the surface currents and the warm surface water mass in the equatorial and subequatorial Pacific Ocean, and (b) geographic distribution of the studied/unstudied samples. Note: Abbreviations used in (a) are Mindanao Eddy (ME), Halmahera Eddy (HE), North Equatorial Current (NEC), North Equatorial Counter Current (NECC), South Equatorial Counter Current (SECC), the South Equatorial Current (SEC), and East Australian Current (EAC) (Tomczak and Godfrey, 1994). Isotherms in (a) were obtained from the World Ocean Atlas (Levitus and Boyer, 1994). The Cruise Code relating to unstudied samples is not shown in (b).

Equatorial Current (SEC) (Fig. 1(a)), and is characterized by longitudinal hydrographic variation. The strong westward flow of the SEC confronts the Philippine and Indonesian archipelagos, forming a Western Pacific Warm Pool (WPWP) in the western equatorial Pacific (Tomczak and Godfrey, 1994). In the WPWP, the surface water is oligotrophic due to strong water stratification. In the Central and Eastern equatorial Pacific, on the other hand, the surface water is relatively cool and remarkably eutrophic due to the Equatorial Divergence (upwelling). Moreover, a strong coastal upwelling off the coast of Ecuador and Peru supplies nutrient-rich, cold, deep water to the surface of the Eastern Pacific (Brown *et al.*, 1989). Therefore, the SEC is a suitable current for studying the floral response to hydrographic changes.

By kindly providing us with several sample sets, Dr. A. McIntyre, formerly at Lamont-Doherty Earth Observatory, and Dr. H. Matsuoka, Kochi University, gave us an opportunity to study the coccolithophore biogeography over a wide area of the Equatorial and Subequatorial Pacific (20°N–20°S). Here we present the floral variation of coccolithophores within the SEC and its adjoining subtropical realms (North/South Pacific Central Gyre) by combining the quantitative floral data of Okada and Honjo (1973b) and those of this study.

Table 1. Samples examined in this study.

Cruise code	Research Vessel	Sampling period	Number of available samples	Number of samples studied in floral composition	Provider of samples
Conrad-9	R/V Conrad	Feb. 1–Feb. 5, 1964	18	7	A. McIntyre
Conrad-10	R/V Conrad	Jan. 30–May 15, 1966	88	5	A. McIntyre
Conrad-11	R/V Conrad	Sep. 1–Oct. 17, 1967	26	15	A. McIntyre
Vema-24	R/V Vema	Feb. 22–Aug. 17, 1967	88	59	A. McIntyre
Conrad-12	R/V Conrad	Feb. 10–Oct. 31, 1968	108	18	A. McIntyre
KH90-3	R/V Hakuho-maru	Nov. 1–Dec. 2, 1990	19	18	H. Matsuoka
KH92-3	R/V Hakuho-maru	Sep. 24–Oct. 2, 1992	4	4	H. Matsuoka

Table 2. Samples of Okada and Honjo (1973b) used in this study.

Cruise code	Research Vessel	Sampling period	Number of available samples	Number of samples studied in floral composition
OM-30	Oshoro-maru	Nov. 19, 1968–Jan. 10, 1969	31	0
HK69-4	R/V Hakuho-maru	Sep. 18–Nov. 5, 1969	103	103

2. MATERIAL AND METHOD

A total of 374 filtered surface water samples were acquired from the equatorial and subequatorial Pacific (20°N–20°S) (Table 1). Each water sample was collected using a bucket, and was filtered through a membrane filter (47 mm diameter, 0.8 μm pore size). Preliminary observations with a cross-polarized microscope revealed that 126 of 374 samples contained a sufficiently large number of coccospheres to study the floral composition in a SEM (Table 1, Fig. 1(b)). The remaining 248 samples were not examined because they were rare/barren in coccospheres (Table 1, Fig. 1(b)). There is no distinct difference between coccosphere-rare/barren and coccosphere-common samples in terms of sampling period, water regimes, collecting method, and preservation method.

The coccolithophore flora was investigated by identifying more than 300 specimens per sample in an SEM. The classification of species followed Young *et al.* (2003). As it is difficult to identify very small, poorly preserved specimens even with the SEM, *Gephyrocapsa crassipons* and *Gephyrocapsa ericsonii* were combined into the small *Gephyrocapsa* complex, and *Reticulofenestra parvula* and *Reticulofenestra punctata* were combined into the small *Reticulofenestra* complex.

Okada and Honjo (1973b) examined 134 surface water samples in the Central equatorial-subequatorial Pacific, and reported quantitative floral data for the 103 coccosphere-common samples by identifying 200 specimens per sample in a TEM (Table 2, Fig. 1(b)). The species names in Okada and Honjo (1973b), partly revised by Okada and McIntyre (1977), were updated to conform to the Young *et al.* (2003) scheme. Their floral data were incorporated into this study, thereby increasing the available floral data to 229 samples (Tables 1 and 2, Fig. 1(b)). The sampling period of all samples studied spans 28 years, and sampling season varies between samples (Tables 1 and 2). Sea surface temperature was the only hydrographic parameter measured at the same time as the sampling.

3. RESULTS AND DISCUSSION

3.1 Floral composition of coccolithophore assemblages

A total of 100 coccolithophore taxa were identified from 229 samples. Fourteen taxa that occupied more than 10% of the flora in any sample and so were recognized as major taxa (Table 3). To determine the degree of similarity in coccolithophore assemblages between samples, a Ward Minimum Variance Cluster Analysis was applied to the samples by using the SYSTAT 4.1 software. This analysis was based on the standardized values of the relative abundance of 14 major taxa and those of miscellaneous taxa. As a result of the analysis, the samples can be classified into three Clusters, I–III, and can be further subdivided into seven subclusters that are identified by affixes a–c (Fig. 2). Based on the floral composition, Clusters I, II, and III are identified as the *Umbellosphaera irregularis* common Assemblage (UCA), the *Gephyrocapsa oceanica* common Assemblage (GCA), and the *Emiliana huxleyi* common Assemblage (ECA),

Table 3. Percentage abundance of each major taxa in the seven subflora.

Major Taxa	UCA-a (subcluster I-a)	UCA-b (subcluster I-b)	UCA-c (subcluster I-c)	GCA-a (subcluster II-a)	GCA-b (subcluster II-b)	ECA-a (subcluster III-a)	ECA-b (subcluster III-b)
<i>Emiliania huxleyi</i> (Lohmann, 1902) Hay and Mohler, in Hay <i>et al.</i> , 1967 var. <i>huxleyi</i>	3.0 (0.0-7.9)	4.9 (0.0-17.3)	15.5 (0.0-49.2)	5.6 (0.0-30.6)	22.5 (1.5-47.5)	27.7 (1.3-57.1)	53.0 (7.6-98.3)
small <i>Gephyrocapsa</i> complex	0.0 (0.0-0.0)	0.1 (0.0-2.0)	1.0 (0.0-4.9)	1.0 (0.0-10.2)	4.4 (0.0-19.0)	13.2 (0.7-37.0)	5.7 (0.0-18.2)
<i>Gephyrocapsa oceanica</i> Kamptner, 1943	16.3 (0.5-41.0)	4.2 (0.0-27.0)	3.2 (0.0-30.3)	56.8 (17.8-94.1)	29.0 (10.0-44.4)	11.0 (0.0-29.4)	5.6 (0.0-22.8)
small <i>Reticulofenestra</i> complex	0.0 (0.0-0.0)	0.0 (0.0-0.6)	0.0 (0.0-0.0)	0.1 (0.0-2.3)	0.0 (0.1-1.0)	10.8 (2.3-40.6)	0.6 (0.0-9.0)
<i>Calciolenia brasiliensis</i> (Lohmann, 1919) Deflandre, 1952	0.2 (0.0-2.3)	0.1 (0.0-1.5)	0.1 (0.0-2.3)	0.8 (0.0-8.5)	0.4 (0.0-2.5)	0.4 (0.0-3.6)	2.5 (0.0-46.2)
<i>Calcidiscus leptoporus</i> (Murray and Blackman, 1898) Loeblich and Tappan, 1978 f. <i>leptoporus</i>	0.2 (0.0-1.0)	0.0 (0.0-0.0)	0.0 (0.0-0.7)	2.0 (0.0-11.8)	16.3 (4.0-28.5)	7.8 (0.0-27.1)	0.1 (0.0-1.7)
<i>Oolithon antillarum</i> (Cohen, 1964) Reinhardt, in Cohen and Reinhardt, 1968	2.8 (0.0-13.5)	0.2 (0.0-2.9)	0.1 (0.0-2.0)	16.6 (0.0-64.0)	8.6 (1.0-18.5)	1.1 (0.0-1.3)	0.1 (0.0-1.3)
<i>Umbilicosphaera lubritiana</i> Gaarder, 1970	3.1 (0.0-11.5)	3.4 (0.0-17.0)	2.5 (0.0-11.2)	2.0 (0.0-9.5)	5.6 (3.0-12.5)	0.4 (0.0-4.9)	0.6 (0.0-2.9)
<i>Umbilicosphaera sibogae</i> (Weber-vanBossche, 1901) Gaarder, 1970	26.5 (13.5-47.7)	1.6 (0.0-10.3)	0.7 (0.0-7.3)	0.5 (0.0-5.5)	0.3 (0.0-1.0)	1.6 (0.0-11.4)	0.6 (0.0-3.6)
<i>Discosphaera tubifera</i> (Murray and Blackman, 1898) Ostentfeld, 1900	2.7 (0.0-12.5)	5.7 (0.0-14.0)	8.7 (1.0-22.6)	0.2 (0.0-3.0)	0.0 (0.0-0.5)	0.0 (0.0-0.3)	1.1 (0.0-5.8)
<i>Rhadinophaera clavigera</i> complex	0.3 (0.0-3.0)	1.1 (0.0-5.5)	2.1 (0.6-16.1)	0.0 (0.0-0.6)	0.0 (0.0-1.5)	0.4 (0.0-3.0)	1.6 (0.0-5.5)
<i>Ophiaster</i> spp.	0.1 (0.0-1.0)	0.3 (0.0-6.1)	0.4 (0.0-3.3)	0.1 (0.0-1.9)	0.0 (0.0-0.0)	3.3 (0.0-11.8)	0.4 (0.0-2.3)
<i>Umbellosphaera irregularis</i> Paasche, in Markali and Paasche 1955	38.7 (6.6-67.0)	65.7 (29.0-85.0)	40.0 (8.9-68.0)	11.4 (0.0-59.0)	9.1 (0.0-24.0)	14.3 (0.0-33.3)	5.4 (0.0-21.6)
<i>Umbellosphaera tenuis</i> (Kamptner 1937) Paasche, in Markali and Paasche 1955	0.0 (0.0-0.3)	1.2 (0.0-14.4)	7.4 (0.0-30.5)	0.0 (0.0-0.3)	0.0 (0.0-0.0)	0.4 (0.0-2.6)	16.3 (0.0-86.5)
miscellaneous	6.2 (1.5-14.6)	11.5 (1.3-44.7)	13.5 (2.0-32.0)	2.9 (0.0-21.7)	2.6 (0.0-6.0)	7.6 (2.5-21.9)	6.4 (0.7-19.7)

Note: The numbers outside and within the parentheses indicate the mean and the variation range of percentage abundances of major taxa, respectively. The understroked number indicates that the all samples of the subflora yielded those taxa.

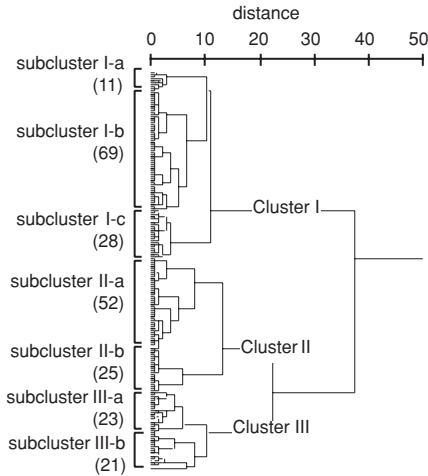


Fig. 2. Simplified dendrogram of the Ward Minimum Variance Cluster Analyses of 229 samples. Note: Metric distance is Euclidean distance based on the standardized values of the relative abundance of 14 major taxa and those of the miscellaneous taxa. Numerals in parentheses indicate the number of samples belonging to each subcluster.

respectively. Furthermore, the seven subclusters are characterized by the composition of the major species (Table 3, Fig. 3).

The UCA-a (=subcluster I-a) is characterized by the common occurrences of *U. irregularis*, *Umbilicosphaera sibogae* and *G. oceanica* with abundances ranging from 6.6–67.2, 13.5–47.7 and 0.5–41.0%, respectively (Table 3). In the UCA-b (=subcluster I-b), *U. irregularis* is the only consistent member of the assemblage, contributing 29.0–85.0% of the total flora. The UCA-c (=subcluster I-c) consistently yielded *U. irregularis* (8.9–68.0%), *Discosphaera tubifera* (1.0–22.6%) and *Rhabdosphaera clavigera* (0.7–16.1%). The GCA-a (=subcluster II-a) is characterized by *G. oceanica* which represents 17.8–94.1% of the total abundance. *Oolithotus antillarum* (up to 64.0%) or *U. irregularis* (up to 59.0%) are the major members of this assemblage. The GCA-b (=subcluster II-b) differs from GCA-a by the consistent occurrence of *E. huxleyi* (1.5–47.5%), *Calcidiscus leptoporus* (4.0–25.5%), *O. antillarum* (1.0–18.5%) and *Umbilicosphaera hulburtiana* (3.0–12.5%). The ECA-a (=subcluster III-a) is characterized by common occurrences of *E. huxleyi* (1.3–27.7%), small *Gephyrocapsa* complex (0.7–37.0%), and small *Reticulofenestra* complex (2.3–40.6%). *E. huxleyi* is the only common member of the ECA-b (=subcluster III-b), contributing 7.6–98.3% of the total flora. The major contributors to this assemblage are *G. oceanica* (up to 22.9%), *Calciosolenia brasiliensis* (up to 46.2%), *U. irregularis* (up to 21.6%), or *U. tenuis* (up to 86.5%).

The identified seven subassemblages showed a zonal distribution (Fig. 3): ECA-a is distributed in the Southeastern equatorial Pacific, and GCA-b is located

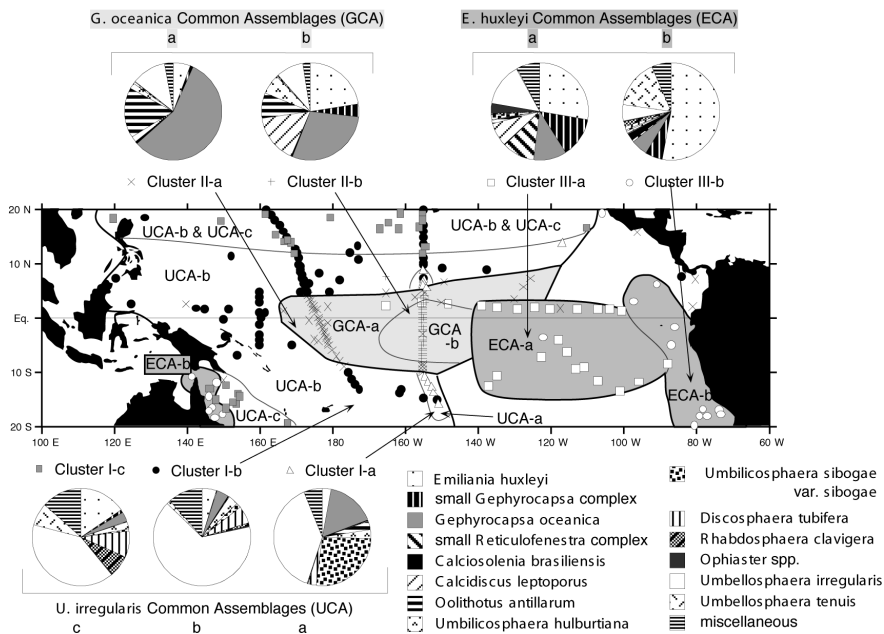


Fig. 3. Geographic coverage of the subclusters and floral subassemblages (map) and average floral composition of each subassemblage (pie graphs).

west of the ECA-a regime. The GCA-a subassemblage surrounds ECA-a and GCA-b. The UCA-a subassemblage occurred in a narrow area to the north and south of GCA-b along the 155°W line. The UCA-b subassemblage circles GCA-a and UCA-a. The UCA-c subassemblage dominates the eastern part of the Coral Sea, coexisting with UCA-b in the North subequatorial Pacific. The ECA-b subassemblage was distributed in two different areas; off the South American Continent and off coast of northern Australia.

In floral composition, UCA and GCA are almost identical to the so-called Subtropical and Tropical assemblages, respectively (Jordan and Chamberlain, 1997). The ECA-a subassemblage resembles the Temperate assemblages in yielding *E. huxleyi*, small *Gephyrocapsa* or *Reticulofenestra* complex (Jordan and Chamberlain, 1997; Broerse *et al.*, 2001). In summary, an ocean-wide latitudinal floral zonation can also be observed along the Equator in the Pacific.

3.2 Correlation between the floral assemblage and environmental parameters

In contrast to the UCA and GCA assemblage, ECA did not occur in warm waters exceeding 27°C (Figs. 4(a) and (b)). Salinity varies slightly between all of the identified assemblages, and so is unlikely to be a factor controlling floral composition (Fig. 4(c)). In the two sub-assemblages of the ECA, nutrient levels vary greatly (Figs. 4(d) and (e)). Therefore, it is evident that the high temperature

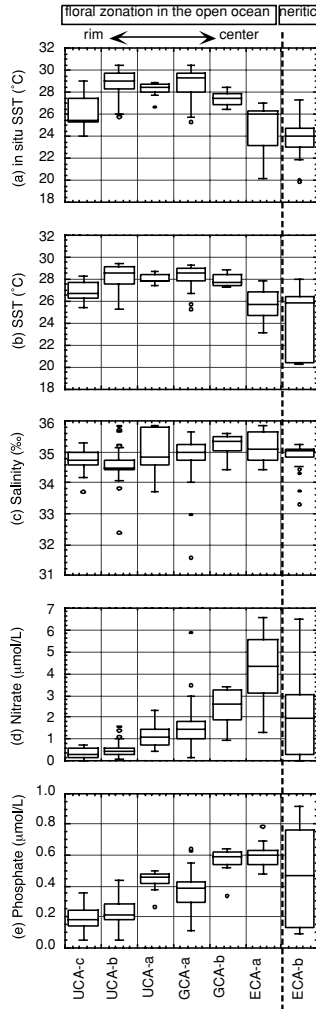


Fig. 4. Variation of in situ sea surface temperature (SST) (a), annual mean SST (b), annual mean salinity (c), annual mean nitrate concentration (d), and annual mean phosphate concentration (e) associated with each floral assemblage. Note: Along the horizontal axis of this graph, the seven floral assemblages are lined up from right to left according to the floral zonation in Fig. 3. The UCA, GCA, and ECA stand for *U. irregularis* common Assemblage, *G. oceanica* common Assemblage, and *E. huxleyi* common Assemblage, respectively. All environmental parameters except in-situ SST were obtained from the World Ocean Atlas (Conkright *et al.*, 1994; Levitus and Boyer, 1994; Levitus *et al.*, 1994).

(>27°C), not the nutrient deficiency, inhibits the occurrence of ECA in the studied area. The ECA-a subassemblage is distributed in the Eastern equatorial-subequatorial Pacific, while ECA-b is restricted to the neritic waters off the Australian and South American Continents (Fig. 3), with ECA-a being

distinguishable from ECA-b due to the presence of the small *Gephyrocapsa* and *Reticulofenestra* complexes. The ECA-a subassemblage occurred in waters with a higher nitrate level compared to ECA-b, and the phosphate ranges of the ECA-a and ECA-b subassemblages overlap. These results suggest that the nitrate concentration affects the occurrence of small *Gephyrocapsa* and *Reticulofenestra* complexes, but the contribution of the nutrient composition is unclear because the nutrient levels used here are decadal averages.

The GCA-a, UCA-a and UCA-b subassemblages are adapted to very warm waters with temperatures exceeding 28°C (Figs. 4(a) and (b)). The nutrient ranges of the GCA-a and UCA-a subassemblages almost overlap, and they tend to be distributed in more eutrophic waters compared to UCA-b (Figs. 4(d) and (e)). The GCA-a and UCA-a floras differ from the UCA-b flora in having a higher relative abundance of placolith-bearing species such as *G. oceanica*, *O. antillarum* and *U. sibogae*. The decline in nutrient concentration and not temperature variation leads to the decrease in placolith-bearing species, and distinguishes UCA-b from GCA-a or UCA-a. The nitrate ranges of the GCA-a and UCA-a subassemblages overlap, but UCA-a occurred in waters with a higher phosphate level compared to GCA-a. These results suggest that the nutrient composition affects the floral composition of coccolithophores, but the contribution of the nutrient composition is unclear, because the nutrient levels used here are decadal averages.

The GCA-b regime was wedged between the ECA-a and GCA-a regimes geographically (Fig. 3), and hydrographic parameters at the GCA-b stations displayed a range intermediate between those of the ECA-a and GCA-a stations (Figs. 4(d) and (e)). Therefore, GCA-b can be regarded as a transitional flora between the ECA-a and the GCA-b floras. Nutrient variation is insignificant between UCA-b and the UCA-c, with the former having a higher temperature range compared to the latter. The UCA-c flora is characterized by the common occurrence of *R. clavigera* and *D. tubifera*. In the North Subtropical Central Gyre, *R. clavigera* decreases in abundance during summer (Reid, 1980). The intolerance of *R. clavigera* to extremely high SSTs differentiates UCA-c from the UCA-b.

3.3 Seasonal variation of coccolithophore assemblages

The observed floral zoning is a truly biogeographical phenomenon and not a result of the difference in seasonality between sample sets. Cruise HK69-4 has two sampling transects; one runs southward along the 155°W line, and the other runs northwestward from 13°S, 172°W to 20°N, 162°E (Fig. 1(b)). All the samples from these two transects were collected during September–November, 1969 (Table 2, Fig. 1(b)). Along the eastern transect, five floral zones can be recognized with GCA-b as the center. Along the western transect, on the other hand, there are three floral zones represented by GCA-a, UCA-b, and UCA-c (Figs. 1(b) and 3). On Cruise KH90-3, winter samples were collected on two latitudinal traverses along 160°W and near the Dateline (Table 1, Fig. 3(a)). The eastern traverse yielded GCA-a and UCA-b, while the western traverse was dominated by UCA-b (Figs. 1(b) and 3). The period during the GCA-a and UCA-b samples were found spans all seasons (data not presented here). From these

observations, there is no doubt that a coccolithophore floral zonation is present all year round in the Central equatorial-subequatorial Pacific, and the latitudinal floral zoning converge westward along the Equator.

Broerse (2000) examined the variation of the suspended coccoliths in two sediment traps moored in the Central equatorial and subequatorial Pacific, and reported that the floral composition in the equatorial station is affected by the intensity of El Niño, not by the season. In the Western Caroline Basin, on the other hand, the coccolith flux displayed a seasonal variation that is related to the monsoonal hydrographic change (Tanaka and Kawahata, 2001). These results suggest that seasonal variation of the coccolithophore flora becomes more prominent in the neritic waters than in the pelagic regions in the equatorial Pacific.

The UCA-b subassemblage coexisted with UCA-c between 20°N and 10°N (Fig. 3). In this region, 78% of the samples yielding the UCA-b flora were collected during autumn (Sept. and Nov.), and 73% of the samples yielding UCA-c were collected during winter to early summer (Feb.–June). The UCA-c subassemblage is characterized by the common occurrence of *R. clavigera* and *D. tubifera*, and *R. clavigera* decreases in abundance during summer in the North Subtropical Central Gyre (Reid, 1980). Therefore, it is evident that the overlapping distribution of UCA-b and UCA-c in the North subequatorial Pacific is caused by the seasonal variation in the *R. clavigera* abundance.

3.4 Floral response of coccolithophores to longitudinal and latitudinal water stratification

The longitudinal, as well as latitudinal, floral zoning can be related to the water stratification within the SEC and its adjoining subtropical realms. The strong upwelling in the Equatorial Divergence Zone facilitates the distribution of the ECA-a flora in the Eastern equatorial Pacific. The coccolithophore flora varied from ECA-a to the UCA-b via GCA-b and GCA-a due to progressive warming and oligotrophication of the surface waters, corresponding to oceanographic changes from the Equatorial Divergence Zone to the WPWP. The latitudinal floral zoning observed between the Equatorial Divergence Zone and the North/South Pacific Central Waters is different from the longitudinal zoning because of the presence of UCA-a and UCA-c (Fig. 3). As UCA-a is not adapted to extremely warm waters such as the WPWP, it occurred only in the central Pacific.

4. CONCLUSION

The results of this study can be summarized as follows:

1. Based on Q-mode Cluster Analysis and floral composition, three main assemblages were identified including one neritic and six pelagic subassemblages as follows; *U. irregularis* common Assemblages (UCA)-a–c, the *G. oceanica* common Assemblages (GCA)-a and b, and the *E. huxleyi* common Assemblages (ECA)-a and b.

2. The seven floral subassemblages displayed a zonal distribution surrounding ECA-a, located in the Eastern Equatorial to Southeastern subequatorial Pacific.

3. Comparison between the subassemblage and environmental parameters revealed that temperature and nutrient levels control the floral composition. ECA subassemblages occurred in temperate waters (<27°C) regardless of nutrient level. In extremely warm conditions (>28°C), GCA-a and UCA-a were distributed in the moderately eutrophic waters, while UCA-b occurred in the oligotrophic waters. The GCA-b subassemblage is adapted to moderately warm, highly eutrophic waters between the ECA-a and GCA-b regimes. The UCA-c flora occurred in moderately warm and nutrient-depleted waters.

4. Seasonal variation is observed in the North subequatorial Pacific with a floral change from winter-spring UCA-c to summer UCA-b. Between 10°N and 20°S, however, the seasonality was unclear within the other floral subassemblages.

5. The westward, as well as latitudinal, oligotrophication associated with the transition from the upwelling center (Equatorial Divergence Zone) to the stratified waters (WPWP and North/South Pacific Central Waters) creates the zonal biogeography in the coccolithophore assemblage in the equatorial-subequatorial Pacific Ocean.

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