Summer and winter distribution and malformation of coccolithophores in the East China Sea

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ABSTRACT: A quantitative scanning electron microscope study of coccolithophores was sampled during the summer and winter from the surface waters over the continental shelf of the East China Sea (ECS) was conducted. In all, only ten coccolithophorid taxa were observed during the investigation periods. *Emiliania huxleyi* (Lohmann) Hay et Mohler and *Gephyrocapsa oceanica* Kamptner were predominant among the coccolithophorid flora during both seasons. *E. huxleyi* increased its relative abundance seaward, while *G. oceanica* concentrated in inner shelf area. These two species accounted for over half of the coccolithophores in the middle shelf of the ECS.

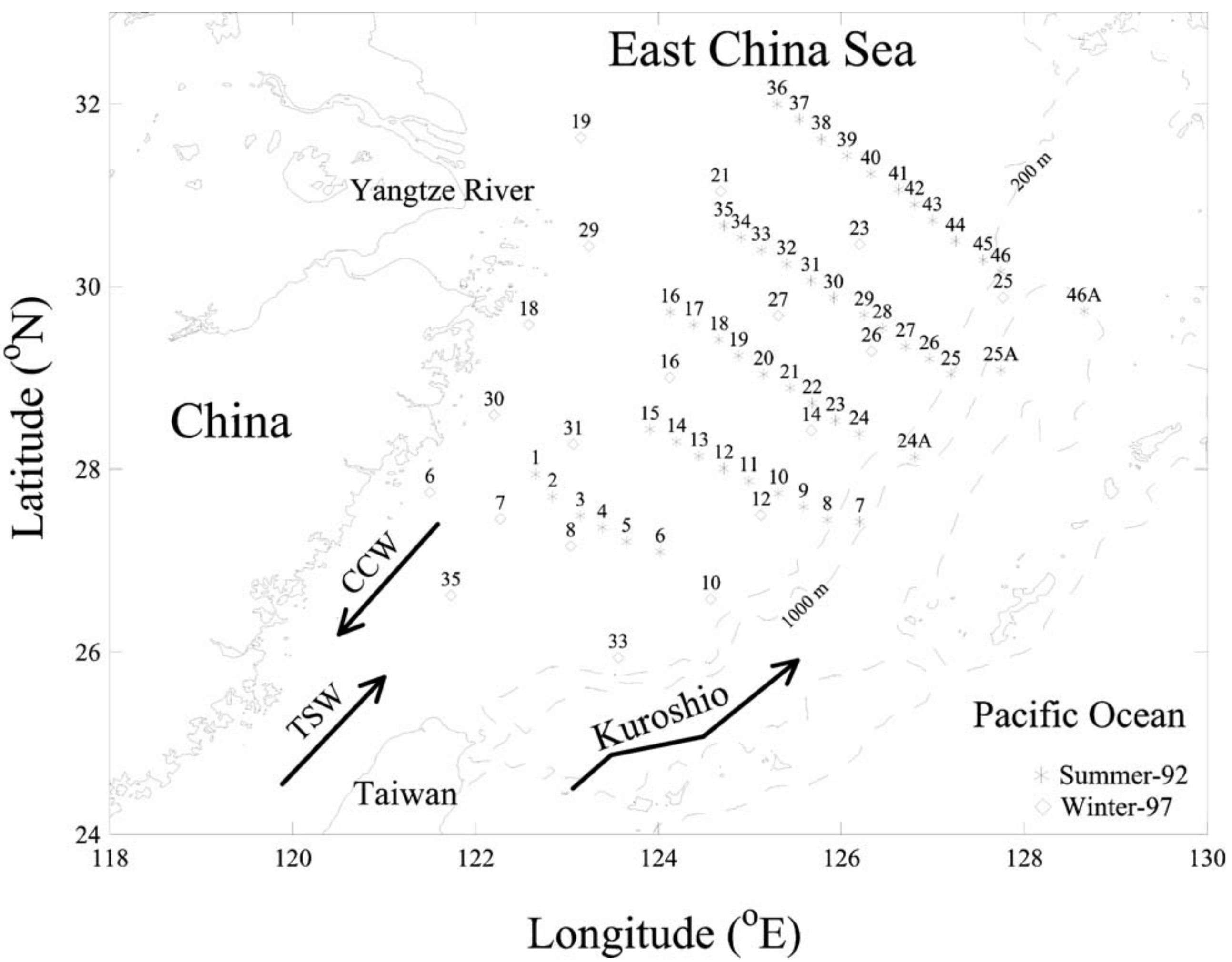
These dominant taxa are eurythermal, occurring in patchy and "bull's-eyes" distributions in both the summer and winter, respectively. Special emphasis has been paid to the overall distribution and intra-species frequency of malformed cells of the two dominant species, as well as other minor species. Malformed cells occurred so frequently in both seasons that the frequency amounted to as much as 80% in both dominant species. The malformation was manifested largely by corroded defects. A comparison of the malformed distribution with the hydrological and nutrient parameters suggests that the malformation was caused mainly by a deficiency of nitrate in the ambient waters.

INTRODUCTION

Marginal seas form an important domain in the global biogeochemical cycles of carbon and nutrient elements in the oceans (Mantoura et al. 1991). The East China Sea (ECS) is the largest marginal sea in the western Pacific with large amounts of nutrients supplied by the Yangtze River and Huanghe (Yellow River). The China Coastal Waters (CCW) together with the year-round upwelled Kuroshio Subsurface Waters off northeastern Taiwan sustains intensive primary production in the shelf water (Milliman and Meade 1983; Edmond et al. 1985; Wong et al. 1991; Liu et al. 1992; Chen 1996; Liu et al. 2000). Apart from the two nutrient-laden water masses, two warm oligotrophic waters, the Taiwan Strait Water (TSW) and Kuroshio Water, also influence the physical, hydrographical and biological properties of the ECS waters (Gong et al. 1996; Wong et al. 2000; Gong et al. 2003).

The ECS is a productive fishing ground (Furuya et al. 2003). It is also a major sink of organic carbon particulate and so CO_2 through the biological pump (Tsunogai et al. 1997; Yanagi 1997; Peng et al. 1999; Wang et al. 2000; Furuya et al. 2003; Gong et al. 2003; Ogawa et al. 2003). It has therefore received intensive attention as a key part of the biogeochemical carbon cycle, particularly during the 10 years' research project on the Kuroshio Edge Exchange Processes (ROC-KEEP) (Wong et al. 2000; Liu et al. 2003, and references in the two issues) and the marginal sea flux experiments in the West Pacific (Japan-MASFLEX) (Tsunogai et al. 2003; and references in the issue). A transect survey conducted by the MASFLEX program from the China coast to the Kuroshio region in the central part of the ECS showed that the shelf water was strongly stratified and depleted in nutrient content during the summer, but well mixed and nutrient enriched in the euphotic surface layer during the winter (Tsunogai et al. 2003). Furuya et al (2003) documented that herbivores controlled the biomass of phytoplankton on the shelf all the time, though the compositions varied seasonally. The ROC-KEEP study showed that nutrient concentrations in the northwestern half of the shelf were enriched all year-round; while in the southeastern part they were seasonally variable (Gong et al. 2003). Their work revealed that primary production (PP) in the northwestern region in the summer was about 3 times higher than that in other seasons, whereas that in the southeastern area showed only slight seasonal variations. Furthermore, the rate of PP was regulated by seawater temperature from winter to early spring, and by the availability of phosphate from summer to autumn (Gong et al. 2003). Coincidently, the concentration of dissolved organic carbon in the northwestern part was higher in the summer and autumn than in the spring and winter, while that in other area displayed insignificant temporal variations (Hung et al. 2003).

Among various studies of the large-scale distribution of living coccolithophores (e.g., McIntyre and Bé 1967; McIntyre et al. 1970; Okada and Honjo 1970; 1973; Okada and McIntyre 1977; Hallegraeff 1984; Kleijne 1991; 1992; 1993; Knappertsbusch 1993; Hagino et al. 2000; Cros and Fortuño 2002), Okada and Honjo (1975) made a monumental study of the coccolitho-



TEXT-FIGURE 1
Map of the East China Sea located in the western Pacific Ocean showing the study sites represented by asterisks (*) and diamonds (◊) and visited on two expeditions in July 1992 and December 1997, respectively. Taiwan Strait Waters (TSW) and Kuroshio flow northward, while China Coast Waters (CCW) southward along the coast. The Yangtze River is the major contributor of fresh water into the sea. For detailed hydrographic conditions refer to the text.

phores in the western Pacific marginal seas and found large numbers of malformed coccolithophores in the areas they studied. Furuya et al. (1996) focused on a restricted area in the northern part of the ECS and showed that the proportion of coccolithophore in the phytoplankton community increased with water depths. Furuya et al. (2003) used High Performance Liquid Chromatography (HPLC) to analyze pigment composition as a proxy of phytoplankton abundance to examine the phytoplankton dynamics in spring and summer. All these works showed that coccolithophores in the northern ECS are present at low abundance and low diversity.

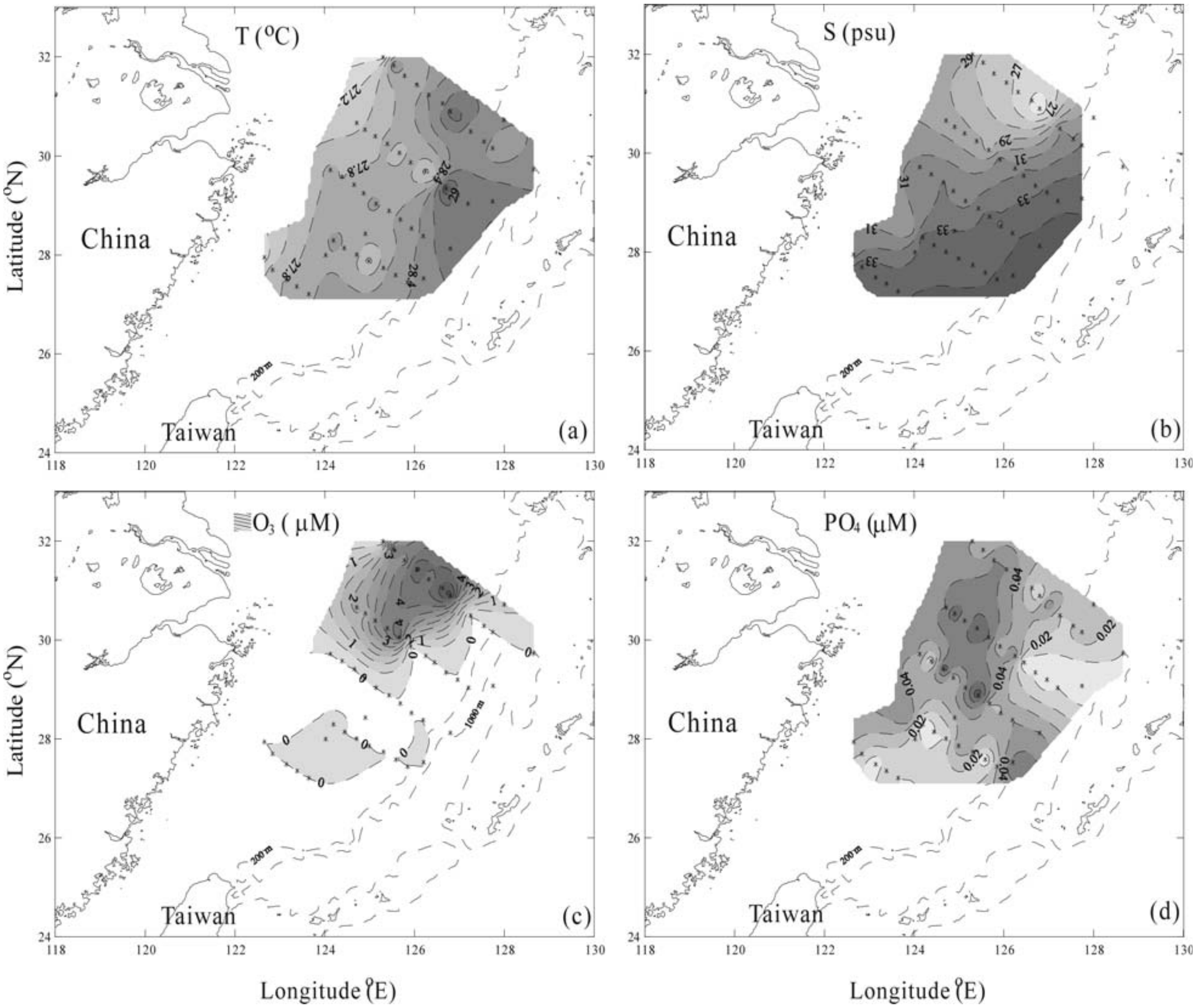
The objective of the current study was to investigate the spatial and temporal (summer vs. winter) dynamics of coccolithophores in surface waters over the East China Sea with special emphasis on the occurrence and distribution of malformed coccolithophores.

MATERIALS AND METHODS

A total of 68 samples filtered from surface water (0~2 m in water depth) were analyzed for the study (tables 1 and 2). These samples were obtained during two cruises, one in the summer and the other in the winter. The joint ROC-Russian joint expedition visited 49 stations from July 10 to August 5, 1992, and the Kuroshio Edge Exchange Processes (ROC-KEEP) study occupied 37 stations from December 19 through December 30, 1997 (text-fig. 1).

Seawater was obtained using a Seabird CTD-General Oceanic Rosette assembly with 12 Go-Flo bottles. About 0.1-1 liters of seawater were filtered on board through a Nuclepore® polycarbonate membrane (47mm in diameter, pore size 0.4 μm) by applying low-pressure (<100mm Hg) generated by a vacuum pump.

Preparation of samples for coccosphere counting followed the protocol of Yang et al. (2001) and can be briefly described. A piece of membrane with filtered particles was cut, about 1 cm^2 each, mounted onto an aluminum stub, and then coated with platinum. Both complete and collapsed coccospheres on the cut membrane portion were examined in horizontal rows and counted in a total of 320 randomly picked viewing fields under 2000 × magnification with a scanning electronic microscope (SEM): a JEOL SEM at the Institute of Oceanography and a



TEXT-FIGURE 2
Contour maps of environmental factors (EFs): (a) temperature, (b) salinity, (c) nitrate and (d) phosphate during the investigation in the summer of 1992.

HITACHI SEM at the Dept. of Geosciences, National Taiwan University, were used. "Cell density" in the present study refers to calcified cells (C-cells) only. The counting fields for these samples with rare specimens were generally more than 320. Plate 1 shows some selected specimens of normal and malformed coccospheres encountered during investigation.

Concentrations of nitrate and phosphate of the sea water were measured following the methods of Parsons et al. (1984). The precision for the determination of nitrate and phosphate were ±0.3μM and ±0.01μM, respectively. Details were given in Gong et al. (1996) for the summer survey and Gong et al. (2003) for the winter survey.

RESULTS

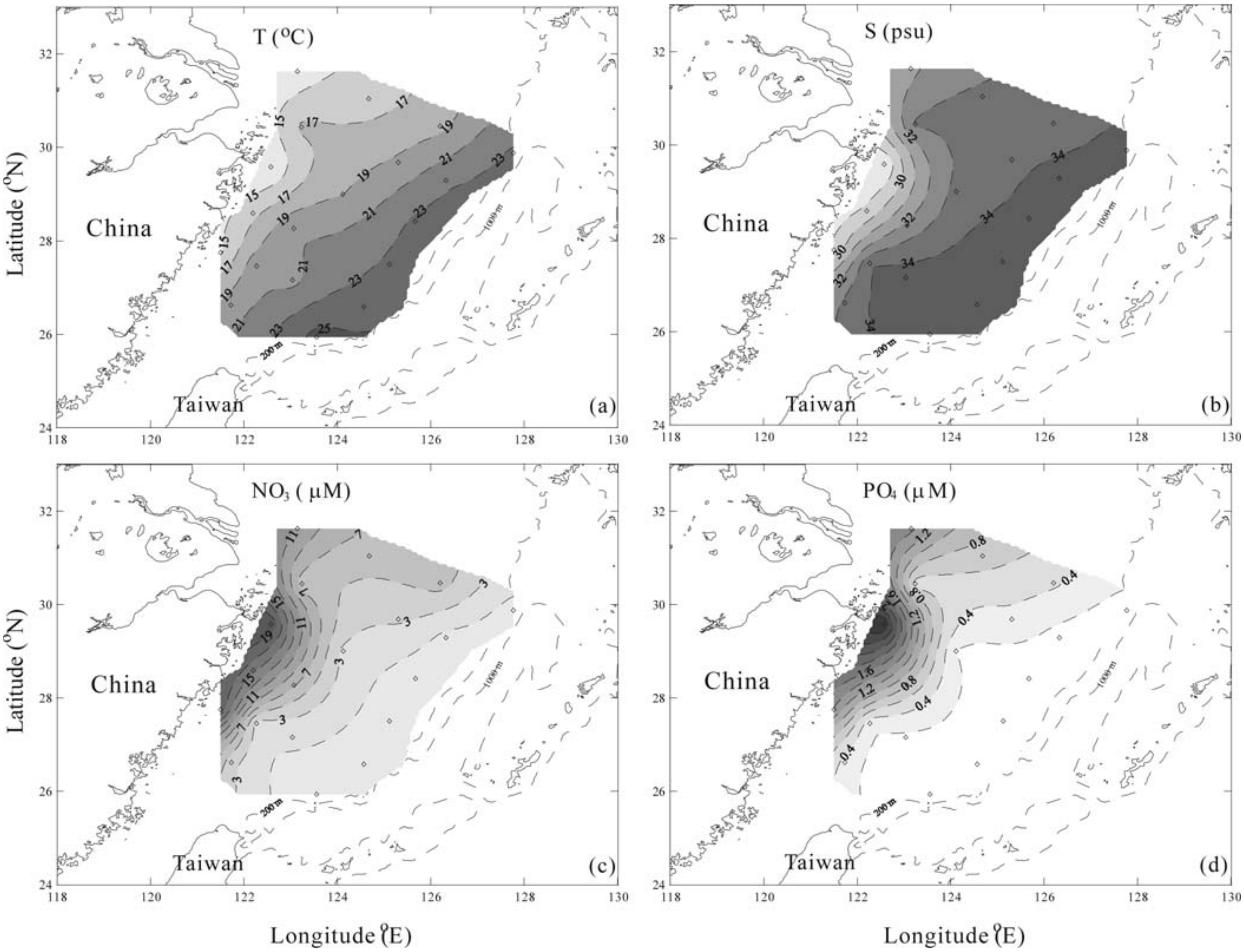
Hydrography

Text-figures 2 and 3 show contour patterns of the environmental parameters: temperature, salinity, nitrate and phosphate, measured in the surface waters of the ECS during supmmer 1992 (text-fig. 2) and winter 1997 (text-fig. 3). The detailed data are also listed in tables 1 and 2. In summer (text-fig. 2) the Yangtze River plume was evident in the northern part of the studied area from its low-salinity and high nitrate content (Gong et al. 1996). The plume signature gradually vanished towards the south. The temperature in the surface layer during summer displayed a somewhat homogenized pattern due to strong solar heating causing the water column to be highly stratified. The distribution of phosphate was patchy during the summer it was investigated.

During the winter (text-fig. 3), the various hydrological parameters exhibited similar patterns, in that all contours are parallel to the Chinese coastline. Temperature and salinity increased from the northwestern part of the shelf near the Yangtze River mouth southeastwardly in the offshore direction, while nitrate and phosphate concentrations decreased consistently.

Summer coccolithophores

The northern part of the studied area was affected by the Yangtze River plume, showing very low species richness (SR) and cell density of coccolithophores. No more than 5 species of coccolithophores were found at any one site, these values (SR = 0-5) are extremely low compared to the SR values of 10-17 in



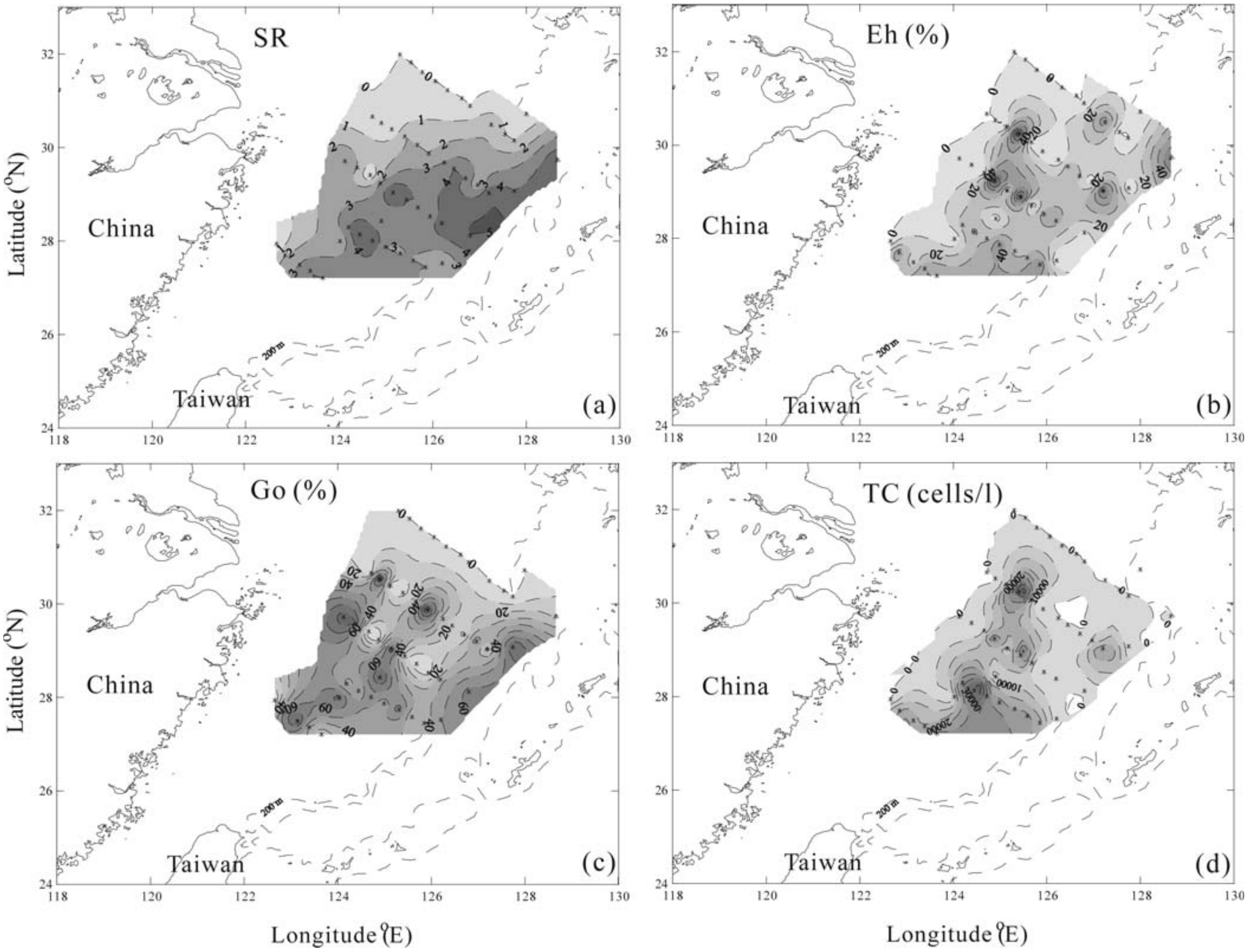
TEXT-FIGURE 3
Contour map of environmental factors (EFs): (a) temperature, (b) salinity, (c) nitrate and (d) phosphate during the investigation in the winter of 1997.

offshore areas off northeastern Taiwan, the Kuroshio (Yang et al. 2001) and in central Pacific waters (e.g., 10-11 from Okada and Honjo 1973; 9-12 from Reid 1980) (text-fig. 4a; table 1). The floral constituents as well as the common occurrence of malformed coccolithophores are in good agreement with the previous work of Okada and Honjo (1975). The species richness increased offshore, i.e. from northwest to southeast. The species richness pattern was notably similar to that of salinity.

Two species, *Emiliania huxleyi* (Lohmann) Hay et Mohler and *Gephyrocapsa oceanica* Kamptner dominated the coccolithophorid flora, and displayed similar patchy distributions (text-figs. 4b, 4c) with high abundances in the central area of the ECS. Some minor taxa, *Helicosphaera* Kamptner spp., *Rhabdosphaera clavigera* Murray et Blackman, *Syracosphaera* Lohmann spp. and *Umbellosphaera* Paasche spp. were only present in the summer. The total cell density (TC) of coccolithophores, including malformed specimens, exhibited large variations with values ranging from 0 to 64,500 cells/l in the surface waters (text-fig. 4d; table 1). A rather abundant occurrence of malformed coccolithophores (MC) ranging up to 36,400 cells/l in shelf waters was also observed, and contributed a large proportion of the total cell numbers (text-fig. 6a; table 1).

Winter coccolithophores

The distributions of coccolithophores, in terms of their SR and dominant species, total and malformed were simpler during the winter than those in the summer, showing a "bull's-eyes" pattern (text-figs. 5, 6b). Very low values of SR (0-3) were documented in the ECS in the winter, relative to offshore Taiwan, including northeastern Taiwan and the northwestern part of the South China Sea (Yang 2003), (table 2). The values of SR were similar to the summer values, but with the higher values concentrated in the middle shelf (text-fig. 5a), rather than the outer shelf. Although the species richness was similar, some different species were present, including *Algirosphaera robusta* (Lohmann) Norris, *Anoplosolenia brasiliensis* (Lohmann) Deflandre, *Calciosolenia murrayi* Gran and *Gephyrocapsa ericsonii* McIntyre et Bé. Dominant species were still *E. huxleyi* and *G. oceanica*, the former being dominant in the outer shelf and the latter in the inner and middle shelf (text-figs. 5b, 5c). The TC values ranged from 0 to 56,400 cells/l (text-fig. 5d; table 2). Malformed coccospheres were also documented, ranging from 0 to 49,900 cells/l, with high numbers concentrated in northern and southern parts of the middle shelf (text-fig. 6d; table 2).



TEXT-FIGURE 4
Contour map showing (a) species richness, (b) relative abundance of *Emiliania huxleyi*, (c) *Gephyrocapsa oceanica*, and (d) total cell density of coccolithophorids (TC) in the summer.

The southern part of the middle shelf witnessed the highest abundance of both total and malformed cells. The northern area contains less coccolithophores, with similar abundance reported in the same regime previously by Okada and Honjo (1975).

DISCUSSION

The coccolithophorid community in the ECS was obviously different from that in the Pacific reported by Okada and Honjo (1973) and Reid (1980), but similar in terms of both composition and frequent malformation to the communities documented in the neritic marginal seas by Okada and Honjo (1975). Ten taxa of coccolithophores were encountered during the counting works. The coccolithophorid taxa in the surface waters of the ECS revealed here were similar to those reported by Tanaka (2003) on the calcareous nannofossil assemblages in surface sediments along a transect from the Yangtze River estuary seaward to the Okinawa Trough. Conversely, the floral composition we observed was different from that documented by Wang and Samtleben (1983) and Zhang and Siesser (1986) from sea-floor sediments. However, most taxa in their census are considered to be forms of subsurface water layer, as well as from lateral transportation.

The cell abundance of coccolithophores and malformed species showed great spatial and temporal variations in surface water of the ECS (text-figs. 4d, 5d, 6), basically in two modes, one being "patchy", and the other, "bull's-eyes" type, in the summer and winter, respectively. To understand the relationships between the distributions of coccolithophores and environmental factors (EFs), plots of TC and the ratio of MC to TC in both seasons, as well as proportions of MC to TC of four major taxa in the summer, versus EFs are shown in text-figs. 7-9. The cell densities of coccolithophores in terms of the predominant species *E. huxleyi* and *G. oceanica* in the sea surface show that these species seem to prefer to a temperature around 28$^{\mathrm{o}}$ C during the summer time, and acclimatize within a large range from 16 $^{\mathrm{o}}$ to 25$^{\mathrm{o}}$ C in the winter. These species appeared to thrive in seawater at most stations with a wide range of salinity from 32 to 35 psu, but disappeared below 29 psu. There is no simple relationship between cell abundance of these species with concentrations of nitrate and phosphate in either season; however, in some stations near

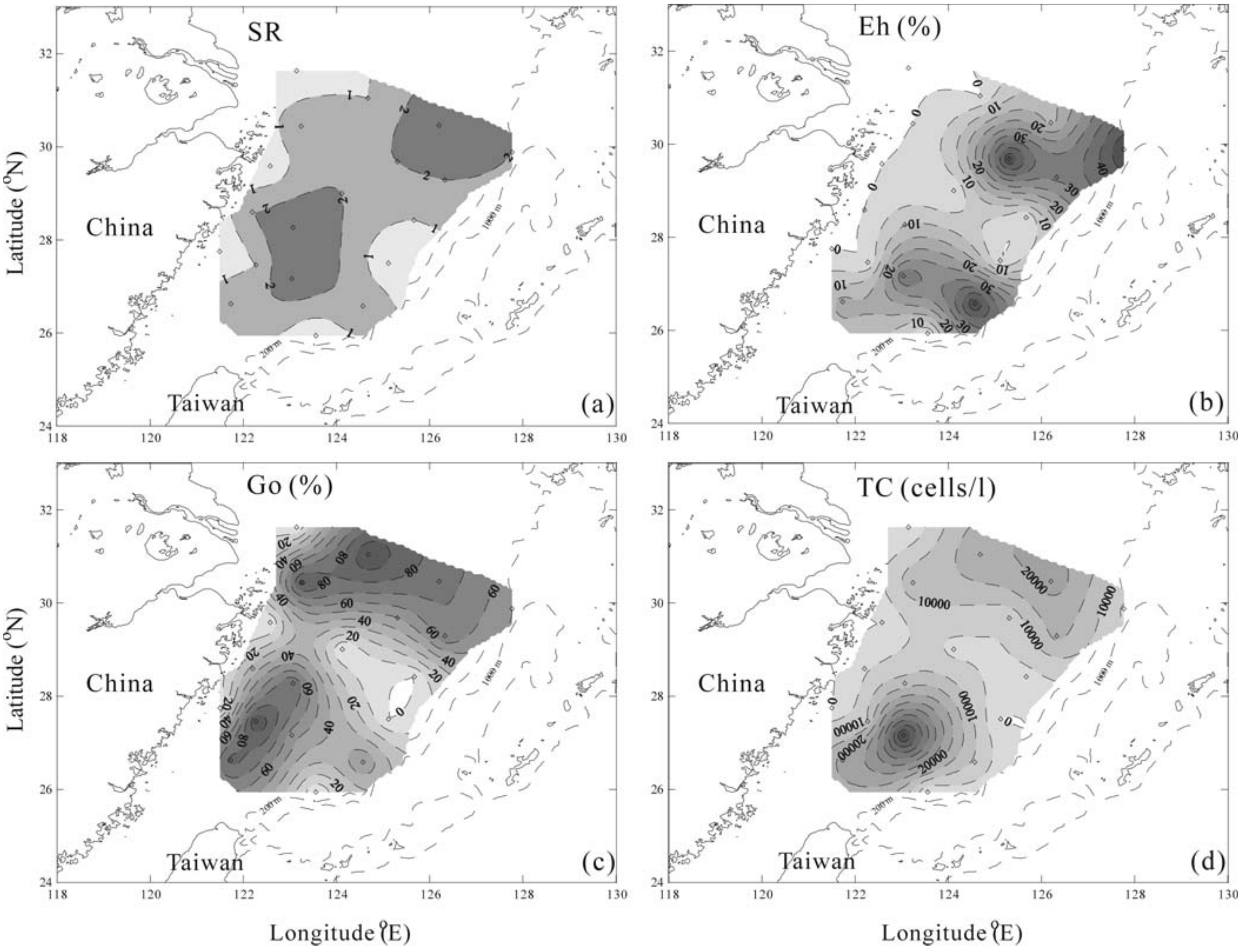
TABLE 1

List of environmental factors: temperature (°C), salinity (per mil), and nitrate and phosphate concentration (μM), and cell numbers of coccolithophores investigated from the surface water in the 1992 summer. *TC: total coccosphere, MC: malformed coccosphere; #n.d.: no data.

Station	1	2	3	4	5	6	7	8	9	10	11	12	13
Temperature	27.06	27.63	27.83	27.88	27.91	28.41	28.46	28.36	28.33	27.99	27.38	27.9	28.06
Salinity	31.55	33.94	33.67	33.65	33.36	34.1	34.39	34.32	33.49	33.77	33.24	33.77	33.59
Nitrate	0	0	0	0	0	0	0	0	0	0	0	0	0
Phosphate	0.03	0.02	0	0.02	0.01	0.01	0.06	0.03	0	0.03	0.04	0.01	0.01
TC*													
E. huxleyi	0	6300	2600	3200	11000	0	0	8800	7100	5000	10400	7100	19200
G. oceanica	0	9900	19800	3100	6200	30	3	5700	6600	13300	9200	15900	24000
Helicosphaera spp.	0	0	0	0	0	0	0	0	0	0	0	0	0
R. clavigera	0	0	1600	500	8400	15	3	2600	8800	1700	1600	3300	9900
Syracosphaera spp.	0	0	0	0	0	0	0	0	0	0	0	800	1000
Umbellsphaera spp.	0	0	0	1000	2600	0	0	0	0	0	400	400	4700
MC*													
E. huxleyi	0	4200	1600	1600	4200	0	0	0	4600	2900	3300	4200	8800
G. oceanica	0	3100	3100	0	500	30	3	0	800	6200	4600	6700	7300
Helicosphaera spp.	0	0	0	0	0	0	0	0	0	0	0	0	0
R. clavigera	0	0	0	500	6800	5	3	2600	4600	1700	800	800	5700
Syracosphaera spp.	0	0	0	0	0	0	0	0	0	0	0	0	1000
Umbellsphaera spp.	0	0	0	1000	2600	0	0	0	0	0	400	400	4700

Station	14	15	16	17	18	19	20	21	22	23	24	24A	25
Temperature	28.18	27.93	27.87	27.78	27.93	27.97	28.21	27.82	28.3	28.2	28.51	28.93	28.85
Salinity	33.37	30.26	31.39	31.71	32.04	31.86	31.53	32.61	33.27	32.89	33.86	34.24	33.78
Nitrate	0.2	0	0	0	0	0	0	0	0	0	0	0	0
Phosphate	0	0.05	0.04	0.01	0.07	0.03	0.05	0.08	0.03	0.03	0.04	0.04	0.01
TC													
E. huxleyi	6800	6	30	0	0	23900	160	34000	3	140	240	20	18400
G. oceanica	9900	130	510	390	0	12400	870	5600	10	20	260	160	4200
Helicosphaera spp.	0	0	0	0	0	0	5	0	3	0	0	0	0
R. clavigera	6300	23	60	78	0	0	45	700	337	90	170	50	600
Syracosphaera spp.	0	3	0	0	0	0	0	0	0	0	9	9	300
Umbellsphaera spp.	4100	0	0	0	0	1000	15	2100	0	110	21	2	4100
MC													
E. huxleyi	8800	5200	6	20	0	0	8300	130	8300	0	120	0	10
G. oceanica	7300	2100	110	400	270	0	6200	250	0	10	10	30	100
Helicosphaera spp.	0	0	0	0	0	0	0	5	0	0	0	0	0
R. clavigera	5700	4200	20	40	60	0	0	40	700	290	70	90	40
Syracosphaera spp.	1000	0	3	0	0	0	0	0	0	0	0	2	9
Umbellsphaera spp.	4700	3600	0	0	0	0	1000	15	700	0	110	11	2

Station	25A	26	27	28	29	30	31	32	33	34	35	36	37
Temperature	29	28.79	29.66	27.72	27.4	28.02	27.58	27.99	27.54	27.56	27.4	26.79	28.39
Salinity	n.d.#	33.43	32.28	32.63	31.27	31.3	28.71	29.37	29.3	29.49	29.39	29.3	27.07
Nitrate	0	0	0	0	0	0	4.3	3.7	3.3	1.9	2.3	0	4.2
Phosphate	0	0	0.01	0	0.05	0.03	0.06	0.07	0.05	0.07	0.05	0.04	0.03
TC													
E. huxleyi	2	0	57	37	0	0	0	60400	0	0	0	0	0
G. oceanica	130	20	20	29	8	3	40	4100	0	49	0	0	0
Helicosphaera spp.	0	0	0	0	0	0	0	0	0	0	0	0	0
R. clavigera	7	20	133	81	30	65	120	0	0	0	0	0	0
Syracosphaera spp.	12	0	0	0	0	0	0	0	0	0	0	0	0
Umbellsphaera spp.	0	0	64	10	0	0	0	0	0	0	0	0	0
MC													
E. huxleyi	2	0	37	10	0	0	0	33300	0	0	0	0	0
G. oceanica	40	20	10	7	8	3	40	3100	0	49	0	0	0
Helicosphaera spp.	0	0	0	0	0	0	0	0	0	0	0	0	0
R. clavigera	7	10	93	69	20	40	120	0	0	0	0	0	0
Syracosphaera spp.	12	0	0	0	0	0	0	0	0	0	0	0	0
Umbellsphaera spp.	0	0	64	10	0	0	0	0	0	0	0	0	0

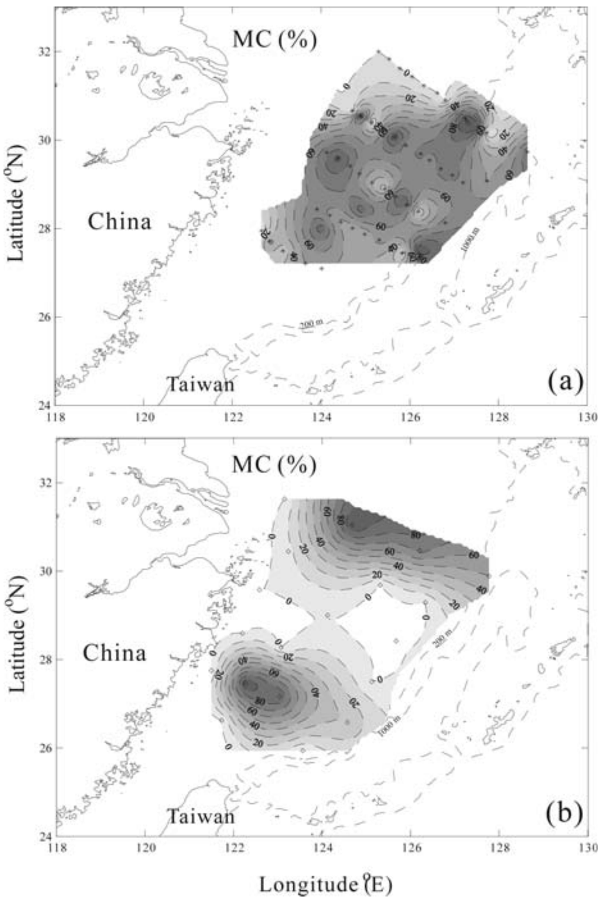


TEXT-FIGURE 5
Contour map showing (a) species richness, (b) relative abundance of *Emiliania huxleyi*, (c) *Gephyrocapsa oceanica*, and (d) total cell density of coccolithophorids (TC) in the winter.

the coast with high nitrate (> 6μM) (text-figs. 3c, 7c) and phosphate (> 0.8μM) (text-figs. 3d, 7d), no coccolithophores occurred in the winter. The limiting factors for coccolithophores in these waters governed by the CCW were probably the low temperature and, particularly, salinity rather than the nutrient supply (text-fig. 3). Nevertheless, enriched nitrate and phosphate indeed induced the increase of cell numbers during optimal temperature and salinity conditions during the winter (text-fig. 7).

Based on an extensive study of the marginal seas in the western Pacific, Okada and Honjo (1975) proposed that nitrogen deficiency results in the deformation of coccolith morphology. Based on their data and previous work, Kleijne (1990) and Giraudeau et al. (1993) discussed the possible reasons for coccolith malformation. Kleijne (1990) discussed the difference between corroded and malformed morphologies of coccoliths and considered nitrogen limitation combined with low sea-surface salinity as a cause of coccolith malformation in the Indonesian Seas surface water. Giraudeau et al. (1993) considered the malformation of coccoliths independent of nitrogen deficiency in the northern Benguela upwelling system off Namibia. Various culture studies have indicated that coccolith-formation was enhanced when nitrogen was limited in cultivated medium, but no malformation appeared (Wilbur and Watabe 1963; Linschooten et al. 1991; Lecourt et al. 1996). Young (1994) observed common presence of malformed coccoliths in late stationary phase cultures, and in cultures grown in artificial seawater. He considered the malformation of coccoliths as a dissolution effect in the waters.

A great number of malformed coccolithophores that are identical to those shown by Okada and Honjo (1975) were found in waters both in summer and winter (tables 1 and 2). Although most of malformed specimens in our work were similar to corroded forms that were defined by Kleijne (1990), we consider them being produced mainly by malformation, not a dissolution effect because the distribution of pH values (8.04-8.22) in the ambient waters indicates that the dissolution of coccoliths should not occur although corrosion between elements of



TEXT-FIGURE 6
Contour map showing percentage of malformed cells (MC) in waters of the (a) summer and (b) winter.

coccoliths might occur in microenvironments (Wang et al., 2000). The relationships between malformed cells and those EFs were shown by ratios of MC and TC for both seasons (text-figs. 8, 9) and by ratios of MC to TC for four major taxa, *E. huxleyi*, *G. oceanica*, *R. clavigera* and *Umbellosphaera* spp. in the summer (text-fig. 10). The malformation existed frequently in stratified and nitrate and phosphate depleted surface waters in the summer (text-figs. 8-10). High proportions of MC to TC for these species occurred patchily in the southern and southwestern parts where the nitrate concentration was below than the detection limit (0.3µM) (text-figs. 2, 8-10), and in the sites where the phosphate concentration was lower than 0.08µM. It is suggested that the availability of phosphate controlled not only the rate of primary production (Gong et al. 2003), but the morphological growth of coccolithophores as well in the ECS. These malformations show no relationship to low salinity. It appears that our data support the hypothesis proposed by Okada and Honjo (1975) that limited nutrient concentration in surface waters during the summer time, especially nitrate, may be a driving force for producing malformed cells, rather than the temperature and salinity (text-fig. 9). Some high values (> 0.5) of ratio of MC and TC, however, were observed in waters where nitrate and phosphate contents range from ~2 to 6µM and 0.27 to 0.71µM, respectively, in both seasons (text-fig. 8) and the other EFs show normal conditions. Since no alkalinity was measured in the winter cruise, and no other parameters were determined in this study, we do not know the reasons for the phenomenon. The malformed coccoliths, however, were manifested largely by corroded defects in our samples as showed in text-figures 1 and 7 and in plate 1. It is possible that, in the samples with very low nitrate no coccolithophore growth is occurring, but old populations of coccolithophorid cells are present and have been subject to water column dissolution (J.R. Young, personal communication).

It is peculiar that no such malformed individuals were reported from investigations on calcareous nannofossils in surface sediments of the Namibian continental margin (Giraudeau 1992) and the ECS continental shelf (Wang and Samtleben 1983; Zhang and Siesser 1986; Tanaka 2003), although some of them were observed in the water columns of these seas. Giraudeau et al. (1993) suggested that the lack of a geological record of this phenomenon might result from the fragile characteristics of the coccoliths due to the disarrangements of the crystal elements. The use of different tools, SEM vs. optical microscope, may result to the different assemblages with/without malformed specimens in samples gained from water column and sea floor sediments, respectively.

CONCLUSION

The cell abundance of coccolithophores and their malformed species showed remarkable spatial and temporal variations in the surface waters of the ECS during the summer of 1992 and winter of 1997. The community structure differed from that in the marginal seas around Taiwan and the open Pacific. In all, only ten coccolithophorid taxa were observed during the investigation periods. Two distribution modes of cell density and dominant species of coccolithophores were observed, “patchy” during the summer and “bull’s-eye” in the winter. Low cell density was observed in areas where the waters were influenced by the Yangtze River plume and CCW. The production of malformed coccoliths is related to the nitrate and phosphate content, and dissolution, instead of temperature and salinity conditions. It is suggested that low temperature and salinity cause low coccolithophorid abundance, while low nutrients cause malformation, although not in all cases.

ACKNOWLEDGMENTS

The authors would like to thank officers and crew of the R/VS *Akademik Aleksandr Vinogradov* and *Ocean Researcher I*, and Prof. F-K Shiah for their help during the expedition’s cruises. We are grateful to A. Kleijne and J.R. Young for their valuable comments on the manuscript. Grants NSC-86-2611-M-002-005-K2 (KYW), NSC 92-2611-M-019-013 (GCG), NSC 83-0209-M002A-021K (FJL) and NSC 92-2119-M-001-003 (TQL) were supported by the National Science Council of the Republic of China.

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TABLE 2
List of environmental factors: temperature (^{O}C), salinity (per mil), and nitrate and phosphate concentration (µM), and cell numbers of coccolithophores investigated from the surface water in the 1997 winter. *TC: total coccosphere, MC: malformed coccosphere; #n.d.: no data.

Station	6	7	8	10	12	14	16	18	19	21	23	25	26
Temperature	14.69	20.35	20.42	23.91	23.32	23.37	18.96	13.01	13.81	16.11	18.47	23.32	22.56
Salinity	29.14	33.92	34.42	34.62	34.7	34.14	33.32	28.08	31.74	33.13	33.32	34.37	34.42
Nitrate	18.6	2.3	1.7	0.1	0.2	0.2	2.5	20.8	10.9	5.8	5.8	0.2	0.4
Phosphate	1.39	0.27	0.17	0.09	0.08	0.08	0.19	2.6	1.46	0.71	0.43	0.11	0.13
TC*													
A. robusta	0	0	5550	0	0	1542	0	0	0	0	0	0	0
C. brasiliensis	0	0	0	0	0	0	1850	0	0	0	0	0	0
C. murrayi	0	0	0	0	0	0	1850	0	0	0	0	0	0
E. huxleyi	0	0	19425	4625	0	0	0	0	0	0	3083	2056	5139
G. ericsonii	0	0	0	0	0	0	0	0	0	0	3083	0	0
G. oceanica	0	10175	30525	4625	0	0	0	0	0	20042	16958	2056	11306
Miscellaneous	0	0	925	0	0	1542	0	0	0	0	0	0	0
MC*													
E. huxleyi	0	0	19425	925	0	0	0	0	0	0	0	0	0
G. ericsonii	0	0	0	0	0	0	0	0	0	0	0	0	0
G. oceanica	0	10175	30525	1850	0	0	0	0	0	20042	16958	2056	0

Station	21	23	25	26	27	29	30	31	33	35
Temperature	16.11	18.47	23.32	22.56	19.39	17.37	16.54	20.73	25.69	19.89
Salinity	33.13	33.32	34.37	34.42	33.76	33.12	29.24	32.28	34.47	33.21
Nitrate	5.8	5.8	0.2	0.4	3.3	5.9	n.d.#	n.d.	0.1	3.8
Phosphate	0.71	0.43	0.11	0.13	0.35	0.52	n.d.	n.d.	0.07	0.33
TC										
A. robusta	0	0	0	0	0	0	0	0	0	0
C. brasiliensis	0	0	0	0	0	0	0	0	0	0
C. murrayi	0	0	0	0	0	0	0	0	0	0
E. huxleyi	0	3083	2056	5139	3083	0	0	1233	0	3700
G. ericsonii	0	3083	0	0	0	925	2846	1233	0	0
G. oceanica	20042	16958	2056	11306	3083	12950	1423	9867	0	18500
Miscellaneous	0	0	0	0	0	0	0	0	0	0
CC										
E. huxleyi	0	0	0	0	0	0	0	0	0	0
G. ericsonii	0	0	0	0	0	925	0	0	0	0
G. oceanica	20042	16958	2056	0	0	0	0	0	0	0

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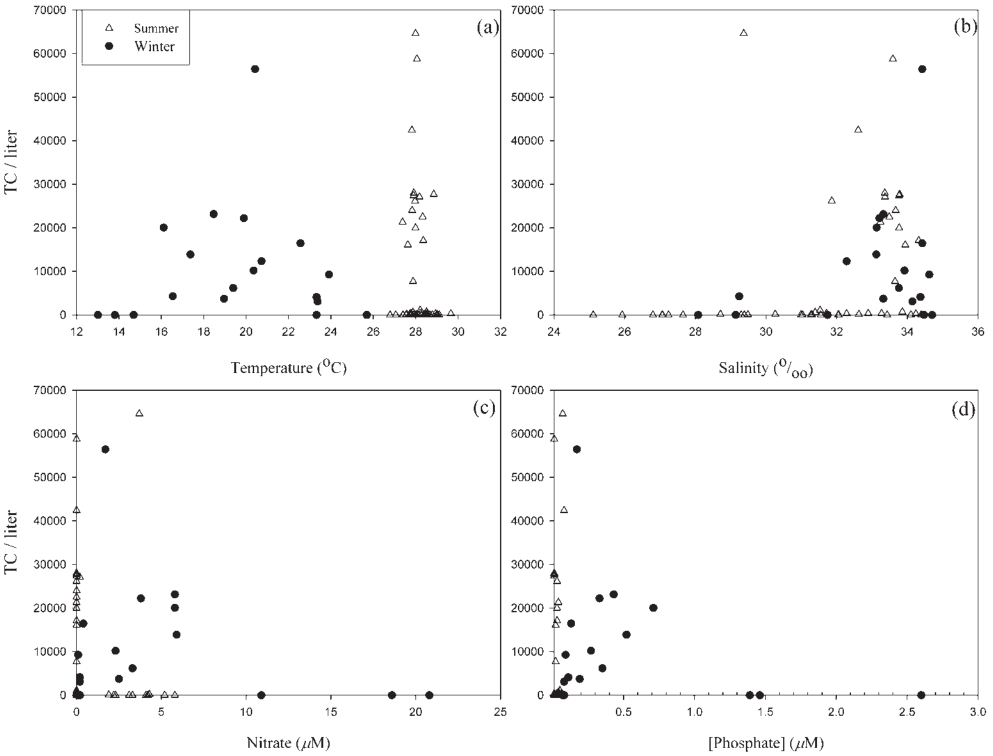
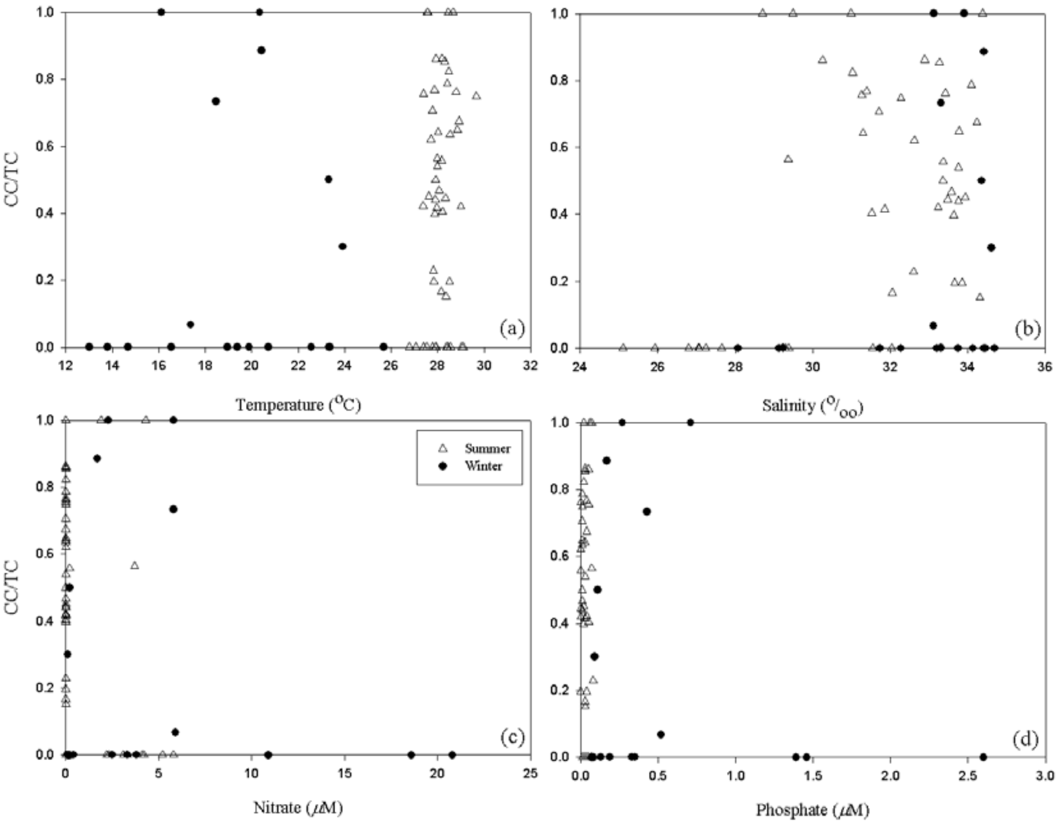
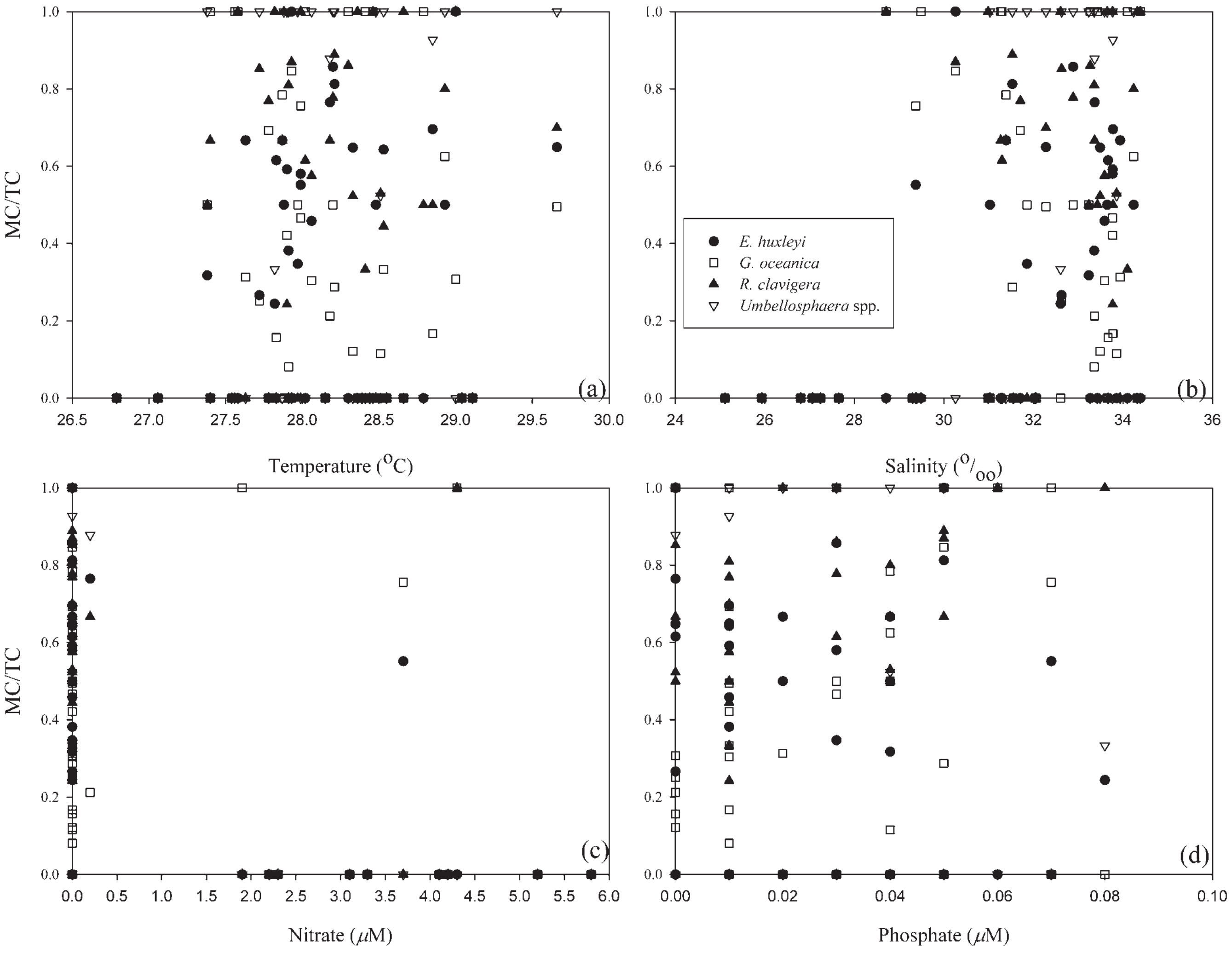


TEXT-FIGURE 7
Plots of total coccolithophore numbers (TC) against environmental factors (Efs): (a) temperature, (b) salinity, (c) nitrate and (d) phosphate. Summer data are marked by open triangle, while those of winter by closed circle.



TEXT-FIGURE 8
Plots of proportion of malformed cells in the total assemblage (MC/TC) against environmental factors: (a) temperature, (b) salinity, (c) nitrate and (d) phosphate. Summer data are marked by open triangle, while those of winter by closed circle.



TEXT-FIGURE 9
Plots of proportions of malformed cells to total cells for four major taxa in the summer against environmental factors: (a) temperature, (b) salinity, (c) nitrate, and (d) phosphate. Data for *E. huxleyi*, *G. oceanica*, *R. clavigera* and *Umbellosphaera* spp. are marked by closed circle, open square, closed triangle and open triangle, respectively.

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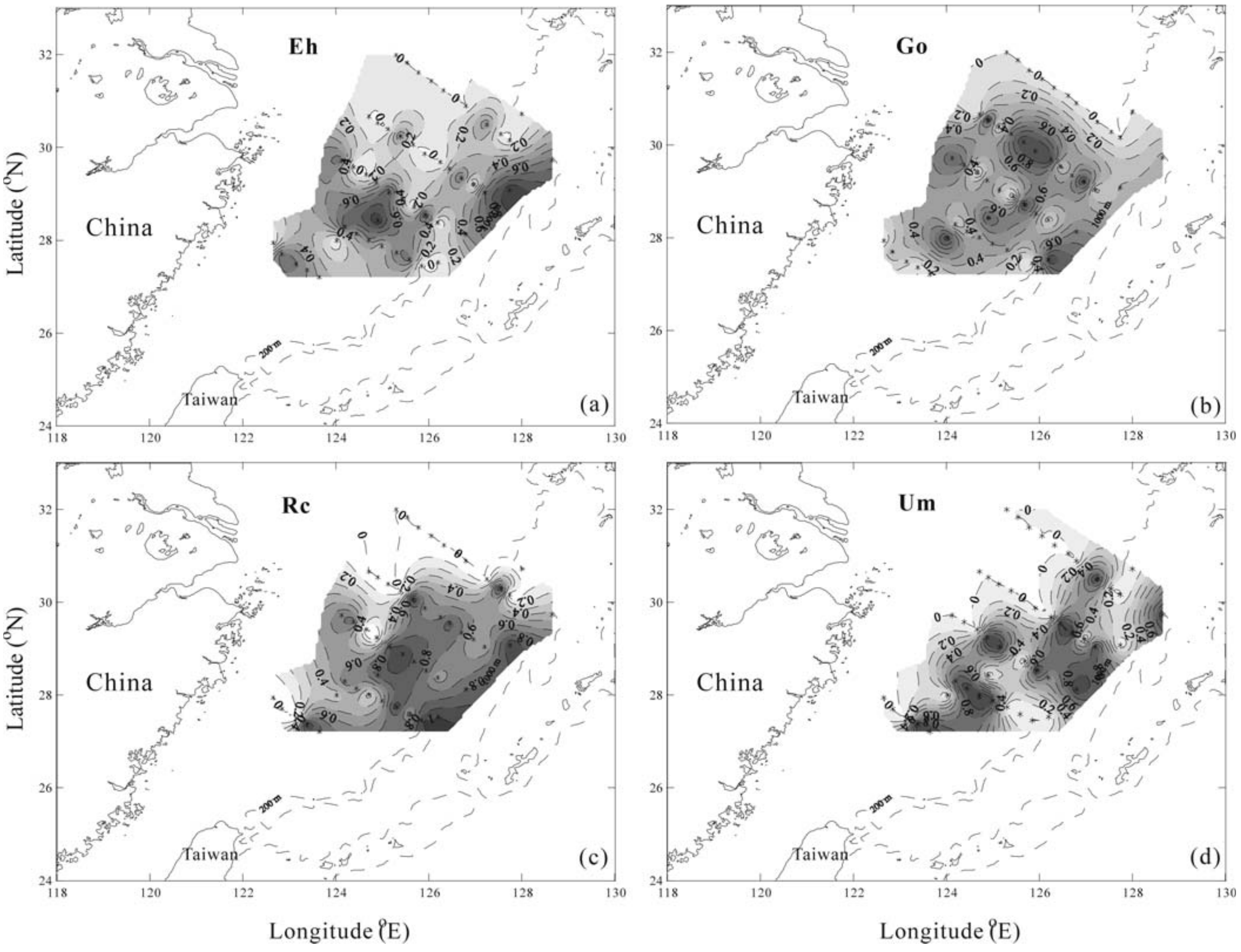

TEXT-FIGURE 10
Contour map showing proportions of malformed cells to total cells for four major taxa in the summer: (a) *E. huxleyi*, (b) *G. oceanica*, (c) *R. clavigera*, and (d) *Umbellosphaera* spp.

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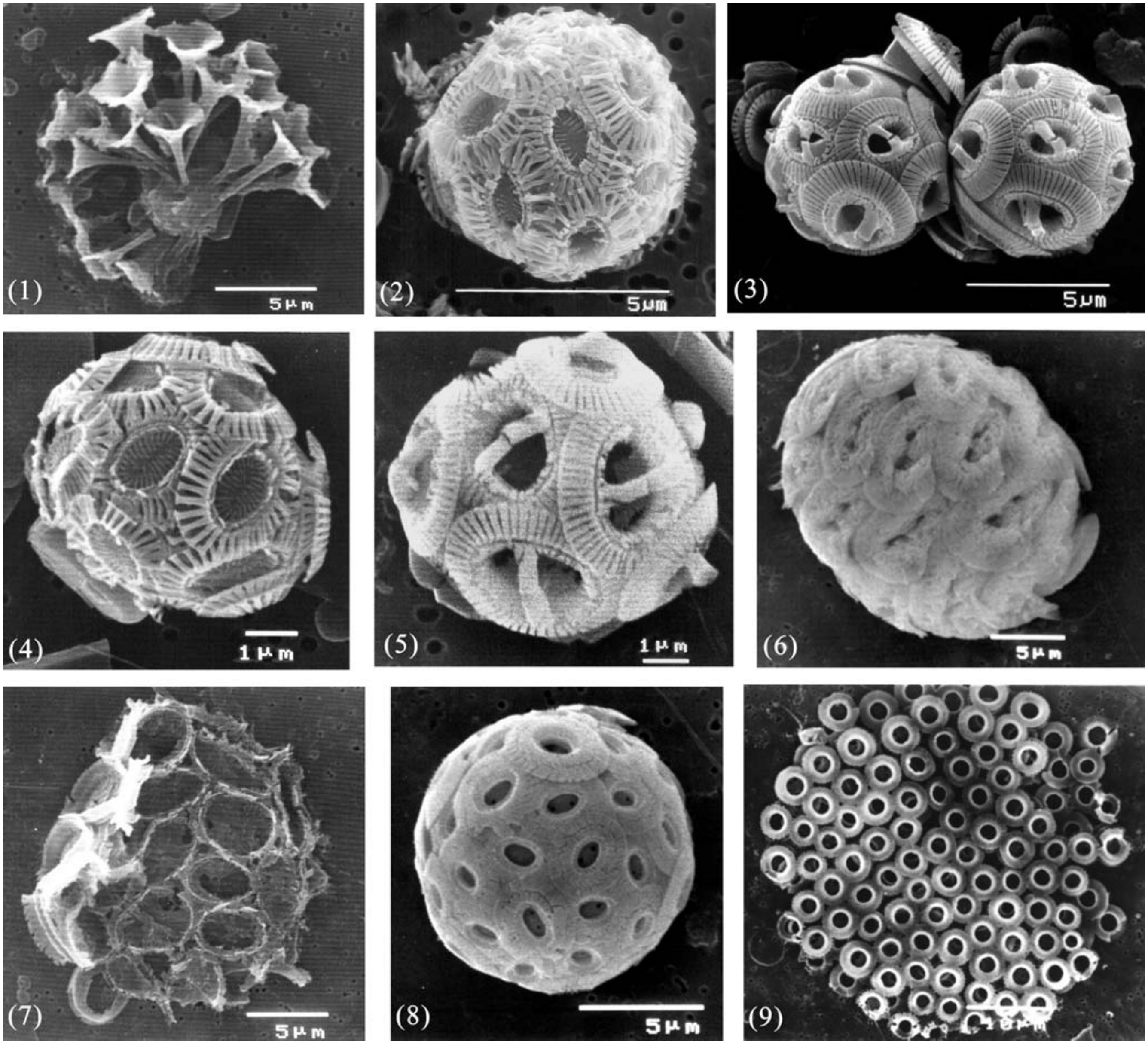

PLATE 1

Figs. 1-3, 6-8: bar = 5µm; Figs. 4, 5: bar = 1µm; Fig. 9: bar = 10µm.

1 *Discosphaera tubifera* (Murray and Blackman) Ostenfeld. Coccosphere with corroded malformed rhabdoliths. (Station 13, summer cruise)

2 *Emiliania huxleyi* (Lohmann) Hay and Mohler. Coccosphere with malformed placoliths. (Station 8, winter cruise)

3 *Gephyrocapsa oceanica* Kamptner. Coccospheres with malformed placoliths. (Station 8, winter cruise)

4 *Emiliania huxleyi* (Lohmann) Hay and Mohler. Coccosphere with malformed placoliths. (Station 5, summer cruise)

5 *Gephyrocapsa oceanica* Kamptner. Coccospheres with malformed placoliths. (Station 13, summer cruise)

6 *Helicosphaera* Kamptner sp. Coccosphere with malformed helicoliths. (Station 20, summer cruise)

7 *Syracosphaera* Lohmann sp. Coccosphere with corroded malformed caneoliths. (Station 5, summer cruise)

8 *Umbilicosphaera hulburtiana* Gaarder. Coccosphere with malformed placoliths. (Station 13, summer cruise)

9 *Umbilicosphaera sibogae* (Weber-van Bosse) Gaarder. Coccosphere with malformed placoliths. (Station 11, summer cruise)

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