



HOKKAIDO UNIVERSITY

Title	Coccolithophore assemblages and morphotypes of <i>Emiliana huxleyi</i> in the boundary zone between the cold Oyashio and warm Kuroshio currents off the coast of Japan
Author(s)	Hagino, Kyoko; 萩野, 恭子; Okada, Hisatake et al.
Citation	Marine Micropaleontology, 55(1-2), 19-47 https://doi.org/10.1016/j.marmicro.2005.02.002
Issue Date	2005-04
Doc URL	https://hdl.handle.net/2115/5939
Type	journal article
File Information	MM55.pdf



Coccolithophore assemblages and morphotypes of *Emiliana huxleyi* in the boundary zone between the cold Oyashio and warm Kuroshio currents off the coast of Japan

Kyoko Hagino¹, Hisatake Okada¹ and Hiromi Matsuoka²

¹ Division of Earth and Planetary Sciences, Graduate School of Science, Hokkaido University, Sapporo, Japan

² Department of Natural Environmental Science, Faculty of Science, Kochi University, Kochi, Japan

Corresponding author: Kyoko Hagino

E-mail: hagino@nature.sci.hokudai.ac.jp

Fax: +81-11-706-3537

Abstract

Living coccolithophore assemblages were studied off the Japanese coast in the boundary zone between the cold Oyashio and the warm Kuroshio Currents as well as in adjacent water masses. A total of 64 coccolithophore taxa were identified. Ten taxa that comprised more than 10% of at least one sample were designated major taxa. Morphological observations and morphometric measurements enabled us to sub-divide the *Emiliana huxleyi* into four morphotypes: Type A, Type B, Type B/C and Type B/C-2.

Based on the composition of major taxa and morphotypes of *E. huxleyi*, four coccolithophore assemblages were recognized, corresponding to distinct water masses: Oyashio Current, Tsugaru Warm Current, Kuroshio Current, and Western North Pacific Central Water (WNPCW). In the Oyashio Current regime, the standing crop of coccolithophores was high, although diversity was low. The floral assemblage was dominated by *E. huxleyi* Type B and consistently contained *Coccolithus pelagicus* ssp. *pelagicus* HOL, *Calciopappus caudatus*, and *Syracosphaera orbiculus*. In the Tsugaru Warm Current regime, the flora was characterized by abundant *E. huxleyi* Type B/C-2

and *Gephyrocapsa oceanica* as well as by relatively common *Braarudosphaera bigelowii*. In the Kuroshio Current regime, *E. huxleyi* Type A, *G. ericsonii*, or *G. oceanica* were abundant. The coccolithophore flora in the WNPCW was characterized by abundant *E. huxleyi* Type A, *Discosphaera tubifera*, and *Umbellosphaera tenuis* Type IV.

Large *E. huxleyi* specimens ($\geq 4.2 \mu\text{m}$ in length) only occurred north of the Oyashio Front, while to the south, *E. huxleyi* were consistently $\leq 4.1 \mu\text{m}$ long, regardless of the morphotype. Large *E. huxleyi* can be a useful paleoenvironmental indicator for reconstructing past migrations of the Kuroshio and Oyashio Currents in the North Pacific Ocean.

Key words: coccolithophores, coccolith, *Emiliana huxleyi*, biogeography, Pacific Ocean,

1. Introduction

Coccolithophores are unicellular marine phytoplankton characterized by calcareous scales called coccoliths. Coccoliths surround the living cell of a coccolithophore and form an extracellular covering called a coccosphere (e.g. Siesser, 1993). Classification of coccolithophores is based on the morphology of the coccoliths and on the combination of coccoliths on the coccosphere (Jordan and Green, 1994; Young et al., 2003). Some cosmopolitan species display intraspecific morphological variation in their coccoliths, and are subdivided into morphotypes. The morphotypes of several major species such as *Emiliana huxleyi*, *Gephyrocapsa oceanica* and *Calcidiscus leptoporus*, have been documented in detail (e.g. Bollmann, 1997; Knappertsbusch et al., 1997; Findlay and Giraudeau, 2000). Immunological and molecular phylogenetic studies have revealed that the morphological variations between the morphotypes stem from genetic differences (e.g. Young and Westbroek, 1991; Medlin et al., 1996; Geisen et al., 2004). The distribution of these morphotypes has been related to hydrographic conditions (e.g. Hagino et al., 2000; Ziveri et al., 2004).

Colmenero-Hidalgo et al. (2002) studied the stratigraphic variation in the size of *E. huxleyi* during the last glacial-interglacial transition and demonstrated that the presence of large *E. huxleyi* specimens ($>4 \mu\text{m}$) can serve as a cold-water indicator in the North Atlantic Ocean and western Mediterranean Sea. Since *E. huxleyi* has dominated the coccolith flora of all oceans for the last 60-80 ky, *E. huxleyi* morphotypes have potential as paleoceanographic indicators in all oceans, not just the Atlantic.

In the northwestern Pacific Ocean, several coccolithophore studies have been conducted over the last 15 years. Tanaka (1991) studied coccolith assemblages in surface sediments from seas around Japan and concluded that temperature and salinity are the key parameters controlling the distribution of coccolithophores. Hagino (1997) (in Japanese) examined living coccolithophores in the northwest Pacific off the Japanese coast and found that the floral composition of the total coccolithophore assemblage, as well as the composition of *E. huxleyi* morphotypes, differ between distinct water masses. Yang et al. (2001) studied the horizontal distribution of living coccolithophores in the waters off northeast Taiwan. Since only Hagino (1997) subdivided *E. huxleyi* into morphotypes, information about *E. huxleyi* morphotypes in

the northwest Pacific Ocean remains scarce.

Hagino (1997) based her classification of *E. huxleyi* morphotypes solely on the morphology of the central area and the proximal shield, following the classification scheme of McIntyre and Bé (1967). However, recent studies of *E. huxleyi* have identified *E. huxleyi* morphotypes by the morphology and/or size of the distal shield, in accordance with the classification scheme of Young and Westbroek (1991) (e.g. Findlay and Giraudeau, 2000; Colmenero-Hidalgo et al., 2002). Therefore, the relationship between the morphotypes of Hagino (1997) and those of other recent studies is unclear.

The aims of this study were 1) to republish the findings of Hagino (1997) in English with additional new floral data and 2) to re-evaluate the *E. huxleyi* morphotypes described by Hagino (1997) based on additional morphological observations and morphometric measurements of the distal shield.

2. Materials and Methods

The thirty-two samples studied by Hagino (1997) were collected from the northwest Pacific Ocean off the coast of northeast Japan during cruise KT90-9 of the R/V *Tansei-Marui* (Kobayashi, 1991) (Table 1, Fig1). An additional 25 samples were collected during cruise KH90-1 of the R/V *Hakuho-Marui* (Tsukawaki and Nemoto, 1991) were examined to investigate the coccolithophore flora and *E. huxleyi* morphotypes in the Kuroshio main stream and the Western North Pacific Central Water (WNPCW) (Table 1, Fig. 1). Cruise KT90-9 samples were collected from the temperate to subarctic zones (34-43°N) between June 23 and July 1, 1990, and cruise KH90-1 samples were collected from the temperate zone (31-34°N) between July 16 and 26, 1990.

Sampling was conducted using a bucket, and water temperature was measured at the time of sampling. Salinity was measured at stations 2-25 during cruise KH90-1, but was not measured during cruise KT90-9 and at station 1 of KH90-1 (Table 1, Fig. 1). After pre-filtration through a 63- μm metal sieve, the water samples were filtered using a Type HA Millipore filter membrane with a pore size of 0.8 μm . The filters were then air-dried and stored in plastic Petri dishes. An elongated strip from the center to the rim

of the filter was cut out and rendered transparent by a drop of immersion oil, so that cell density could be counted by light microscopy. Another portion of the filter (ca. 5 x 5 mm) was mounted onto a brass SEM stub using adhesive agents and then sputter-coated with gold/platinum for SEM observation. The absolute abundance of coccolithophores was calculated by counting the number of coccospheres on ca. 1.0-4.8 mm² of the filter (corresponding to ca. 10 ml) in cross-polarized light. To ascertain the floral composition of the total coccolithophore assemblage, we identified >300 specimens per sample in the SEM.

3. Hydrology

During the two sampling cruises, the Oyashio Front was situated around 37-39°N, and three surface water masses –Oyashio Current, Tsugaru Warm Current, and Kuroshio Current regimes – were present in the study area (Fig. 1a) (Japan Coast Guard, 1990a, b). Of the 25 samples collected north of the Oyashio Front, three (stations 1-3, KT90-9)

were under the influence of the Tsugaru Warm Current, and the other 22 were from the Oyashio Current regime. *In situ* sea surface temperature (SST) was low at the Oyashio Current stations (mostly $<14^{\circ}\text{C}$), but was higher at the Oyashio Front (17.8°C) and in the Tsugaru Warm Current (ca. 15.0°C).

To the south of the Oyashio Front, the surface water is dominated by the Kuroshio Current (Fig. 1a). In the northern part of the Kuroshio Current regime ($34\text{-}38^{\circ}\text{N}$), *in situ* SST increases southward (Fig. 1b-1) (Japan Coast Guard, 1990c). However, in the southern part of the Kuroshio Current regime ($31\text{-}34^{\circ}\text{N}$), water was not always warmer than at the more northern stations, because the SST south of 34°N increased greatly during the sampling cruise (Figs. 1b-2 and 1-b3) (Japan Coast Guard, 1990d, e). Based on the *in situ* SST and sea surface salinity (SSS), sigma-T values were calculated for 24 samples collected at stations 2-25 of KH90-1. The sigma-T values differed across the 141°E longitudinal line (Fig. 1c). A change in sigma-T values can be interpreted as representing two different water masses (Brown et al., 1989). High sigma-T values in the eastern stations indicate that those samples were collected from the WNPCW, not from the Kuroshio Current. The *in situ* SST in the Kuroshio Current regime and

WNPCW ranged from 17.8-29.8°C and 27.2-29.2°C, respectively (Fig. 1b-3).

The Hakodate Marine Observatory (1990) recorded spatial variations in temperature, salinity, and nutrient concentrations in the Oyashio Current, Tsugaru Warm Current, and Kuroshio Current regimes between June 23 and July 31, 1990. At the sea surface level, nitrite and nitrate concentrations were almost equal among the three water regimes (NO_2 : 0.00-0.01 $\mu\text{mol/L}$; NO_3 : 0.1-0.2 $\mu\text{mol/L}$), but salinity and phosphate concentration differed. Surface waters from the Oyashio Current regime off Hokkaido Island were characterized by a low salinity (<33.4 psu) and a relatively high phosphate concentration (typically >0.1 $\mu\text{mol/L}$). In the Tsugaru Warm Current, SSS was essentially uniform (ca. 33.7 psu), while phosphate concentration decreased from 0.21 to 0.03 ($\mu\text{mol/L}$) in waters leaving from the Tsugaru Strait. Off Boso Peninsula, Honshu, in waters dominated by the Kuroshio Current (35°N, 140°E – 36°N, 141°E), salinity was relatively high (>33.8 psu), and phosphate concentration was 0.02-0.05 $\mu\text{mol/L}$.

4. Taxonomy

The classification of species sampled on cruise KH90-1 followed Young et al. (2003) (Table 1). The species names used by Hagino (1997) were revised to conform to those of Young et al. (2003). In this study, *Emiliana huxleyi* and *Braarudosphaera bigelowii* displayed intraspecific morphological variation. Criteria for their morphological grouping are discussed below.

4-1. *Emiliana huxleyi*

Morphological variations in *E. huxleyi* were first reported by McIntyre and Bé (1967), who subdivided *E. huxleyi* into warm- and cold-water types based on the morphology of the central area and the proximal shield (Table 2). Subsequent studies reported several morphotypes of *E. huxleyi* from various oceans, but related the distribution of morphotypes to water regimes rather than water temperatures. Okada and Honjo (1973a) documented the subarctic variety from an area of the North Central Pacific Ocean influenced by the Oyashio Extension (Table 2). Winter (1985) recognized warm and cold morphotypes in the California Current system and stated that the

composition of *E. huxleyi* morphotypes in samples taken in March reflected distinct water masses.

Young and Westbroek (1991) reported that the intensity of calcification (i.e., proximal shield slitting) varies with changes in culture conditions, and distinguished Types A-C of *E. huxleyi* based on morphology and the size of the distal shield (Table 2). Recent studies on *E. huxleyi* have followed Young and Westbroek (1991) in the classification of the morphotypes. Findlay and Giraudeau (2000) reported the occurrence of Types A, C, and D in the Southern Ocean. They regarded Type D as synonymous with the subarctic variety (Okada and Honjo, 1973a) and concluded that the irregularly shaped “T” elements of Type D resulted from dissolution (Table 2). Young et al. (2003) reviewed the classification of *E. huxleyi* morphotypes and revised medium-sized Type C specimens from the Antarctic Ocean (Findlay and Giraudeau, 2000) to be Type B/C (Table 2).

Hagino (1997) subdivided *E. huxleyi* into cold-water, intermediate, and warm-water types based on the morphology of the proximal shield and the central area (Table 2). The warm-water type described by Hagino (1997) is comparable to Type A of Young

and Westbrook (1991). However, the relationship between other morphotypes used by Hagino and those of Young and Westbrook (1991) is not clear because Hagino (1997) did not consider the morphology and size of the distal shield. Therefore, we combined the cold-water and intermediate types of Hagino (1997) together as types B and C (see section 5-2 on general floral variation).

To re-evaluate the *E. huxleyi* morphotypes of Hagino (1997), we used an SEM to examine the morphology of the distal shield elements in samples containing Types B and C (i.e., intermediate and cold water types). In addition, morphometric measurements were made on samples from seven stations: the Oyashio Current regime (station 11, KT 90-9); the Oyashio Front (station 34, KT90-9); the Tsugaru Warm Current regime (station 1, KT90-9); the northern part of the Kuroshio regime (station 35, KT90-9); the central part of the Kuroshio regime (station 38, KT90-9); the main pass of the Kuroshio Current (station 9, KH90-1); and the WNPCW (station 18, KH90-1) (Table 1, Fig 1). More than 50 *E. huxleyi* coccosphere images per sample were stored and measured electronically using the software program PC-I. To measure the overall size of the distal shield, a coccolith that appeared in an almost horizontal view on the

coccosphere was selected. If the entirety of the distal shield of the most horizontal coccolith was not exposed because it was overlapped by other coccoliths, the overall coccolith size was obtained by doubling the measurements of their exposed half-lengths. Most coccoliths were measured for only distal shield length, but those with both the proximal and distal shields exposed were measured for both shield lengths.

4-2. *Braarudosphaera bigelowii*

Extremely small specimens of *B. bigelowii* were observed at station 3 of KT90-9 (Hagino, 1997) (Plate II, 4-6). To find a suitable criterion for separating the *B. bigelowii* size groups, 100 coccosphere photographs of *B. bigelowii* were taken by SEM, and pentalith side length was measured using a ruler. Among the 100 specimens measured, 31 were $<2.2 \mu\text{m}$, while the remaining 69 were $>4.0 \mu\text{m}$ (Fig. 2). The taxonomic position of the small *B. bigelowii* specimens is unknown.

5. Results

5-1. Cell density and species diversity of total coccolithophores

Coccolithophores occurred in 52 of the 57 samples. Coccospheres were absent in three samples collected from the Oyashio Current and two samples collected from the Kuroshio Current (Table 1, Fig. 3a). Cell density and species diversity (D_H : Shannon-Wiener's Function) (Berger and Parker, 1970) differed between Subarctic and temperate waters (Fig. 3).

In the Subarctic Oyashio Current regime, the standing crop of coccolithophores was high (usually $>10^5$ cells/L), and species diversity was low (D_H : <1.0), consisting of only four to five taxa. The highest concentration of coccolithophores (3.9×10^5 cells/L) occurred at station 21, KT-90-9. At station 5, KT90-9, *E. huxleyi* monopolized the coccolithophore flora, and species diversity was the lowest ($D_H = 0.0$). In the warm water regimes of the Tsugaru Warm Current, the Kuroshio Current, and the WNPCW, coccolithophore cell density varied between 3.0×10^2 and 2.7×10^4 cells/L, and species diversity was relatively high compared to the Oyashio Current regimes. The highest species diversity occurred at station 35, KT90-9, in the northernmost part of the Kuroshio Current regime, and yielded 40 coccolithophore taxa.

5-2. Geographic distribution of coccolithophore assemblages and morphotypes of

Emiliana huxleyi

A total of 64 coccolithophore taxa were identified from the 52 samples in which coccospheres were common. Ten taxa that comprised more than 10% of the flora in any sample were designated major species (Fig. 4). From the data on standing crop, species diversity, and floral composition, four distinctive coccolithophore assemblages were identified, and can be correlated to the Oyashio Current, the Tsugaru Warm Current, the Kuroshio Current, and the Western North Pacific Central Water (WNPCW).

5-2-1. Oyashio Current flora

The Oyashio Current flora was characterized by a high standing crop (usually $>10^5$ cells/L) and low species diversity ($< DH: 1.0$) (Table 1, Figs. 4-5). In this regime, the coccolithophore assemblage was dominated by *Emiliana huxleyi* (64-100%). *Coccolithus pelagicus* ssp. *pelagicus* HOL (up to 32%), *Calciopappus caudatus* (up to 22%), and *Syracosphaera orbiculus* (up to 16%) were common components of the flora (Fig. 4).

Except at the Oyashio Front (station 34, KT90-9), the *E. huxleyi* population of the Oyashio Current regime was dominated by Types B and C (Fig. 4). Types B and C specimens were characterized by delicate, irregularly arranged, elevated distal shield elements and a hollow or solid central area (Plate I, 4-6). Distal shield lengths at station 11, KT90-9, ranged from 2.7 μm to 4.9 μm , and the proximal shield was usually larger than distal shield (Plate I, 4-6) (Figs. 5 and 6).

At the Oyashio Front (station 34, KT90-9), the *E. huxleyi* population comprised Type A and Types B and C almost equally (Fig. 4). The distal shield length of Type A and Types B and C measured 2.4-3.8 μm and 3.2-5.4 μm , respectively (Fig. 4). Three Type A specimens <2.7 μm were abnormal: the size range of normal Type A specimens at the Oyashio Front was 2.7-3.8 μm . Types B and C specimens from the Oyashio Front station had elevated T-shaped elements similar to those from the Oyashio Current regime.

5-2-2. Tsugaru Warm Current Flora

In the Tsugaru Warm Current regime, the standing crop of coccolithophores was

low ($< 7.5 \times 10^3$ cells/L), but species diversity was relatively high compared to those in the Oyashio Current regime (Table 1, Figs. 3-4). *E. huxleyi* (ca. 50%) and *Gephyrocapsa oceanica* (ca. 40%) dominated the coccolithophore assemblage, and *Braarudosphaera bigelowii* was a common component of the flora (2-17%).

In the Tsugaru Warm Current regime, *E. huxleyi* type A was rare while *E. huxleyi* Types B and C was abundant (Fig. 4). The distal shields of Types B and C in this regime were composed of non-elevated T-shaped elements (Plate II, 1-3). Morphometric measurements, applied only to Type B and C specimens, showed that distal shield lengths at station 1, KT90-9, ranged from 3.0 μm to 5.1 μm (Fig. 5). The proximal shields of Types B and C were smaller than the distal shields (Plate II, Figs. 3) (Fig. 6).

5-3-3. Kuroshio Current Flora

In the Kuroshio Current, the standing crop of coccolithophores varied between 1.4×10^3 cells/L and 4.1×10^5 cells/L, and species diversity (D_H) varied from 0.3 to 1.9. The highest species diversity in this study ($D_H = 1.9$) occurred at station 35, the northernmost station of this water regime. The flora was characterized by abundant *E.*

huxleyi (20.0-73.7%) and rare to abundant *Gephyrocapsa ericsonii* (up to 20.7%) and *G. oceanica* (up to 79.3%). The relative abundance of the major taxa in this regime differed between the continental shelf side and the open ocean side of the main stream of the Kuroshio Current. *E. huxleyi* dominated the flora on the continental shelf-side, while *G. oceanica* increased in abundance (>50%) in the boundary zone between the Kuroshio main stream and the WNPCW, where the temperature of the surface waters was high (>28°C) (Figs. 1 and 4).

In the Kuroshio Current regime, *E. huxleyi* Type A was abundant, while Types B and C were rare to absent. The distal shield length of Type A coccoliths measured 2.1-4.1 µm. Type A specimens smaller than 2.7 µm were malformed, while the size range of intact Type A coccoliths was 2.7-4.1 µm. Coccoliths of Types B and C specimens from the Kuroshio Current regime were medium-sized (3.2-4.1µm) and did not have elevated distal shield elements (Fig. 4).

5-4-4. Western North Pacific Central Water Flora

The standing crop of coccolithophores in the WNPCW regime was consistently

lower than 5.1×10^3 cells/L, but species diversity was relatively high (D_H : 0.97-1.63) (Table 1, Figs. 3-4). The coccolithophore flora was characterized by an abundance of *E. huxleyi* (up to 53.2%), *Discosphaera tubifera* (up to 72.7%), and *Umbellosphaera tenuis* Type IV (up to 26.0%). *Umbellosphaera hulburtiana*, *Coronosphaera* spp., and *Syracosphaera pulchra* HOL *oblonga* occurred consistently as minor taxa. In this regime, the *E. huxleyi* population was dominated by Type A, and the distal shield length ranged from 2.6-3.9 μm (Figs. 4 and 5). As the smallest Type A specimen was malformed, the size range of Type A was 2.8-3.9 μm .

6. Discussion

6-1. Comparison of the coccolithophore flora with those in previous studies

Okada and Honjo (1973a) documented the Subarctic coccolithophore assemblage from the Central North Pacific Ocean, which is influenced by the Oyashio Extension. SST and SSS were essentially uniform for the Oyashio Current (this study)

and Central North Pacific (Okada and Honjo, 1973a, b) samples. The coccolithophore flora from the Oyashio Current in this study was similar to the Subarctic assemblage of Okada and Honjo (1973a, b) in terms of density ($>10^5$ cells/L) and the dominance of *E. huxleyi*, but it differed from the Subarctic assemblage in the composition and vertical distribution of minor taxa. *Coccolithus pelagicus* ssp. *pelagicus* HOL, which was an abundant taxon in the Oyashio Current regime, was not observed in the Subarctic assemblage. The Subarctic assemblage commonly yielded *Syracosphaera pulchra* or *S. histrica* instead of *S. orbiculus*, which is an abundant species in the Oyashio Current flora (this study). In the North Atlantic Ocean, *C. pelagicus* ssp. *pelagicus* HOL was abundant between April and early June, and *S. orbiculus* increased in abundance in July and November (Okada and McIntyre, 1979). Samples from the Oyashio Current (this study) and the Central North Pacific (Okada and Honjo, 1973a, b) were collected in late June and late autumn, respectively. Therefore, the differences in the minor taxa in the Oyashio Current and Subarctic assemblages may result from seasonal floral variations. *Calciopappus caudatus*, which was a common species in the surface water of the Oyashio Current regime (this study), was found only in the middle to lower photic zone

(75-150 m) in the Central North Pacific (Okada and Honjo, 1973b). The hydrographic parameters that may control the vertical distribution of *C. caudatus* are not known.

Data on coccolithophores in the Tsugaru Warm Current regime is limited. Tanaka (1991) documented coccolith thanatocoenoses in surface sediments from the seas around Japan and reported that the fossil assemblage in the sediments off northeastern Honshu (in the Tsugaru Warm Current regime) is dominated by *Gephyrocapsa oceanica* and is characterized by the occurrence of *C. pelagicus*. *E. huxleyi*, which was one of the major species in the Tsugaru Warm Current flora in this study, comprised less than 20% of the fossil assemblage (Tanaka, 1991). The differences in floral composition between the living assemblage studied here and the fossil assemblage (Tanaka, 1991) may result from the selective dissolution of coccoliths during sedimentation.

Yang et al. (2001) studied summer coccolithophore assemblages in the surface waters of the seas off northeastern Taiwan and identified three communities: 1) the continental shelf community dominated by *E. huxleyi*, *G. oceanica*, and *Calciosolenia murrayi*; 2) the Kuroshio community dominated by *Umbellosphaera*

spp.; and 3) the WNPCW community dominated by *Calicasphaera* spp. and *Palusphaera vandellii*. Coccolithophore assemblages sampled from the Kuroshio Current regime and the WNPCW for our study differed from those of Yang et al. (2001) in the higher abundance of placolith-bearing species, such as *E. huxleyi* and *Gephyrocapsa* spp. As a result, the composition of the Kuroshio and WNPCW floras we studied resemble those of the continental shelf and Kuroshio communities of Yang et al. (2001), respectively.

During the two sampling cruises of KT90-9 and KH90-1, the Kuroshio Current meandered around 138°E, and a cold eddy was observed north of the current (Fig. 1) (Japanese Coast Guard, 1990a, b, e). Nitrate concentration in the Kuroshio regime (around 34-35°N, 140-141°E) ranged from 0.1-0.2 $\mu\text{mol/L}$ during late July 1990 (Hakodate Marine Observatory, 1990). On the other hand, nitrate was depleted at sea surface level in the waters off Taiwan (Yang, 2001). Placolith-bearing species prefer more eutrophic conditions than do umbelliform species such as *U. irregularis* and *D. tubifera* (e.g. Young, 1994; Hagino and Okada, 2004). Therefore, it can be inferred that the cold eddies off Honshu Island (Japan), formed by the meandering of the Kuroshio

Current, supplied nutrients to the surface water, resulting in a higher abundance of placolith-bearing species in the Kuroshio regime and the WNPCW than in the waters off Taiwan.

In the Kuroshio Current regime, the composition of placolith-bearing species was different between the continental shelf side and the open-ocean side (Fig. 4). Higher sea surface temperatures ($>28^{\circ}\text{C}$) caused a change in the flora from an assemblage in which *E. huxleyi* was common to an assemblage in which *G. oceanica* was common, regardless of nutrient concentration (Hagino et al., 2000; Hagino and Okada, 2004). Therefore, the higher abundance of *G. oceanica* than *E. huxleyi* in the boundary zone between the Kuroshio main-pass and the WNPCW may be related to the high sea surface temperature ($>28^{\circ}\text{C}$) (Figs. 1 and 4).

The WNPCW flora observed in this study resembled the transitional assemblage in the Central North Pacific (Okada and Honjo, 1973a, b) and the early summer surface assemblage documented in May 1974 from the Eastern North Pacific Central Water, which was characterized by the presence of *E. huxleyi*, *D. tubifera*, *S. pulchra* HOL *oblonga*, and *U. tenuis* (Reid, 1980). Data on nutrient concentrations are

not available for this regime; however, the common occurrence of umbelliform species (*D. tubifera* and *U. tenuis*) suggests that surface nutrient concentrations are lower than those of the Kuroshio Current regime.

6-2. Taxonomic implications for the morphotypes of *Emiliania huxleyi*

The distal shield length of intact Type A specimens of *E. huxleyi* ranged from 2.7-4.1 μm and displayed bimodal peaks at 3.1 μm and 3.5 μm , regardless of the water regime (Figs. 4, 5). There was no morphological difference between the small (<3.1 μm) and medium-sized Type A coccoliths (>3.6 μm), and small and medium-sized coccoliths were often observed in the same coccosphere. Morphological observations and morphometric measurements suggest that the Type A specimens in our study can be included in the Type A of Young et al. (2003), although the size range of the distal shield of our samples was slightly larger than that of Young et al. (2003) (Tables 2 and 3).

Types B and C specimens from the Oyashio Current regime are characterized by elevated distal shield elements and a very large coccolith size (Plate I, 4-6). Distal

shield lengths ranged from 2.7-5.4 μ m (Figs. 4 and 5), and the length of the proximal shield was generally larger than that of the distal shield (Fig. 6). Hagino (1997) identified Type B and C specimens from the Oyashio Current regime as a cold-water type based on the solid proximal shield. Young and Westbroek (1991), however, reported that the morphology of the proximal shield varied depending on culture conditions, while the distal shield morphology was independent of culture conditions. Morphological and morphometric studies suggest that the cold-water type of Hagino (1997) (i.e., Types B and C in the Oyashio Current regime) is identical to the subarctic variety (Okada and Honjo, 1973a) and to Type B (Young and Westbroek, 1991; Young et al., 2003), but not to the cold-water type of McIntyre and Bé (1967) (Table 3).

Okada and Honjo (1973a) recognized the subarctic variety based on its irregularly arranged distal shield elements. However, we found that the irregular arrangement of distal shield elements varied on individual coccospheres (Plate I, 5). Subarctic varieties shown in the plates of Okada and Honjo (1973a) have elevated distal shield elements. Therefore, the Subarctic variety and Type B (Young and Westbroek, 1991) should be distinguished by their possession of elevated distal shield elements, not by the irregular

distal shield element arrangement. Since data on the geographical distribution of this morphotype are limited, we prefer to use the neutral term Type B, rather than subarctic variety (Table 3).

The maximum size of Types B and C specimens from the Tsugaru Warm Current is $>5.0 \mu\text{m}$, but their distal shield elements are not elevated (Plate II, 1-3) (Figs. 4 and 5). Therefore, the relationship between Types B and C from the Tsugaru Warm Current regime (i.e., the intermediate type of Hagino, 1997) and the morphotypes of Young et al. (2003) is unclear. The morphology of the distal shield element is stable and independent of culture conditions (Young and Westbroek, 1991). Therefore, we have tentatively called the Types B and C specimens from the Tsugaru Warm Current regime Type B/C-2, largely based on the morphological characters of the distal shield elements (Table 3). Types B and C specimens from the Kuroshio Current regime are characterized by medium-sized coccoliths ($3.2\text{-}4.1 \mu\text{m}$) consisting of non-elevated distal shield elements, and are comparable to Type B/C of Young et al. (2003) (Table 3).

6-3. Oceanographic observations of the morphotypes of *Emiliana huxleyi*

Emiliana huxleyi Type A was abundant in the warm Kuroshio Current regime and the Western North Pacific Central Water, rare in the Tsugaru Warm Current regime, and absent in the cold Oyashio Current regime. The Tsugaru Warm Current originates in the Tsushima Current, which is a branch of the Kuroshio Current. In the Tsugaru Warm Current regime, the abundance of Type A specimens decreased in waters leaving from the Tsugaru Strait (Fig. 4). The decrease of Type A abundance in the Tsugaru Warm Current regime can be interpreted as a decline in the influence of the Kuroshio waters.

Type B had a restricted distribution in the Oyashio Current regime. Okada and Honjo (1973a) documented Type B (their subarctic variety) from the central North Pacific, which is under the influence of the Oyashio Extension. Therefore, it is evident that Type B is distributed in the subarctic zone of the North Pacific along the longitudinal flow of the Oyashio Current and its extension.

The populations of large *E. huxleyi* ($\geq 4.2 \mu\text{m}$) consisting of Type B or Type B/C-2 were distributed north of the Oyashio Front. South of the Oyashio Front, Type A and type B/C coexisted, and the maximum size of *E. huxleyi* was $4.1 \mu\text{m}$ (Fig. 4). Colmenero-Hidalgo et al. (2002) studied size variation of *E. huxleyi* in cores from the

North Atlantic Ocean and the western Mediterranean Sea, and demonstrated that large *E. huxleyi* specimens ($>4 \mu\text{m}$) are useful cold-water indicators. Therefore, we can use large *E. huxleyi* ($\geq 4.2 \mu\text{m}$) to reconstruct the position of the boundary zone between the subpolar and subtropical gyres in both the North Atlantic and Pacific oceans, regardless of their morphotype assignment.

Summary

1. A total of 64 coccolithophore taxa was identified from 52 samples in which coccospheres were common, collected in the NW Pacific Ocean off the coast of northeast Japan. Ten taxa that comprised more than 10% of at least one sample were designated major species.
2. *Braarudosphaera bigelowii* was subdivided into two size groups, small ($<2.5 \mu\text{m}$) and normal ($>4.0 \mu\text{m}$), based on morphometric measurements of the side lengths of the pentoliths

3. The morphotypes of *Emiliana huxleyi* documented by Hagino (1997) were re-evaluated on the basis of morphological observations and morphometric measurements of the distal shield as follows: Type B is the cold-water type from the Oyashio Current regime, Type B/C is the cold-water type from the Kuroshio Current regime, Type B/C-2 is the intermediate type from the Tsugaru Warm Current regime, and Type A is the warm-water type from the Kuroshio Current and Tsugaru Warm Current regimes of Hagino (1997).
4. Based on the floral composition and morphotypes of *E. huxleyi*, we recognized four coccolithophore assemblages corresponding to distinct water masses: the Oyashio Current, the Tsugaru Warm Current, the Kuroshio Current, and the Western North Pacific Central Water.
5. The Oyashio Current flora was dominated by *E. huxleyi* Type B and characterized by the common occurrence of *Coccolithus pelagicus* ssp. *pelagicus* HOL, *Calciopappus caudatus*, and *Syracosphaera orbiculus*.
6. The Tsugaru Warm Current flora was characterized by the occurrence of abundant *E. huxleyi* Type B/C-2 and *G. oceanica*, as well as the relatively common occurrence of

Braarudosphaera bigelowii.

7. The Kuroshio Current Flora yielded abundant placolith-bearing species. In this assemblage, *E. huxleyi* Type A was abundant and Type B/C was rare.
8. The Western North Pacific Central Water flora was characterized by the abundance of *E. huxleyi*, *Discosphaera tubifera*, and *Umbellosphaera tenuis* Type IV. The *E. huxleyi* population was composed exclusively of Type A.
9. Large *E. huxleyi* specimens ($\geq 4.2 \mu\text{m}$) were collected from waters north of the Oyashio Front. South of the Oyashio Front, *E. huxleyi* coccoliths were consistently $< 4.1 \mu\text{m}$, regardless of the composition of the morphotypes. Large *E. huxleyi* coccoliths can be useful as paleoenvironmental indicators to reconstruct the latitudinal distribution of the boundary zone between the Subarctic and subtropical gyres in the North Pacific Ocean.

Acknowledgement

We are grateful to M. Okamura and Y. Tanaka for their helpful suggestions. We thank to L. Beaufort, R.W. Jordan, and J.R. Young, for their critical reviews and comments. We are indebted to E. Thomas for her valuable suggestions. We also thank the chief scientists, captain and crew of the Cruises KT90-9 and KH90-1 for their assistance. This research is supported by a 21st Century COE Program on "Neo-Science of Natural History" at Hokkaido University financed by the Ministry of Education, Culture, Sports, Science and Technology, Japan.

Reference

- Berger, W.H. and Parker, F.L., 1970. Diversity of planktonic foraminifera in deep-sea sediments. *Science*, 168, 1345-1347.
- Bollmann, J., 1997. Morphology and biogeography of *Gephyrocapsa* coccoliths in Holocene sediments. *Mar. Micropaleontol.*, 29, 319-350.
- Brown, J., Colling, A., Park, D., Phillips, J., Rothery, D. and Wright, J., 1989. In: Bearman, G., (Editor), *Ocean Circulation*, Open University + Pergamon Press, pp. 238.
- Colmenero-Hidalgo, E., Flores, J.A., and Sierro, F., 2002. Biometry of *Emiliana huxleyi* and its biostratigraphic significance in the Eastern North Atlantic Ocean and Western Mediterranean Sea in the last 20000 years. *Mar. Micropaleontol.*, 46, 247-263.
- Findlay, C.S. and Giraudeau, J. 2000. Extant calcareous nannoplankton in the Australian sector of the Southern Ocean (austral summers 1994 and 1995). *Mar. Micropaleontol.*, 40(4): 417-439.

Geisen, M., Young, J.R., Probert, I., Sáez, A.G., Baumann, K.-H., Sprengel, C.,
Bollmann, J., Cros, L., de Vargas, C. and Medlin, L.K., 2004, Species level
variation in coccolithophores. In: Thierstein, H.R. and Young, J.R., (Editor),
Coccolithophores. Springer, pp. 327-366.

Hagino, K., 1997, Distribution of living coccolithophores in the western Pacific Ocean
off the coast of Northeast Japan. *Fossils*, 63: 1-19. *In Japanese with English
Abstract*

Hagino, K., Okada, H., and Matsuoka, H., 2000, Spatial dynamics of coccolithophore
assemblage in the Equatorial Western-Central Pacific Ocean, *Marine
Micropaleontology*, 39, p. 53-57.

Hagino, K. and Okada, H., 2004, Floral response of coccolithophores to progressive
oligotrophication in the South Equatorial Current, Pacific Ocean, *In H.
Kawahata et al. (Ed), Global environmental change in the ocean and on land,
TERRAPUB*, pp. 121-132.

Hakodate Marine Observatory, 1990, Oceanographic observation report of the Hakodate
Marine Observatory, 28 (3), Hakodate Marine Observatory, 28pp. *in Japanese*

Japan Coast Guard, 1990 a. Ocean Current Forecastings, No. 25 of Heisei 2nd. *in*

Japanese

Japan Coast Guard, 1990 b. Ocean Current Forecastings, No. 28 of Heisei 2nd. *in*

Japanese

Japan Coast Guard, 1990 c. Quick Bulletin of Ocean Conditions, No. 13 of Heisei 2nd.

in Japanese

Japan Coast Guard, 1990 d. Quick Bulletin of Ocean Conditions, No. 14 of Heisei 2nd.

in Japanese

Japan Coast Guard, 1990 e. Quick Bulletin of Ocean Conditions, No. 15 of Heisei 2nd.

in Japanese

Jordan, R.W. and Green, J.C., 1994, A check-list of the extant Haptophyta of the world.

J. mar. Biol. Ass., 74, 149-174.

Knappertsbusch, M., Cortes, M.Y., and Thierstein, H.R., 1997. Morphologic variability

of the coccolithophorid *Calcidiscus leptoporus* in the plankton, surface

sediments and from the Early Pleistocene. Mar. Micropaleontol., 30, 293-317.

Kobayashi, K., 1991, Preliminary Report of the Hakuho Maru Cruise KH90-1. Ocean

Research Institute, University of Tokyo.

McIntyre, A. and Bé, A.W.H., 1967. Modern Coccolithophoridae of the Atlantic Ocean

– 1. Placoliths and cyrtoliths. *Deep-Sea Res.*, 14: 561-597.

Medlin, L.K., Barker, G.L.A., Campbell, L., Green, J.C., Hayes, P.K., Marie, D.,

Wrieden, S., and Vaultot, D., 1996. Genetic characterization of *Emiliana*

huxleyi (Haptophyta). *J. Mar. Syst.* 9, 13-31.

Okada, H. and Honjo, S., 1973a. The distribution of oceanic coccolithophorids in the

Pacific. *Deep-Sea Res.*, 20: 355-374.

Okada, H. and Honjo, S., 1973b. Distribution of coccolithophorid in the North and

Equatorial Pacific Ocean: Quantitative data on samples collected during Leg

30, Oshoro-Marui, 1968 and Leg HK69-4, Hakuho-Marui, 1969. WHOI Tech.

Rep., WHOI-73-81, Woods Hole Oceanogr. Inst., 59pp.

Okada, H. and McIntyre, A., 1979. Seasonal Distribution of Modern Coccolithophores

in the Western North Atlantic Ocean. *Mar. Biol.*, 54: 319-328.

Reid, F.M.H. 1980, Coccolithophorids of the North Pacific Central Gyre with notes on

their vertical and seasonal distribution, *Micropaleontol.*, 26(2), 141-176.

- Siesser, W.G. 1993, Calcareous nannoplankton, In: Lipps, J.H., (Editor), Fossil Prokaryotes and Protists. Blackwell Scientific Publications, pp. 169-201.
- Tanaka, Y., 1991. Calcareous Nannoplankton Thanatocoenoses in Surface Sediments from Seas Around Japan. Science Reports of the Tohoku University, 61 (2), 127-198.
- Tsukawaki, S. and Nemoto, N., 1991. Preliminary Results on Tansei-maru Cruise KT90-9 in Forearc Areas off Northern Tohoku and Hokkaido, and Sagami Bay, Japan. The Science Reports of the Hirosaki University, 38(1). pp.86.
- Winter, A., 1985. Distribution of living coccolithophores in the California Current System, Southern California Borderland. Mar. Micropaleontol., 9, 385-393.
- Yang, T.-N., Wei, K.-Y. and Gong, G.-C., 2001. Distribution of coccolithophorids and coccoliths in surface ocean off northeast Taiwan. Bot. Bull. Acad. Sin., 42, 287-302.
- Young, J.R. Function of coccoliths. In: Winter A. and Siesser, W.G. (Editor), Coccolithophores. Press Syndicate of the University of Cambridge, pp. 63-82.
- Young, J.R., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I., and Ostergaard,

J., 2003. A guide to extant coccolithophore taxonomy. Journal of Nannoplankton Research Special Issue 1. 125pp.

Young, J.R. and Westbroek, P., 1991. Genotypic variation in the coccolithophorid species *Emiliana huxleyi*, Mar. Micropaleontol., 18, 5-23.

Ziveri, P., Baumann, K.-H., Böckel, B., Bollmann, J., and Young, J.R., 2004. Biogeography of selected Holocene coccoliths in the Atlantic Ocean. In: Thierstein, H.R. and Young, J.R., (Editor), Coccolithophores. Springer, pp. 327-366.

Plate Captions

Plate. I Scanning electron micrographs of *Emiliana huxleyi*

Fig. 1. *E. huxleyi* Type A. st.35 of KT90-9.

Fig. 2. *E. huxleyi* Type A. st.35 of KT90-9.

Fig. 3. *E. huxleyi* Type A. st.35 of KT90-9.

Fig. 4. *E. huxleyi* Type B (Types B and C), st.11 of KT90-9.

Fig. 5. *E. huxleyi* Type B (Types B and C), st.21 of KT90-9.

Fig. 6. *E. huxleyi* Type B (Types B and C), st.21 of KT90-9.

Plate. II Scanning electron micrographs of *Emiliana huxleyi* and *Braarudosphaera*

bigelowii

Fig. 1. *E. huxleyi* Type B/C-2 (Types B and C), st.1 of KT90-9.

Fig. 2. *E. huxleyi* Type B/C-2 (Types B and C) , st.1 of KT90-9.

Fig. 3. *E. huxleyi* Type B/C-2 (Types B and C) , st.1 of KT90-9.

Figs. 4 and 6. Normal sized coccosphere of *B. bigelowii*, st.3 of KT90-9.

Figs. 5 and 7. Very small coccosphere of *B. bigelowii*, st.3 of KT90-9.

Note: Figs. 6 and 7 were taken at the same magnification.

Figure Captions

Fig.1. Distributions of: (a) surface water samples and surface water masses; (b1-b3) in situ and half-month average temperatures; and (c) calculated sigma-T values.

Distribution of surface water masses and isotherms were cited from Japan Coast Guard (1990a-d). Numbers within the parentheses and on the isotherms in figs. b1-b3 are in situ and average temperature, respectively.

Fig.2. Schematic diagram indicating the actual measurement conducted for *Braarudosphaera bigelowii* (a) and frequency distribution for the coccolith size of *B bigelowii* at st.3 of KT90-9.

Fig. 3. Distributions of: (a) standing crop of total coccolithophores; and (b) species diversity index.

Fig. 4. Geographic distribution of surface water masses, standing crop of total coccolithophores, percentage abundance of major taxa (a), and frequency distribution of the coccolith length of *Emiliana huxleyi* from seven selected samples (b). Note: Diameter of each Pie Chart indicates the standing crop of

coccolithophore assemblage, and the sector angle indicates the percentage values for the major taxa.

Fig. 5. Coccolith length variation in each *E. huxleyi* morphotypes: Type A (a), Type B (b), Type B/C-2 (c) and Type B/C (d). Note: Numerals in the parentheses are the number of coccoliths measured.

Fig. 6. Correlations between the lengths of proximal and distal shields of *Emiliana huxleyi*. Results show that the *E. huxleyi* population has different linear correlations among different water masses.

Table 2: Morphotypes of *Emiliana huxleyi* documented in the previous studies

McIntyre and Bé (1967) Warm Water form: open work grill covering the central pore and T-shaped elements in both shield

Cold water type: solid proximal shield and pore (=central area) covering

Okada and Honjo (1977) subarctic variety: poorly developed and formed of irregularly oriented T-shaped dorsal (=distal shield) elements

Hagino (1997) warm water type: open proximal shield consists of T-shaped elements, central area covered by grill-like structure.

cold water type: solid proximal shield consists of rod-like elements, central area open or covered by thin solid plate.

intermediate type: open proximal shield consists of T-shaped elements, central area open or covered by thin solid plate.

Findlay and Giraudeau Type A: heavily calcified form with a central grill structure, average coccolith length 2.5-3.1 μm

Type C: less calcified form with either no central structure or adjoining thin plate, average coccolith length 2.5-3.1 μm

Type D: irregular shaped "T" elements (synonymous with subarctic variety of Okada and Honjo, 1973a)

Young and Westbroek Type A: liths medium-sized (3-4 μm), distal shield elements robust, central area elements curved.

and Young et al (2003) Type B: liths large (3.5-5 μm), distal shield elements delicate and elevated, central area elements irregular laths. proximal shield often wider than distal shield.

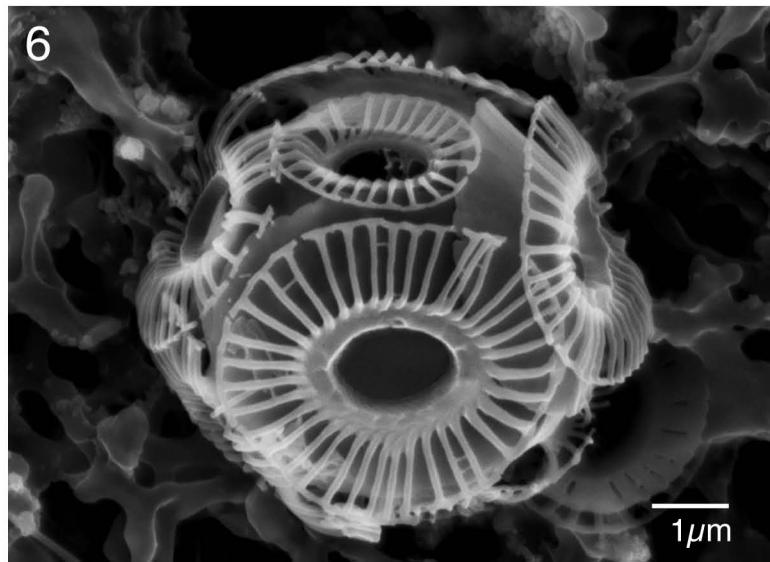
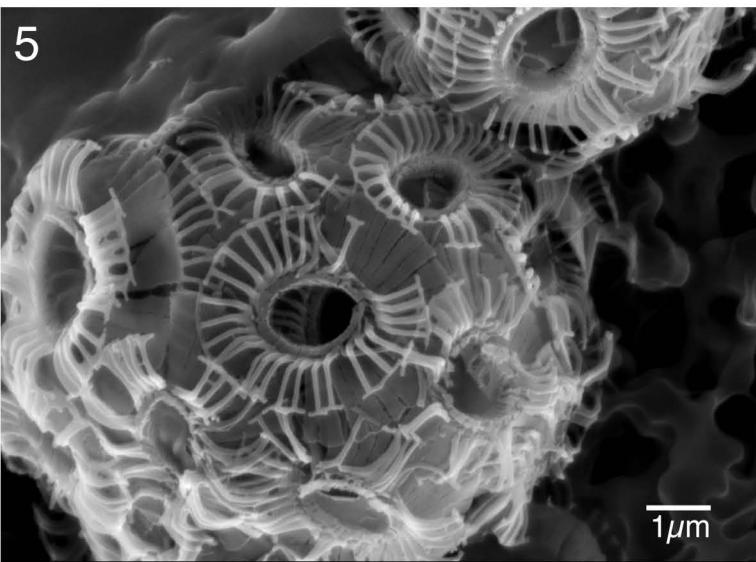
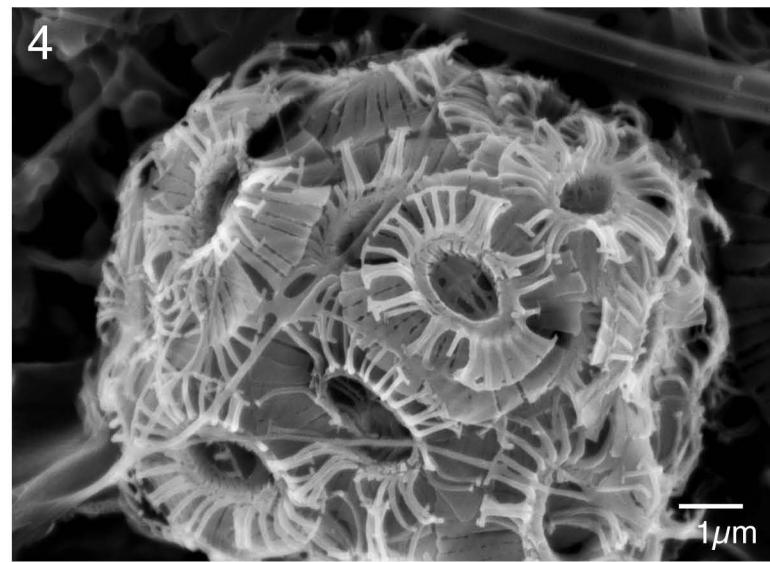
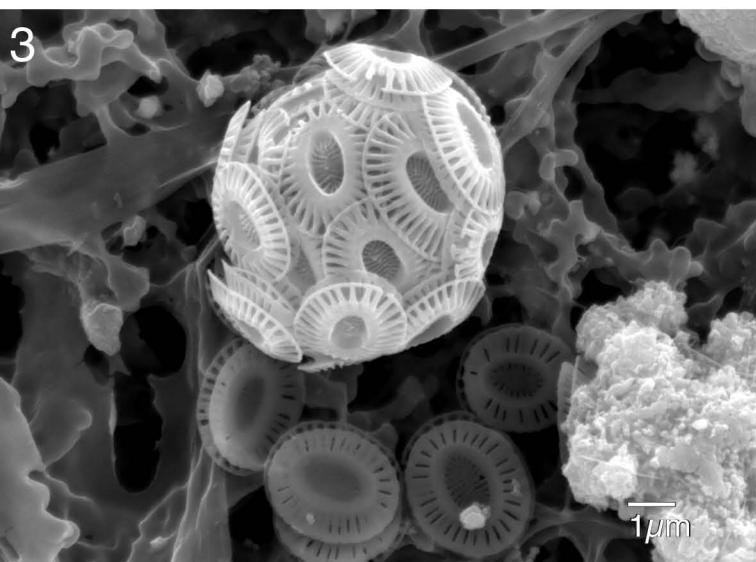
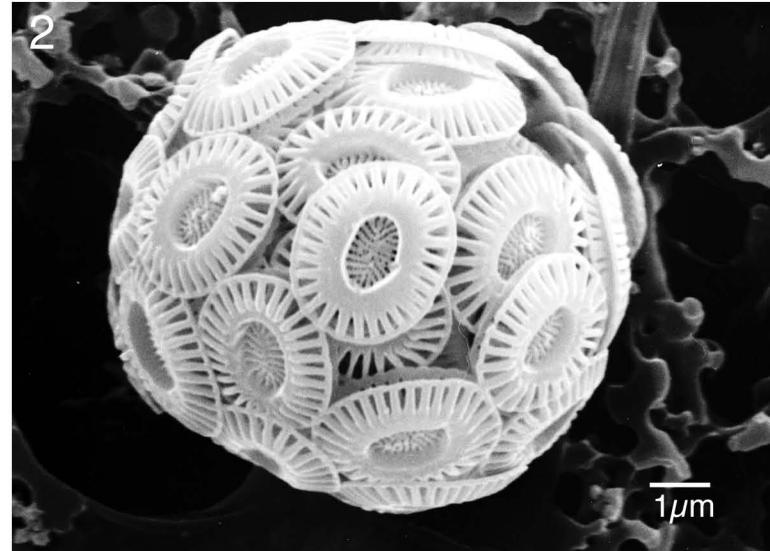
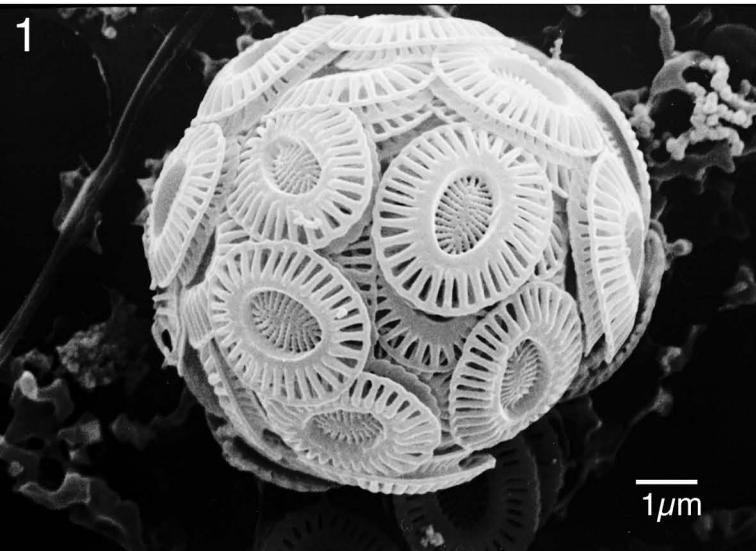
Type C: liths small (2.5-3.5 μm), distal shield elements delicate, central area open or covered by thin plate.

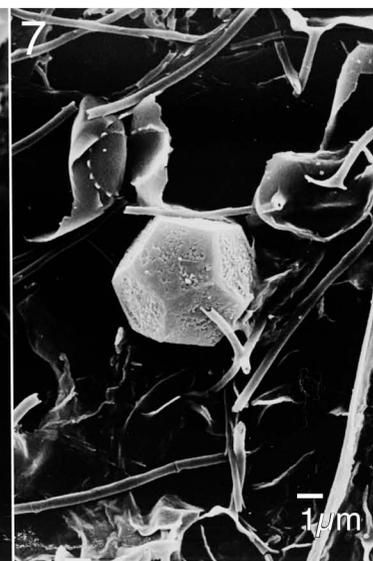
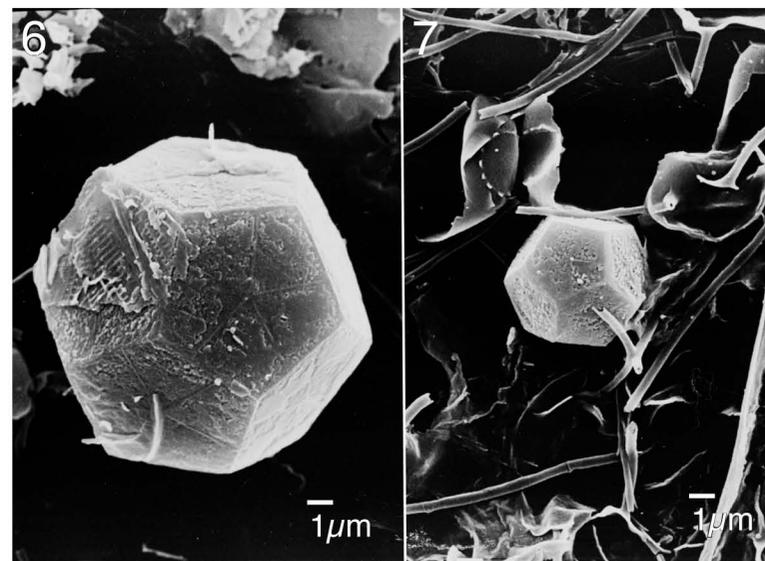
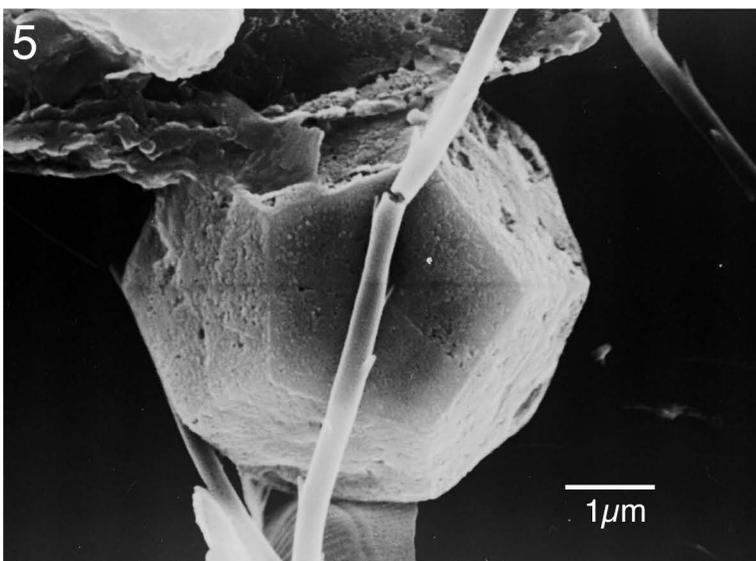
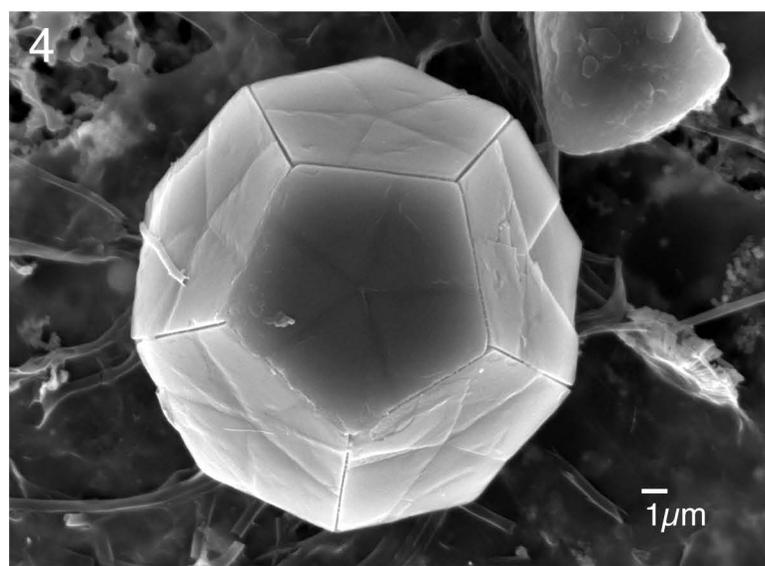
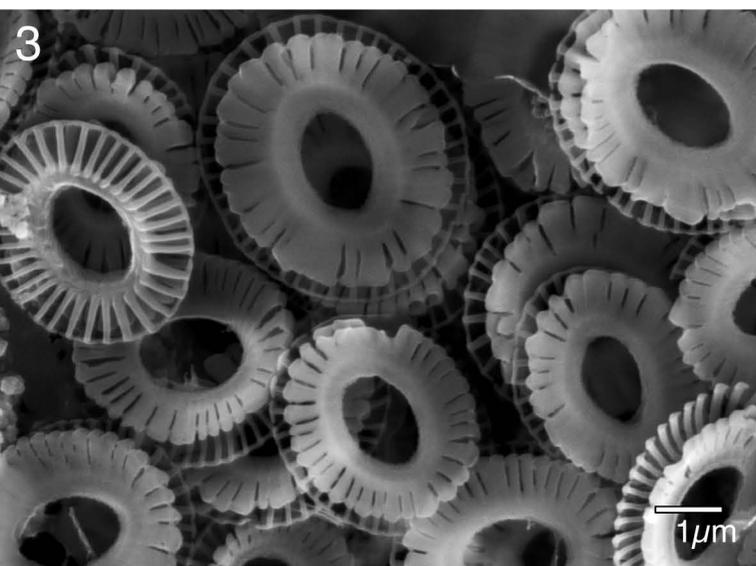
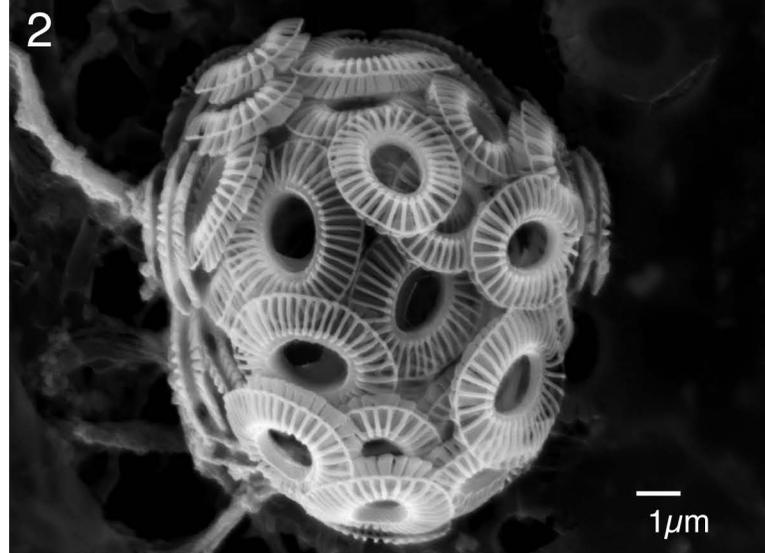
Type B/C: liths medium-sized (3-4 μm), distal shield elements delicate, i.e. similar in morphology to types B & C, but intermediate in size.

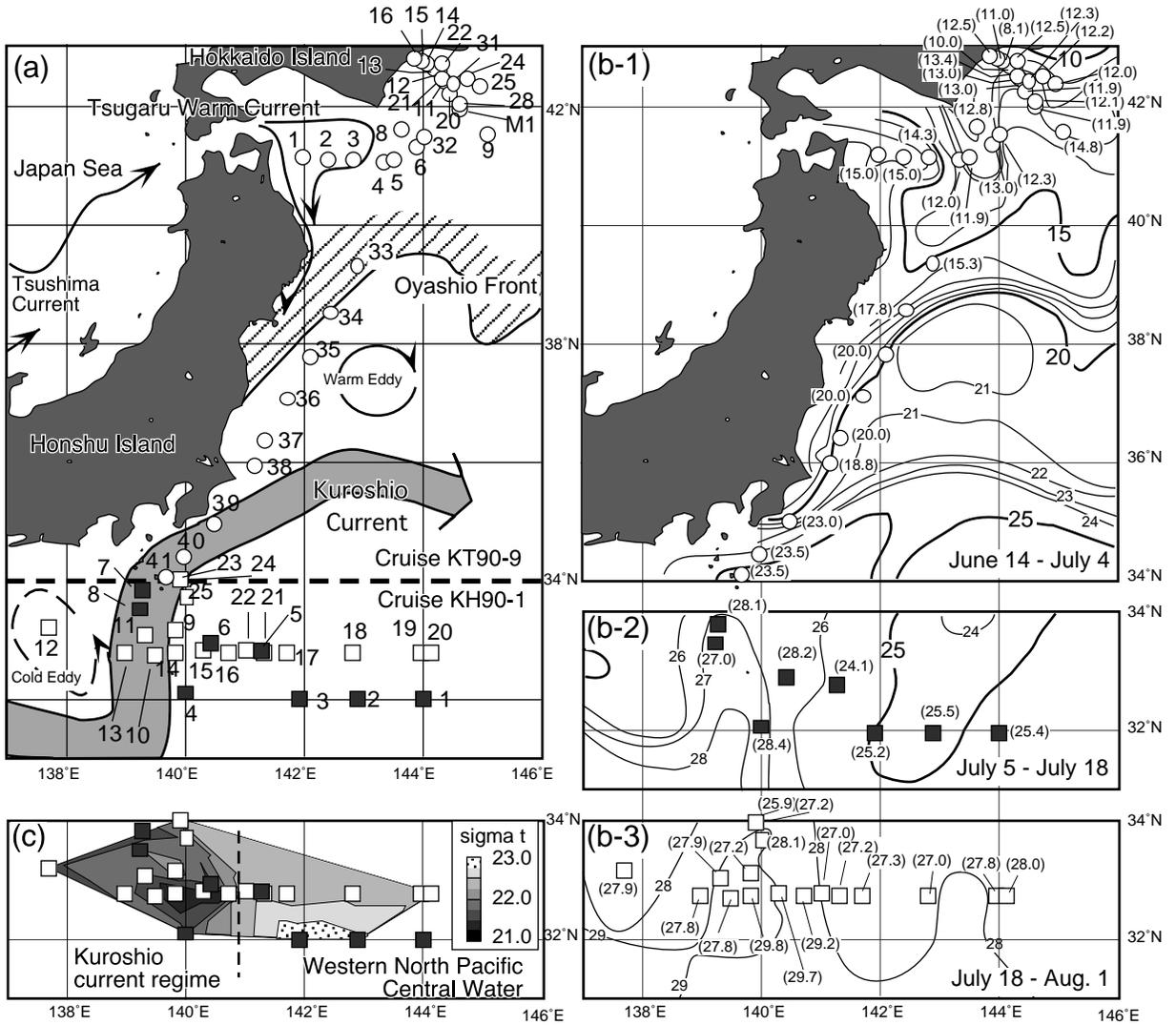
Type R: Form similar to type A but with heavily calcified shield elements, indeed slits often closed giving a Reticulofenestra-like appearance.

Table 3. Morphotypes of *Emiliana huxleyi* observed in this study

Morphotype	Morphological characters	Distribution	old name in Hagino 1997
Type A	liths medium -sized (2.7-4.1 μm), distal shield elements robust, central area covered by grill-like structure.	Kuroshio Current regime	Warm water type
Type B	liths large (2.7-5.4 μm), distal shield elements delicate and elevated, central area open or covered by thin plate. Proximal shield often larger than distal shield.	Oyashio Current regime	Cold water type
Type B/C	liths medium (3.2-4.1 μm), distal shield elements delicate and non-elevated, central area open or covered by thin plate.	Kuroshio Current regime	Cold water type
Type B/C-2	liths medium (3.0-5.1 μm), distal shield elements delicate and non-elevated, central area open or covered by thin plate. Proximal shield smaller than distal shield.	Tsugaru Warm Current	Intermediate Type

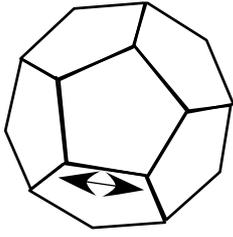




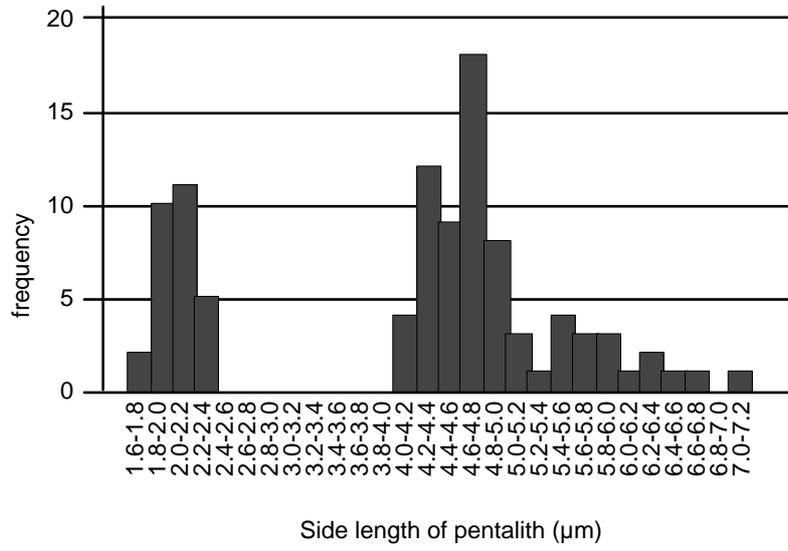


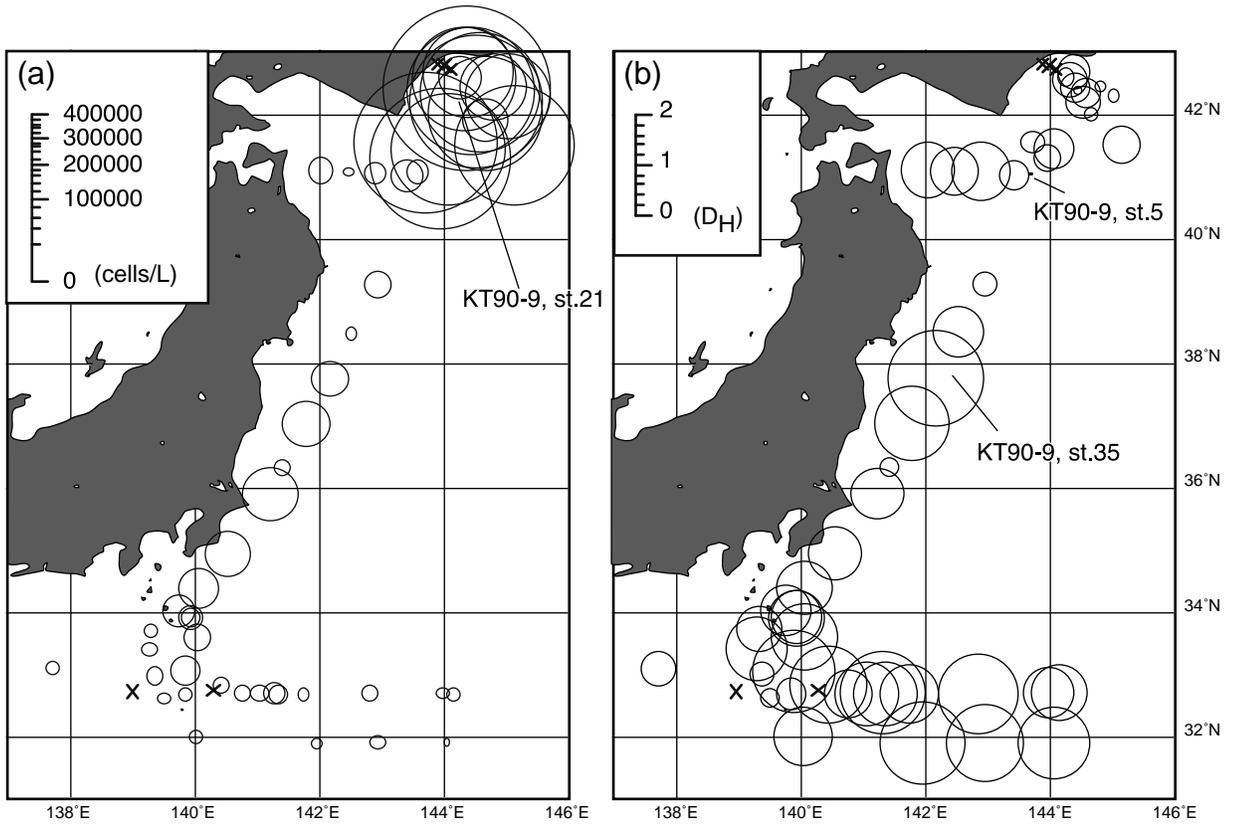
- Samples collected during Cruise KT90-9 (June 23-July 1, 1990)
- Samples collected during the first half of Cruise KH90-1 (July 16-19, 1990)
- Samples collected during the second half of Cruise KH90-1 (July 20-26, 1990)

(a)

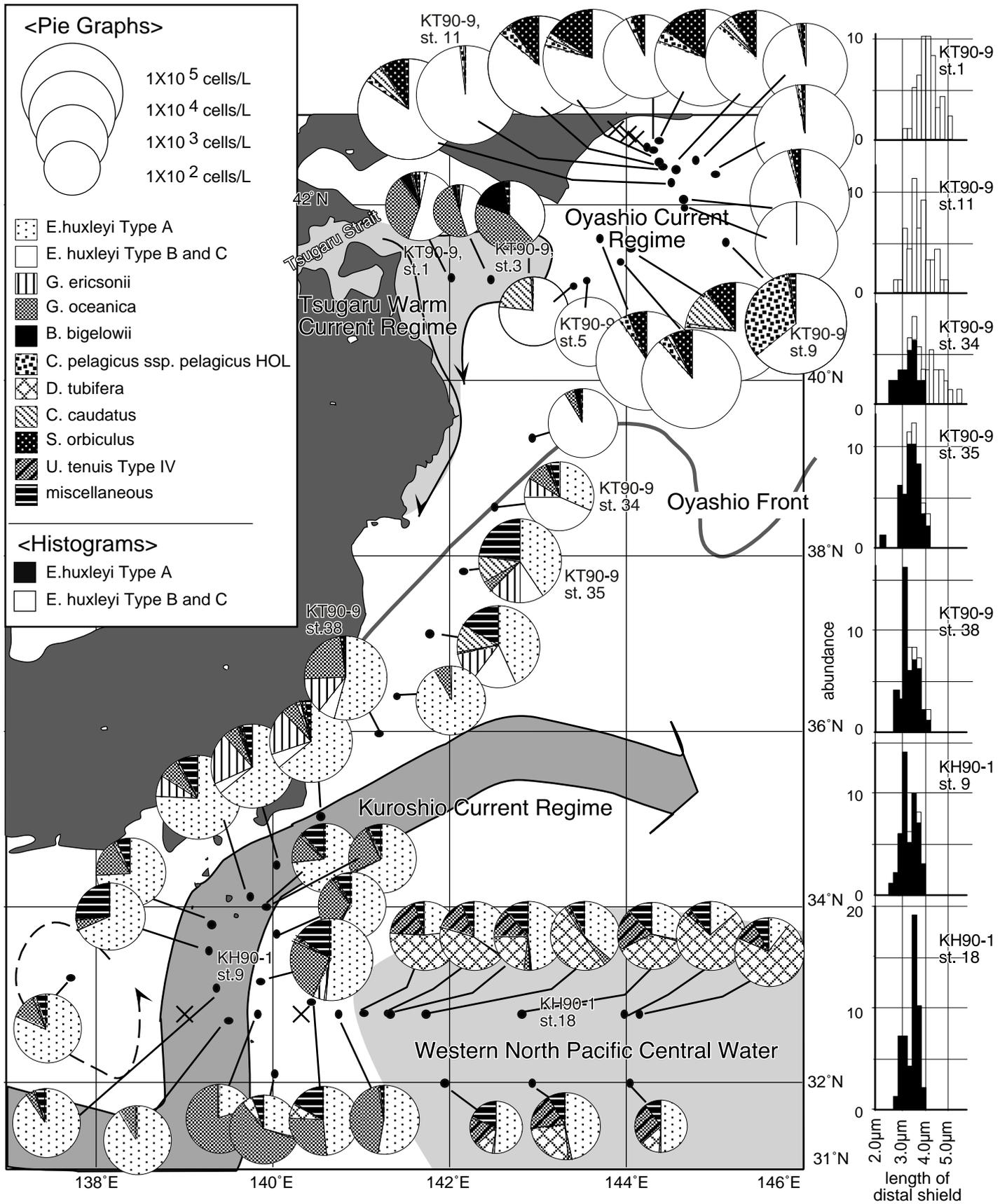


(b)



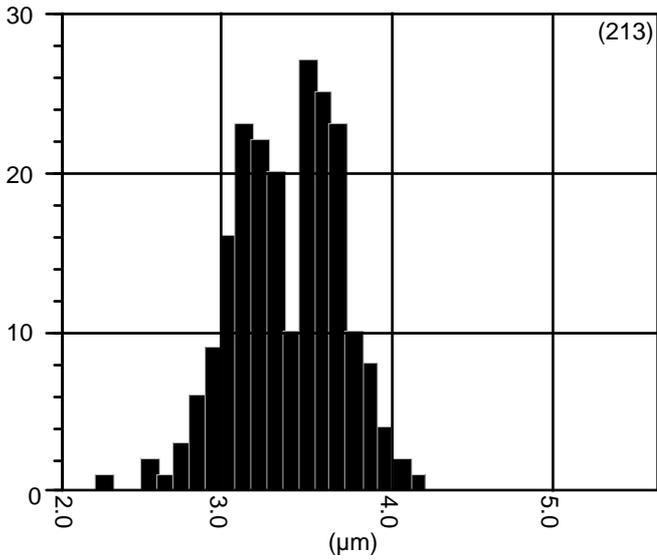


Hagino et al. Fig.3

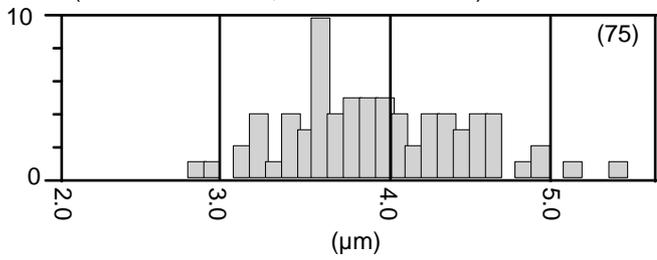


Hagino et al., Fig. 4

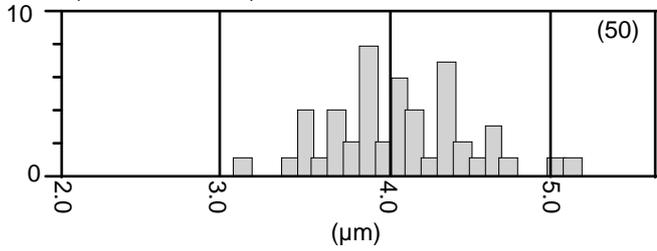
(a) Type A :
 Kuroshio Current regime and Western North Pacific Central Water
 (st.35 of KT90-9, st.38 of KT90-9, st.9 of KH90-1, st.18 of KH90-1)



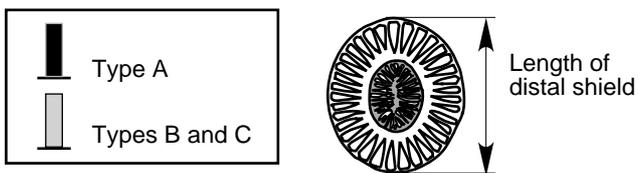
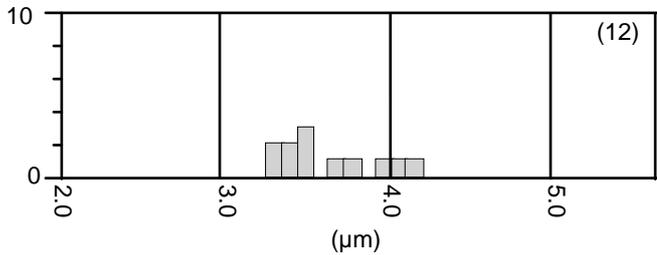
(b) Type B: Oyashio Current regime
 (st.11 of KT90-9, st.34 of KT90-9)



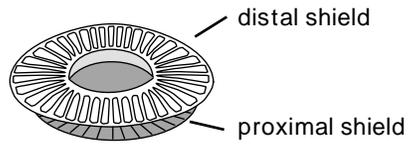
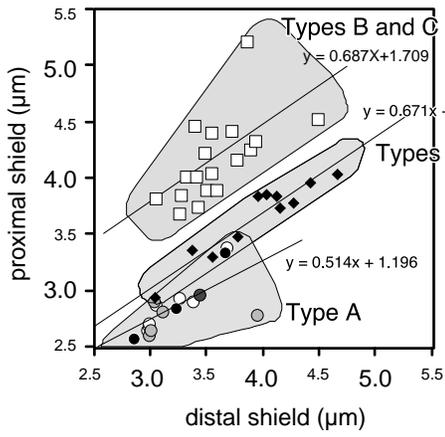
(c) Type B/C-2: Tsugaru Warm Current regime
 (st.1 of KT90-9)



(d) Type B/C: Kuroshio Current regime
 (st.35 of KT90-9, st.38 of KT90-9, st.9 of KH90-1)



Hagino et al., Fig. 5



- Type A at st. 35, KT90-9
 - Type A at st. 38, KT90-9
 - Type A at st. 9, KH90-1
 - Type A at st. 18, KH90-1
 - Types B and C at st.11, KT90-9 (Oyashio Current regime)
 - ◆ Types B and C at st.1, KT90-9 (Tsugaru Warm Current regime)
- } Kuroshio Current regime and Western North Pacific Central Water

Hagino et al., Fig. 6