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LATITUDINAL VARIATIONS IN DISTRIBUTION AND ABUNDANCE OF PLANKTON AND SALMONIDS IN THE NORTHERN PACIFIC OCEAN AND BERING SEA IN EARLY SUMMER

by

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ABSTRACT

Latitudinal changes in the distribution and abundance of phytoplankton, macrozooplankton and salmonids were surveyed during the cruises of the R/V *Wakatake maru* conducted from-mid June to early July in 1992 and 1993 along a transect at 179°30'W from 38°30'-58°30'N. In the Bering Sea (52°00'-58°30'N) where salmonids were abundant, macrozooplankton biomass was low whereas phytoplankton abundance was high. However, in the transition domain (42°00'/43°00'-46°00'N) where salmonid catch was low, macrozooplankton biomass was high but phytoplankton stock was at a low level. In the subarctic domain (46°00'-52°00'N), salmonid abundance varied between years but it had a negative relationship to macrozooplankton biomass and a positive relationship to phytoplankton stock. These 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 net phytoplankton (>10 μm) was indeed low but that of copepods was high, possibly because reduced predation pressure of salmonids may have enhanced the copepod grazing on those phytoplankters. Moreover, the macrozooplankton biomass in the transition domain is controlled by the feeding of planktivorous fishes migrating from the more southerly transition zone (38°30'-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 density is low.

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; Pearcy, 1991). Recently, Odate (1994) found that the early summer macrozooplankton abundance in the transition domain is highly affected by planktivorous fish (i.e., Pacific saury *Cololabis saira*) and suggested a top-down control theory in that the feeding of this fish reduces the macrozooplankton biomass in that domain, which enhances the abundance of microzooplankton and net phytoplankton (>10 μm) due to suppressed grazing by macrozooplankton on the latter plankters.

The aim of the present study is to test such a top-down control theory with focusing on Pacific salmon (*Oncorhynchus* spp.), as top predators, that predominate in oceanic waters of the subarctic North Pacific Ocean and Bering Sea. This study examines latitudinal changes or between-domain differences in chlorophyll *a* concentration, macrozooplankton biomass, and abundance of salmonids and other epipelagic fishes.

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 Bering Sea (Ishida et al., 1992; Nagasawa et al., 1994). Samplings were made 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 (NO_2 + NO_3, PO_4, SiO_2) 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 to remove large zooplankton through a 200 μm mesh screen. For assessing the total phytoplankton abundance, the seawater was filtered through a Whatman GF/F filter. For estimation of size-fractioned chlorophyll *a* concentration, the seawter was also filtered through both Nuclepore filters of 2 and 10 μm 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 μm, 2-10 μm, and >10 μm. In this study the fractions smaller than 2 μm and larger than 10 μm are defined, respectively, as picophytoplankton and net phytoplankton.

MACROZOOPLANKTON

Macrozooplankton samples were collected using a Norpac 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 Norpac net was towed vertically from 150 m to the surface with 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 10% Formalin in sea water.

The macrozooplankton samples were sorted to various taxonomic categories (i.e., euphausiids, copepods, amphipods, pteropods, appendicularians, chaetognaths, fishes, squids, others) in the laboratory. Macrozooplankton biomass at each station is defined here as the total weight of these categories. Large (>2 cm) gelatinous organisms were excluded for data analysis. Detailed data on macrozooplankton biomass used in this paper have been published elsewhere (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 no gillnets were 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 for 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.

RESULTS

OCEANOGRAPHIC STRUCTURE

The subarctic boundary, denoted as a vertical 34.0 isohaline from the surface to 200 or 400m (Dodimead et al., 1963), was located near 42°00'N and 43°00'N in 1992 and 1993, respectively. Thus, the transition zone (Roden, 1991; Pearcy, 1991), south of the subarctic boundary, was located south of approximately 42°00'N and 43°00'N in these years (Fig. 1).

The transition domain, north of the subarctic boundary and distinguished by cold waters less than 4°C at depths below 100m (Favorite at al., 1976), extended from 42°00'-46°00'N in 1992 and from 43°00'-46°00'N in 1993.

Although the surface layer north of the transition domain can be divided into 4 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 domain (46°00'-52°00'N) and Bering Sea (52°00'-58°30'N).

The concentration of nitrogenous nutrients (NO_2 + NO_3) in the surface layer was lowest in the transition zone but increased northward to the transition domain and subarctic domain although it decreased in the Bering Sea in 1993 (Fig. 2). Similar trends were recorded for other macronutrients: phosphate and silicate.

DISTRIBUTION AND ABUNDANCE OF PHYTOPLANKTON

There was a substantial difference in total chlorophyll *a* concentration between the four oceanographical regions (transition zone, transition domain, subarctic domain, and Bering Sea)(Fig. 3). The most prominent feature was that the chlorophyll concentration remained at the lowest level in the transition domain in both 1992 and 1993. However, it was much higher in both the transition zone and Bering Sea than in the transition domain. The concentration in the subarctic domain varied markedly between years, low in 1992 but high in 1993.

There were also annual differences in mean chlorophyll concentration between 1992 and 1993 in the northern region, combined by the subarctic domain and Bering Sea, where salmonids were abundantly distributed (see below): mean value (0.90 μ g/l) in this vast region for 1993, high salmonid adundance year, was much higher than that (0.36 μ g/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 subarctic domain in 1992 and transition domain in 1993) picophytoplankton (<2 μ m) predominated but the proportion of net phytoplankton (>10 μ m) was low.

DISTRIBUTION AND ABUNDANCE OF MACROZOOPLANKTON

Latitudinal changes in the biomass of macrozooplankton definitely showed opposite patterns to those in total chlorophyll *a* concentration (Fig. 5). Macrozooplankton abundance was low in the transition zone, but it was high in the transition domain. Macrozooplankton in the subarctic domain were abundant in 1992 but remained 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 domain and 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 all stations (except for one station), followed by chaetognaths and euphausiids. The lowest proportion of copepods was recorded in the transition zone but its percentage peaked in the transition domain and then slightly decreased northerly to the subarctic domain and Bering Sea (Fig. 6).

DISTRIBUTION AND 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 catch in 1992 (N=1359) and 1993 (N=1248). There were annual variations 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). Fishes other than salmonids were Pacific pomfret (*Brama japonica*) from the transition zone and transition domain, and Atka mackerel (*Pleurogrammus monopterygius*) and walleye pollock (*Theragra chalcogramma*) from the northern subarctic domain and Bering Sea. No Pacific sauries were collected in the transition zone by longlines but they were taken by gillnets there.

In the transition zone, most of the catch were Pacific pomfret with only a few salmonids being captured (Fig. 7). In the transition domain, the catch of Pacific pomfret decreased greatly and salmonids predominated although their abundance was quite low. There were between-year variations in salmonid catch, low in 1992 and at a moderate level in 1993, in the subarctic domain. Salmonids were abundant in the Bering Sea.

As to relationships to macrozooplankton biomass, in the subarctic domain where annual salmonid catch was lower in 1992 than in 1993, mean macrozooplankton biomass (383 mg/m^3) for 1992 was higher than that (152 mg/m^3) for 1993.

DISCUSSION

The most interesting fact found in the present study is that there were close associations between the distribution and abundance of phytoplankton, macrozooplankton, and salmonids. In other words, this study indicates that a top-down (fish-zooplankton-phytoplankton) controlling process exists in the open subarctic Pacific Ocean and Bering Sea, as has been recently suggested by Odate (1994) for the northern North Pacific. 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 catch was low, macrozooplankton biomass was high but phytoplankton stock was at a low level. Salmonid abundance annually varied in the subarctic domain but it had a negative relationship to macrozooplankton biomass but a positive relationship to phytoplankton stock. These imply that salmonid foraging may have resulted in the low abundance of macrozooplankton, which may have enhanced the phytoplankton stock due to suppressed grazing by macrozooplankton on phytoplankton, in particular net phytoplankton (see below).

The proportion of net phytoplankton (>10 μ m) was indeed low in the regions with low salmonid abundance (i.e., the transition domain and subarctic domain in 1992 and 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 net 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 net phytoplankton.

The concentrations of nitrogen, phospahte, and silicate recorded from the transition domain and subarctic domain 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 association between micro- and macrozooplankton. Thus, to better understand quantitative relationships between macrozooplankton and phytoplankton, it is necessary to study the distribution and abundance of microzooplankton in our future research, as well.

Cooney (1988) found that a weak but significant correlation between zooplankton and pink salmon abundance in the Gulf of Alaska: one year after higher than average salmon abundance, the stock of zooplankton was generally lower that the average. Shiomoto (1994) reported that phytoplankton stock was suppressed at a low level by intense grazing pressure by zooplankton in the year when pink salmon abundance was small. Similar between-year difference trends were 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 suggest that the feeding of salmonids may be partially responsible for interannual variations in abundance of phyto- and zooplankton in the oceanic subarctic Pacific. However, since little information is available on this, more studies are desired to evaluate the magnitude of salmonid foraging impacts on organisms at lower trophic levels.

It has been reported that the macrozooplankton abundance in the transition domain is lower than in the subarctic domain (Taniguchi, 1981; Pearcy, 1991). However, this is not necessarily true, particularly in the early summer season. 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 transition domain and reduced the abundance of macrozooplankton. Following these observations, it is plausible that macrozooplankton biomass in the transition domain varies markedly in early summer before and after the arrival of migratory planktivorous fishes from the more southerly transition zone.

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 as predators of macrozooplankton in this domain appears to be much higher than that of salmonids.

Recently, 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 controlling the macrozooplankton abundance in this region, as well as planktivorous fishes. There is yet sparse information on prey-predator relationships at lower and higher trophic levels in the transition domain, further study is needed in terms of the top-down control theory.

In conclusion, the present study indicates that a top-down controlling process, in which salmonids and other migratory epipelagic planktivorous fishes play as top predators, is present in the open subarctic Pacific and Bering Sea in early summer. In considering the biological productivity in this region, this idea will not be able to neglect and we should deepen it more quantitatively.

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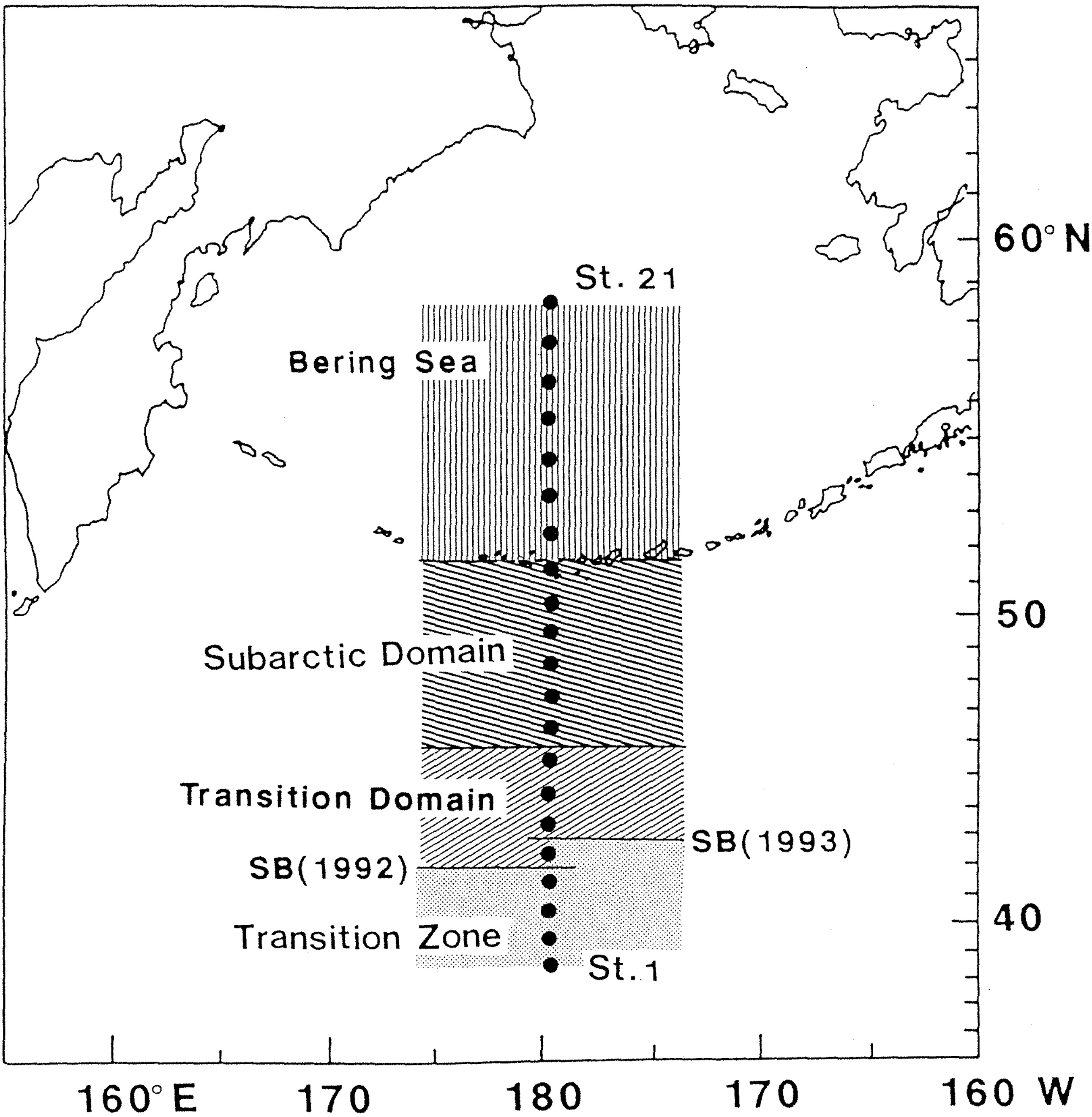

Fig. 1. Location of sampling stations during the cruises of the R/V *Wakatake maru* along a transect at 179° 30'W longitude from mid-June to early July in 1992 and 1993. The survey region was divided into four water masses: transition zone, transition domain, subarctic domain, and Bering Sea. SB: subarctic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

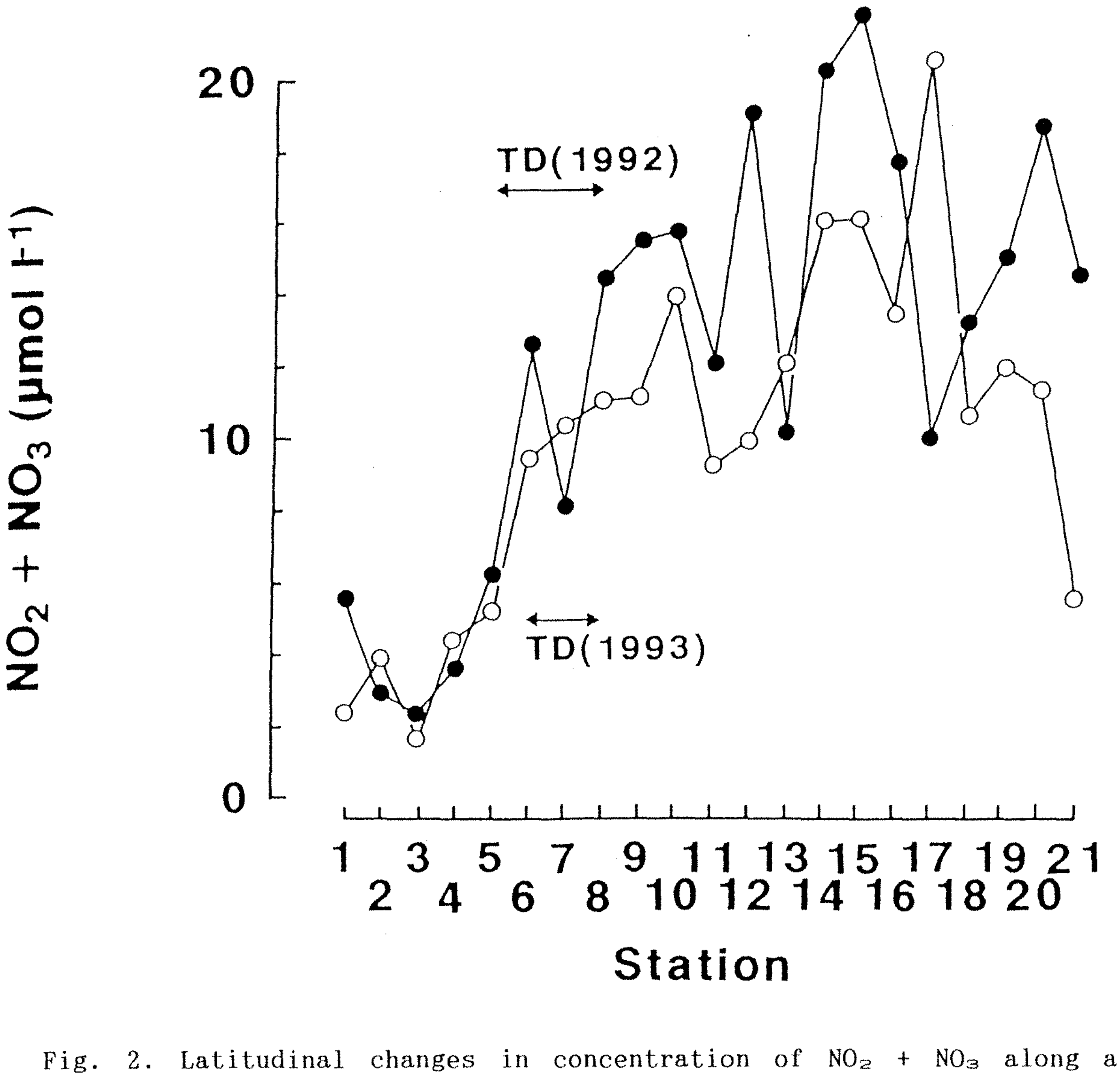

Fig. 2. Latitudinal changes in concentration of NO_2 + NO_3 along a transect at 179° 30'W from mid-June to early July in 1992 (○) and 1993 (●). TD: transition domain.

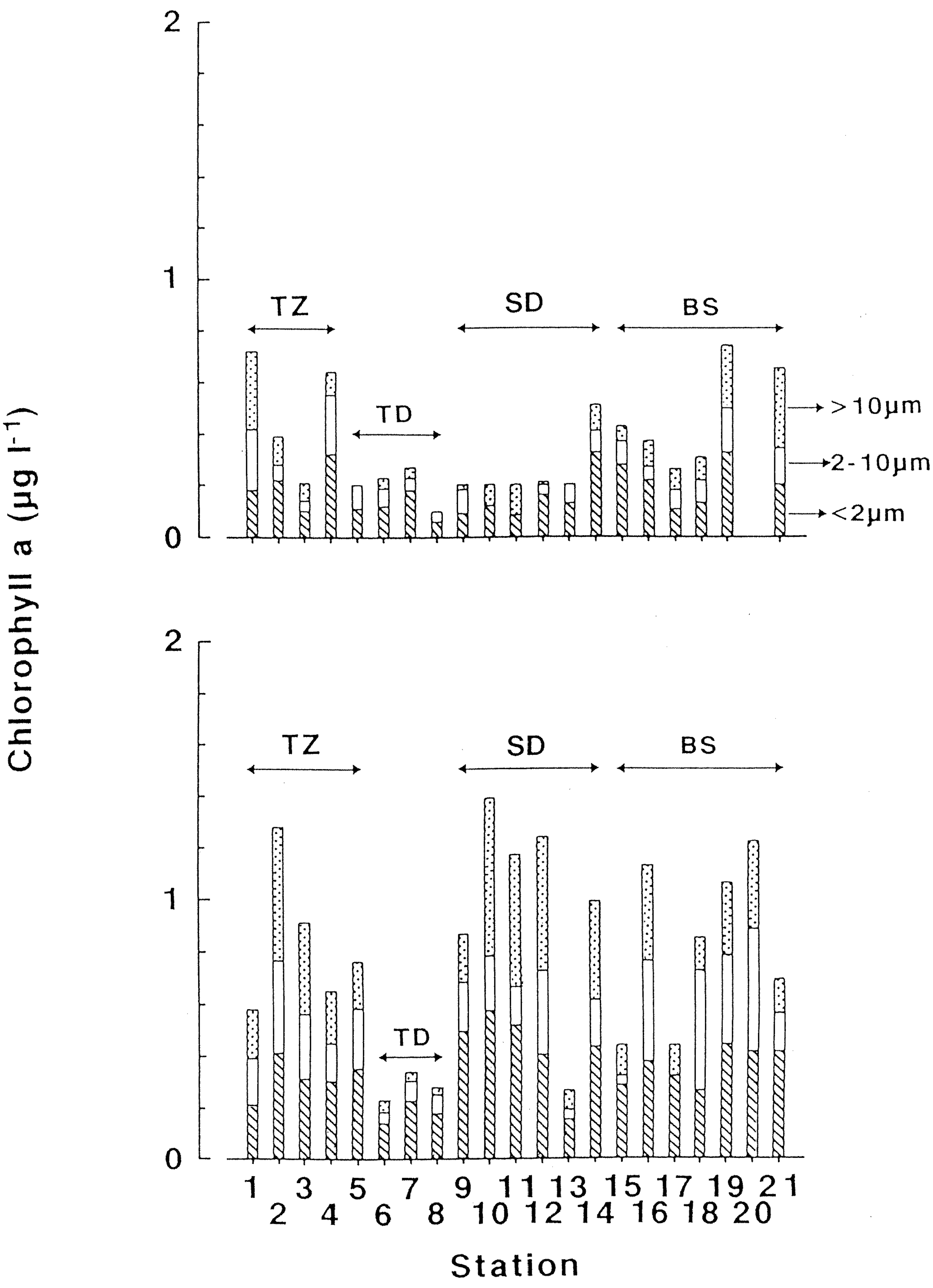

Fig. 3. Latitudinal changes in total chlorophyll *a* concentration along a transect at 179°30'W from mid-June to early July in 1992 (top) and 1993 (bottom). TZ: transition zone, TD: transition domain, SD: subarctic domain, BS: Bering Sea.

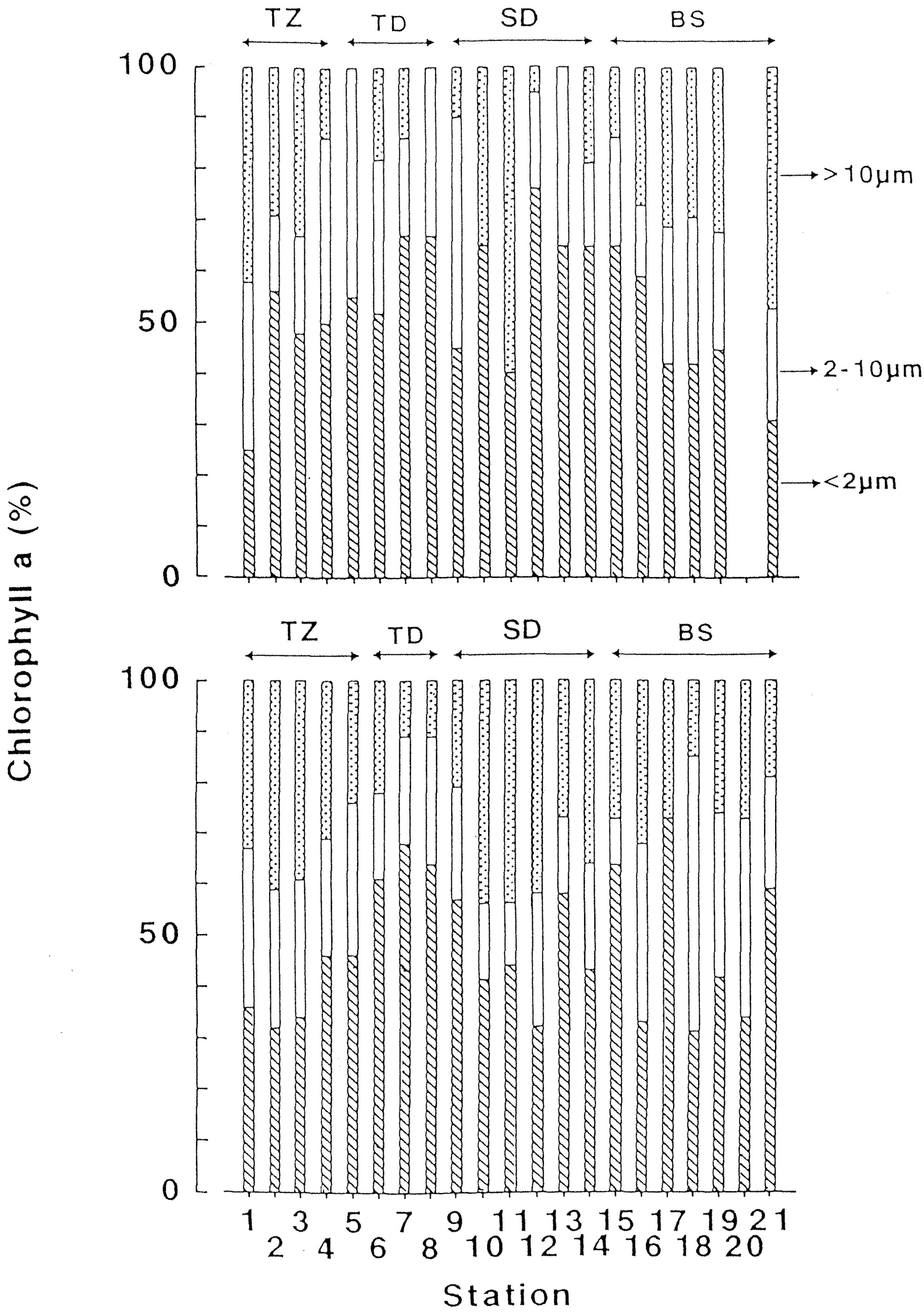

Fig. 4. Latitudinal changes in percentage of three size fractions of chlorophyll *a* along a transect at 179° 30'W from mid-June to early July in 1992 (top) and 1993 (bottom). TZ: transition zone, TD: transition domain, SD: subarctic domain, BS: Bering Sea.

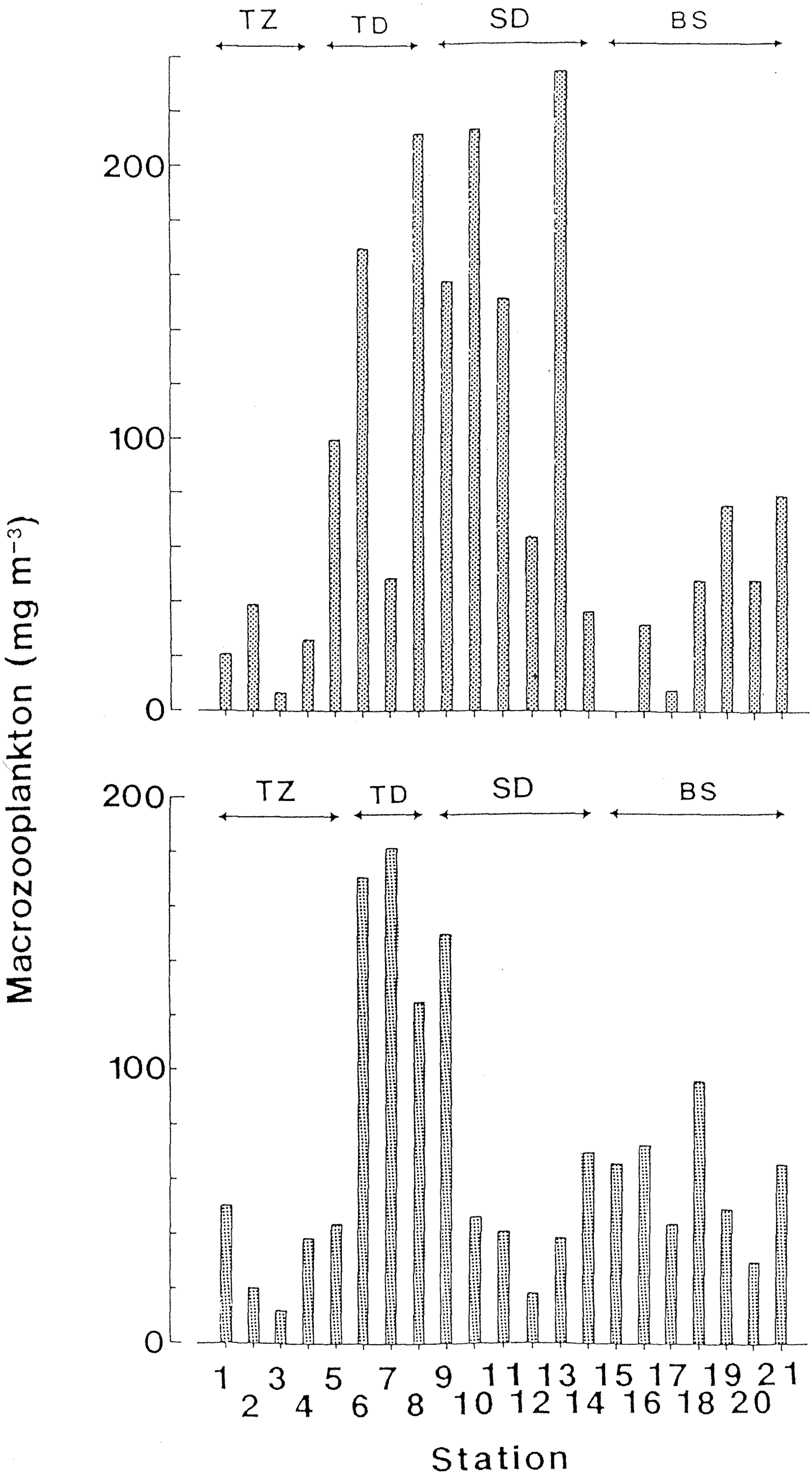

Fig. 5. Latitudinal changes in macrozooplankton biomass along a transect at 179°30'W from mid-June to early July in 1992 (top) and 1993 (bottom). TZ: transition zone, TD: transition domain, SD: subarctic domain, BS: Bering Sea.

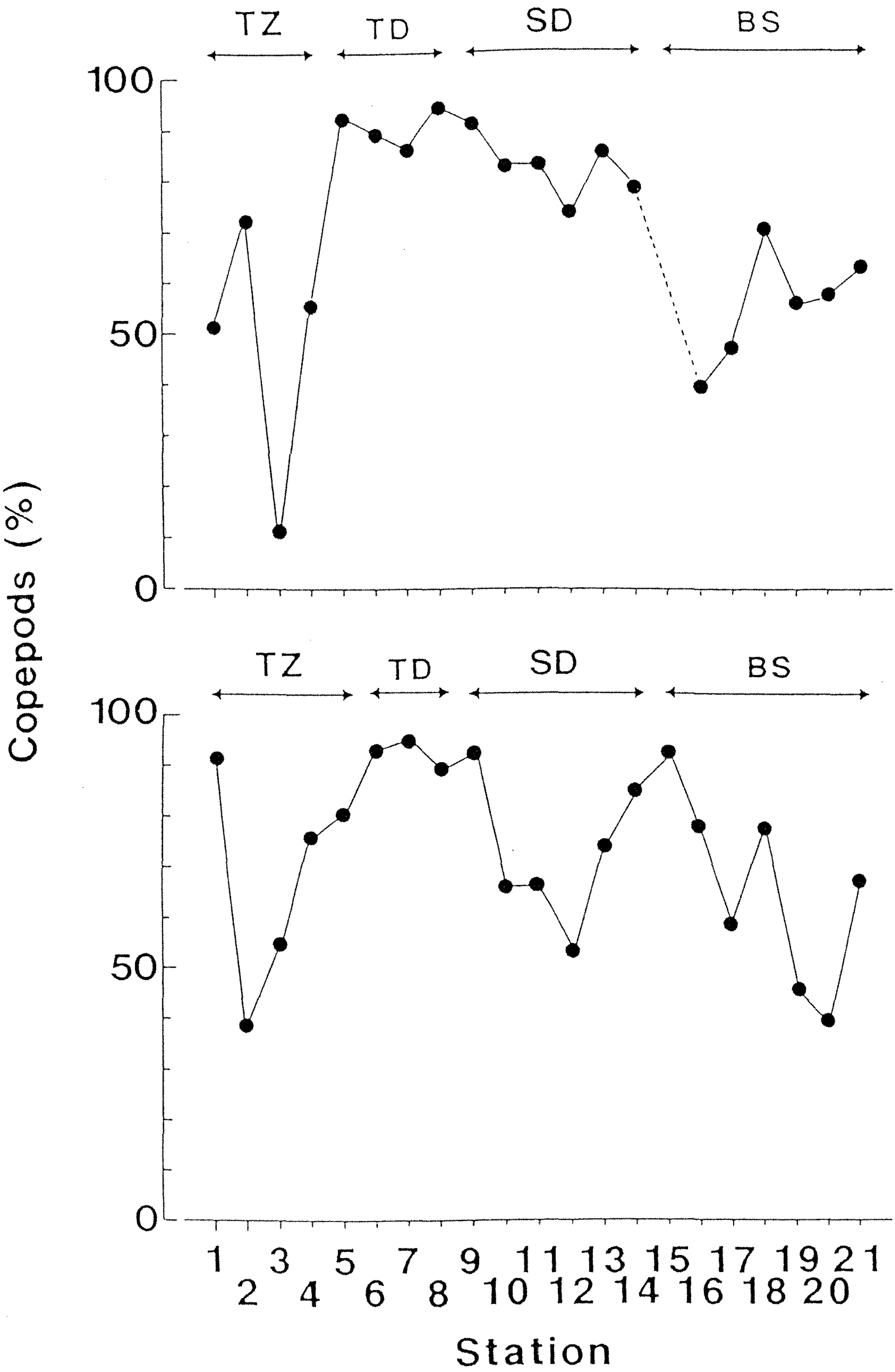

Fig. 6. Latitudinal changes in percentage of copepods in macrozooplankton biomass along a transect at 179° 30'W from mid-June to early July in 1992 (top) and 1993 (bottom). TZ: transition zone, TD: transition domain, SD: subarctic domain, BS: Bering Sea.

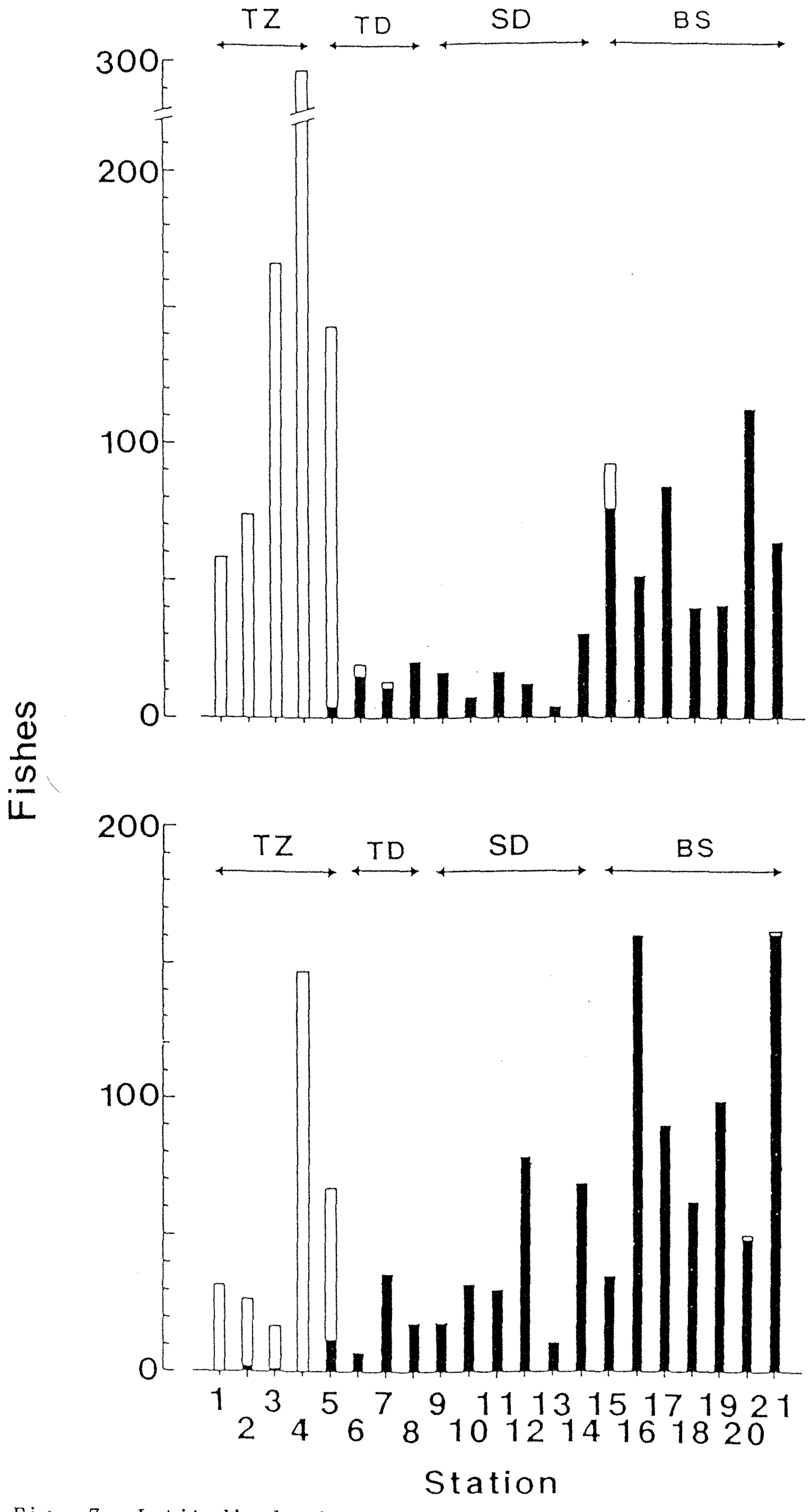

Fig. 7. Latitudinal changes in number of salmonids (closed histograms) and other epipelagic planktivorous fishes (open histograms) caught along a transect at 179°30'W from mid-June to early July in 1992 (top) and 1993 (bottom). TZ: transition zone, TD: transition domain, SD: subarctic domain, BS: Bering Sea.