

Interdecadal change in the upper water column environment and spring diatom community structure in the Japan Sea: an early summer hypothesis

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ABSTRACT: Diatom community structure in the offshore Tsushima Current area of the Japan Sea was studied from 1972 to 1999 in relation to temporal variability of the upper water environment. We observed a distinct change in the community structure in spring during the 1980s, the period after the 1976/77 climate regime shift which has been reported to occur in the vast areas of the North Pacific. Chlorophyll *a* (chl *a*) concentration and chl *a* per cell were markedly low, and summer species including *Pseudonitzschia* spp. dominated the diatom community in spring during the 1980s. Mixed layer phosphate concentrations during the 1980s were lower in spring compared to the 1970s and 1990s, suggesting that nutrient depletion to levels limiting diatom growth might occur early. This change seemed subsequently to cause a shift in the dominant diatom species from those adapted to eutrophic conditions to those adapted to oligotrophic conditions. Density profiles between the surface and 300 m showed the thickness of the surface Tsushima Current water and the cold subsurface water decreasing and increasing, respectively, from the late 1970s to the late 1980s. In addition, spring solar radiation increased during the 1980s. These conditions indicate intensified stratification of the upper water column. Increases in the phosphate gradient between the surface and subsurface layers suggested that the intensified stratification reduced nutrient supply to the surface and may be responsible for early formation of the summer-like oligotrophic conditions. Based on these results, we propose the 'early summer hypothesis' as the cause of the apparent decline of the spring phytoplankton biomass in the Japan Sea during the 1980s.

KEY WORDS: Interdecadal change · Diatom · Japan Sea

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INTRODUCTION

Since the climate regime shift was reported to occur in the North Pacific in the late 1970s with an intensification of the Aleutian Low Pressure (ALP) system (Trenberth 1990, Hanawa 1992, Miller et al. 1994, Trenberth & Hurrell 1994, 1995), there has been accumulating evidence that the lower trophic level marine ecosystem changed corresponding to the large-scale climatic events. Zooplankton biomass doubled in the

Gulf of Alaska (Brodeur & Ware 1992, McFarlane & Bermish 1992, Brodeur et al. 1996) while it declined in the California Current (Roemmich & McGowan 1995) after the late 1970s. Summer chlorophyll *a* (chl *a*) markedly increased in water north of the Hawaii Islands after the mid-1970s (Vernrick et al. 1987). In the central and western subarctic North Pacific (Sugimoto & Tadokoro 1998) and the Oyashio water (Tomosada & Odate 1995) summer zooplankton biomass decreased after the regime shift. Positive correlations were found between winter wind intensity and summer zooplankton biomass in the Gulf of Alaska (Brodeur & Ware

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1992) and summer chl *a* north of the Hawaii Islands (Venrick et al. 1987). Positive and negative correlations were also reported between zooplankton biomass and water temperature in the Oyashio water (Tomosada & Odate 1995) and the California Current (Roemmich & McGowan 1995), respectively.

However, such correlations did not always reflect causes and effects, nor explain the detailed processes and mechanisms of the observed change in the ecosystem. Moreover, since the majority of studies on interdecadal scale interactions between climate and ecosystems have been conducted using total quantity-based data such as total plankton biomass and/or chl *a*, ecological consequences of the regime shift, in terms of food web structure and function of the biological carbon pump, remain unknown. What determines the downward particulate organic carbon flux in a marine food web is the structure of the lower trophic level, such as size and species composition of plankton communities (Boyd & Newton 1995, 1999). There is now increasing recognition of the importance of taxonomic or functional breakdowns of plankton community structure for studies of ecosystem change on a decadal to interdecadal scale, rather than use of the conventional, total biomass-based approach (e.g. Venrick 1993).

In contrast to the eastern North Pacific, where many process studies on long-term ecosystem change have been conducted, less information is available for the western North Pacific region, particularly for the Japan Sea. However, since recent studies revealed a warming trend over a period of several decades of the Japan Sea Proper Water (JSPW), which lies below 500 m (Minami et al. 1999a,b), there has been increasing scientific attention to large-scale interactions between climate and the oceanic environment, and biological feedback to the observed changes in the Japan Sea. The Japan Sea has characteristics of a great ocean despite its small size and semi-closed geographical feature: its average depth is over 1000 m and it contains large-scale oceanic gyres driven by wind stress and thermohaline circulation (Takematsu et al. 1999). We may expect to gain good insight into the mechanisms of climate-ecosystem interaction in the widespread North Pacific by studying this miniature ocean.

The Maizuru Marine Observatory of the Japan Meteorological Agency has been conducting routine oceanographic/biological observations along the PM line (Fig. 1) across the central Japan Sea 4 times a year from 1972 to the present. They have found that interdecadal variability of PM line zooplankton biomass (wet weight) was positively correlated with that of the 0 to 150 m mean water temperature (Minami et al. 1999b). Both variables were low during the 1980s after the North Pacific climate regime shift. The PM line water column chl *a* also decreased during the 1980s

(Imai & Ebara 1989, Maizuru Marine Observatory 1999). Studying the distributional patterns of key diatom species for cold and warm waters, Kubo & Ebara (1992) pointed out that the occasional appearance of cold water species during the 1980s corresponded well to the low temperature period. However, these links are insufficient to explain the details of the process and the ecological consequence of the observed change.

By analyzing the PM line diatom community structure, we attempt here to reveal how interdecadal change in the physical and chemical environment within an upper water column could alter the lower trophic level marine ecosystem in the Japan Sea. Possible consequences of the observed diatom community change in terms of food web structure and biological carbon pump are further discussed.

MATERIALS AND METHODS

PM line data sets with sampling and measurement information. The PM line observations were conducted from aboard the RV 'Seifu-Marui II' from 1972 to 1992 and RV 'Seifu-Marui III' from 1993 to 1999 at up to 11 stations (Fig. 1). The cruise dates were late Janu-

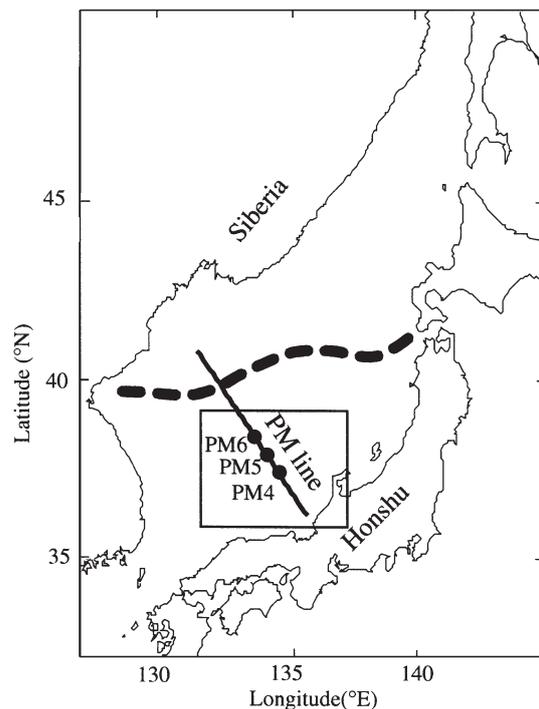


Fig. 1. Location of the PM observation line and stations. Dotted line indicates the approximate location of the polar front. Square indicates the region (36 to 39°N, 132 to 137°E) of which solar radiation data sets were used (data on land are not included)

ary to mid-February in winter, late April to mid-May in spring, mid-July to early August in summer and late September to mid-October in autumn. The locations of the northern stations, PM7 to 11, were changed or the stations abolished during the course of decades, and the hydrographic conditions of the southern most stations, PM1 to 3, may have been affected to a large extent by the coastal environment. Therefore to detect the effect of large-scale dynamics of the oceanic gyre on the local ecosystem, variability at Stns PM4, 5 and 6, which are located south of the polar front within the offshore Tsushima Current area (Minami et al. 1999b; Fig. 1), was investigated in this study. The phytoplankton bloom peaks in this study area twice in April and November (Kim et al. 2000). The autumn PM line observation had been made long before the autumn bloom started when the chl *a* level was quite low. Therefore, we particularly focused on the variability in spring, the most productive season, in conjunction with the environmental/biological succession from the pre-spring bloom (winter) to the post-spring bloom (summer).

From the PM line observation data sets, we used diatom abundance at the surface, and water temperature, salinity, phosphate and chl *a* at the surface, and at 10, 20, 30, 50, 75, 100, 125, 150, 200, 250 and 300 m. As for nutrients, we used only phosphate data since measurements of nitrate and silicate were less frequent. Water density profiles were obtained from temperature and salinity values. The bottom of the mixed layer (MLD) was defined as the depth at which density increased by 0.125 kg m^{-3} from the surface following Levitus (1982), and MLD was estimated by linearly interpolating the density profile. Water column integrated chl *a* and mean phosphate concentration within a mixed layer were estimated by the trapezoidal approximation method.

Water samples for salinity, phosphate and chl *a* analyses were taken by Nansen casts prior to 1988 (Minami et al. 1999). Water temperature and salinity were measured by a reversing thermometer equipped on a Nansen bottle and a salinometer, respectively (Minami et al. 1999b). After 1988, water temperature and salinity were measured by conductivity, temperature depth (CTD) profiler casts and water samples for the other analyses were taken using a Rosette multi-sampler with Niskin bottles mounted on the CTD frame (Minami et al. 1999b). Phosphate was measured following the method of Murphy & Riley (1961), and chl *a* was measured using the fluorometric technique (Yentsch & Menzel 1963, Japan Meteorological Agency 1999).

Water samples for diatom analysis were taken from the surface using a bucket. Five hundred ml of the surface water was transferred into a bottle and fixed with a final solution of 1% neutral formalin. After settling in a tube, 10 ml of sample water was centrifuged at

2500 rpm for 15 min. Diatom species, in a concentrated 0.5 or 1.0 ml sample, were identified and each species counted with an optical microscope. A Sedgwick-Rafter chamber was used to estimate numerical abundance (cell l^{-1}) at each sampling station (Japan Meteorological Agency 1999). Total cell number was counted for each sample and identification of diatom species was done from 1973 until 1998 but not after 1999.

Analysis of diatom community structure. To reveal the interaction between the diatom distribution pattern and environmental effects in an objective way (Day et al. 1971), we analyzed the variability of the whole community instead of focusing on a few indicator species for distinctive water masses such as cold, warm and coastal ones. For each season, species accounting for more than 4% of the total cell numbers for any year and location, or appearing at more than 1/3 of the stations in any year, were defined as dominant species. As for the spring diatom community, a dissimilarity matrix between stations was constructed using the Bray-Curtis Index (Bray & Curtis 1957) based on differences in the percentage composition of the dominant species. The Bray-Curtis Index is a powerful tool for analysis of ecological data including a large portion of '0' values because it is not biased by the 'joint absences' effect (Field et al. 1982). Based on the matrix, cluster analysis coupled with an unweighted pair group method using arithmetic mean (UP-GMA) was applied to classify the stations into several groups, each of which had a distinctive community structure and spatio-temporal distribution pattern.

Solar radiation. From 1972 to 1996, $1^\circ \times 1^\circ$ gridded solar radiation data in the region of $36^\circ 00'$ to $39^\circ 00'$ N and $132^\circ 00'$ to $137^\circ 00'$ E were extracted from North Pacific surface heat flux data sets (Japan Meteorological Agency, Tokyo; Fig. 1). The data were collected by volunteer ships and processed as a monthly composite for each grid. We calculated first the monthly mean values of the region for each year, and obtained seasonal means by averaging December to January means for winter and March to May means for spring (note: values of December were of the previous year). The number of data points for each month of the year is larger than 10 (except in December 1976) and 85% were more than 30, and were therefore considered sufficient to represent the monthly values.

RESULTS

Seasonal and decadal scale variability of diatom abundance and surface chl *a*

Cell number of total diatoms varied spatio-temporally between 76 and 6590 cell l^{-1} (mean \pm SD: 1309 ± 1120) in

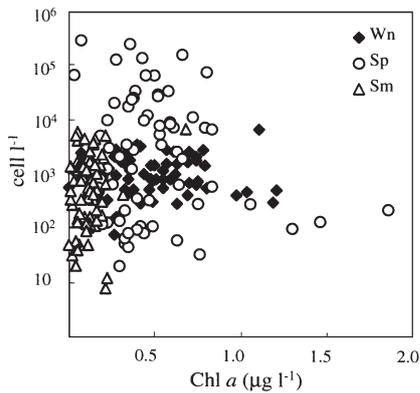


Fig. 2. Relationship between total diatom cell number (cell l^{-1}) and surface chl a ($\mu\text{g l}^{-1}$) for winter (\blacklozenge), spring (\circ) and summer (\triangle) at all stations from 1973 to 1999

winter, 20 and 287 660 cell l^{-1} ($22\,571 \pm 53\,144$) in spring, and 8 and 6536 cell l^{-1} (1230 ± 1496) in summer. Surface chl a varied between 0.13 and 0.93 $\mu\text{g l}^{-1}$ (mean \pm SD: 0.51 ± 0.18) in winter, 0.17 and 1.36 $\mu\text{g l}^{-1}$ (0.52 ± 0.32) in spring, and 0.01 and 0.37 $\mu\text{g l}^{-1}$ (0.11 ± 0.08) in summer. The mean cell numbers were similar in winter and sum-

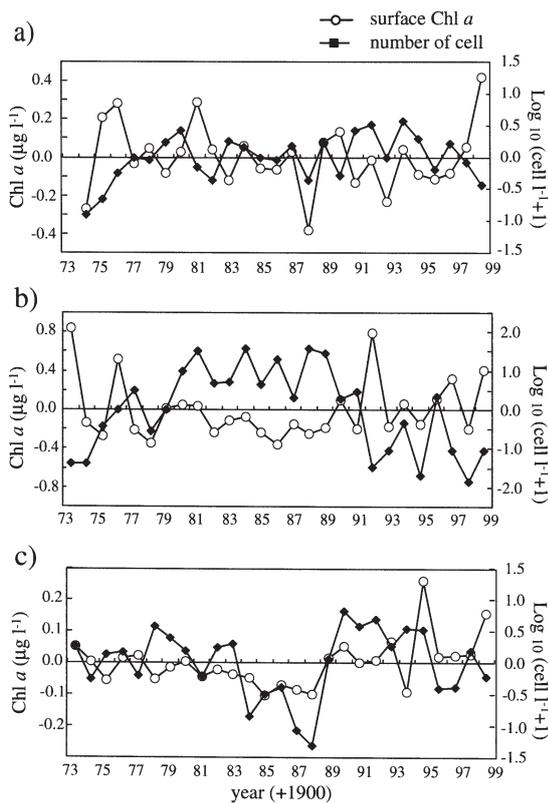


Fig. 3. Time series of anomalies for surface chl a ($\mu\text{g l}^{-1}$) and total diatom cell number ($\log_{10}(\text{cell l}^{-1} + 1)$) between 1973 and 1999 for (a) winter, (b) spring and (c) summer. Each data point of a year is the mean value at PM4, 5 and 6

mer while mean chl a was much higher in the former, giving a higher chl a per cell in winter (Fig. 2). Although the mean values for both cell number and chl a were high in spring, the variances were greatest (Fig. 2).

Decadal scale change in the relationship between chl a and diatom cell number was most notable in spring, when the cell number markedly increased while surface chl a remained low during the 1980s (Fig. 3b). This condition resulted in a marked decrease in chl a per cell during the period, suggesting that a considerable change in quality and/or physiological states might occur in the spring diatom community. In summer, on the other hand, chl a and cell number varied in a similar manner in terms of decadal scale: decrease in the 1980s and increase in the 1990s (Fig. 3c). No decadal scale variability was evident in winter (Fig. 3a).

Diatom community structure

A total of 26, 30 and 26 dominant species were identified for winter, spring and summer, respectively (Table 1). Synonymy of the species name on the original data set was corrected following Tomas (1996). As for the spring diatom community, 7 groups with distinctive species compositions were identified at the 93% dissimilarity level by cluster analysis (Fig. 4). The cutting score of dissimilarity level was quite high, indicating that species composition differed largely between cluster groups as well as between individual stations in each cluster group. Major species (more than 1% of the total composition) for each group are listed in Table 2, among which species dominating not only in spring but also in summer or winter (Table 1) were defined as summer species or winter species, respectively. Groups 1, 2 and 3 consisting of summer species in a large portion (53.7, 53.5 and 58.7%, respectively) were defined as the 'summer-type' communities. Groups 4, 5 and 6 included more winter species (25.8, 14.4 and 33.7%, respectively) and were defined as the 'winter-type' communities. Group 1, the largest group dominated by *Bacteriastrium varians* and *Pseudonitzschia* spp., occurred at almost all stations during the 1980s (Fig. 5). Both of the other 2 summer-type communities appeared after 1992 (1992, 1996 and 1997). On the other hand, winter-type communities were distributed in the mid-1970s and after 1989: Group 4 and Group 6 appeared exclusively in the 1970s and 1990s, respectively (Fig. 5).

Interannual and decadal scale variability of the upper water column environment

To investigate how change in the upper water column environment could affect the phytoplankton pro-

Table 1. List of dominant species for winter, spring and summer. Season(s) that each species dominated was (were) indicated by asterisks. Species accounting for more than 4% of the total abundance on any occasion or appearing at more than 1/3 of stations in any year were defined as dominant species

Species	Season dominated		
	Winter	Spring	Summer
<i>Asterionellopsis glacialis</i>		*	*
<i>Bacteriastrium delicatulum</i>			*
<i>B. furcatum</i>		*	
<i>Chaetoceros affinis</i>	*	*	
<i>C. aequatorialis</i>			*
<i>C. atlanticus</i>	*	*	*
<i>C. coarctatus</i>	*	*	
<i>C. compressus</i>	*	*	*
<i>C. concavicornis</i>	*		
<i>C. convolutus</i>	*		
<i>C. curvisetus</i>		*	*
<i>C. debilis</i>	*		*
<i>C. decipiens</i>			*
<i>C. didymus</i>		*	
<i>C. diversus</i>		*	*
<i>C. peruvianus</i>	*		
<i>C. radicans</i>	*	*	
<i>C. simplex</i>			*
<i>C. socialis</i>			*
<i>C. tetrastichon</i>			*
<i>C. tortissimus</i>			*
<i>Climacodium biconcavum</i>	*		
<i>C. frauenfeldianum</i>	*		
<i>Corethron</i> spp.			*
<i>Coscinodiscus wailesii</i>		*	
<i>Cylindrotheca closterium</i>	*		
<i>Dactyliosolen fragilissimus</i>	*	*	
<i>Detonula pumila</i>		*	
<i>Eucampia zodiacus</i>		*	*
<i>Guinardia flaccida</i>		*	*
<i>G. striata</i>			*
<i>Haslea wawrikan</i>			*
<i>Hemiaulus hauckii</i>	*		
<i>H. membranaceus</i>		*	
<i>Lauderia annulata</i>	*		*
<i>Leptocylindrus danicus</i>	*		
<i>L. mediterraneus</i>	*	*	
<i>L. minimus</i>			
<i>Meuniera membranacea</i>	*		
<i>Neodenticula seminiae</i>	*	*	
<i>Nitzschia longissima</i>	*	*	
<i>Proboscia alata</i>	*	*	
<i>Pseudonitzschia</i> spp.		*	
<i>Pseudosolenia calcar avis</i>	*	*	
<i>Rhizosolenia castracanei</i>	*		
<i>R. hebetata</i>	*		
<i>R. setigera</i>		*	
<i>R. styliformis</i>			
<i>Skeletonema costatum</i>			
<i>Thalassionema nitzschioides</i>			
<i>T. frauenfeldii</i>			
<i>Thalassiosira angulata</i>			
<i>T. gravida</i>			
<i>T. rotula</i>			

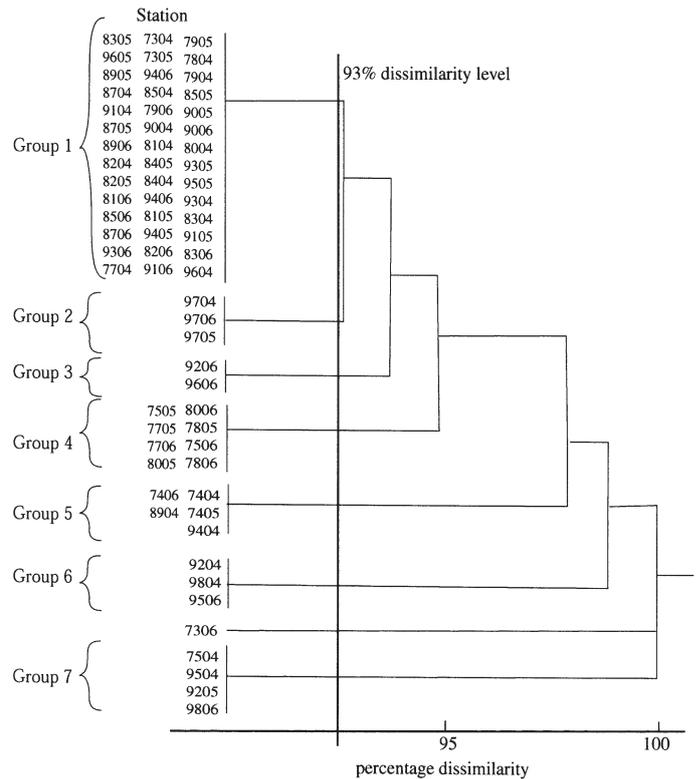


Fig. 4. Dendrogram derived by cluster analysis on the spring diatom community. Stations were classified into 7 groups based on the difference in species composition at the 93% dissimilarity level. Left 2 digits of the station name indicate the year and the right 2, are the station: '8304' means 'Stn PM4 in 1983'

ductivity from winter to spring, temporal variability of the mean MLD, mean phosphate concentration within the mixed layer (ML phosphate) and water column integrated chl *a* were compared. The mean MLD varied interannually between 48 and 196 m (mean \pm STD: 104 ± 36) in winter and 5 and 35 m (mean \pm STD: 19 ± 7) in spring. The mean phosphate concentration within the mixed layer (ML phosphate) varied between 0.29 and 0.58 μM (mean \pm STD: 0.41 ± 0.06) in winter, and 0.02 and 0.28 μM (0.09 ± 0.06) in spring. Water column integrated chl *a* varied between 8.17 and 125.32 mg m^{-2} (mean \pm STD: 52.09 ± 21.40) in winter and 4.76 and 172.38 mg m^{-2} (57.4 ± 32.4) in spring.

Winter chl *a* was positively correlated to winter MLD (Spearman rank correlation test, $r_s = 0.339$, $N = 26$, $p < 0.05$; Fig. 6b). In addition, spring chl *a* was positively correlated to spring ML phosphate ($r_s = 0.427$, $N = 27$, $p < 0.05$; Fig. 6f). No significant correlations were identified between winter ML phosphate and winter MLD ($r_s = 0.078$, $N = 28$; Fig. 6a), winter chl *a* and winter ML phosphate ($r_s = 0.044$, $N = 26$) (Fig. 6c), spring chl *a* and winter ML phosphate ($r_s = 0.008$, $N = 27$; Fig. 6d) or

Table 2. List of major species (>1 % of total abundance) for each diatom community group in spring derived by cluster analysis. Species which dominated not only in spring but also in winter or summer were defined as the winter or summer species. Community type of each group (summer or winter type) was determined by comparing the sum of composition of the summer and winter species

Cluster group	Major spp.	Composition (%)	Abundant in other seasons		Winter spp. (%)	Summer spp. (%)	Community type
			Winter	Summer			
Community type							
Group 1	<i>Bacteriastrum furcatum</i>	30.4		*	1.3	53.7	Summer
	<i>Pseudonitzschia</i> spp.	19.9		*			
	<i>Leptocylindrus danicus</i>	6.8		*			
	<i>Guinardia striata</i>	2.0		*			
	<i>Chaetoceros decipiens</i>	1.3		*			
	<i>C. socialis</i>	1.3	*				
Group 2	<i>Pseudosolenia calcar avis</i>	34.2		*	1.7	53.5	Summer
	<i>C. decipiens</i>	12.0		*			
	<i>Pseudonitzschia</i> spp.	5.6		*			
	<i>C. convolutus</i>	1.7	*	*			
Group 3	<i>G. striata</i>	49.9		*	10.4	58.7	Summer
	<i>C. convolutus</i>	7.0	*	*			
	<i>C. atlanticus</i>	3.4	*				
	<i>Pseudonitzschia</i> spp.	1.8		*			
Group 4	<i>C. socialis</i>	21.7	*		25.8	6	Winter
	<i>B. delicatulum</i>	13.1					
	<i>Dactyliosolen fragilissimus</i>	6.6					
	<i>L. minimus</i>	2.7	*	*			
	<i>C. decipiens</i>	2.1		*			
	<i>Meuniera membranacea</i>	1.4	*				
Group 5	<i>Pseudonitzschia</i> spp.	1.1		*	14.4	3.0	Winter
	<i>R. hebetata</i>	35.4					
	<i>C. concavicornis</i>	13.2	*				
	<i>C. pervianus</i>	7.6					
	<i>C. decipiens</i>	1.9		*			
	<i>Thalassionema frauenfeldii</i>	1.2	*				
	<i>B. delicatulum</i>	1.1					
<i>G. striata</i>	1.1		*				
Group 6	<i>T. frauenfeldii</i>	17.5	*		33.7	0.0	Winter
	<i>R. setigera</i>	16.2	*				
	<i>L. danicus</i>	11.1					
	<i>C. aequatorialis</i>	3.7					
Group 7	<i>L. danicus</i>	13.8			8.3	8.3	–
	<i>L. minimus</i>	8.3	*	*			
	<i>G. flaccida</i>	6.7					

spring chl *a* and spring MLD ($r_s = 0.031$, $N = 27$; Fig. 6e). These results suggested that phosphate supply to the upper water by winter water mixing might enhance the winter phytoplankton growth, and not necessarily be preserved to benefit the spring bloom.

No distinctive decadal scale change was seen in the MLD, ML phosphate and chl *a* in winter. On the other hand, MLD, ML phosphate and chl *a* in spring showed a negative anomaly during the 1980s, suggesting that phytoplankton growth was hindered by nutrient depletion.

Vertical hydrographic structure and water column stratification

Following the criteria of Ohwada & Tanioka (found in Kadono 1999), we assumed isopycnals of $25.5 \sigma_t$ and $27.05 \sigma_t$ as indices of the Tsushima Current Core Water and Lower Cold Water located below the Tsushima Current, respectively. The Tsushima Current Core Water and the Lower Cold Water were also represented by water temperature ($^{\circ}\text{C}$) ranging between $14.0 \leq T < 17.0$ and $2.0 \leq T < 5.5$, and salinity (PSU)

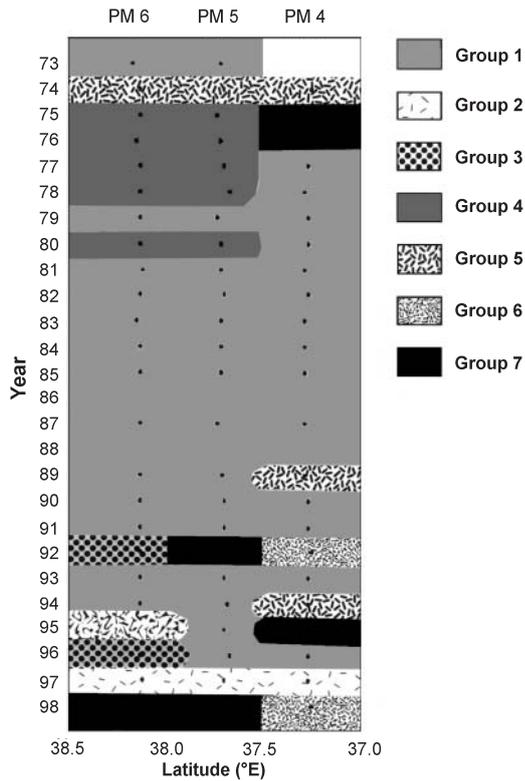


Fig. 5. Spatio-temporal distribution of diatom community groups in spring derived by cluster analysis

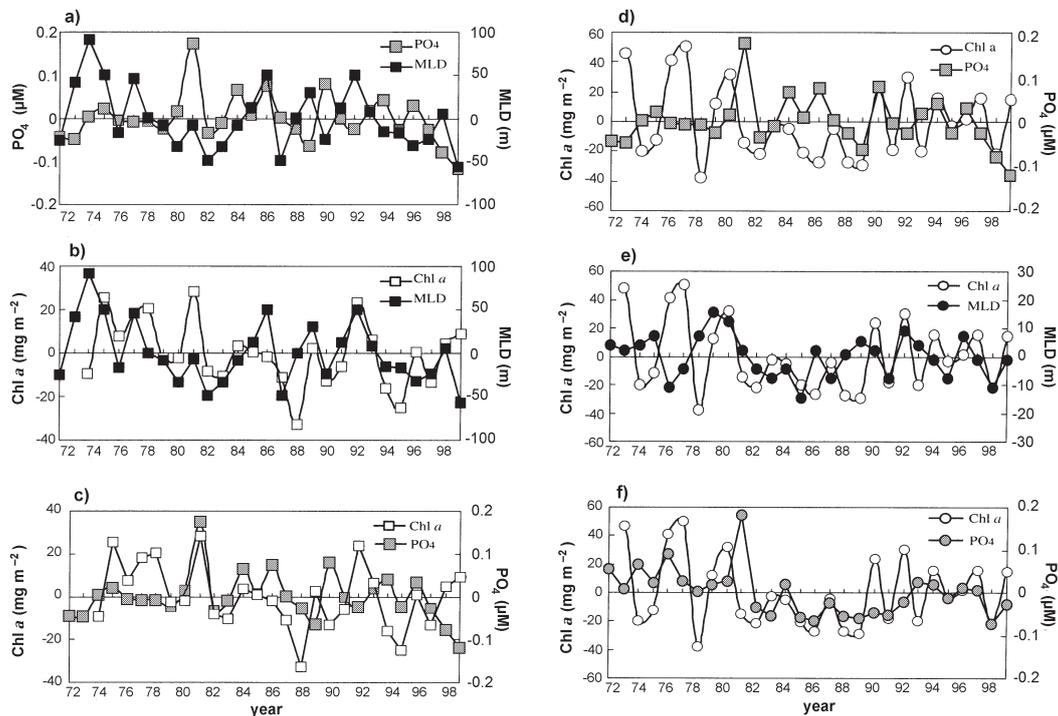


Fig. 6. Time series of anomalies of mixed layer depth (MLD; m), water column integrated chl *a* (mg m^{-2}) and mixed layer phosphate concentration (μM) for winter and spring. (a) Winter MLD and phosphate, (b) winter MLD and chl *a*, (c) winter chl *a* and phosphate, (d) winter phosphate and spring chl *a*, (e) spring MLD and chl *a* and (f) spring chl *a* and phosphate. Each data point of a year is the mean value at PM4, 5 and 6

ranging between $34.33 \leq S$ and $34.00 \leq S < 34.20$, respectively (Ohwada & Tanioka 1971, found in Kadono 1999).

Time series of water density profiles (0 to 300 m) for winter, spring and summer at Stn PM5 showed a convex pattern of $27.05 \sigma_t$ isopycnal from the late 1970s to the late 1980s and also in the mid-1990s (Fig. 7). Time series of water temperature and salinity profiles in spring showed that the observed density profile pattern was well reflected in temperature but not in salinity (Fig. 8a,b). The isopycnal of $25.5 \sigma_t$ was well recognized in summer, reflecting an increase of the Tsushima Current flow (Fig. 7c). In addition, the $25.5 \sigma_t$ isopycnal occurred at shallower depth during 1980s and mid-1990s corresponding to the rise of $27.05 \sigma_t$ isopycnal. The distribution pattern of the time series of the $27.05 \sigma_t$ isopycnal was coherent from winter to summer, indicating that the surface, warm Tsushima Current water became thinner while cold subsurface water became thicker during those years.

Time series water density gradient ($\Delta\sigma_t$) between surface and subsurface in spring markedly increased in the 1980s (Fig. 9a), suggesting an intensification of the upper water column stratification. As for spring phosphate concentration profile, subsurface concentration increased while surface concentration was decreased somewhat in the 1980s (Fig. 9b), implying

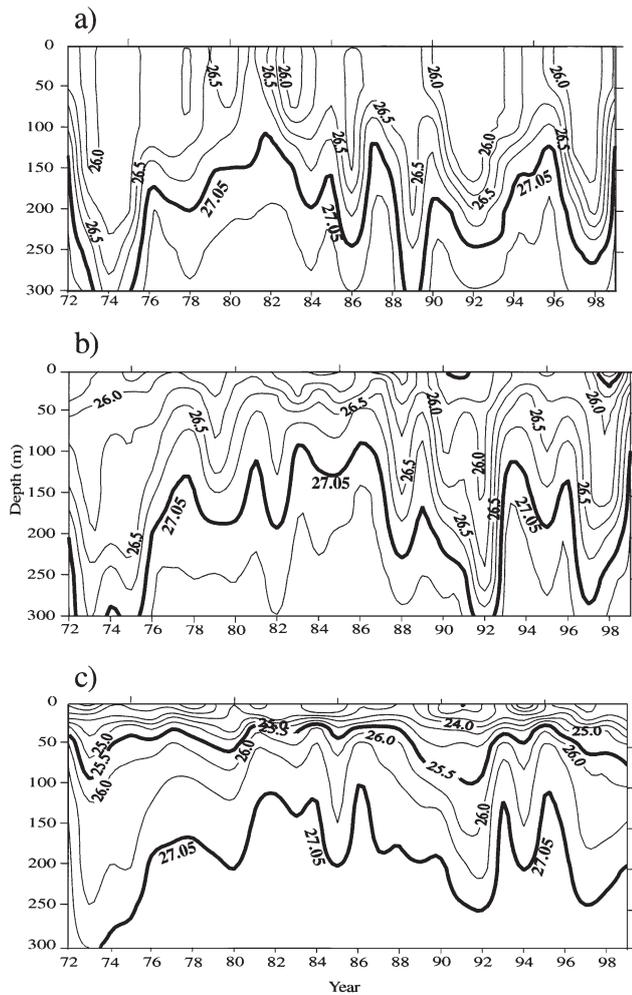


Fig. 7. Time series of water density profiles between 0 to 300 m at PM5 in (a) winter, (b) spring and (c) summer. Isopycnals of indices for the Tsushima Current Core Water ($25.5 \sigma_t$) and the Lower Cold Water ($27.05 \sigma_t$) are shown by bold lines

that nutrient supply from subsurface to surface was limited by the intensified stratification.

Solar radiation

Monthly means (\pm SD) of solar radiation from 1972 to 1996 were: 63 W m^{-2} (± 9) in December, 72 W m^{-2} (± 8) in January, 105 W m^{-2} (± 6) in February, 160 W m^{-2} (± 12) in March, 228 W m^{-2} (± 15) in April and 262 W m^{-2} (± 20) in May. Mean solar radiation for winter and spring was 80 and 217 W m^{-2} , respectively. The 5 yr running mean of the winter solar radiation (December to February) showed a slight increasing trend throughout the study year (Fig. 10). On the other hand, the spring solar radiation (March to May) reached a peak in the mid-1980s and remained low in the 1970s and 1990s (Fig. 10).

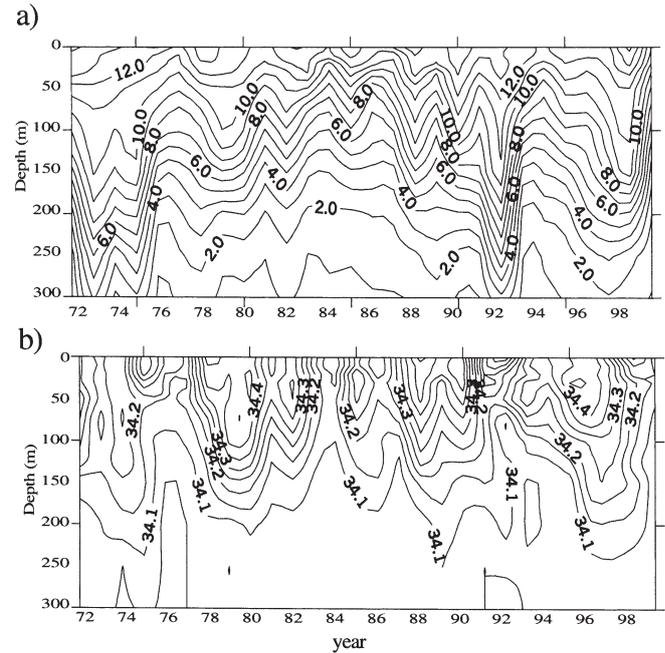


Fig. 8. (a) Time series profiles of water temperature ($^{\circ}\text{C}$). (b) Salinity (PSU) at PM5 in spring

DISCUSSION

Early summer hypothesis

This study showed that the upper water column environment and phytoplankton assemblages in spring changed considerably during the 1980s in this research area. All of the results suggested that summer-like conditions formed earlier in spring during these years. We propose here the 'early summer hypothesis' as the process accounting for the apparent decline in spring phytoplankton biomass and productivity in the Japan Sea during the 1980s.

Considering that the summer surface chl *a* per cell observed was much lower than that of winter (Fig. 2), the marked decrease in spring surface chl *a* per cell during the 1980s suggested that the diatom community might have changed into the summer-type one. The result of species composition analysis revealed that communities dominated by summer species occurred exclusively during the 1980s while communities dominated by winter species appeared in the 1970s and 1990s; this supports the early summer hypothesis. In addition, decrease in spring surface chl *a* during the 1980s indicated the low surface primary productivity as there was a significant correlation between the two (Nagata 1998).

Kim et al. (2000) concluded from satellite observation data that chl *a* concentration reached its maximum in April and May in this area when the critical depth

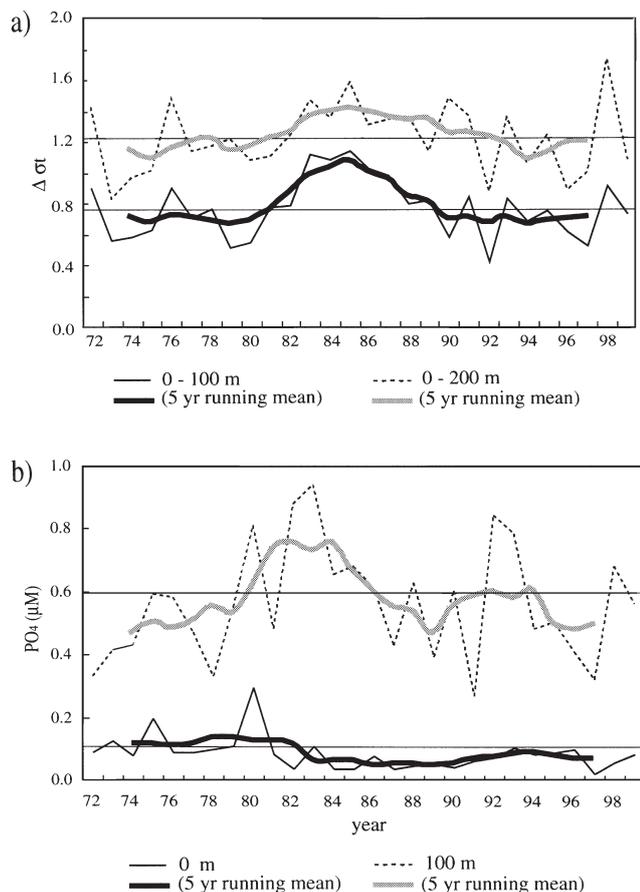


Fig. 9. (a) Time series of water density gradient ($\Delta\sigma_t$) between the surface and subsurface in spring. (b) Phosphate concentration ($\mu\text{g l}^{-1}$) at surface and subsurface in spring. Thick line indicates 5 yr running mean, and horizontal straight line indicates the mean value of the respective index. Each data point of a year is the mean value at PM4, 5 and 6

becomes deeper than MLD, and rapidly declines in summer as nutrients become depleted within a shallow ML. The observed decrease in ML phosphate, chl *a* and MLD in spring during the 1980s (Fig. 6) denoted an oligotrophic condition that is characteristic of the highly stratified upper water environment in summer. In addition, we observed that the spring upper water column stratification intensified to the level limiting nutrient supply to the surface in the 1980s (Fig. 9). Thus, formation of early and intensive stratification was likely responsible for the dominance of summer diatom species, which were adapted to the oligotrophic conditions. A Pennate diatom, *Pseudonitzschia* sp., has been reported to grow at low Si/N ratios in comparison to Centric diatom species (Sommer 1994). With this information, the dominance of *Pseudonitzschia* species in the 1980s might be a result of changes in nutrient availability within the surface

water, although we did not have sufficient data on macronutrients other than phosphate in order to substantiate this.

Our finding of the dominance of a summer-type diatom community in the 1980s may be counterintuitive as previous studies reported a water temperature decline (Minami et al. 1999b) associated with the appearance of cold water species (Kubo & Ebara 1992) during the 1980s. Studying the same PM line data, Imai & Ebara (1989) attributed the decline in chl *a* during the 1980s to the lower water temperature. Water temperature data used in Minami et al. (1999b) were mean temperature between the surface and 150 m, and those of Imai & Ebara (1989) were from 100 m depth. Therefore, their data are considered to have reflected the effect of a subsurface cold deep water rise while our results show that sea surface temperature had been relatively constant. It is thus possible that the cold water allowed a small population of cold water species to survive and reproduce during the 1980s in the area as Kubo & Ebara (1992) suggested. In terms of the community structure, however, our results showed that the dominant diatom species were summer ones during these years. For example, *Chaetoceros atlanticus*, which is a cold water index species in Kubo & Ebara (1992) and

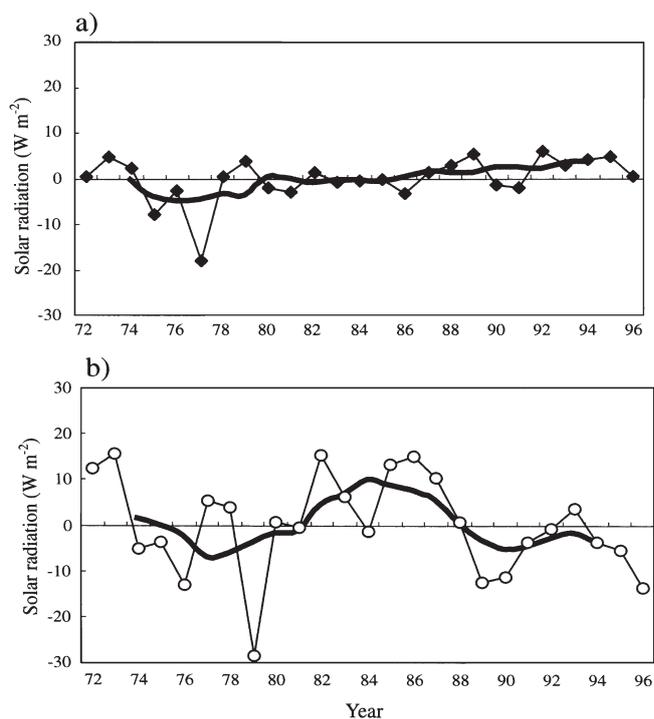


Fig. 10. Time series of anomalies of seasonal mean solar radiation (W m^{-2}) in the area of 36 to 39°N and 132 to 137°E for (a) winter (mean of December to February) and (b) spring (mean of March to May). Thick line indicates the 5 yr running mean

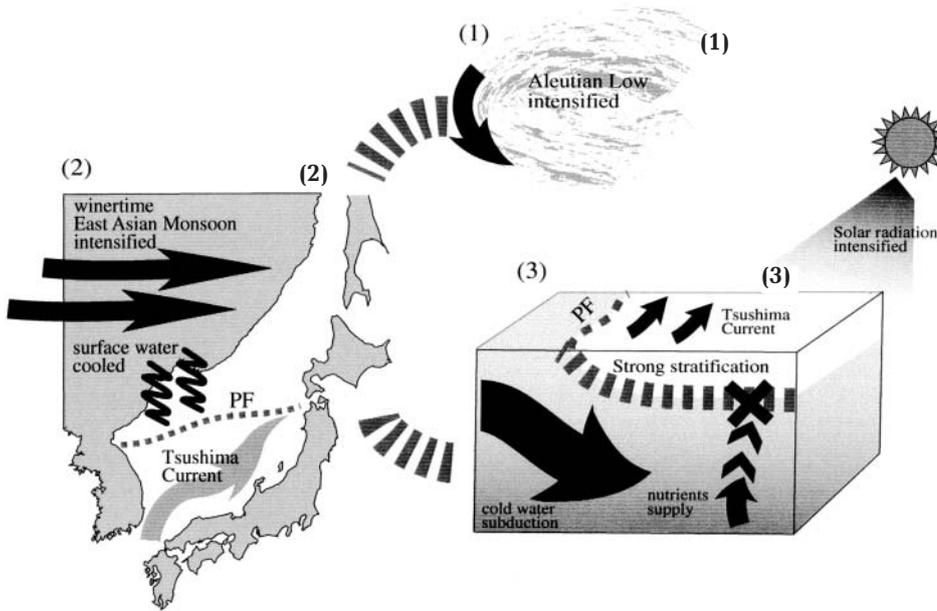


Fig. 11. Diagrams illustrating processes of formation of the early summer-like condition in the Japan Sea between the 1976/77 and 1988 North Pacific climate regime shifts. PF: approximate location of the polar front. Intensification of the Aleutian Low pressure system (1) strengthened the wintertime East Asian Monsoon over Siberia and the northern Japan Sea (2). The strong westerlies cooled surface water of the northern Japan Sea and facilitated subduction of cold water below the warm Tsushima Current (2)(3). In addition, springtime solar radiation increased during the 1980s (3). These conditions led to enhancement of stratification between subsurface and surface waters in spring, resulting in limiting the nutrient supply to the surface to the level that only a summer-adapted plankton community was favored (3)

was classified into the winter species in this study, appeared in Group 1 but accounted for less than 1% of the total. This result indicates that the change in mean water temperature within the water column was unlikely to be a direct factor determining the interdecadal scale variability in diatom community structure and phytoplankton production in the Japan Sea. Instead, our results suggest that the timing and degree of the upper water column stratification was the more important factor.

We cannot determine from the present data whether the observed 'early summer' condition meant a shift in the timing of the spring bloom or overall decrease in the phytoplankton production of the yr. However, both cases could be responsible for the decline zooplankton biomass during the 1980s (Minami et al. 1999b), and thus might affect the food web structure of the region. An overall decrease in phytoplankton food would obviously have a negative effect on zooplankton production. In addition, a shift of the spring bloom might also reduce the food availability for zooplankton due to the 'match-mismatch' effect (Cushing 1972) as zooplankton biomass usually reaches its peak in April to May in the offshore Japan Sea (Hirota & Hasegawa 1999). Furthermore, the mismatch of the production peaks of phytoplankton and zooplankton could influence the vertical carbon flux of the region (Townsend et al. 1994).

Climate regime shift and upper water environment

The next question is as to how interdecadal scale climatic variability could affect the timing and degree of

upper water column stratification. One of the possible factors is the observed increase in spring solar radiation during the 1980s (Fig. 10). Surface water warming would facilitate water stratification. However, surface temperature showed no increase during the 1980s (Fig. 8), which might be due to the rise of the cold subsurface water from the late 1970s to the late 1980s (Figs. 7 & 8). It is reported that the 1976/77 climate regime shift in the North Pacific was characterized by the intensification of the ALP system which persisted until 1988 (Trenberth 1990). The period of a strong ALP was roughly coincident with the year of the cold subsurface water rise in this study. In light of this, we propose here a schematic process linking climate and the upper water column environment that determines the lower trophic level marine ecosystem in the central Japan Sea (Fig. 11).

The strong ALP system induced the southward shift of westerly winds and strengthening of the winter circulation at mid latitudes (Hanawa 1992, Miller 1994, Trenberth & Hurrell 1994; Fig. 11 [1]). The Monsoon Index (MOI) indicates winter-time wind stress over the Eurasian Continent to the North Pacific, and is defined as differences in atmospheric pressure between Nemuro, Japan (43.02° N, 145.45° E), and Irkutsk, Russia (52.16° N, 104.21° E). It is possible that a slight increase in the winter (December to February) MOI after the mid-1970s (Kim & Isoda 1998, Limsakul et al. 2001) occurred in conjunction with the Aleutian Low intensification. Observing the significant correlation between winter-time MOI and water temperature at 100 and 200 m along the PM line, Kim & Isoda (1998) concluded that the winter MOI was a useful indicator of the subsurface water cooling in the Japan

Sea (Fig. 11 [2]). Wind driven circulation is prominent during winter in the Japan Sea (Sekine 1992). Senju (Senju & Sudo 1994, Senju 1999) suggested that cooled surface water is subducted off Siberia, north of the polar front during winter and transported to the PM line observation area. The convex distribution pattern of the cold subsurface water on our σ_t profiles (Fig. 7) might reflect the enhancement of transportation and/or subduction of cold water during the 1980s (Fig. 11 [3]). In the same years, the surface water was warmed by intensified solar radiation during spring, resulting in an early formation of the summer-like stratified environment (Fig. 11 [3]). The relationship between the intensification of winter wind stress and spring solar radiation is not clear. Furthermore, we may have to consider the influence of interannual variability in the formation and horizontal transportation of Tsushima Current Water on the water stratification process.

Comparison to the other region

Our results showed that the 1976/77 climate regime shift altered diatom community, and possibly, food web structure by changing the upper water column structure from winter to spring. It has been reported that vertical water mixing during winter and subsequent water column stratification (stabilization) during spring are important for effective nutrient utilization by phytoplankton, but might function differently depending on the local conditions. For example, Polovina et al. (1995) pointed out that moderate winter mixing and early water stabilization could enhance spring plankton productivity in the subarctic ocean, where light availability limits phytoplankton growth, while strong winter mixing may increase the spring productivity in the subtropical ocean, where nutrient availability is the limiting factor. Thus, it is noteworthy that different mechanisms may work to determine plankton biomass in conjunction with the 1976/77 climate regime shift between the Japan Sea and other regions in the Western North Pacific.

In the Oyashio water, Minobe (1997) reported that water temperature declined due to advection of northern, cold water, which was induced by intensification of winter circulation in the subarctic gyre after the climate regime shift. Tomosada & Odate (1995) attributed the observed decrease in zooplankton biomass to the decline in phytoplankton productivity due to low water temperature and reduced solar radiation. Their result follows the subarctic ocean process by Polovina et al. (1995). Our study, however, suggested that mean water temperature decline was not the direct factor which limited phytoplankton productivity in the Japan

Sea. On the other hand, it has been reported that deep mixing during winter after the regime shift had a positive influence on phytoplankton growth in the western North Pacific Subtropical Gyre, where nutrient availability is a limiting factor (Limsakul et al. 2001). Their result follows the subtropical ocean process by Polovina et al. (1995). However, our Japan Sea data suggested that nutrients supply by winter deep mixing might not determine the spring phytoplankton production (Fig. 6). Our results showed that neither the subarctic or the subtropical processes as Polovina et al. (1995) reported were sufficient to explain the interaction between climate, the upper water column environment, and lower trophic level ecosystem in transitional regions of warm and cold water masses such as the central Japan Sea.

Ecological consequences of diatom community change

We observed that interdecadal climate change altered the diatom community structure in the Japan Sea. It is well known that diatoms are generally large phytoplankton which play a fundamental role in a grazing food chain while nano- and pico-sized phytoplankton are the major primary producers in a microbial loop dominated ecosystem. However, ecological and physiological characteristics as well as size are quite diverse, even between diatom species (e.g. Tomas 1996). We consider it possible to elucidate change in a food web structure by examining diatom community structure, particularly in a region where springtime diatom bloom was eminent such as the Japan Sea (Ebara 1984).

During the 1980s, we found an increase of pennate diatom, *Pseudonitzschia* spp. Recent experimental studies have shown that large herbivorous copepods do not actively feed on Pennate diatoms (Boyd & Newton 1999). Several *Pseudonitzschia* species are reported to produce a toxic substance, domoic acid, under certain environmental conditions (reviewed in Bates et al. 1998). Although it is still unclear if domoic acid is capable of inhibiting copepod grazing, Bates et al. (1989) suggested that the toxin might play a role as an anti-predation substance due to its insecticidal properties (Maeda et al. 1984). Therefore, the increase in *Pseudonitzschia* spp. during the 1980s might have had a negative influence on the production of herbivorous copepods.

In conclusion, besides the overall decline of the phytoplankton food and mismatch of the timing of spring bloom, shifts of the diatom community structure might also be responsible for the observed decline in zooplankton biomass during the 1980s.

CONCLUSION

Detailed investigations of biological variables has long been neglected in long-term change studies as it requires significant work and time for microscopic analyses. However, this study demonstrated that taxonomic and functional breakdown of the plankton community structure, when compared to conventional total quantity based studies, offers useful indicators which can help us better understand the processes and consequences of climate-ecosystem interactions.

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