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Distribution of chlorophyll-*a* concentration in the Transition Domain and adjacent regions of the central North Pacific in summer

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Abstract: Chlorophyll-*a* (Chl-*a*) concentrations and phytoplankton productivities, as well as physical and chemical environmental factors, were measured in the Transition Domain (TD) and its adjacent regions to the south and north in the central North Pacific during the summers of 1991 to 1996. The Chl-*a* concentrations in the surface layer in the TD were not intermediate between those in the southern and northern regions. The concentration seems to be rather constant and low in the TD compared to the adjacent regions. In contrast, temperature and nutrient levels were found to be intermediate in the TD compared to regions to the north and south. Chl-*a*-specific phytoplankton productivity (an index of phytoplankton growth rate) of the <2, 2–10 and 10–200 μm fractions in the TD did not substantially differ from that in the adjacent regions. Phytoplankton growth rate is therefore unlikely to be responsible for the low Chl-*a* concentration in the TD. The standing stock of copepods tended to be largest in the TD. From these results and the previous information about zooplankton in and around the TD, we suggest that heavy grazing by zooplankton in the TD reduced the phytoplankton standing stock and, therefore, the concentration of Chl *a* in the area.

Key words: chlorophyll *a*, Transition Domain, central North Pacific, summer, grazing

Introduction

The Transition Domain (TD) is located just north of the Subarctic Boundary, defined by the vertical 34.0 isohaline at approximately 42°N, and divides the North Pacific into subtropical and subarctic regions (Dodimead et al. 1963; Favorite et al. 1976). The northern boundary of the TD is defined as the location where the 4°C isotherm descends below 100 m (Favorite et al. 1976).

Saury, spotlined sardine, Pacific pomfret, chub mackerel, blue shark, neon flying squid, etc. migrate into the TD and the subarctic North Pacific in summer, whereas salmon migrate into the TD and subtropical North Pacific (Mishima 1981; Pearcy 1991). The TD is thus an important feeding ground for pelagic fish and cephalopods. Consequently, it is important to reveal the distribution pattern of phytoplankton standing stock in and around the TD.

The TD has the character of a frontal zone in which there are rapid changes in physical, chemical and biological factors. Temperature and nutrient concentrations in the surface layer of the TD are intermediate between those in the subtropical and subarctic regions in spring and summer (Dodimead et al. 1963; Sagi 1970; Kawarada & Sano 1972; McGowan & Williams 1973; Favorite et al. 1976; Maita & Toya 1986; Matsunaga et al. 1986; Odate & Maita 1988/89; Shiomoto & Maita 1990; Odate 1994; Shiga 1994; Takagi et al. 1997). Some spring and summer studies indicated that the biological features in the surface layer are also intermediate in the TD, including the associations of planktonic diatom species (Venrick 1971), chlorophyll-*a* (Chl-*a*) concentrations (McGowan & Williams 1973; Odate & Maita 1988/89), and daily and annual phytoplankton productivities (Taniguchi 1981). However, there are several summer

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studies indicating that Chl-*a* concentrations in the surface layer are not intermediate in the TD (Kawarada & Sano 1972; Shiomoto & Maita 1990; Odate 1994; Shiga 1994; Sugimoto & Tadokoro 1997; Takagi et al. 1997). Hence, we have attempted to clarify whether or not Chl-*a* concentration is intermediate in the TD with the help of six sets of cruise data from the TD and adjacent regions of the central North Pacific in the summers of 1991 to 1996. In this paper, we show that some physical and chemical features are intermediate in the TD compared to the north and south, however, Chl-*a* concentration seems to be rather lower in the TD than in adjacent regions, and we discuss factors that contribute to the low Chl-*a* concentration.

Materials and Methods

Water sampling and incubation experiments were conducted during the cruises of the R/V *Wakatake Maru*, owned by the Education Bureau of Hokkaido, in June and July of 1991 to 1996 (e.g. Ishida et al. 1997). Stations were located every 1° between 38°30'N and 50°30'N along 179°30'W (Fig. 1A). Surface and subsurface seawater samples were collected around noon using an acid-cleaned plastic bucket and an acid-cleaned 10-liter PVC Niskin or Go-Flo sampler. These samples were sieved through a 200-μm mesh screen to remove large zooplankton. The samples were then used to determine Chl-*a* concentration and phytoplankton productivity, and to measure physical and chemical environmental factors.

Every year, Chl-*a* concentration at the surface was measured, and in 1993 and 1994 Chl-*a* concentrations were measured at 0, 10, 20, 30, 50, 75 and 100 m. A Whatman GF/F filter was used to determine the surface and subsurface Chl-*a* concentrations. In 1992 and 1993, surface seawater samples were filtered separately through Nuclepore filters with pore sizes of 10 (>10-μm fraction) and 2 μm (>2-μm fraction), and a Whatman GF/F (about 0.7-μm pore size; total), in order to determine the Chl-*a* concentration of the 10–200, 2–10 and <2-μm fractions. Samples collected onto Nuclepore filters with a pore size of 10 μm were used to determine Chl-*a* concentrations of the 10–200 μm fraction. Chl-*a* concentration of the 2–10 μm fraction was obtained from the difference between the >2 and >10-μm fractions. The concentration of the <2-μm fraction was obtained from the difference between the total and the >2-μm fraction. The filters were stored frozen at −20°C until analysis ashore. Chl-*a* concentration was measured by in vitro fluorometry using a Hitachi F-2000 fluorometer calibrated by standards derived from commercially prepared Chl *a* (Wako Pure Chemical Industries, Ltd., Tokyo), according to Parsons et al. (1984).

In 1992 and 1993, surface seawater samples were used to determine size-fractionated (10–200, 2–10 and <2-μm fractions) phytoplankton productivity. The productivity experiments were started within 1 h of sample collection. The samples (1 liter) were dispensed into six acid-cleaned 1-liter polycarbonate bottles and enriched by the addition of $NaH^{13}CO_3$ (99 atom% ^{13}C; Shoko Co. Ltd. Tokyo) to about 10% of the total inorganic carbon in ambient water. Incubations were conducted under sunlight, being cooled with near-surface seawater, for 2–3 h. Fractionation of samples into size classes was done after incubation. Immediately following incubation, two of six samples were filtered through precombusted (450°C for 4 h) 47-mm Whatman GF/F filters (total). Two of the remaining four samples were filtered through Nuclepore filters with a pore size of 2 μm and the other two with a pore size of 10 μm. The latter four filtrates were refiltered through 47-mm Whatman GF/F filters (<2 or <10-μm fraction). The particulate matter on

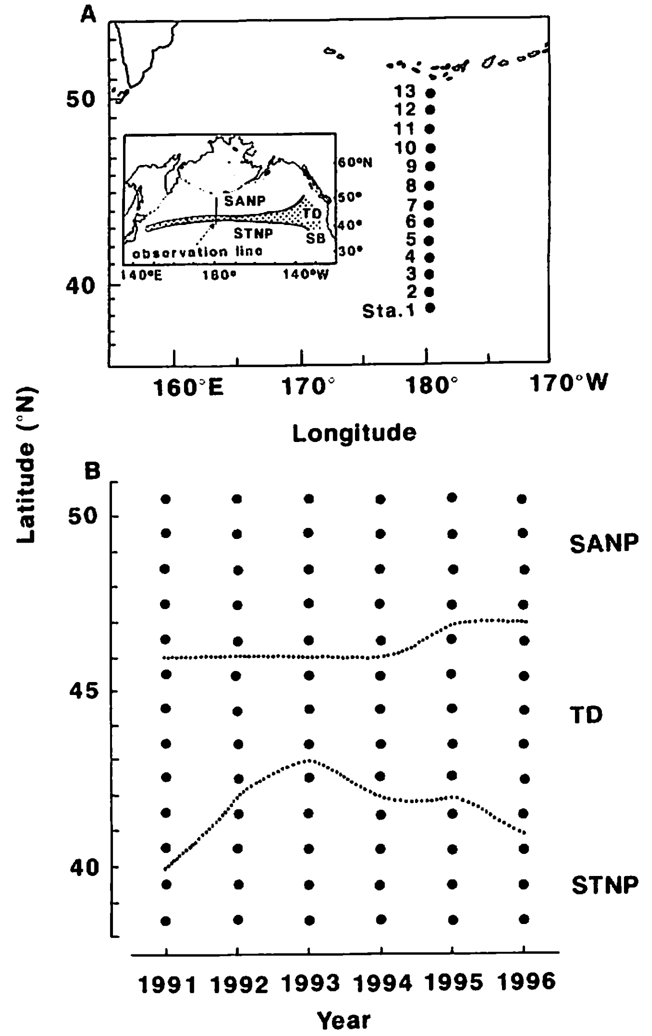

Fig. 1. A. Location of sampling stations in the Transition Domain (TD) and adjacent regions of the North Pacific in the summers of 1991 to 1996, and schematic diagram indicating extent of the TD in the North Pacific. *Dotted area* indicates the TD. SB, the Subarctic Boundary; STNP, the subtropical North Pacific located south of the TD; SANP, the subarctic North Pacific located north of the TD. **B.** Interannual changes in the locations of STNP, TD and SANP. *Solid circles* indicate the position of sampling stations. *Dotted lines* indicate the southern and northern limits of the TD.

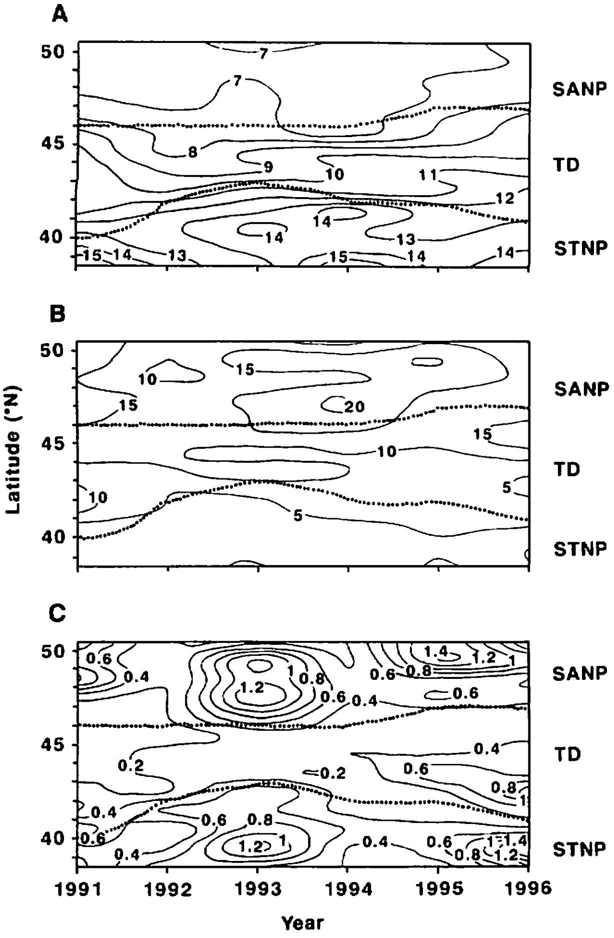

Fig. 2. Latitudinal and interannual changes of temperature (°C) (A), nitrite+nitrate concentration (μM) (B) and chlorophyll-*a* concentration (μg l^{-1}) (C) at the surface during the summers of 1991 to 1996. Abbreviations and symbols as in Fig. 1.

the Whatman GF/F filters was rinsed with prefiltered seawater and the filters were stored frozen at −20°C until isotope analysis ashore. They were treated with HCl fumes for 4 h to remove inorganic carbon, and thoroughly dried in a vacuum desiccator. The isotopic ratios of ^{13}C to ^{12}C and particulate organic carbon were determined through infrared absorption spectrometry using a JASCO EX-130S $^{13}CO_2$ analyzer (cf. Satoh et al. 1985). Total inorganic carbon in the water was measured with a Shimadzu TOC 5000 infrared analyzer. Phytoplankton productivity was calculated according to the equation described by Hama et al. (1983). The productivity of the 10–200 μm fraction was obtained from the difference between the total and the <10-μm fraction. The productivity of the 2–10 μm fraction was obtained from the difference between the <10 and <2-μm fractions.

Surface temperature and salinity were measured with a thermometer and an Auto-Lab salinometer. Subsurface temperature and salinity were recorded at 1-m intervals down to 600 m using an Alec memory STD sensor. Surface water samples for nutrient determinations were stored frozen at −20°C and analysed using a Bran & Luebbe TRAACS 800.

Table 1. Mean±standard deviation (σ_{n-1}) of total chlorophyll-*a* concentration (μg l^{-1}) at the surface in the subtropical Narth Pacific (STNP), Transition Domain (TD) and subarctic North Pacific (SANP), 1991–1996. The number of data is given in parentheses.

Year	STNP	TD	SANP
1991	0.21 (2)	0.26±0.25 (6)	0.62±0.40 (5)
1992	0.49±0.23 (4)	0.20±0.07 (4)	0.20±0.00 (5)
1993	0.84±0.28 (5)	0.28±0.06 (3)	0.98±0.45 (5)
1994	0.43±0.11 (4)	0.32±0.07 (4)	0.39±0.07 (5)
1995	0.40±0.16 (4)	0.41±0.19 (5)	0.98±0.45 (4)
1996	1.00±0.57 (3)	0.53±0.29 (6)	0.54±0.25 (4)

Results

According to the definition (see above) of Favorite et al. (1976), we determined the location of the TD based on the prevailing temperature and salinity (Fig. 1B). The stations were thus divided into three regional groups in the TD, the subtropical North Pacific (STNP), located south of the TD and the subarctic North Pacific (SANP), located north of the TD.

From 1991 to 1996, surface seawater temperature was generally 12–15°C in the STNP, 8–12°C in the TD and 6–8°C in the SANP (Fig. 2A). Surface nitrite+nitrate concentrations were generally less than 8 μM in the STNP, 8–15 μM in the TD and 10–20 μM in the SANP (Fig. 2B).

Surface Chl-*a* concentrations fluctuated latitudinally and interannually in the STNP and SANP, within the range of 0.1 and 1.6 μg l^{-1} and 0.1 and 1.4 μg l^{-1} (Fig. 2C). Values exceeding 1 μg l^{-1} were occasionally observed in the SANP. In the TD, the Chl-*a* concentrations ranged from 0.1 to 1.1 μg l^{-1} and were generally within the range of 0.2 and 0.5 μg l^{-1}. High concentrations of more than 0.5 μg l^{-1} were found at Stn 3 in 1991 (0.76 μg l^{-1}), Stn 6 in 1995 (0.73 μg l^{-1}) and Stns 5 and 6 in 1996 (1.09 and 0.52 μg l^{-1}). The high concentrations were not limited to any one year. The share of the concentration of 0.2–0.5 μg l^{-1} was 82% in the TD, whereas the share was 45% in the STNP and 57% in the SANP. The Chl-*a* concentration was constant both latitudinally and interannually in the TD compared to in the STNP and SANP. Mean concentration was highest every year in either the STNP or SANP (Table 1). The mean values in the TD were lower or nearly equal to the lowest value found in either the STNP or SANP. Moreover, Chl-*a* concentrations in the upper 100 m were generally in the range of 0.2 and 0.4 μg l^{-1} in the TD in 1993 and 1994 (Fig. 3). In contrast, Chl-*a* concentrations exceeding 0.4 μg l^{-1} were frequently observed in the STNP and SANP, especially in 1993. Consequently, the Chl-*a* concentrations in the TD were not intermediate between those in the STNP and SANP, a pattern which did not follow from

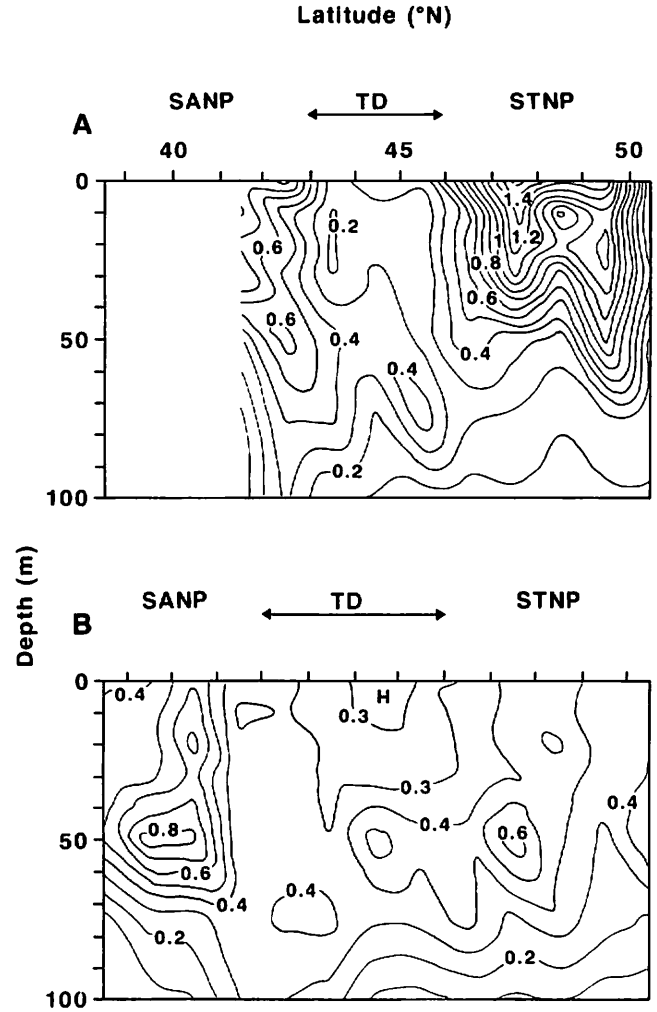

Fig. 3. Vertical sections of chlorophyll-*a* concentration (μg l^{-1}) along 179°30'W during the summers of 1993 (A) and 1994 (B). Abbreviations and symbols as in Fig. 1.

Table 2. Mean±standard deviation (σ_{n-1}) of size-fractionated (in μm) chlorophyll-*a* concentration (μg l^{-1}) at the surface in the subtropical Narth Pacific (STNP), Transition Domain (TD) and subarctic North Pacific (SANP), 1992 and 1993. The number of data is given in parentheses.

Year	Size	STNP	TD	SANP
1992	<2	0.21±0.09 (4)	0.12±0.05 (4)	0.12±0.03 (5)
	2–10	0.49±0.23 (4)	0.20±0.07 (4)	0.20±0.00 (5)
	10–200	0.14±0.11 (4)	0.02±0.02 (4)	0.05±0.06 (5)
1993	<2	0.32±0.07 (5)	0.18±0.05 (3)	0.43±0.17 (5)
	2–10	0.23±0.08 (5)	0.06±0.02 (3)	0.18±0.10 (5)
	10–200	0.29±0.15 (5)	0.04±0.01 (3)	0.38±0.24 (5)

Table 3. Mean±standard deviation (σ_{n-1}) of size-fractionated (in μm) chlorophyll-*a*-specific phytoplankton productivity (μgC μgChl-a^{-1} h^{-1}) at the surface in the subtropical North Pacific (STNP), Transition Domain (TD) and subarctic North Pacific (SANP), 1992 and 1993. The number of data is given in parentheses.

Year	Size	STNP	TD	SANP
1992	<2	7.52±2.92 (4)	7.06±3.88 (4)	4.68±1.58 (5)
	2–10	6.40±5.91 (4)	4.18±1.73 (4)	4.97±3.30 (3)
	10–200	3.13±2.48 (4)	2.38 (2)	5.43±6.49 (4)
1993	<2	2.91±0.70 (5)	2.28±0.62 (3)	1.39±0.72 (5)
	2–10	2.98±1.79 (5)	2.02±3.02 (3)	2.29±0.10 (5)
	10–200	1.63±1.27 (5)	2.90±2.76 (3)	1.09±0.39 (5)

the physical and chemical environmental factors. The Chl-*a* concentration seems to be rather constant and low in the TD compared to the STNP and SANP.

Mean values for surface Chl-*a* concentrations of the <2 and 2–10 μm fractions in the TD and SANP were equal, and lower than those in the STNP in 1992 (Table 2). The mean values for the three size fractions were lowest in the TD in other cases. The mean values for the <2 and 2–10 μm fractions in the TD were 4 times lower at most than those in other regions, and those for the 10–200 μm fraction were 2.5 to 9.5 times lower in the TD than in other regions.

Mean values of the surface Chl-*a*-specific phytoplankton productivity (μgC μgChl-a^{-1} h^{-1}), an index of phytoplankton growth rate (Lalli & Parsons 1993), for the<2 μm fraction were intermediate in the TD in 1992 and 1993, and that for the 10–200 μm fraction was highest in the TD in 1993 (Table 3). The mean values were lowest in the TD for the other cases. However, the Chl-*a*-specific phytoplankton productivity of the three size fractions in the TD did not substantially differ from that in the STNP and SANP.

Discussion

The physical and chemical environmental factors in the TD were intermediate between those in the STNP and SANP (Fig. 2A, B) and the results were in agreement with previous results (Dodimead et al. 1963; Sagi 1970; Kawarada & Sano 1972; McGowan & Williams 1973; Favorite et al. 1976; Maita & Toya 1986; Matsunaga et al. 1986; Odate & Maita 1988/89; Shiomoto & Maita 1990; Odate 1994; Shiga 1994; Takagi et al. 1997). On the contrary, the Chl-*a* concentration seems to be rather constant and low in the TD compared to the STNP and SANP (Figs 2C, 3). Such patterns have been found in other studies (Kawarada & Sano 1972; Odate 1994; Shiga 1994; Sugimoto & Tadokoro 1997; Takagi et al. 1997). In addition, the Chl-*a* concentrations of the three size fractions at the surface were low in the TD compared to the STNP and SANP, especially for the 10–200 μm fraction (Table 2). Size composition of Chl-*a* concentration at the surface was roughly representative of the size composition of Chl-*a* concentration in the water column (0–200 m) in the TD and adjacent regions (Odate & Maita 1988/89). Low concentrations of phytoplankton of every size, especially the large ones, con-

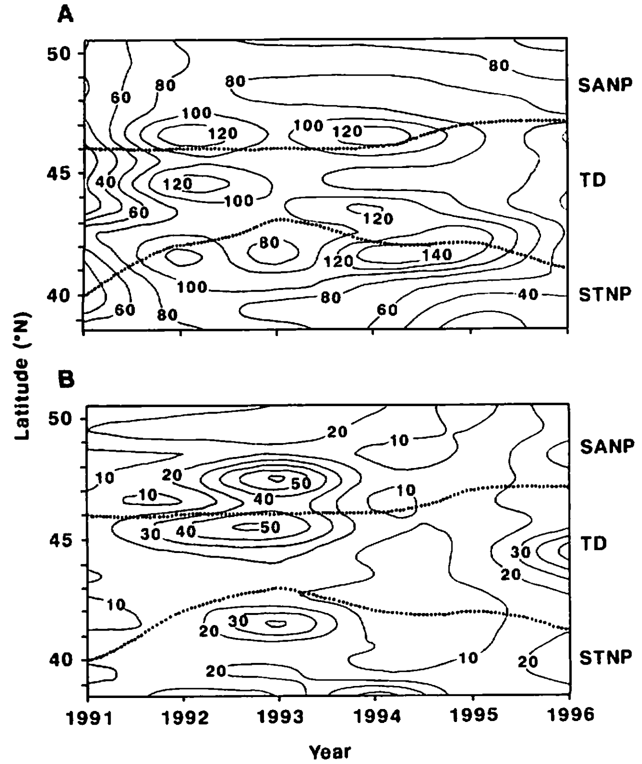

Fig. 4. Latitudinal and interannual changes of depth of surface mixed layer (m) (A) and vertical gradient of sigma-*t* in the pycnocline ($\times 10^{-3}$ kg m^{-4}) (B) during the summers of 1991 to 1996. Abbreviations and symbols as in Fig. 1.

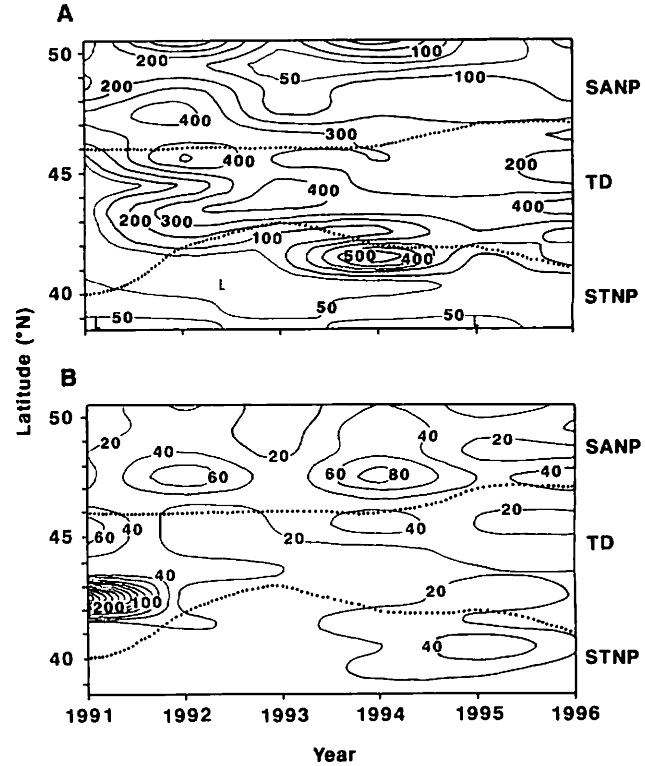

Fig. 5. Latitudinal and interannual changes of wet weight (mg m^{-3}) of copepods (A) and carnivores (amphipods+pteropods+chaetognaths) (B) obatined by Norpac-net operations from 150 m to the surface during the summers of 1991 to 1996. Abbreviations and symbols as in Fig. 1. (Data from Tadokoro et al. 1995, and Nagasawa & Ishida 1997.)

tribute to the low Chl-*a* concentration in the TD.

The surface Chl-*a*-specific phytoplankton productivity of the three fractions were not substantially lower in the TD than in the STNP or SANP (Table 3). Phytoplankton growth rate is thus unlikely to be responsible for the low Chl-*a* concentration in the TD. Accordingly, we suggest that losses in phytoplankton, especially large ones, are higher in the TD than elsewhere, and thus the Chl-*a* concentration is lower in the TD. Possible losses of phytoplankton include respiration, sinking and zooplankton grazing. Below, we discuss whether these three factors can be thought to contribute to the low Chl-*a* concentration in the TD.

According to Sverdrup's (1953) critical depth model, net production of phytoplankton can take place if the critical depth is deeper than the depth of the surface mixed layer, and no net production can take place in the opposite case, because respiration loss exceeds production in the water column. The depth of the surface mixed layer was defined as the uppermost steepest vertical gradient of sigma-*t*. Every year, the depth of the surface mixed layer was generally within the range of 50 and 100 m in the STNP, TD and SANP, though depths of 100–150 m and shallower than 50 m were sometimes observed (Fig. 4A). Global monthly critical depth, according to Sverdrup, was estimated by Obata et al. (1996). The critical depths are 100–200 m in our study area. Thus, it can be said that water column conditions do not account for much greater loss through respiration in our study area. Respiratory loss is unlikely to cause the low Chl-*a* concentration in the TD.

A small density gradient in the surface layer will reduce the standing stock of phytoplankton because a small gradient favors a greater loss of cells through their sinking below the surface layer. Semina & Tarkhova (1972) observed a positive correlation between the standing stock of phytoplankton and the density gradient in the main pycnocline. The density gradient in the pycnocline in the TD was not substantially different from those in the STNP and SANP (Fig. 4B). Accordingly, the sinking of phytoplankton is unlikely to cause the low Chl-*a* concentration in the TD.

Standing stock (wet weight) of macrozooplankton was estimated from midnight (2100–0100 h) Norpac-net (335-μm mesh size) tows from 150 m to the surface conducted at the same locations as this study in 1991–1996 (Tadokoro et al. 1995; Nagasawa & Ishida 1997). Copepods represented most of the standing stock of the macrozooplankton in the TD, except in 1991 (0–63% in 1991 and 73–96% in 1992–1996). In the TD, the standing stock of copepods tended to be largest, except in 1991 when the wet weight of carnivorous macrozooplankton, the sum of the wet weight

Table 4. Mean±standard deviation (σ_{n-1}) of wet weight of copepods (mg m^{-3}) in the upper 150 m of the water column in the subtropical Narth Pacific (STNP), Transition Domain (TD) and subarctic North Pacific (SANP), 1991–1996. The number of data is given in parentheses. (Re-arranged from Tadokoro et al. 1995, and Nagasawa & Ishida 1997.)

Year	STNP	TD	SANP
1991	42 (2)	23±25 (6)	156±112 (5)
1992	34±29 (4)	306±175 (4)	351±148 (5)
1993	63±43 (5)	370±79 (3)	117±131 (5)
1994	177±266 (4)	245±126 (4)	205±126 (5)
1995	62±35 (4)	281±40 (5)	94±72 (4)
1996	69±27 (3)	257±127 (6)	102±43 (4)

of amphipods, pteropods and chaetognaths, was high (Fig. 5A, B, Table 4). The small standing stock of copepods in the TD in 1991 may have been due to the intense grazing effect of carnivores. Grazing copepods live in the surface layers (roughly 0 to 150 m) from spring to mid-summer in the oceanic subarctic Pacific (Miller et al. 1984; Mackas et al. 1993). Copepod grazing generally has an effect on large phytoplankton (more than 8-μm cell size; Landry et al. 1993). Moreover, Spearman rank correlation showed a significant negative relationship between the wet weight of copepods and the surface Chl-*a* concentration (Fig. 6). This implies that copepod grazing was related to variation in the phytoplankton standing stock. From the discussion above, heavy grazing by copepods could reduce the large phytoplankton standing stock in the TD. Heavy grazing by copepods in the TD was suggested by Odate (1994) and Shiga (1994). On the other hand, the standing stock of microzooplankton in the TD tended to be intermediate between those in the southern and northern adjacent regions (Odate & Maita 1994; Odate 1994). Moreover, Shiga (1994) implied that tunicates (doliolids and salps) actively graze on phytoplankton in summertime in the TD. Tunicates are able to collect large amounts of particulate matter, ranging from about 1 mm to less than 1 μm (Madin 1974; Alldredge & Madin 1982). Heavy grazing on small phytoplankton can also be expected in the TD. It is possible that this study illustrates a case in which zooplankton grazing is responsible for the low Chl-*a* concentration in the TD of the central North Pacific.

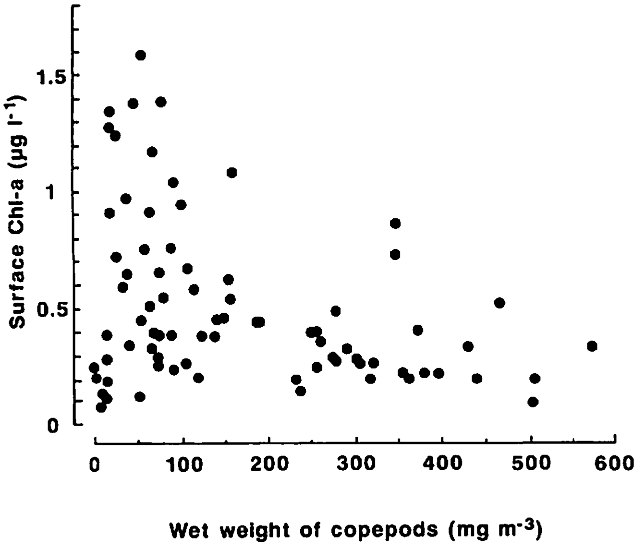

Fig. 6. Relationship between the wet weight of copepods in the upper 150 m of the water column and the surface chlorophyll-*a* concentration during the summers of 1991 to 1996. $r_s = -0.23$, $n = 78$, $p < 0.05$ (two-tailed test).

Copepods are considered important predators of phytoplankton and prey for fishes (e.g. Lalli & Parsons 1993). Hence, high grazing loss by copepods leads us to expect that energy and materials from primary production flow rapidly to high trophic levels in the summertime ecosystem of the TD in the central North Pacific. We thus feel that the summertime TD in the central North Pacific is a region that can support a large biomass of fishes. We also feel that zooplankton grazing is the driving force in energy and materials flow in the summertime ecosystem of the TD in the central North Pacific.

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