

Latitudinal Variations in Abundance of Phytoplankton, Macrozooplankton, Salmonids, and Other Epipelagic Fishes in the Northern Pacific Ocean and Bering Sea in Summer

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Latitudinal changes in abundance of phytoplankton, macrozooplankton, salmonids (*Oncorhynchus* spp.) and other epipelagic fishes were surveyed from mid-June to early July in 1992 and 1993 along a transect at 179° 30'W from 38° 30'N-58° 30'N. In the Bering Sea (52° 00'N-58° 30'N) where salmonids were abundant, macrozooplankton biomass was low whereas phytoplankton abundance was high. In the Transition Domain (42° 00'/43° 00'N-46° 00'N) with low salmonid abundance, macrozooplankton biomass was high but phytoplankton stock was at a low level. Salmonid abundance annually varied in the subarctic North Pacific, and when salmonids were abundant there, macrozooplankton biomass was low but phytoplankton stock was high, and vice versa. These results imply that salmonid predation may have resulted in the low abundance of macrozooplankton, which may have enhanced the phytoplankton stock. In the regions with low salmonid abundance, the proportion of large-sized phytoplankton (>10 μm) was low but that of copepods was high, possibly because reduced predation pressure of salmonids may have enhanced the copepod grazing on large-sized phytoplankton. The catch of pink salmon (*O. gorbuscha*) was high in 1993 and this species seems to play an important role in reducing the macrozooplankton biomass in central North Pacific in summer. Since the macrozooplankton biomass in the Transition Domain is controlled by the feeding of planktivorous fishes (e.g., Pacific saury *Cololabis saira*) migrating from the more southerly subtropical North Pacific (38° 30'N-42° 00'/43° 00'N), these fishes appear to give stronger negative effects, than salmonids, on the abundance of macrozooplankton in the Transition Domain where salmonid abundance is low.

Key words: top-down control of biomass, salmonids, zooplankton, phytoplankton, North Pacific Ocean, Bering Sea

Introduction

It has been generally accepted that the abundances of phytoplankton and macrozooplankton vary between oceanic water masses of the North Pacific Ocean (McGowan and Williams, 1973; Taniguchi, 1981; Hayward and McGowan, 1985; Percy, 1991). Recently, Odate (1994) found that the early summer macrozooplankton abundance in the Transition Domain is highly affected by planktivorous fishes (i.e., Pacific saury *Cololabis saira*) and suggested a top-down control theory in that the feeding of this fish reduces the macrozooplankton biomass and enhances the abundance of microzooplankton and large-sized phytoplankton (>10 μm) due to suppressed grazing by macrozooplankton on the latter plankters. Shiimoto et al. (1997) also made a similar suggestion in the relationship between Pacific salmon (*Oncorhynchus* spp.) and macrozooplankton abundance in the subarctic North Pacific Ocean.

The aim of the present paper is to test such a top-down control theory of biomass, focusing on latitudinal changes or between-domain differences in chlorophyll-*a* concentration, macrozooplankton biomass, and abundance of salmonids and other epipelagic fishes in oceanic waters of the subarctic North Pacific Ocean and the Bering Sea.

Materials and Methods

The study was conducted at 21 stations along a south-to-north transect at 179° 30'W from 38° 30'N to 58° 30'N (Fig. 1) in the central North Pacific Ocean and the Bering Sea (Ishida et al., 1992; Nagasawa et al., 1994). Sampling was done from mid-June to early July in 1992 and 1993.

Oceanography

At each station, oceanographic data including temperature and salinity were recorded at 1-m intervals to a depth of 600 m or more using an Alec Memory STD sensor (Alec Electronics Co. Ltd., Japan). Surface seawater was collected for later precise salinity measurements in the laboratory. Subsamples of the seawater were frozen and brought to the laboratory, where macronutrients (NO₂ + NO₃) were measured using a TRAACS-800 Auto Analyzer (Bran and Lube Co. Ltd., Germany) (Parsons et al., 1984).

Phytoplankton

Surface seawater was collected using a plastic bucket around noon at each of 21 stations, where it was sieved through a 200 μm mesh screen to remove large zooplankton. For assessing the total phytoplankton stock, the seawater was filtered through a Whatman GF/F filter. For estimation of size-fractioned

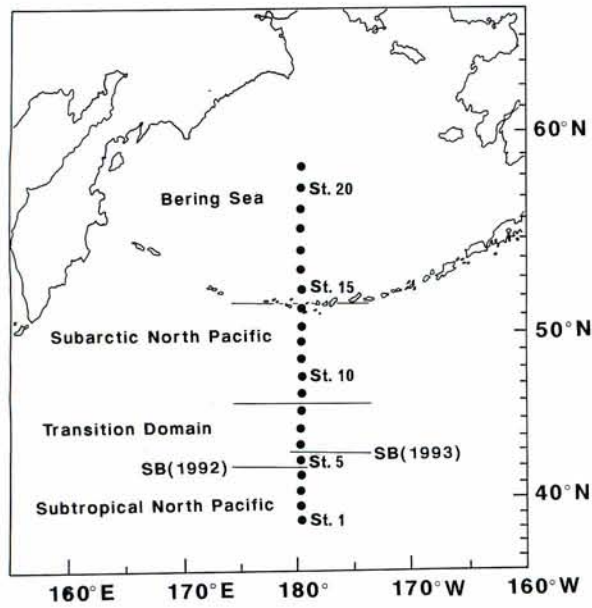


Fig. 1. Location of sampling stations during the cruises of the R/V *Wakatake maru* along a transect at 179° 30' W longitude from mid-June to early July in 1992 and 1993. The survey region was divided into four water masses: subtropical North Pacific, Transition Domain, subarctic North Pacific, and Bering Sea. SB: Subarctic Boundary.

chlorophyll-*a* concentration, the seawater was also filtered, through both Nuclepore filters of 10 and 2 μ m pore sizes and a Whatman GF/F filter. These filters were frozen, brought to the laboratory, where they were put into in glass vials containing 90% acetone for extraction of chlorophyll-*a*. Fluorescence was measured with a Hitachi F-2000 fluorophotometer (Hitachi Co Ltd., Japan) (Parsons et al., 1984) and chlorophyll-*a* concentration was determined for three fractions, i.e., <2 μ m, 2-10 μ m, and >10 μ m. In this study, the fractions smaller than 2 μ m and larger than 10 μ m are defined as small- and large-sized phytoplankton, respectively. Latitudinal changes in distribution of chlorophyll-*a* concentration in the study area (excluding the Bering Sea) have been reported by Shiimoto et al. (1999).

Macrozooplankton

Macrozooplankton was collected using a North Pacific standard plankton net (0.45 m diameter, 1.95 m length, 0.335 mm mesh size) (Motoda, 1957) after the evening longline operation at every station. The plankton net was towed vertically from 150 m to the surface at a speed of 1 m per second. Filtered water volume was measured using a calibrated flow meter (Rigosha Co. Ltd., Japan). The samples were fixed in a 10% formalin-seawater solution.

The macrozooplankton samples were sorted to nine taxonomic categories, such as euphausiids, copepods, amphipods, pteropods, appendicularians, chaetognaths, fishes, squids, and others, in the laboratory. Total macrozooplankton biomass at each station is defined here by summing the wet weight of these categories. Large (>2 cm) gelatinous organisms were excluded

from data analysis. Detailed data on macrozooplankton biomass used in this paper have been published by Tadokoro et al. (1995).

Salmonids and Other Fishes

Distribution of salmonids and other epipelagic fishes was surveyed at each of 21 stations. Although two types of fishing gear, longlines and gillnets, were used to collect those fishes, only data from longline catch are used here because gillnets were not employed within the U.S. 200-mile EEZ. The longlines were set 30 minutes before sunset and hauled 30 minutes after sunset. The longlines comprised 30 hachi (one hachi was about 111 m long and had 49 hooks), and salted Japanese anchovy (*Engraulis japonicus*) was used as bait. Soon after removal from the longlines, fishes were sorted to the species level, counted, and their biological data (body length, body weight, sex, gonad weight, stomach contents, etc.) were taken. The longline catch represents the abundance of salmonids occurring at each station but may underestimate the abundance of small planktivorous fishes such as Pacific saury.

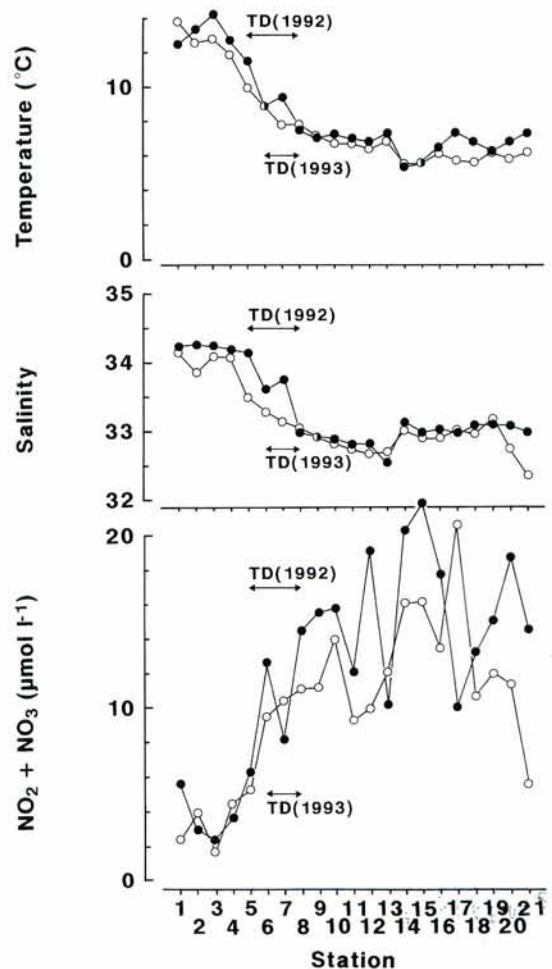


Fig. 2. Latitudinal changes in sea-surface temperature (top), sea-surface salinity (middle), and concentration of $\text{NO}_2 + \text{NO}_3$ (bottom) along a transect at 179° 30' W from mid-June to early July in 1992 (○) and 1993 (●). TD: Transition Domain.

Results

Oceanographic Structure

The Subarctic Boundary, indicated by a vertical 34.0 isohaline from the surface to 200 or 400 m (Dodimead et al., 1963), was located near 42° 00'N in 1992 and 43° 00'N in 1993. The subtropical North Pacific was located south of the Subarctic Boundary (Fig. 1). The Transition Domain, distinguished by cold waters less than 4° C at depths below 100 m (Favorite et al., 1976), extended from 42° 00'N-46° 00'N in 1992 and from 43° 00'N-46° 00'N in 1993, being located north of the Subarctic Boundary. Although the surface water north of the Transition Domain can be divided into four water masses (i.e., Subarctic Current System, Alaska Current System, Bering Current System, and Bering Sea Gyre)(Favorite et al., 1976), these are combined into two regions in this study: subarctic North Pacific (46° 00'N-52° 00'N) and Bering Sea (52° 00'N-58° 30'N)(Fig. 1).

Both sea-surface temperature and salinity were the highest in the subtropical North Pacific and decreased northward to the Transition Domain (Fig. 2). They remained low in the subarctic North Pacific and the Bering Sea. The concentration of nitrogenous nutrients (NO₂ + NO₃) in the surface water was the lowest in the Transition Zone (Fig. 2). They increased northward to the Transition Domain and subarctic North Pacific

although it decreased in the Bering Sea in 1993.

Regional Abundance of Phytoplankton

There was a substantial difference in total chlorophyll-*a* concentration between the four oceanographic regions (subtropical North Pacific, Transition Domain, subarctic North Pacific, and Bering Sea)(Fig. 3). The most prominent feature was that the chlorophyll-*a* concentration remained at the lowest level in the Transition Domain in both 1992 and 1993, whereas it was much higher in both the subtropical North Pacific and the Bering Sea. The concentration in the subarctic North Pacific varied markedly between years, low in 1992 but high in 1993.

There were also annual differences in mean chlorophyll-*a* concentration between 1992 and 1993 in the northern region (combined by the subarctic North Pacific and the Bering Sea), where salmonids were abundantly distributed (see below): mean value (0.90 μg/l) in this vast region for 1993, high salmonid abundance year, was much higher than that (0.36 μg/l) for 1992, low salmonid abundance year.

Although there were some variations among surveyed locations in percent composition of three size fractions of phytoplankton (Fig. 4), there was a tendency that in the regions where the total chlorophyll-*a* concentration was low (i.e., the Transition Domain and the subarctic North Pacific in 1992 and the Transition Domain in 1993) small-sized hytoplankton (<2 μm) predominated but the proportion of large-sized

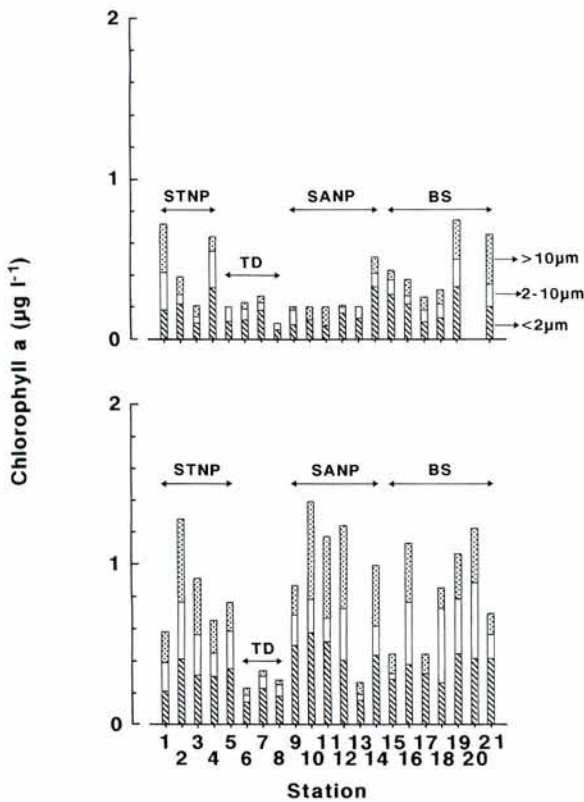


Fig. 3. Latitudinal changes in total chlorophyll-*a* concentration along a transect at 179° 30'W from mid-June to early July in 1992 (top) and 1993 (bottom). STNP: subtropical North Pacific, TD: Transition Domain, SANP: subarctic North Pacific, BS: Bering Sea.

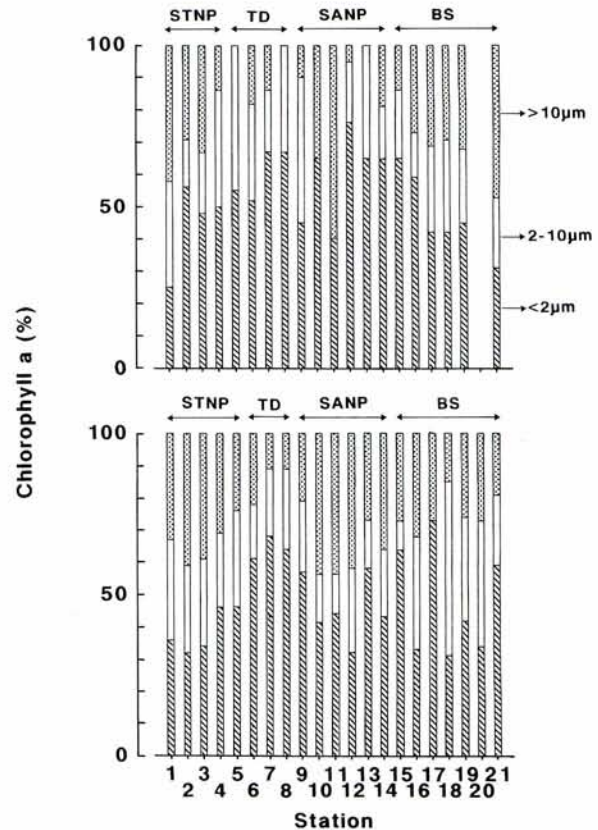


Fig. 4. Latitudinal changes in percentage of three size fractions of chlorophyll-*a* along a transect at 179° 30'W from mid-June to early July in 1992 (top) and 1993 (bottom). STNP: subtropical North Pacific, TD: Transition Domain, SANP: subarctic North Pacific, BS: Bering Sea.

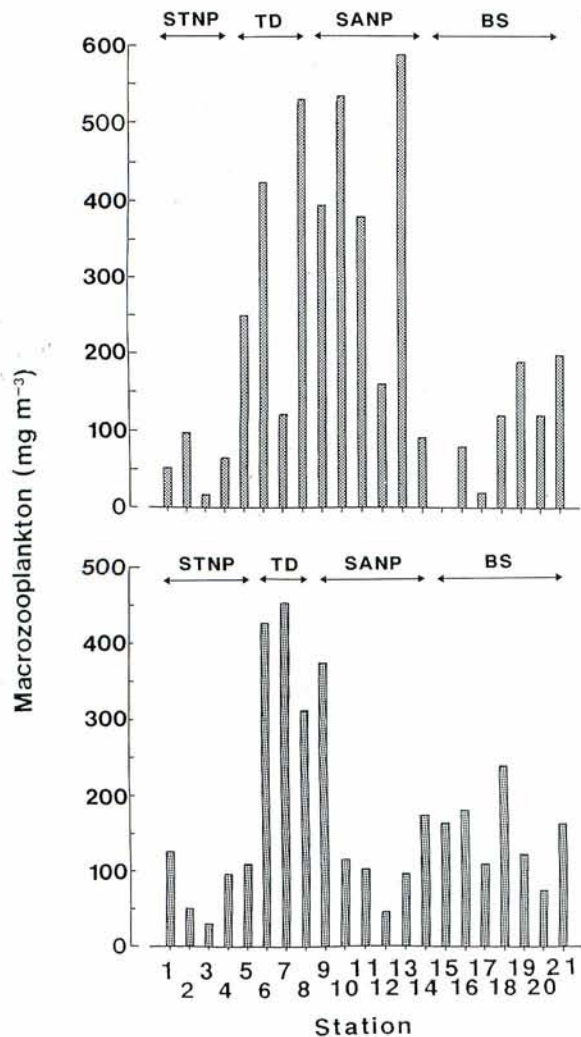


Fig. 5. Latitudinal changes in macrozooplankton biomass along a transect at $179^{\circ} 30'W$ from mid-June to early July in 1992 (top) and 1993 (bottom). STNP: subtropical North Pacific, TD: Transition Domain, SANP: subarctic North Pacific, BS: Bering Sea.

phytoplankton ($>10 \mu m$) was low.

Regional Abundance of Macrozooplankton

Latitudinal changes in the biomass of macrozooplankton showed a opposite pattern to those in total chlorophyll-*a* concentration (Fig. 5). Macrozooplankton abundance was low in the subtropical North Pacific, but it was high in the Transition Domain. Macrozooplankton in the subarctic North Pacific were abundant in 1992 but was at a low level in 1993. The biomass of macrozooplankton in the Bering Sea showed relatively lower values.

In addition, macrozooplankton biomass in the northern region (combined by the subarctic North Pacific and the Bering Sea), where salmonids were mainly distributed (see below), varied between 1992 and 1993: mean value (262 mg/m^3) in this region for 1992, low salmonid abundance year, was higher than that (152 mg/m^3) for 1993, high salmonid abundance year.

Copepods predominated at most of the stations,

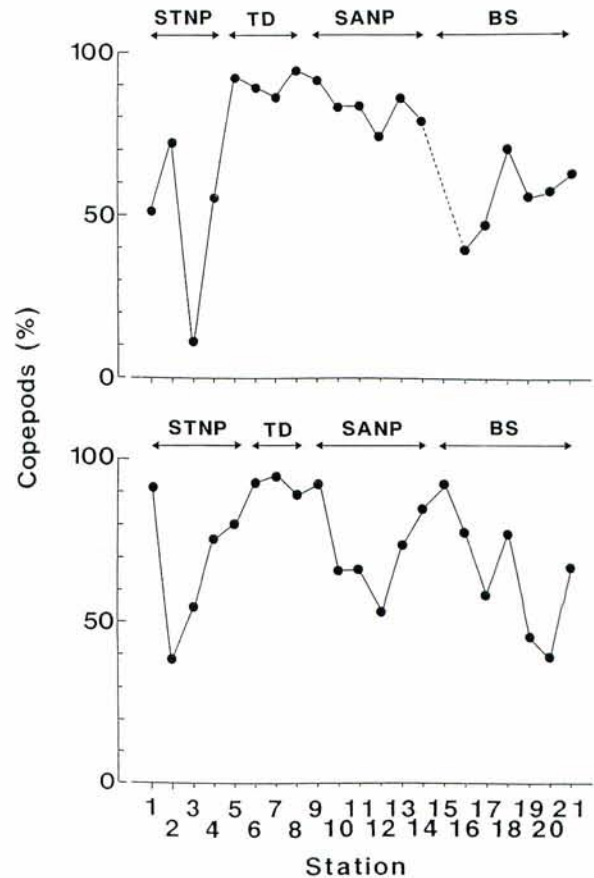


Fig. 6. Latitudinal changes in percentage of copepods in macrozooplankton biomass along a transect at $179^{\circ} 30'W$ from mid-June to early July in 1992 (top) and 1993 (bottom). STNP: subtropical North Pacific, TD: Transition Domain, SANP: subarctic North Pacific, BS: Bering Sea.

followed by chaetognaths and euphausiids. Their percentage peaked in the Transition Domain and then slightly decreased northerly to the subarctic North Pacific and the Bering Sea, while their lowest proportion was recorded in the subtropical North Pacific (Fig. 6).

Regional Abundance of Salmonids and Other Fishes

Salmonids caught consisted of six species: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), coho salmon (*O. kisutch*), chinook salmon (*O. tshawytscha*), and steelhead trout (*O. mykiss*). These salmonids accounted for 44.7% and 77.8% of the total fish catch in number in 1992 (N=1359) and 1993 (N=1248). There was an annual variation in salmonid abundance between 1992 and 1993: their catch per longline operation being higher in 1993 (46.2 fish) than in 1992 (28.7 fish). Although chum and pink salmon predominated among the salmonids, the catch of the latter species was high in 1993. Fishes other than salmonids were Pacific pomfret (*Brama japonica*) from the subtropical North Pacific and the Transition Domain, and Atka mackerel (*Pleurogrammus monopterygius*) and walleye pollock (*Theragra chalcogramma*) from the northern subarctic North Pacific and the Bering Sea. No Pacific sauries

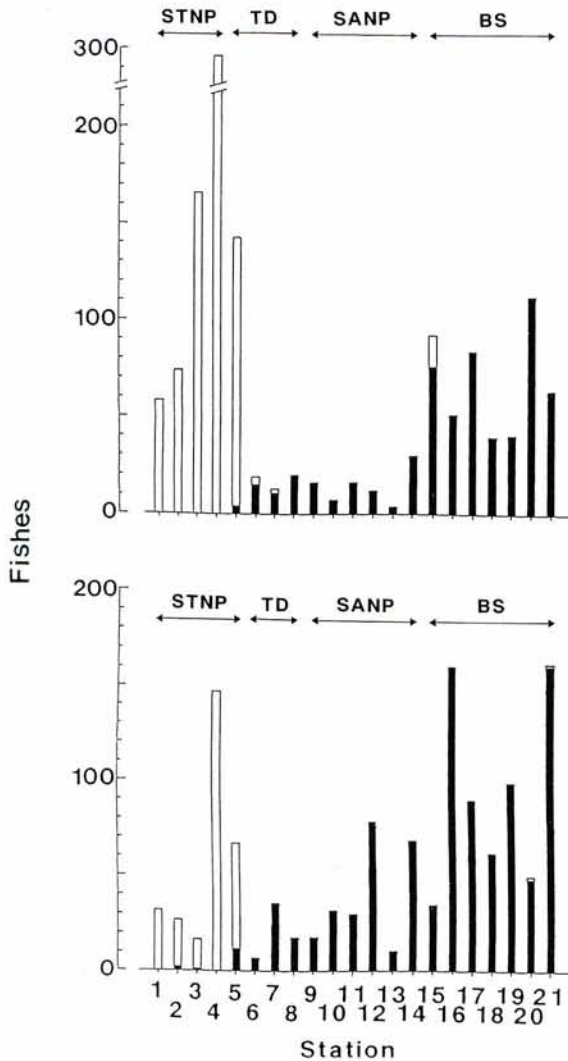


Fig. 7. Latitudinal changes in number of salmonids (closed histograms) and other epipelagic planktivorous fishes (open histograms) caught along a transect at 179° 30' W from mid-June to early July in 1992 (top) and 1993 (bottom). STNP: subtropical North Pacific, TD: Transition Domain, SANP: subarctic North Pacific, BS: Bering Sea.

(*Cololabis saira*) were collected in the subtropical North Pacific by longlines but they were taken by gillnets there.

In the subtropical North Pacific, the catch was mostly Pacific pomfret with only a few salmonids (Fig. 7). In the Transition Domain, Pacific pomfret decreased greatly and salmonids predominated although their abundance was quite low. There was a between-year variation in salmonid catch, low in 1992 and high in 1993, in the subarctic North Pacific. Salmonids were abundant in the Bering Sea.

In the subarctic North Pacific where annual salmonid catch was lower in 1992 than in 1993, mean macrozooplankton biomass (383 mg/m³) for 1992 was higher than that (152 mg/m³) for 1993.

Discussion

The most important fact found in the present study is that there were close relationships between the abundances of phytoplankton, macrozooplankton, and salmonids. In the Bering Sea where salmonids were abundant, macrozooplankton biomass was low whereas phytoplankton abundance was high. Contrary to this, in the Transition Domain where salmonid abundance was low, macrozooplankton biomass was high but phytoplankton stock was at a low level. Salmonid abundance annually varied in the subarctic North Pacific, and when salmonids were abundant there, macrozooplankton biomass was low but phytoplankton stock was high and *vice versa*. These results imply that a top-down (fish-macrozooplankton-phytoplankton) controlling process exists in the open subarctic Pacific Ocean and the Bering Sea, as has been suggested by Odate (1994) and Shiimoto et al. (1997). In other words, salmonid foraging might have resulted in the low abundance of macrozooplankton, which in turn enhanced the phytoplankton stock due to suppressed grazing by macrozooplankton on phytoplankton, particularly large-sized phytoplankton.

The proportion of large-sized phytoplankton (>10 μm) was low in the regions with low salmonid abundance (i.e., the Transition Domain and the subarctic North Pacific in 1992 and the Transition Domain in 1993). This can be explained by the above top-down control theory because decreased predation by salmonids may have enhanced the copepod grazing on those phytoplankters. Copepods are known as grazers of large-sized phytoplankton (Marshall and Orr, 1956). The proportion of copepods was highest in those regions, and this situation may have caused high copepod grazing pressure on large-sized phytoplankton. Shiimoto et al. (1999) currently have suggested that heavy grazing by macrozooplankton reduces the phytoplankton standing stock in the Transition Domain in summer.

Based on a discussion on the potential effect of salmonid feeding on their prey abundance in the subarctic North Pacific, Perry et al. (1998) suggested that exceptionally high abundance of salmonids (e.g., Asian pink salmon) can affect the abundance of local zooplankton biomass. In our study, the abundance of pink salmon increased in 1993, when macrozooplankton biomass in the subarctic North Pacific was low. Thus, pink salmon feeding may play important role in affecting the macrozooplankton abundance. Numerous maturing adult pink salmon (mostly of Kamchatkan origin) are present in the central North Pacific and the central Bering Sea in summer in odd-number years (Takagi et al., 1981). Although pink salmon do not feed only on macrozooplankton, their feeding may reduce the macrozooplankton biomass in seasons and years when their abundance is high (e.g., summer in 1993) and in areas where they are numerous (e.g., the subarctic North Pacific in 1993). We also think that a top-down predator control is not found in the entire subarctic North Pacific in all seasons but occurs in some limited areas and times when salmonids,

especially pink salmon and Pacific saury (see below), are very abundant.

The concentrations of nitrogen, phosphate, and silicate recorded from the Transition Domain and subarctic North Pacific were not at low levels. This indicates that these nutrients were not responsible for the observed low abundance of phytoplankton.

The present study did not examine the abundance of microzooplankton, which are recently regarded as important grazers of phytoplankton (Frost, 1987, 1991). Also, microzooplankton are major food items of macrozooplankton (Gifford, 1993). According to Odate (1994) who surveyed the abundance of phytoplankton, micro-, and macrozooplankton along 180° longitude in the northern North Pacific in early summer, there was a reverse relationship between micro- and macrozooplankton. Thus, to understand quantitative relationships between macrozooplankton and phytoplankton, it is necessary to study the distribution and abundance of microzooplankton in future research, as well.

Shiomoto et al. (1997) reported that phytoplankton stock was suppressed at low level by intense grazing pressure by zooplankton in the year when pink salmon abundance was small. A similar between-year difference trend was found in the present study: low abundance of salmonids and phytoplankton but high biomass of macrozooplankton in 1992 whereas high abundance of salmonids and phytoplankton but low biomass of macrozooplankton in 1993. These results suggest that the feeding of salmonids may be partially responsible for interannual variations in abundance of zoo- and phytoplankton in the oceanic subarctic North Pacific.

It has been reported that the macrozooplankton abundance in the Transition Domain is lower than in the subarctic North Pacific (Taniguchi, 1981; Pearcy, 1991). However, this is not always true, particularly in summer. In our study, high macrozooplankton biomass was recorded for mid-June in the Transition Domain. Based on the top-down control theory, this is caused by the fact, in addition to low abundance of salmonids, most of migratory planktivorous fishes, such as Pacific pomfret and Pacific saury, have not yet arrived in the Transition Domain and thus gave little impacts on macrozooplankton biomass. In the case of Odate (1994) who also surveyed in mid-June in the central Pacific, Pacific sauries have already entered the southern part of the Transition Domain and reduced the abundance of macrozooplankton. Following these observations, it is plausible that macrozooplankton biomass in the Transition Domain varies markedly in summer before and after the arrival of numerous migratory planktivorous fishes from the more southerly subtropical North Pacific. The abundance of salmonids in the Transition Domain is low because this region corresponds to the southern limit of their distribution. Thus, the importance of migratory planktivorous fishes from south as predators of macrozooplankton in this domain appears to be much higher than that of salmonids.

Fishes that were not caught by longlines are not considered here, but myctophids, for example, are very

abundant and some species migrate to the near-surface water at night (Pearcy et al., 1977; Nagasawa et al., 1997). We should evaluate the importance of such fishes to control the macrozooplankton biomass, as well.

Shiga et al. (1995) found that the early summer abundance of macrozooplankton varied among years in the Transition Domain and attributed it to the different abundance of salps. This suggests that large filter-feeding zooplankton grazing is important in determining the macrozooplankton abundance in this region. There is yet sparse information on prey-predator relationships at lower and higher trophic levels in the Transition Domain, further study is needed to understand a relationship of prey and predators in this area. In addition, Contrary to our implication, Dagg (1993) found that grazing by copepods does not control phytoplankton production in the eastern subarctic Pacific region. There may be regional differences in controlling the structure and function of biological production in the subarctic Pacific. We need more information about area-specific features of biological production in the northern North Pacific.

In conclusion, the present study implies at least that a top-down controlling process, in which salmonids and other migratory epipelagic planktivorous fishes play as top predators, is present in the central subarctic North Pacific and the central Bering Sea in summer.

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夏季の北部北太平洋とベーリング海における動植物プランクトン現存量及びさけ・ます類と他の浮魚類の豊度の緯度別変化

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摘 要

1992年と1993年の6月中旬～7月上旬に西経179度30分線上の北緯38度30分～58度30分において、動植物プランクトン現存量及びさけ・ます類と他の浮魚類の豊度の緯度別分布を調べた。さけ・ます類が多く分布したベーリング海（北緯52度～58度30分）では、動物プランクトン量が少なかったが植物プランクトン量は多かった。しかし、さけ・ます類が少なかった移行領域（北緯42/43度～46度）では、動物プランクトン量は多かったが植物プランクトン量は少なかった。亜寒帯水域（北緯46度～52度）ではさけ・ます類の豊度が年によって異なり、さけ・ます類が多かった年には動物プランクトン量は少なく、植物プランクトン量は多かった。逆にさけ・ます類が少なかった年には、動物プランクトン量が多く、植物プランクトン量は少なかった。これらの結果は、さけ・ます類の摂餌が動物プランクトン量を低くする結果、植物プランクトン量の増加を招くことを示唆する。実際、さけ・ます類が少なかった水域では、大型植物プランクトン（10 μ m以上）が少なく、カイアシ類が多かった。これは、さけ・ます類によるカイアシ類への捕食圧が減少した結果、カイアシ類による植物プランクトンの摂食が高まったことに原因すると考えられた。さらに、移行領域の動物プランクトン量は、さけ・ます類に加えて、南の亜熱帯水域から回遊してくるプランクトン食性魚類（サンマ）の摂餌によってもコントロールされていると推察された。

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