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Formation of a diatom assemblage distributed widely in the North Pacific Polar Frontal Zone

Kuo-Ping CHIANG* and Akira TANIGUCHI

Abstract

Diatom populations distributed in the North Pacific Polar Frontal Zone east of northern Honshu in winter are investigated in relation to distribution of water types.

Three water types and four diatom assemblages were defined by principal component analyses. Distributional patterns of the water types and the diatom assemblages were not always consistent with each other. Although the warm water assemblage effectively indicated the Tsugaru Warm Current, other assemblages of cold water nature could not strictly indicate the Oyashio Cold Current probably because active growth of diatoms does not occur in the cold water in winter. Background assemblage which is distributed widely over the frontal zone and composed of cold oceanic and neritic cosmopolitan species is likely to be formed by winter convection of water which selects tolerant species to winter conditions.

1. Introduction

The Kuroshio Extension forms in the sea area east of Honshu a marked ocean front, the Kuroshio Front. The Oyashio Current from the north flows into the sea area and also forms a front, the Oyashio Front. These two large-scale fronts border the Polar Frontal Zone in the western North Pacific Ocean. The less prevailng Tsugaru Warm Current intrudes from the Japan Sea through the Tsugaru Straits into the western edge of the Polar Frontal Zone and flows southward along the east coast of Honshu. Therefore, oceanographic condition in the Frontal Zone is very complicated by several different water masses such as warm and cold core rings and streamers, coastal water mass, etc., which scatter over the mixed water mass (cf. KAWAI, 1972; HANAWA and MITSUDERA, 1987). The mixed water mass can be considered as the background water mass in the Frontal Zone and many small-scale secondary fronts are formed between this background water and other water masses mentioned above.

Because fish shoals tend to aggregate at fronts, the excellent fishing grounds are formed there. This phenomenon is known as Kitahara's law (KITAHARA, 1913). Enhanced productivity of the accumulated plankton communities at fronts has been considered as the primary cause of this phenomenon and whole area of the Polar Frontal Zone has been generally considered as productive fishing ground (UDA, 1938; UDA and ISHINO, 1958). On the other hand, it is also reported that productivity and standing crops of plankton are not uniformly high over the Frontal Zone but high at the limited areas such as the Kuroshio Front (YAMAMOTO *et al.*, 1981, 1988). This implies that the plankton community in the background mixed water is not always productive.

We also have found in warm seasons that standing crops of the diatom assemblage inhabiting the mixed water (background assemblage) are small comparing to assemblages formed in other water masses (CHIANG, 1993). In this paper, we report the possible formation mechanism of the background

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Laboratory of Biological Oceanography, Faculty of Agriculture, Tohoku University, Sendai 981, Japan

* Present address: College of Fisheries Science, National Taiwan Ocean University, 2 Pei-Ning Road, Keelung 20224 Taiwan, R.O.C.

assemblage in winter. Detail of summer feature will be given elsewhere.

2. Materials and Methods

Samplings and Analyses

Samples to determine standing crops and species composition of the phytoplankton assemblages were collected on the Cruise WK-91-1 of R/V Wakataka Maru in 23-26 January, 1991 (Fig. 1). A CTD-RMS was employed to record temperature and salinity profiles and to collect the water samples from 9-13 layers down to 200 m at eight stations, which were occupied at 10 mile intervals. Each samples was offered to phytoplankton examination and nutrient determination. A 500 ml subsample was preserved by adding 25 ml of neutralized formalin (37% conc.) with sodium borate ($Na_2B_2O_7$) and the rest was deep-frozen for later nutrient analyses.

The preserved sample was thoroughly shaken and a 100 ml aliquot was taken and set in a plastic bottle

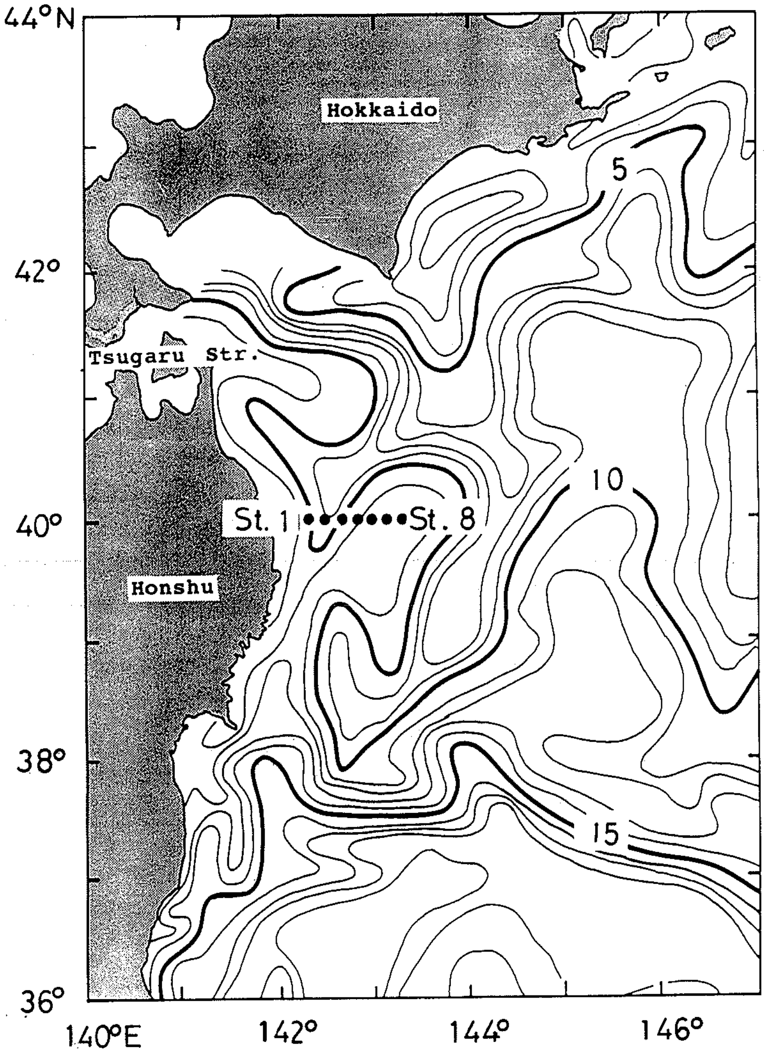

Fig. 1. Sampling stations occupied on the Cruise WK-91-1 of R/V Wakataka Maru to the sea area off the northern Honshu during the period from 23 to 26 January, 1991. Isotherms at the surface are adapted from Japan Fisheries Information Service Center (1991)

for 24 hrs. After removing supernatant water with a glass siphon, concentrated plankton into about 10 ml of water was transferred to a counting chamber and set again for 24 hrs. Identification and cell count of phytoplankters were made under a Nikon-MSDR inverted microscope at 200× or 400×. Of the countings of diatoms, silicoflagellates and dinoflagellates, the results on diatoms are used in the following discussion. Determination of nutrient concentration such as dissolved silica, phosphate, nitrite plus nitrate and ammonia by the methods described in STRICKLAND and PARSONS (1972) was made by and the data were provided by the Tohoku National Fisheries Research Institute.

Data Processing

Principal component analyses (PCAs) and cluster analyses (PIELOU, 1984) of the results obtained were made by using the Statistical Analysis System (S.A.S.). PCAs were done separately for an oceanographic data set (OD) and a diatom data set to see the relationship between diatom assemblages and water types in distribution. The diatom data set was processed in two ways. The first, diatom species were grouped into 14 types according to their distributional nature reported in literature (KOKUBO, 1960; MARUMO *et al.*, 1966; YAMAJI, 1984). That is, cold oceanic centric diatoms (COC), warm oceanic centric diatoms (WOC) and so on (see Fig. 4). The second, 13 species which occurred in more than 50% of samples were selected for PCA. These grouping and selection were necessary to handle many identified species up to 160 species including summer species (CHIANG, 1993). In the following section, we describe the first as distributional characteristics (DC) and the second as dominant species (DS).

The first principal component PC_1 (X axis) and the second principal component PC_2 (Y axis) in the above mentioned three PCAs (OD, DC, DS) were used to identify subgroups by average linkage clustering method (Euclidean distance=1.0); the water types were defined by OD and the diatom assemblages by DC and DS.

3. Results

Hydrography

Sea surface temperature in the sampling area for January, 1991, was reported by the Japan Fisheries Information Service Center (1991) (Fig. 1). It can be roughly seen that the Oyashio Current north of 10℃ isotherm and the Tsugaru Warm Current west of 9℃ met in the present sampling area and the Kuroshio Current flowed along the isotherms of 16-18℃. The rest area was occupied by the mixed water.

Vertical profiles of temperature and salinity were nearly uniform except below 100 m depth around St. 6 (Fig. 2). By the method of T-S analysis described by HANAWA and MITSUDERA (1987) this water below 100 m is identified as Oyashio Water System (<7℃, <33.7), and the rest is as Tsugaru Warm Current Water System (>5℃, >33.7). In this paper, because water types are defined by PCA-OD and the results of PCA-OD are not always identical with those of T-S analysis, the term "water type" is used for the results of PCA-OD separately from the term "water system" defined by HANAWA and MITSUDERA (1987).

The result of PCA-OD based on the data on temperature, salinity, dissolved silica, phosphate, nitrite plus nitrate and ammonia is summarized in Table 1. PC_1 explains 63.84% of the total variance and shows positive correlation with nitrate+nitrite, silica and phosphate, and negative correlation with temperature. PC_2 accounts for 17.72% and positively correlates with ammonia.

On the scatter diagram of PC_2 on PC_1 four clusters are shown (Fig. 3) and the results are given for each sampling depth in Table 4 (Column OD). Three well-defined water types can be finally recognized: surface water (cluster A), mixed water (clusters B, C) and Oyashio water (cluster D) in order of PC_1 values from smaller to larger (Fig. 3). In the vertical plane, these three water types are stratified in this order (Fig. 7). The Oyashio water is detected in the depths as indicated by T-S analysis.

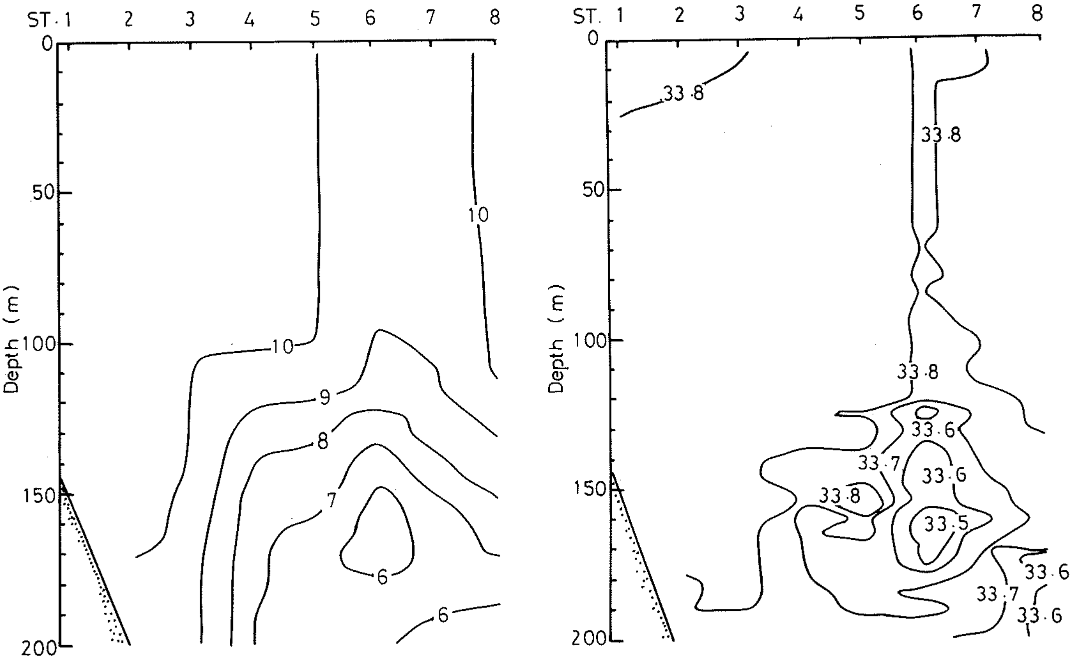

Fig. 2. Distributions of temperature (left) and salinity (right) in vertical section along the line from St. 1 near Honshu to offshore St. 8 observed with a CTD in January, 1991

Table 1. Oceanographic data used as variables for the PCA-OD and their eigenvectors of PC_1 and PC_2. Percentage of variance explained is indicated below each of PC_1 and PC_2.

Variables	PC_1 63.84%	PC_2 17.72%
Temperature	−0.479	0.048
Salinity	−0.326	0.338
Dissolved silica	0.472	0.083
Phosphate	0.449	0.114
Nitrate+nitrite	0.489	0.031
Ammonia	0.030	0.929

Phytoplankton populations

Diatom standing crops in cell number were low and relatively homogeneous in distribution being $2.0\text{-}5.0 \times 10^3$ cells/l (Fig. 6). This feature seems to be common in most subarctic sea areas when water is vertically mixed and lower light flux limits active phytoplankton growth.

In PCA-DC, the first and second principal components account for 39.82% of the total variance (Table 2). PC_1 positively correlates with cold neritic centric diatoms and warm neritic pennate diatoms, and PC_2 positively correlates with neritic cosmopolitan centric diatoms and negatively correlates with warm neritic centric diatoms. In PCA-DS, PC_1 and PC_2 account for 36.46% of the variance; PC_1 is influenced by *Nitzschia* sp. and *Navicula* sp. and PC_2 by *Thalassionema nitzschioides* and *Corethron criophilum* (Table 3).

Figs. 4 and 5 illustrate the scatter of PC_2 on PC_1 in DC and DS respectively, and four clusters could be identified in both analyses. These results are summarized in the columns of DC and DS in Table 4. Among the four clusters, clusters A and B are similar to each other as indicated by their closer positions in Figs. 4 and 5, while clusters C and D are clearly separated from others. Since cluster B could be recognized as an intermediate one between cluster A and clusters C and D rather than an independent cluster, assignment of individual points in cluster B was determined by their position in the

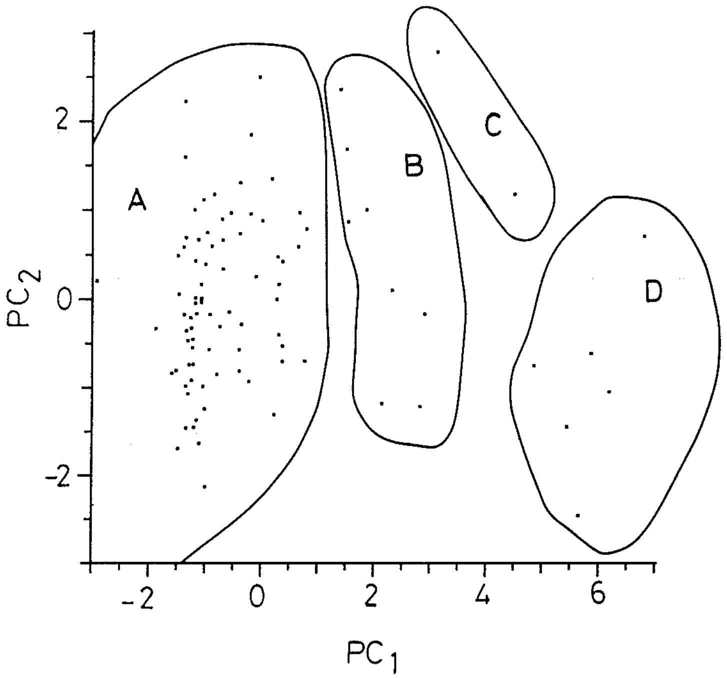

Fig. 3. Plot of PC_2 on PC_1 in PCA using oceanographic data (OD) (See also Table 1)

Table 2. Eleven types of diatoms grouped by their distributional characteristics used as variables for the PCA-DC and their eigenvectors of PC_1 and PC_2. Percentage of variance explained is indicated below each of PC_1 and PC_2. For abbreviations of variables see Fig. 4

Variables	PC_1 22.21%	PC_2 17.61%
COC	0.269	0.338
CNC	0.407	−0.292
WOC	0.273	0.089
WNC	0.212	−0.488
OCC	0.094	0.260
NCC	0.025	0.466
OC	0.332	−0.025
COP	0.321	0.267
WNP	0.457	−0.013
NCP	0.307	0.330
OP	0.343	−0.298

Table 3. Thirteen dominant diatom species, which occurred more than 50% of samples, used as variables for the PCA-DS and their eigenvectors of PC_1 and PC_2. Percentage of variance explained is indicated below each of PC_1 and PC_2.

Variables	PC_1 20.93%	PC_2 15.53%
Corethron criophilum	−0.039	0.432
Denticulopsis marina	0.313	0.359
Navicula sp.	0.431	−0.138
Nitzschia closterium	0.387	−0.275
Nitzschia seriata	0.306	−0.145
Nitzschia sp.	0.423	0.042
Paralia sulcata	0.159	0.169
Pleurosigma elongatum	0.086	0.246
Pseudoeunotia doliolus	0.261	0.280
Thalassionema nitzschioides	0.021	0.514
Thalassiosira angstii	−0.080	−0.023
Thalassiosira oestrupii	0.387	−0.230
Thalassiosira sp.	0.186	0.284

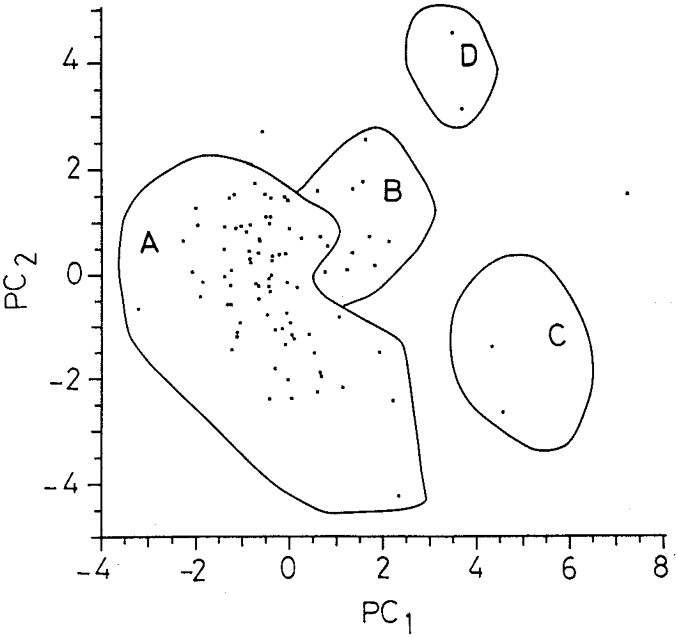

Fig. 4. Plot of PC_2 on PC_1 in PCA using 14 types of diatoms grouped by their distributional characteristics, i.e., cold oceanic centric diatoms (COC), cold neritic centric diatoms (CNC), warm oceanic centric diatoms (WOC), warm neritic centric diatoms (WNC), oceanic cosmopolitan centric diatoms (OCC), neritic cosmopolitan centric diatoms (NCC), other centric diatoms (OC), cold oceanic pennate diatoms (COP), cold neritic pennate diatoms (CNP), warm oceanic pennate diatoms (WOP), warm neritic pennate diatoms (WNP), oceanic cosmopolitan pennate diatoms (OCP), neritic cosmopolitan pennate diatoms (NCP), other pennate diatoms (OP) (See also Table 2). Four points out of envelopes A-D are marked # in Table 4, two of which are far out of this diagram.

scatter diagram (Figs. 4 and 5). Compiling the results of DC and DS, four diatom assemblages are finally defined as described below (Table 5).

(1) Warm water assemblage: The assemblage defined by cluster C and a part of clusters A and B. Combination of clusters in DC and DS are cluster C in DC+cluster C in DS (C-C), cluster A in DC+ cluster B in DS (A-B), and cluster B in DC+cluster A in DS (B-A) in this assemblage. C-C were found only at 0 m and 95 m at St. 1 (Table 4) where neritic species predominated. A-B and B-A scattered among A-A in the water column at Sts. 1-4 could be regarded as a transition from C-C to A-A (cf. Figs. 4 and 5). The dominant species forming this assemblage were *Pseudoeunotia doliolus, Nitzschia closterium* and *Thalassionema nitzschioides*. The species having a peak of their distribution in this assemblage were *Chaetoceros curvisetum, Eucampia zodiacus, P. doliolus* and *Thalassiosira oestrupii*. All of these dominant and peak-forming species have been reported as warm neritic or neritic cosmopolitan species (Table 5).

(2) Oyashio assemblage: The assemblage clearly defined by D-D and found at 150 m at St. 6 (Table 4). D-A identified at 100 m and 200 m at the same station could be considered as a transition from A-A to D-D. The dominant species were *Corethron criophilum, Denticulopsis marina* and *T. nitzschioides*, and the peak-forming species were *C. criophilum* and *T. nitzschioides* (Table 5). These species indicate the relatively oceanic cold nature of this assemblage.

(3) Mixed assemblage: The assemblage defined by #-D, D-#, and B-A found at Sts. 7 and 8. The sign "#" indicates the samples which are different from all others in species composition or indepen-

Table 4. Distribution of the clusters separated by the PCAs based on the oceanographic data (OD), the abundance of distributional groups (DC) and dominant diatoms (DS) as variables for the Cruise WK-91-1 of R/V Wakataka Maru.

ST & Dep	OD	DC	DS	ST & Dep	OD	DC	DS	ST & Dep	OD	DC	DS	ST & Dep	OD	DC	DS	ST & Dep	OD	DC	DS	ST & Dep	OD	DC	DS	ST & Dep	OD	DC	DS	ST & Dep	OD	DC	DS
St. 1				St. 2				St. 3				St. 4				St. 5				St. 6				St. 7				St. 8			
0	A	C	C	0	A	A	A	0	A	A	B	0	A	B	A	10	A	A	A	0	A	A	A	0	A	A	A	0	A	#	D
5	A	A	A	5	A	A	A	5	A	A	A	5	A	A	B	15	A	A	A	5	A	A	A	5	A	A	A	5	A	A	A
15	A	B	A	10	A	A	B	10	A	A	A	10	A	A	A	20	A	A	A	10	A	A	A	10	A	A	A	10	A	A	A
20	A	A	B	15	A	A	A	15	A	A	A	15	A	A	A	25	A	A	A	15	A	A	A	15	A	A	A	15	A	A	A
25	A	A	B	20	A	A	A	20	A	A	A	20	A	A	A	30	A	A	A	25	A	A	A	20	A	A	A	20	A	A	A
35	A	#	B	25	A	A	B	25	A	A	A	25	A	A	A	40	A	A	A	30	A	A	A	25	A	B	A	25	A	A	A
45	A	A	B	35	A	A	B	35	A	A	A	30	A	A	A	50	A	#	#	40	A	A	A	30	A	A	A	30	A	B	A
70	A	A	B	45	A	A	B	45	A	A	A	40	A	A	A	75	A	A	A	50	B	A	A	40	A	A	A	40	A	A	A
95	—	C	C	70	A	A	B	70	A	A	A	50	A	A	A	100	—	A	A	75	B	A	A	50	A	A	A	50	A	A	A
				95	A	A	A	95	A	A	A	75	A	A	A	200	C	A	A	100	B	B	A	75	B	A	A	75	A	B	A
				145	A	A	B	145	A	A	A	100	A	A	A					150	D	D	D	100	C	A	A	100	A	B	A
				195	B	B	A	195	B	A	A	150	B	A	A					200	D	B	A	150	D	A	A	150	B	B	A
												200	D	#	A									200	D	A	A	200	D	D	#

'—': Sample were not collected from the layer.
'#': The samples which are different from all others in species composition.

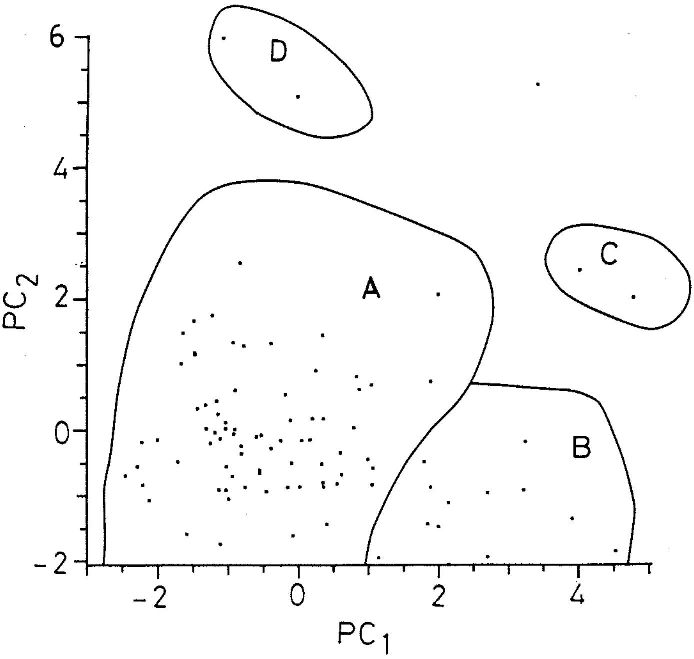

Fig. 5. Plot of PC_2 on PC_1 in PCA using 13 dominant diatom species which occurred in more than 50% of samples (See also Table 3). Two points out of envelops A-D are marked # in Table 4, one of which is far out of this diagram.

Table 5 Distribution and some features of diatom assemblages in winter defined by PCAs in the sea area east of nothern Honshu.

Assemblage	Warm	Oyashio	Mixed	Background
DS	C	D	#,D	A
DC	C	D	#,D	A
Distribution (St. & depth)	St. 1 (0, 15-95) St. 2 (10, 25-70 145-195) St. 3 (0) St. 4 (0-5)	St. 6 (100-200)	St. 7 (25) St. 8 (0, 30, 70-200)	All the rest
Dominant species				
	N. closterium (NC) *P. doliolus* (WN) *T. nitzschioides* (NC)	*C. criophilum* (CO) *D. marina* (CO) *T. nitzschioides* (NC)	*D. marina* (CO) *P. doliolus* (WN) *N. closterium* (NC) *T. nitzschioides* (NC)	*D. marina* (CO) *N. closterium* (NC) *P. doliolus* (WN) *T. nitzschioides* (NC)
Peak-forming species				
	C. curvisetum (WN) *E. zodiacus* (WN) *P. doliolus* (WN) *T. oestrukii* (WN)	*C. criophilum* (CO) *T. nitzschioides* (NC)	*C. criophilum* (CO) *P. doliolus* (WN)	*None*

WO: Warm oceanic diatoms, WN: Warm neritic diatoms, CO: Cold oceanic diatoms, CN: Cold neritic diatoms, NC: Neritic cosmopolitan diatoms.

dent points out of four envelopes (clusters) in Figs. 4 and 5. The dominant species were *D. marina, P. doliolus, N. closterium* and *T. nitzschioides*, and peak-forming species were *C. criophilum* and *P. doliolus* (Table 5). These species indicate that this assemblage was formed by mixing of warm neritic species such as *P. doliolus* into the Oyashio assemblage.

(4) Background assemblage: The assemblage defined by A-A. This assemblage was small in cell number and heterogeneous in distributional nature but was very widely distributed over entire section, being found at all stations. The dominant species were cold oceanic *D. marina*, warm neritic *P. doliolus* and neritic cosmopolitan *N. closterium* and *T. nitzschioides*. Since abundance of this assemblage was small, no peak-forming species was there.

4. Discussion

The distribution of four diatom assemblages and the stratification of three water types are illustrated in Fig. 7. It is clear that distribution patterns of water types and assemblages were not consistent

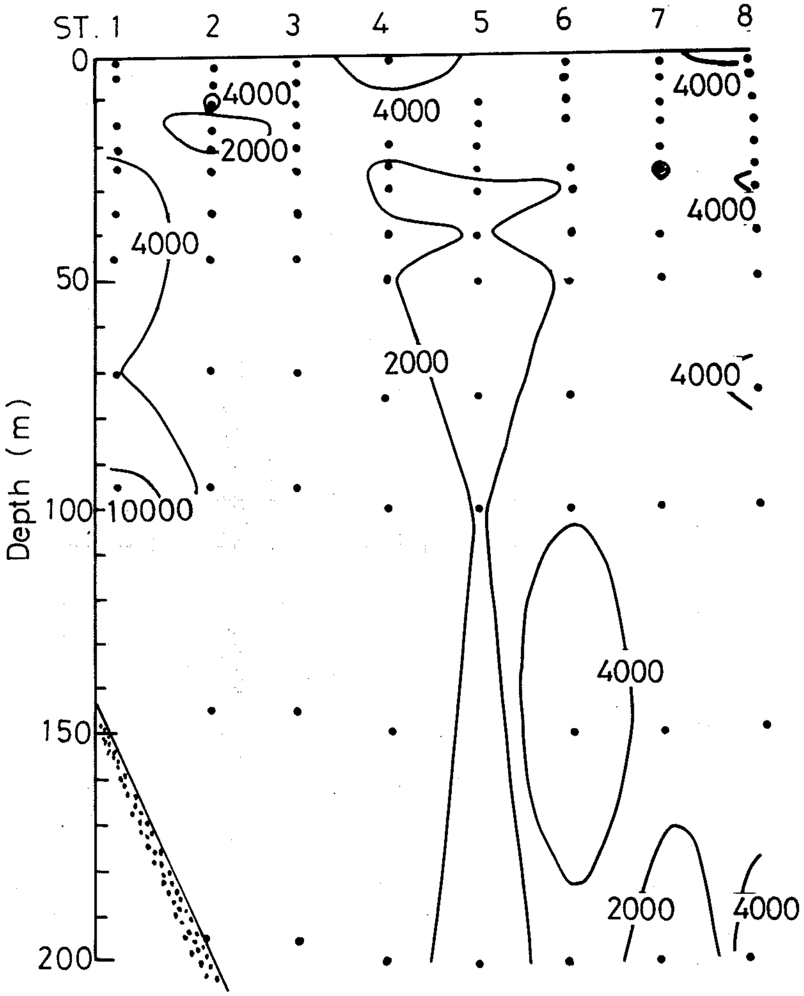

Fig. 6. Distribution of diatoms in cell number (cells/l) in vertical section along the line from St. 1 to St. 8 observed in January, 1991

with each other. The warm water assemblage and the mixed assemblage were distributed in mosaic manner among the background assemblage, while water types were simply layered. The warm water assemblage scattered in the coastal side (Sts. 1-4), and the mixed assemblage in the oceanic side (Sts. 7-8).

Plankters which can be used to trace particular water masses transported by the ocean current are the indicator species (Russel, 1935; Hada, 1957; Hart and Currie, 1960; Schwenke, 1971; Taniguchi, 1983; Fryxell *et al.*, 1985; Kaczmarska *et al.*, 1986). In this work, *Chaetoceros curvisetum*, *Eucampia zodiacus* and *Thalassiosira oestrupii* forming the warm water assemblage at Sts. 1-4 are examples of the indicators of the Tsugaru Warm Current. The warm water assemblage as a group of several species is also an effective tracer of the Tsugaru Warm Current.

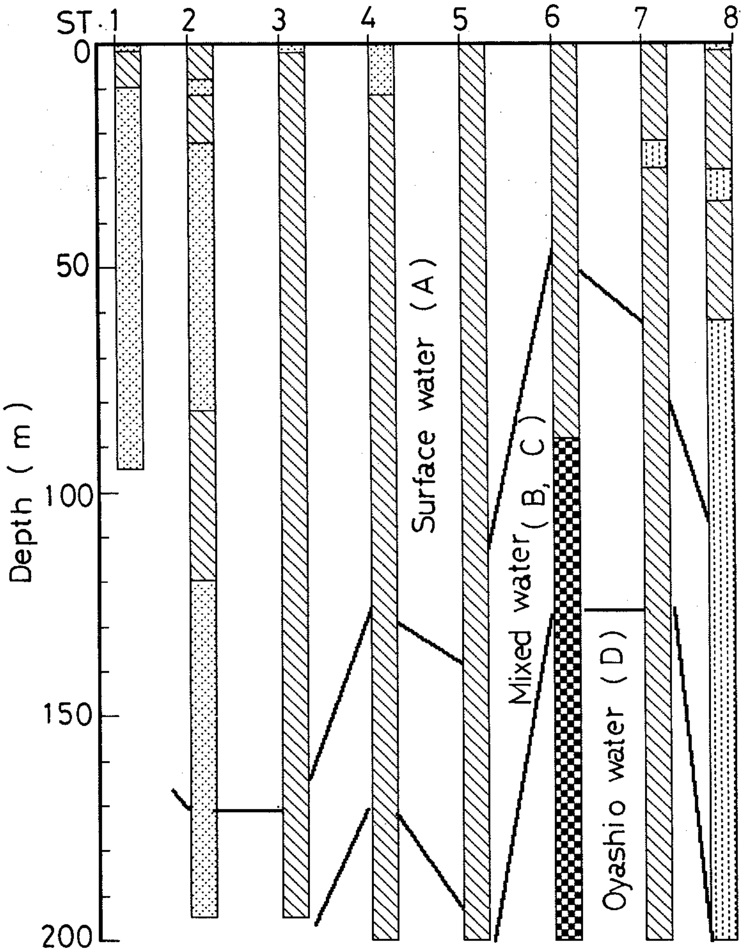

Fig. 7. Distributions of the water types and the diatom assemblages defined by PCAs (See also Table 5). Stratification of the water types is indicated by their own names, and the assemblages are indicated in vertical columns by the following marks:
▧: Background assemblage
░: Warm water assemblage
▩: Oyashio assemblage
▦: Mixed assemblage

On the other hand, the Oyashio assemblage, mixed assemblage and background assemblage are similar in species composition which were mainly composed of cold and cosmopolitan species. Therefore, indicator capability of these assemblages are not definite. This might result in discordance in distribution of the Oyashio water type and the Oyashio assemblage: the latter was limited in deeper layers at St. 6, while the Oyashio water type was seen at Sts. 4, 6 and 7 (Fig. 7). These facts imply that the Oyashio water type can not strictly be indicated by diatom species or assemblage in winter, since no species actively grow in the Oyashio in winter.

The most widely distributed background assemblage was the mixture of the cold Oyashio species and neritic species, mostly cosmopolites, and small in standing crops. The same nature was observed for the background assemblage in warm seasons, although individual species forming the assemblage were not always identical by the seasons and geographical positions (CHIANG, 1993).

SANO (1966) also reported that the diatom assemblage in the same sea aea in winter was homogeneously distributed and its standing crops were low, being about 2,000-4,000 cells/l. The dominant species were *T. nitzschioides, Thalassiosira decipiens* and *Paralia sulcata* (as *Melosira sulcata*): again mixture of cold Oyashio species and neritic cosmopolites. These indicate that the background assemblage in the Polar Frontal Zone is formed by tolerant species which survive winter convection period following the surface cooling and diminution of solar radiation. These species may not essentially be productive under warmed condition and/or thermally stratified condition in offshore areas where no nutrient supply from coastal water occurs. Under such condition, different assemblages might be formed in the surface layer above the background assemblage in the subsurface layer and the assemblages differentiate into the twin-layer structure as reported by GOULD *et al.* (1986) and VENRICK (1988, 1992).

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北太平洋の極前線海域に広く分布する珪藻群集の形成過程

蒋国平*・谷口旭

本論文では，本州北部東方沖の北太平洋極前線域に分布している冬期の珪藻プランクトン群集と水塊の分布の関係について調査した。主成分分析によって，三つの水塊と四つの珪藻群集が識別された。しかし，水塊と珪藻群集の分布は必ずしも一致しないことがわかった。珪藻の暖水群集は，津軽暖流の影響を受けた海域を良く指標したが，他の冷水性格を帯びた群集は親潮水塊のよい指標にはなっていなかった。その原因は，冬期には親潮域では珪藻群集が活発に生長しないためと推定される。この海域において最も広く分布し，冷水外洋性種および沿岸コスモポリタン種からなる背景群集は，冬の鉛直混合によって形成されると考えられる。すなわち，その混合過程で，環境抵抗力の強い少数の種が生残し，背景群集が形成されるものと推定される。

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* 東北大学農学部生物海洋学講座
〒981 仙台市青葉区堤通雨宮町 1-1
現住所：国立台湾海洋大学水産学院
台湾省基隆市 20224 北寧路 2 號