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Pan-North Pacific comparison of long-term variation in *Neocalanus* copepods based on stable isotope analysis

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ABSTRACT

Regional differences in the mechanisms of temporal variation in the lower trophic levels in the western, central, and eastern subarctic North Pacific were studied using the nitrogen stable isotope ratio (δ^{15}N) of the major copepod species, *Neocalanus cristatus*, *Neocalanus flemingeri*, and *Neocalanus plumchrus*. We used formalin-preserved specimens collected in the Oyashio region (OY), three sections from north to south along the 180° longitudinal line (180LineSA, TN, and TS), off Vancouver Island (Off-Van), and at Sta. P, during the periods of 1960–2000, 1979–1997, 1981–2007, and 1996–2007, respectively. The regional mean δ^{15}N of the three species roughly corresponded to the surface nitrate distribution and the extent of its drawdown from winter to spring; it was higher in regions of larger seasonal drawdown as observed in the coastal regions OY and Off-Van (7–10‰), but lower in regions with less seasonal drawdown, such as in the offshore regions at St. P and stations along the 180Line (3–6‰). Time series analysis revealed possible region-specific mechanisms for temporal variation in *Neocalanus* δ^{15}N. First, δ^{15}N indicated shifts in feeding strategies between herbivorous to omnivorous/carnivorous at OY and 180LineSA, where δ^{15}N tended to be lower in the years with warmer winters, suggesting that *Neocalanus* took advantage of enhanced phytoplankton production under favorable light availability due to increased stratification. Conversely, wind-induced latitudinal advection of surface water was considered to be the initial cause of interannual variation in *Neocalanus* δ^{15}N at 180LineTN, 180LineTS, and Off-Van, where δ^{15}N was higher in the years with strong southerly or westerly winds at 180LineTN and TS, and the Off-Van site. This suggests that pole-ward transport of relatively oligotrophic, southern water might enhance the uptake of the heavier isotope by phytoplankton, which *Neocalanus* feed upon. Another possibility at the Off-Van site, where high δ^{15}N was observed (*c.a.*, 8–10‰), is a switch in the *Neocalanus* feeding strategy induced by decreased phytoplankton availability. This study demonstrated the usefulness of zooplankton δ^{15}N as an indicator of interannual variation in lower trophic level environments and food web structures, which are caused by region-specific mechanisms.

1. Introduction

Retrospective studies have revealed that historically collected zooplankton samples/data sets can provide useful information about how marine ecosystems respond to climatic and environmental change at various spatiotemporal scales (*e.g.*, Perry et al., 2004). Based on the community-level breakdown of zooplankton data, phenological changes (Mackas et al., 1998; Edwards and Richardson, 2004; Chiba et al., 2006) and the biogeographical shift (Beaugrand et al., 2002; Batten and Welch, 2004; Mackas et al., 2006; Chiba et al., 2009) of the lower trophic levels in response to large-scale climatic forcing, such as the North Atlantic Oscillation and Pacific Decadal Oscillation, have been reported.

In the North Pacific (NP), the Aleutian Low is reported to drive the spatiotemporal temperature pattern as shown by the Pacific Decadal Oscillation index (PDO; Mantua et al., 1997). Although well documented as a temperature anomaly, the Aleutian Low influences the extent of wintertime vertical mixing and springtime stratification that determines nutrient and light availability within the euphopic zone, and thereby influences phytoplankton production (Polovina et al., 1995). Zooplankton abundance/biomass and community structure has varied according to the PDO, particularly

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during the climatic regime shift in the mid-1970s (Miller et al., 1994) and late 1980s (Hare and Mantua, 2000) in both the western (Sugimoto and Tadokoro, 1998; Chiba et al., 2008) and eastern NP (Brodeur et al., 1996; Mackas et al., 2004). Although these studies suggested that changes in seasonal and annual phytoplankton availability might affect secondary production, the detailed mechanisms linking changes in the environment, phytoplankton, and zooplankton are less clear.

Previous studies have reported that surface nitrate concentration was negatively correlated with nitrate δ^{15}N (Sigman et al., 2000) as well as δ^{15}N in particulate organic nitrogen ($\delta^{15}\mathrm{N}_{\mathrm{sus}}$) (Saino and Hattori, 1987) in regions, including the subarctic NP, where nitrate is the major nitrogen source for phytoplankton production. After finding a negative correlation between the depth of the nitricline and $\delta^{15}\mathrm{N}_{\mathrm{sus}}$ in a mid-latitude region (−45°N) under nitrate-depleting conditions, Mino et al. (2002) concluded that $\delta^{15}\mathrm{N}_{\mathrm{sus}}$ might be a useful indicator of algal production and nitrate utilization. While robust time-series data are not available for phytoplankton δ^{15}N, data for zooplankton δ^{15}N, which have been collected over the course of various time-series studies, can provide information about long-term changes in nitrate availability and primary production.

In fact, the nitrogen stable isotope ratios (δ^{15}N) of oceanic zooplankton and higher trophic levels can be used as indicators of variation in regional trophic structure (*e.g.* Welch and Parsons, 1993; Brodeur et al., 2002; Bode et al., 2004; Kaeriyama et al., 2004). δ^{15}N at the consumer level increases by approximately 3.4‰ as trophic level increases (reviewed in Minagawa and Yoshioka (2005)). Recently, additional studies have investigated the changes in δ^{15}N (and δ^{13}C) of zooplankton in conditions with different food sources and availability in the lab (Aberle and Malzahn, 2007) and the field (Sommer et al., 2005). Other studies reported spatio-temporal variation in the δ^{15}N of specific species in relation to environmental and climatic variation; *e.g.* decadal change in Pacific salmon (Satterfield IV and Finney, 2002) and ENSO scale change in zooplankton in the California Current System (Rau et al., 2003).

Neocalanus cristatus, *Neocalanus flemingeri*, and *Neocalanus plumchrus* are dominant, widely-distributed herbivorous copepods in the subarctic NP (Miller and Clemons, 1988; Tsuda and Sugisaki, 1994). Under oligotrophic conditions, the *Neocalanus* δ^{15}N is expected to increase due to (1) phytoplankton fractionation and (2) a shift toward an omnivorous feeding strategy under conditions of low phytoplankton availability (Gifford, 1993; Kobari et al., 2003a), and vice versa. Thus, we hypothesized that time-series evaluations of *Neocalanus* δ^{15}N might provide insights that would help clarify the mechanisms of spatio-temporal variation in lower trophic-level environments and the bottom-up control of secondary production.

We analyzed the time series δ^{15}N of three *Neocalanus* species collected in the western, central, and eastern subarctic NP to investigate how its variation is related to climatic and hydrographic conditions. Changes in biomass/abundance and phenology of *Neocalanus* species have been reported in response to NP regime shifts (Mackas et al., 1998; Tadokoro et al., 2005; Chiba et al., 2006). Because large-scale climatic forcing, such as the Aleutian Low, derives cool-warm conditions in different ways among the western, central, and eastern NP (*e.g.* Miller et al., 2004), mechanisms determining interannual variation in *Neocalanus* δ^{15}N are likely to differ among regions. To further clarify relationships among nitrate availability, phytoplankton composition/δ^{15}N, and zooplankton δ^{15}N, we conducted an additional case study in the Oyashio region based on data collected during a monthly routine observation program. The goal of this study was to clarify the regionally specific process linking climate, environment, phytoplankton, and zooplankton in the subarctic NP based on δ^{15}N values of three *Neocalanus* species, and to examine the usefulness of the zooplankton stable isotope ratios for understanding bottom-up control of interannual variation in lower trophic level ecosystems.

2. Materials and methods

2.1. Sampling and measurements

We analyzed specimens of *N. cristatus*, *N. flemingeri*, and *N. plumchrus* collected in the western, central, and eastern subarctic NP by the Tohoku National Fisheries Institute, Hokkaido University, and the Institute of Ocean Sciences, respectively (Table 1 and Fig. 1). The western NP samples collected in Oyashio waters (OY) were extracted from the Odate Collection (Odate, 1994). The central NP samples were collected along the 180° longitudinal line; this area was subdivided into the subarctic (180LineSA), transition north (180LineTN), and transition south (180LineTS) based on the interannual variation in water mass properties following the description of Kobari et al. (2003b). The eastern NP samples were collected at either Sta. P in the Alaska Gyre or off Vancouver Island (Off-Van).

Neocalanus were collected via 150–0 m vertical tow of a NORPAC net in the western and central regions, whereas 0–250 m oblique tow using a Bongo net was used in the eastern regions (Table 1). We considered the bias caused by using different sampling methods to be negligible because we examined only fifth-stage (CV) copepodites, which mainly distribute within the upper 100 m during reproductive seasons (Mackas et al., 1993; Kobari and Ikeda, 2000).

All specimens were preserved in 5% formalin in seawater. Because δ^{13}C is unstable in specimens that have been preserved in formalin for many years (*e.g.*, Rau et al., 2003), we used only δ^{15}N data for regional comparisons. Although a single *Neocalanus* specimen of the CV stage was sufficient for the measurements, we used up to 10 individuals for each measurement for *N. cristatus*, and up to 20 individuals whenever available for *N. flemingeri* and *N. plumchrus*, to obtain the community mean. We did not measure the δ^{15}N of *N. flemingeri* at 180LineTS because this species was rarely collected at this location. Before measurement, specimens selected from each sample were washed in distilled water, dried in a drying oven at 60 °C for 24 h, and ground into a homogeneous powder. The stable isotope ratio was measured using the Thermo Fisher Scientific, EA1112, DELTA V ConFlo III System, which exhibits an instrument error of ±0.1‰. Isotopic values are expressed as standard δ notation relative to the atmospheric N_2 standard (AIR) as, $\delta^{15}\mathrm{N}\ (‰) = [(^{15}\mathrm{N}/^{14}\mathrm{N}_{\mathrm{sample}}/^{15}\mathrm{N}/^{14}\mathrm{N}_{\mathrm{AIR}}) - 1] \times 1000$. For mass spectrometric analysis, alanin ($\delta^{15}\mathrm{N} = -2.5‰$) was used as the running standard, and glycine ($\delta^{15}\mathrm{N} = 0.6‰$) was measured in every 10 samples as the reference standard to ensure accuracy of measurement.

Samples from the western and eastern NP were collected between April and July, and the mean δ^{15}N for April to July was used for regional comparison because the monthly mean δ^{15}N did not differ significantly for any species within a given region (ANOVA, $P > 0.05$). The three species perform ontogenetic migration; i.e., they stay in the surface layers during the reproductive season in spring and summer and remain dormant in the deep layer during winter. Although the approximate timing and duration of the reproductive season differs among species (February–July for *N. cristatus*, March–May for *N. flemingeri,* and May–July for *N. plumchrus* (Kobari and Ikeda, 2000)), our sampling was conducted during the reproductive and thus active feeding season for all species over the subarctic NP.

Correlations between time-series measurements of *Neocalanus* δ^{15}N and biomass were tested for in each region to examine if δ^{15}N indicates a mechanism of bottom-up control linking nutrients – phytoplankton – zooplankton of interannual zooplankton production. The mean biomass/abundance during the respective

Table 1
Information of sampling and analysis of *Neocalanus* specimen used for nitrogen stable isotope measurement for western, central and eastern North Pacific.

	West	Central (180° Line)			East	
	Oyashio	Subarctic (SA)	Transition North (TN)	Transition South (TS)	Off-Vancouver Island (Off-Van)	St.P
Area	38°–41°N 142°–145°E	47°–48°30′N	44°–46°N	39°30′–42°N	48°–51°N 124°30″–130°W	50°N 145°W
Year	1960–2002	1980–1997	1979–1997	1979–1997	1981–2007	1996–2007
Sample holder	Tohoku National Fisheries Institute[a]	Hokkaido University			Institite of Ocean Sciences, DFO	
Sampling season	April-July	June			April-July	
Sampling method	NORPAC net 0–150 m haul	NORPAC net 0–150 m haul			Bongo net 0–250 m tow (max)	
Preservation	5% formalin sea water					
Specimen	CV (4–20 individual per sample)					
SI measurement	Thermo Fisher Scientific, EA1112-DELTA V ConFlo III System					

[a] Specimens of the Oyashio was extracted from the Odate Collection (Odate, 1994; Chiba et al., 2006).

research season/month was used for regional comparisons. For OY, the wet weight (g m^{-3}) of second- to fifth-stage (CII–CV) copepodites of the three *Neocalanus* species (Tadokoro et al., 2005) was used. Log abundance data were used for 180LineSA, TN, and TS (Kobari et al., 2003b), Off-Van, and Sta. P. For the 180Line data, only CV abundance was counted. The Off-Van abundance data comprised only *N. cristatus* and *N. plumchrus* because *N. flemingeri* was rare in this location. Biomass/abundance time-series data were normalized prior to the analysis to give a whole year mean = 0 and standard deviation = 1.

2.2. Climate and oceanic data sets

Interannual and interdecadal climatic forcing affects seasonal hydrographic conditions. For example, the Aleutian Low causes decadal changes in wind stress over the NP, affecting the extent of vertical water mixing during winter and subsequently the yearly nitrate input to surface water and its availability for phytoplankton. Therefore, we expected interannual change in *Neocalanus* δ^{15}N to be significantly correlated with climatic indices. Temporal coverage of the *Neocalanus* δ^{15}N time series data differed largely among the western, central, and eastern NP, making it difficult to conduct a direct comparison of interannual variation in relation to common climatic forcing for a specific year. Therefore, we used the following climate indices (Table 2) to clarify the relationships between climatic forcing and interannual variation in *Neocalanus* δ^{15}N, which are considered to be region-specific: Monsoon Index (MOI; December to February) (Hanawa et al., 1988), PDO, wintertime North Pacific Index (NPI; November to March; Trenberth and Hurrell, 1994), wintertime Arctic Oscillation index (AO; November to March; Thompson and Wallace, 1998), the Aleutian Low Pressure Index (ALPI; Beamish et al., 1997), wintertime Southern Oscillation index (SOI of November to March average; Trenberth, 1984), and North Pacific Gyre Oscillation index (NPGO) (Di Lorenzo et al., 2008).

Observational climate and ocean data, cloud cover, sea level pressure (SLP), sea surface temperature (SST), zonal wind, and meridional wind from winter to summer for the western, central, and eastern subarctic NP, were also used for comparison with the *Neocalanus* time series (ICOADS, Climate Diagnostics Center, NOAA, http://icoads.noaa.gov/products.html). The areas covered by the data set are 34–50°N and 140–156°E for OY, 40–56°N and 174–186°E for 180LineSA, TN, and TS, 44–56°N and 234–246°W for Off-Van, and 46–56°N and 220–246°E for Sta. P. All of the climatic and ocean time-series data were normalized to give a whole year mean = 0 and standard deviation = 1.

2.3. Seasonal nitrate consumption and plankton δ^{15}N in the Oyashio

To determine how temporal changes in nitrate conditions affect phytoplankton composition and δ^{15}N, and consequently *Neocalanus* δ^{15}N, we needed to clarify those relationships at a specific time and location, rather than comparing spatio-temporally averaged climatological values. For this purpose, we conducted a case study in the Oyashio Current in 2007, collecting monthly data on size-fractionated Chl *a*, diatom abundance, nitrate concentration, and δ^{15}N of POM and *Neocalanus*.

Water and zooplankton were sampled monthly from March to July 2007 at several stations during the A-line observation cruise (Kasai et al., 2001) by the R/V Wakataka-maru of the Tohoku National Fisheries Research Institute. Among the water samples collected with a Niskin bottle at 10, 20 or 30 m depths, 4 L was filtered through a GFC filter, and the POM collected on the GFC filter was preserved at −40 °C. No correction for residual inorganic carbon was made during filtration because the POM sample volume was large enough and contamination of inorganic carbon was

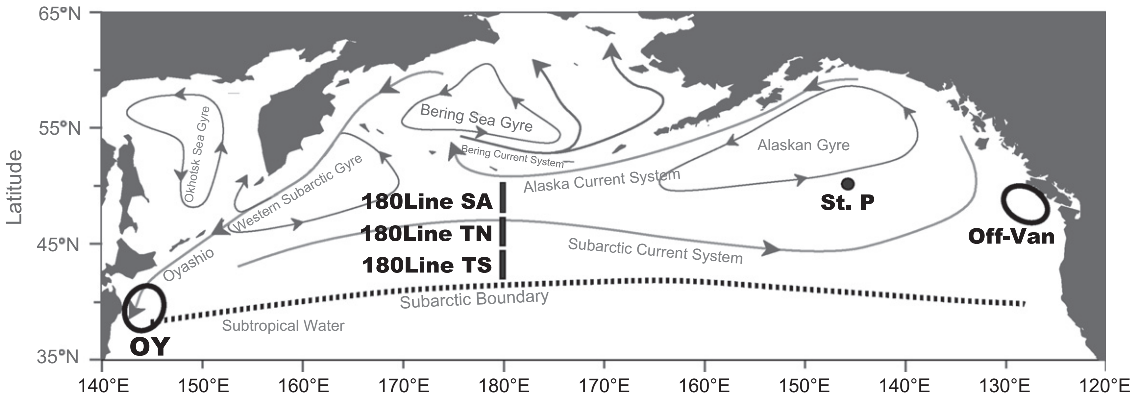

Fig. 1. Sampling locations of the *Neocalanus* species. Note that latitudinal boundaries of the180Line regions were determined based on the interannual variation in water mass properties following the description of Kobari et al. (2003b).

Table 2
Brief description of climate index compared to time-series *Neocalanus* $\delta^{15}N$.

Climate index	Climatic/hydrographic condition indicated	URL
MOI	Wintertime wind stress over the western NP	http://www.data.kishou.go.jp/kaiyou/db/obs/knowledge/stmw/moi.html
PDO	SST anomaly over the NP	http://tao.atmos.washington.edu/pdo/
NPI	Sea Level pressure over the NP	http://www.cgd.ucar.edu/cas/jhurrell/npindex.html
AO	Intensity of Polar atmospheric circulation	http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml
ALPI	Intensity of wintertime Aleutian Low	http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/downloads/alpi.txt
SOIwin	SST anomaly of tropical Pacific, also emerged as SST anomaly over the NP	http://www.bom.gov.au/climate/current/soihtm1.shtml
NPGO	Intensity of the central and eastern branches of the North Pacific gyre circulations	http://www.o3d.org/npgo/data/NPGO.txt

considered negligible. Considering that the vertical distribution of *Neocalanus* during reproductive season is mainly within the upper 50 m for *N. flemingeri* and *N. plumchrus* and approximately 50–150 m for *N. cristatus* (Mackas et al., 1993; Kobari and Ikeda, 1999), zooplankton were collected by a VMPS plankton sampler (Tsurumi Seiki, http://www.tsk-jp.com/tska/plankton_sampler.html) with a 100-μm mesh and specimens were taken from several layers between 0 and 225 m. Fresh *Neocalanus* specimens were preserved at −40 °C soon after sampling. Before measuring the stable isotope ratio after the cruise, the POM was dried at 60 °C for 24 h. *Neocalanus* specimens were prepared using the same procedures as the long-term samples described above. The stable isotope ratio of POM and *Neocalanus* was measured using the Thermo Fisher Scientific EA1112 as well as the DELTA V ConFlo III System (see Section 2.1).

For size-fractionated Chl *a*, ca. 200 ml water was filtered through 10, 2, and 0.2 μm nucleopore filters. Pigment collected on the filters was extracted in 6 ml dimethylformanide (Suzuki and Ishimaru, 1990) and fluorescence was measured by fluorometric methods using a Turner Designs fluorometer Model 10 (Holm-Hansen et al., 1965). Diatoms in 1 L water were preserved in 4% Lugol's solution and condensed by reverse filtration and cell numbers were counted using an inverted microscope (following Utermöhl (1958)). For nitrate, 10 ml water was taken and frozen in a polypropylene tube, and nitrate concentration was measured using a Bran + Luebbe Traac 800 autoanalyzer, following the method of Parsons et al. (1984).

3. Results

3.1. Regional differences in mean $\delta^{15}N$

The area mean *Neocalanus* $\delta^{15}N$ indicated clear regional gradients in which all three species showed similar distribution patterns: high in the western and eastern NP and low in the central NP (Fig. 2a) with the highest values at OY and Off-Van (7–10‰) and the lowest at 180LineTN and 180LineTS (2–4‰). The distribution of the high- and low-$\delta^{15}N$ areas roughly corresponded to the areas of low and high surface wintertime nitrate distribution (World Ocean Atlas 2005; http://www.nodc.noaa.gov/General/nutrients.html, Fig. 2b, top), which is based on a set of objectively analyzed (1° grid) climatological fields of *in situ* nitrate for seasonally compositing periods since the early 20th century.

The association between $\delta^{15}N$ and nitrate distribution was strengthened when compared to seasonal nitrate drawdown, which shows differences in nitrate concentration from winter to summer (Fig. 2b, top and bottom). Specifically, high $\delta^{15}N$ values occurred in the area of larger nitrate drawdown (i.e., OY and Off-Van), where summer concentrations drop below 1 μM, and low $\delta^{15}N$ values were seen in areas of less nitrate drawdown (180LineSA, TN and TS and St. P), where summer concentrations remain >5–10 μM. The $\delta^{15}N$ differed among regions for all species: it was significantly higher at OY and Off-Van than at the other four stations (ANOVA with Scheffe's *post hoc* test, $P < 0.05$).

Conversely, the mean $\delta^{15}N$ did not differ significantly among species within each area (ANOVA with Scheffe's *post hoc* test, $P < 0.05$), except for *N. flemingeri* at 180LineTN, for which $\delta^{15}N$ was significantly higher than the other two species (ANOVA, $P < 0.05$). The all-area mean and standard deviation of $\delta^{15}N$ was 5.82 ± 2.43‰ for *N. cristatus*, 6.68 ± 2.13‰ for *N. flemingeri*, and 5.47 ± 3.15‰ for *N. plumchrus*.

3.2. Time series $\delta^{15}N$

Because the interannual variation for each pair of the three *Neocalanus* species was significantly coherent (Pearson's *r*, $P < 0.05$) in all regions except Sta. P, we used the three-species mean $\delta^{15}N$ for the time series analysis. At Sta. P, *N. flemingeri* and *N. plumchrus*

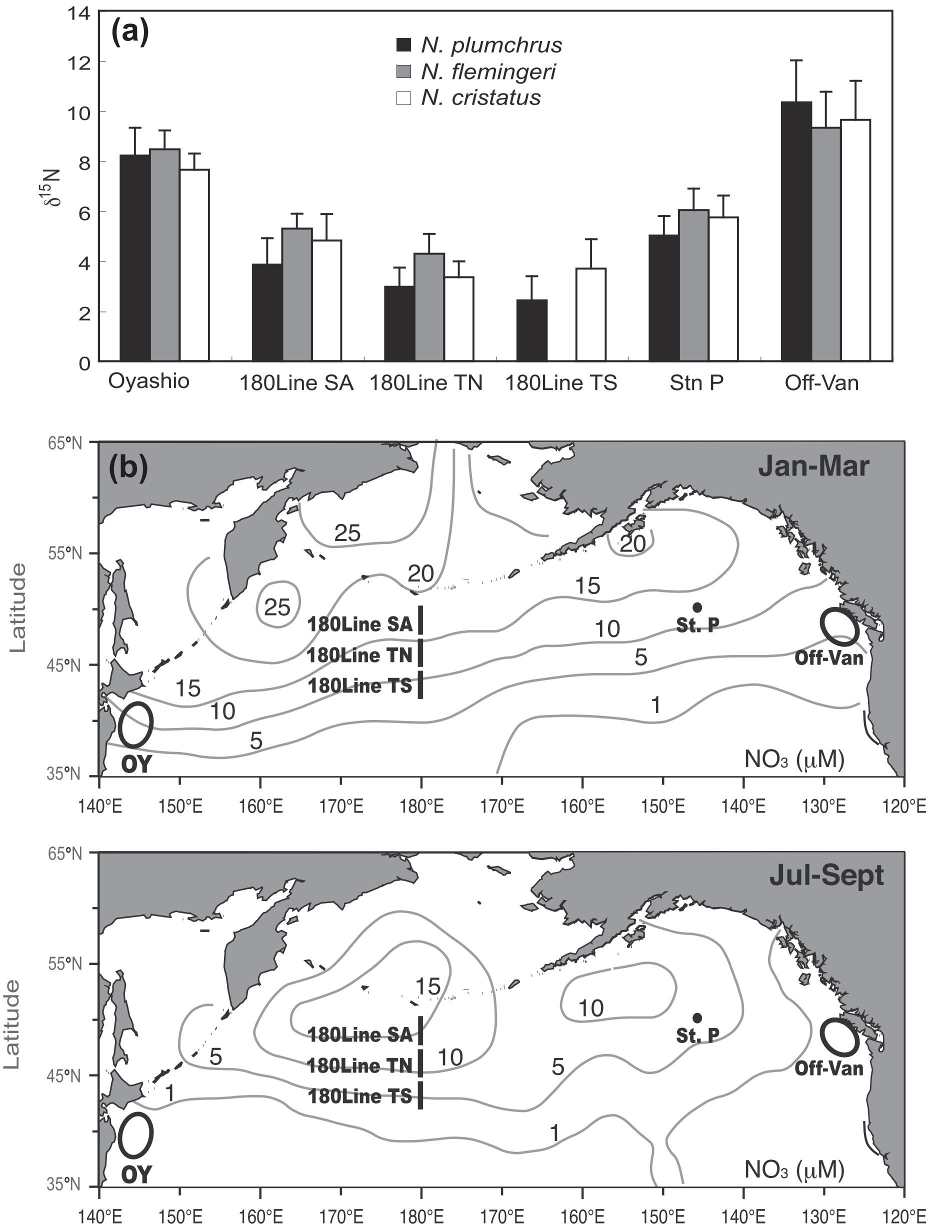

Fig. 2. (a) The stable nitrogen isotope ratio (δ^{15}N in ‰) of the three *Neocalanus* species in each sampling area. The values are means for the sampling periods for the respective areas and the error bars indicate the standard deviation. (b) Climatological surface nitrate distribution in the sampling area (μM) for winter (January–March) (top) and summer (July–September) (bottom), based on the World Ocean Atlas 2005 (http://www.nodc.noaa.gov/General/nutrients.html).

varied in a similar manner (Pearson's *r*, $P < 0.05$), whereas *N. cristatus* varied differently from the other two species. The differences in δ^{15}N between the highest and lowest years were c.a. 3–4‰ for all regions, which is equivalent to a change in one trophic level.

At OY, δ^{15}N was high from mid 1960s until the late 1980s, with the exception of a few years (including 1981), and then declined at the end of the 1980s (Fig. 3a). In the central NP, δ^{15}N varied in a different manner among 180LineSA, TN, and TS (Fig. 3b–d). For Off-Van, a more positive anomaly was observed during the 1980s, whereas the yearly variation was large during the 1990s, and there was a more negative anomaly after 2000 (Fig. 3e). Similar to OY, a higher or lower anomaly was observed more frequently before and after the end of the 1980s for 180LineSA and Off-Van. Although the time series is short at Sta. P, δ^{15}N fluctuated over a several-year cycle for both the *N. flemingeri*/*N. plumchrus* composite and *N. cristatus* (Fig. 3f and g).

No significant correlation was detected between biomass/abundance and δ^{15}N in any regions at the interannual scale (Pearson's *r*, $P > 0.05$). In OY, however, biomass tended to be small in the years with high δ^{15}N from the mid-1970s through the 1980s, while it was large in the years with low δ^{15}N during the 1990s; the relationship was less clear before the mid-1970s. For Off-Van, although no interannual correlation was observed between *Neocalanus* δ^{15}N and abundance, a more negative δ^{15}N anomaly was observed when the abundance increased slightly after the mid-1990s.

3.3. Comparison with the climatic/environmental time series

No significant correlation between any climatic index and the three-species composite δ^{15}N was detected, except for NPI and 180LineSA (Pearson's *r*, $P < 0.05$), indicating that δ^{15}N tended to be higher in cool winters. At Sta. P, the δ^{15}N of *N. cristatus*, which

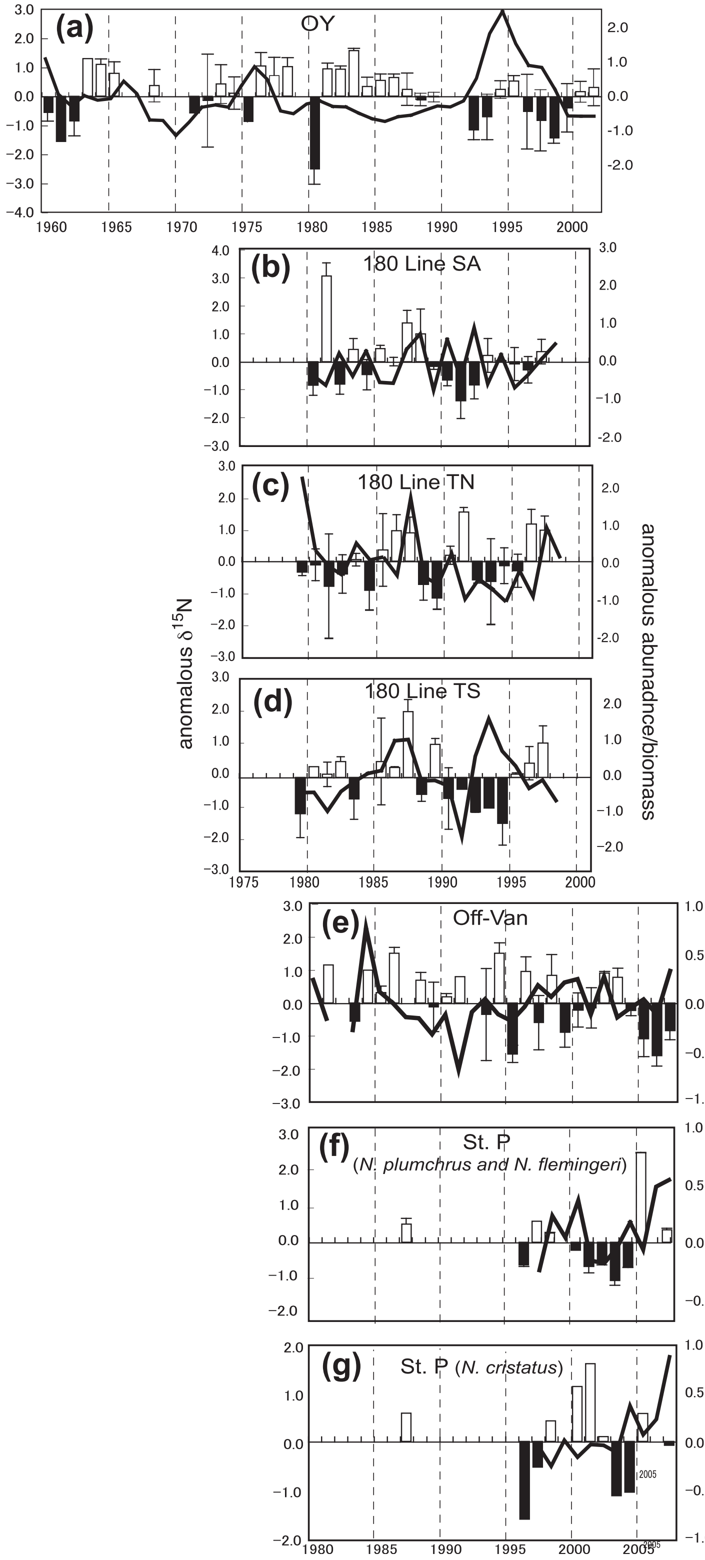

Fig. 3. Time series anomaly in δ^{15}N and biomass/abundance in the three *Neocalanus* species in each sampling area. The bar and thick line indicate δ^{15}N and abundance/biomass, respectively. The anomalous value of δ^{15}N is the mean for the three species and the error bars indicate the standard deviation for OY and 180LineSA, TN, and TS. For Off-Van δ^{15}N was a composite of three species while biomass was a composite of *N. cristatus* and *N. plumchrus* only. For Sta. P, *N. cristatus* was plotted separately because its interannual variation in δ^{15}N differed significantly from the other species. Biomass/abundance time-series data were normalized to give a whole year mean = 0 and standard deviation = 1.

varied differently from the other two species (Fig. 3g), had a significant positive correlation with NPGO.

Regarding the relationship between climatic/environmental variables and *Neocalanus* (Table 3), the study regions could be roughly classified into three sections: (1) OY and 180LineSA; (2) 180LineTN and TS and Off-Van; and (3) Sta. P. For OY, *Neocalanus* δ^{15}N had a significant negative correlation with the wintertime SST (January to March) and wintertime meridional wind (Table

Table 3
Pearson correlation coefficient between climatic variables (COADS) and time series of nitrogen stable isotope ratio (δ^{15}N) of *Neocalanus* species. δ^{15}N value is the mean of three *Neocalanus* species except for St. UP, at which *Neocalanus cristatus* varied differently from *N. flemingeri* and *N. plumchrus*.

		OY	180LineSA	180LineTN	180LineTS	Off-Van	St.P (*N. cristatus*)	St.P (*N. flemingeri* & *N. plumchrus*)
	(N)	(35)	(18)	(19)	(18)	(24)	(11)	(11)
Cloud cover	January–March	n.s.	n.s.	n.s.	n.s.	$0.366^{\triangle}$	n.s.	n.s.
Cloud cover	March–May	$-0.285^{\triangle}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Cloud cover	March–July	n.s.	n.s.	n.s.	n.s.	n.s.	$0.630^{\triangle}$	n.s.
SLP	January–March	n.s.	-0.495^{*}	n.s.	n.s.	n.s.	n.s.	n.s.
SLP	March–May	n.s.	n.s.	n.s.	n.s.	$0.390^{\triangle}$	n.s.	n.s.
SLP	March–July	n.s.	n.s.	n.s.	n.s.	0.569^{*}	n.s.	$-0.618^{\triangle}$
SST	January–March	-0.407^{*}	-0.550^{*}	$0.453^{\triangle}$	n.s.	n.s.	n.s.	n.s.
SST	March–May	$-0.322^{\triangle}$	$-0.504^{\triangle}$	n.s.	n.s.	n.s.	n.s.	n.s.
SST	March–July	$-0.333^{\triangle}$	$-0.447^{\triangle}$	n.s.	n.s.	n.s.	$-0.556^{\triangle}$	n.s.
Zonal wind	January–March	$-0.316^{\triangle}$	$0.414^{\triangle}$	n.s.	n.s.	n.s.	n.s.	n.s.
Zonal wind	March–May	n.s.	n.s.	n.s.	n.s.	$0.396^{\triangle}$	n.s.	n.s.
Zonal wind	March–July	n.s.	n.s.	n.s.	n.s.	0.498^{*}	$0.628^{\triangle}$	n.s.
Meridional wind	January–March	-0.349^{*}	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Meridional wind	March–May	n.s.	n.s.	0.534^{*}	0.699^{*}	n.s.	n.s.	n.s.
Meridional wind	March–July	n.s.	n.s.	0.530^{*}	0.521^{*}	n.s.	n.s.	n.s.

n.s.: not significant.
* Significant correlation ($P < 0.05$).
$^{\triangle}$ Weak correlation ($P < 0.1$).

3). In OY, the wintertime meridional wind had an exclusively northerly component (<0). These results indicate that the *Neocalanus* δ^{15}N increased (decreased) in the years with a cool (warm) winter with strong (weak) northerly winds. No decadal variation was conspicuous in the northerly time series (Fig. 4a), while the SST time series showed cool conditions from the mid-1970s to the late 1980s and warm conditions during the 1990s (Fig. 4b). Along 180LineSA, *Neocalanus* δ^{15}N had a significant negative correlation with the wintertime SLP and wintertime SST (Table 3), suggesting that *Neocalanus* δ^{15}N increased conspicuously in cool conditions, from the mid-1970s to the late 1980s (Fig. 4c and d), as observed in OY.

Along 180LineTN and 180LineTS, *Neocalanus* δ^{15}N had a significant positive correlation with the spring–summer meridional wind (Table 3). Because the meridional wind has an exclusively southerly component in the 180Line region (>0), this suggests that *Neocalanus* δ^{15}N tended to increase in years with a strong southerly wind from spring to summer at 180LineTN and TS. The southerly wind was weak from 1990 and strengthened after 1995 (Fig. 4e), corresponding well with the *Neocalanus* δ^{15}N time series.

In Off-Van, *Neocalanus* δ^{15}N had significant positive correlations with the spring–summer SLP and spring–summer zonal wind (Table 3). Because the zonal wind has an exclusively westerly component (>0) in Off-Van, this suggests that *Neocalanus* δ^{15}N increased in years with sunny conditions with strong westerly winds from spring to summer. Both SLP and westerly winds tended to be a negative anomaly after the early to mid-1990s (Fig. 4f and g), corresponding well with the decline in *Neocalanus* δ^{15}N.

At Sta. P, the δ^{15}N of *N. cristatus* showed no significant correlation with any of the climatic/environmental variables, although there was a weak positive relationship with the spring–summer cloud cover and zonal wind and a negative relationship with the spring–summer SST (Table 3), suggesting that the δ^{15}N increased in years with cloudy conditions with strong westerly winds during the spring–summer. The δ^{15}N of *N. flemingeri*/*N. plumchrus* showed only a weak correlation with the spring–summer SLP.

3.4. Seasonal nitrate consumption and plankton δ^{15}N in the Oyashio

Based on the A-line monthly observation in the Oyashio, seasonal variation in nitrate concentration, δ^{15}N of POM, and Chl *a* within the upper 30 m were detected (Fig. 5). δ^{15}N – POM linearly increased as nitrate decreased from March to July. Chlorophyll a peaked in April and decreased in July while nitrate markedly dropped in May, indicating that post-bloom, relatively oligotrophic conditions were present as water column stratification increased after May. Although the data show high nitrate concentrations (>15 μM) at 30 m depth in July, this depth was below the seasonal mixed layer (data not shown) and was considered not to contribute to phytoplankton production. The linear seasonal increase in δ^{15}N – POM suggested changes in isotope fractionation by phytoplankton associated with nitrate availability. Chlorophyll *a* was positively correlated with the ratio of large phytoplankton (>10 μm) (Spearman's $r = 0.705$, $P < 0.01$) (Fig. 6a) and exponentially correlated to diatom abundance (Spearman's $r = 0.825$, $P < 0.01$) (Fig. 6b). Thus seasonal variation in Chl *a* indicated change in phytoplankton composition from diatom-dominated conditions during bloom and smaller phytoplankton-dominated conditions during the pre- and post-blooming periods.

For all species, the δ^{15}N of *Neocalanus* and surface POM (20 and 30 m) from March through July had a significant positive correlation (Pearson's r, $P < 0.05$; Fig. 7). No clear relationship was observed between the δ^{15}N of *Neocalanus* and POM at 10 m, presumably because only a small population of *Neocalanus* was distributed around 10 m. The slope was most and least acute for *N. cristatus* (>1.0) and *N. flemingeri* (*c.a.* 0.6), respectively, indicating that the δ^{15}N of *N. ctistatus* was relatively stable while that of *N. flemingeri* was sensitive to change in phytoplankton δ^{15}N. The δ^{15}N of *N. plumchrus* increased constantly as phytoplankton δ^{15}N increased (slope, *c.a.* = 1.0). The mean and standard deviation of the δ^{15}N of POM (20 and 30 m) was 4.39 ± 1.66‰, and those of *N. cristatus*, *N. flemingeri*, and *N. plumchrus* were 6.70 ± 0.76, 8.12 ± 1.27, and 7.59 ± 1.36‰, respectively, with levels approximately 2–4‰ higher for *Neocalanus* δ^{15}N. Among the three species, the δ^{15}N was highest for *N. flemingeri*, as observed for the long-term variation.

4. Discussion

4.1. Canonical distribution of Neocalanus δ^{15}N

We observed that regional variation in *Neocalanus* δ^{15}N was high in coastal regions both in the eastern and western NP and low in offshore regions (Fig. 2). Given that all three species showed coherent regional distribution patterns, we considered that this is the canonical distribution of δ^{15}N, which is determined by basin scale isotope composition of substrates and/or degree of isotope fractionation influenced by nitrate availability for phytoplankton.

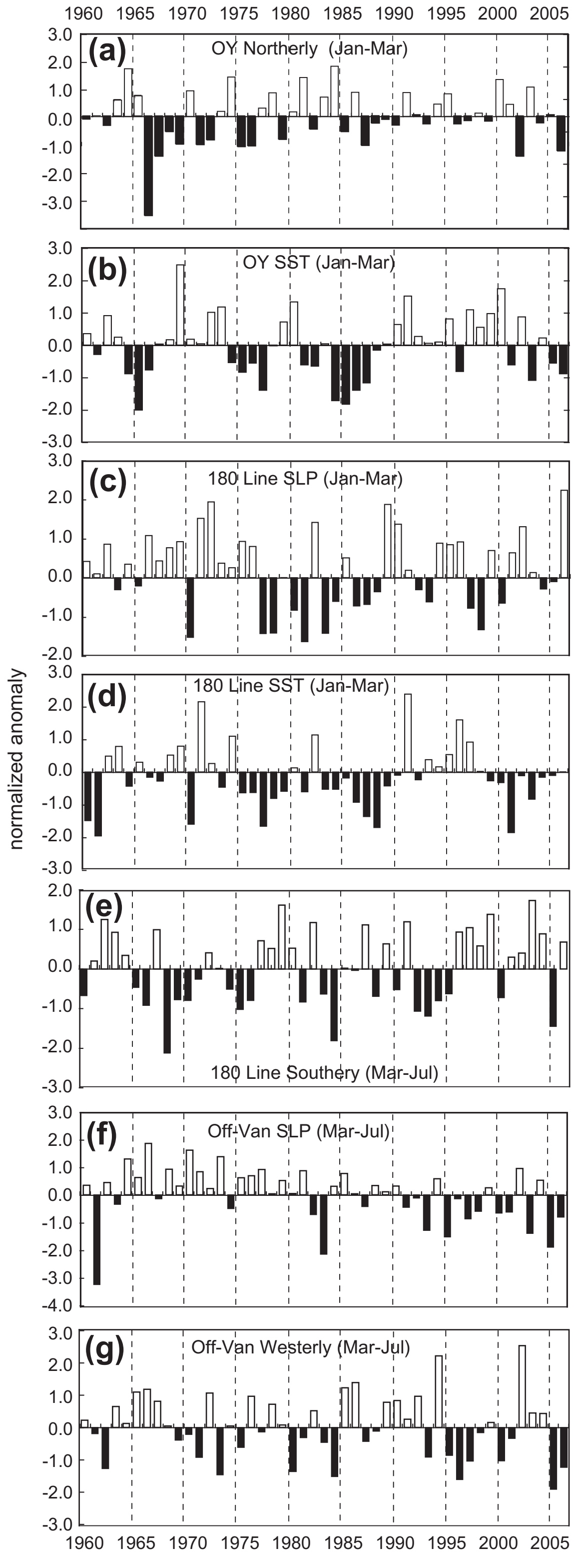

Fig. 4. Time series anomaly in the climatic and environmental variables that have a significant correlation with *Neocalanus* δ^{15}N in the respective regions (Table 2): (a) northerly winds (January to March) for OY, (b) SST (January to March) in OY, (c) SLP (January to March) for 180Line, (d) SST (January to March) for 180Line, (e) southerly winds (March to July) for 180Line, (f) SLP (March to July) for Off-Van, and (g) westerly winds (March to July) for Off-Van. The anomaly was normalized to give a whole-year mean = 0 and standard deviation = 1.

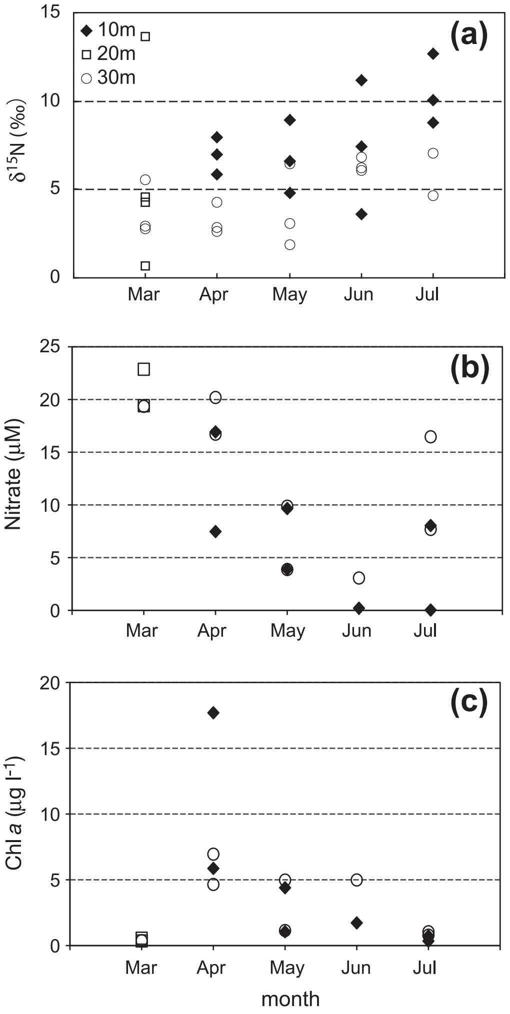

Fig. 5. Seasonal variation in the (a) δ^{15}N (‰) of POM, (b) nitrate concentration (µM), and (c) Chl *a* (µg l^{-1}) at different depths (10, 20, and 30 m) at the A-line stations in the Oyashio waters.

Neocalanus δ^{15}N was well correlated with nitrate distribution and the extent of its drawdown from winter to spring. Specifically, it was higher in regions of larger seasonal drawdown as observed in coastal regions, OY and Off-Van, while lower in regions of smaller seasonal drawdown as at St. P and stations along the 180Line (Fig. 2). Phytoplankton δ^{15}N are reportedly subject to temporal variation depending on the availability of ambient nitrate caused by isotopic fractionation in mid- to high-latitude regions, where nitrate is a major nutrient resource for primary production (Saino and Hattori, 1987; Mino et al., 2002). The annual mean surface phytoplankton abundance based on ocean color satellite observations is approximately twice as large in OY and the Off-Van area than at St. P and 180Line (Sarmient and Gruber, 2006). Assuming that regional variation in seasonal nitrate drawdown is due to the extent of nitrate consumption by phytoplankton, *Neocalanus* δ^{15}N is likely to act as an isotopic signal in phytoplankton production derived by regionally specific nitrate availability. However, it is important to be cautious about *Neocalanus* δ^{15}N in an extensive high-nutrient, low-chlorophyll (HNLC) region such as the St. P area, where the major nitrogen source for phytoplankton is NH_4 rather than NO_3. The next section includes a more detailed discussion of this issue.

Capturing the canonical distribution of *Neocalanus* δ^{15}N is crucial premise for regional comparison of its temporal variation. Similar to our results, it was reported that *Neocalanus* δ^{15}N showed concordant spatial distribution pattern during 1998–2004 in the Gulf of Alaska, higher in coastal region and lower in offshore, in spite of large interannual variations of the mean value (Kline,

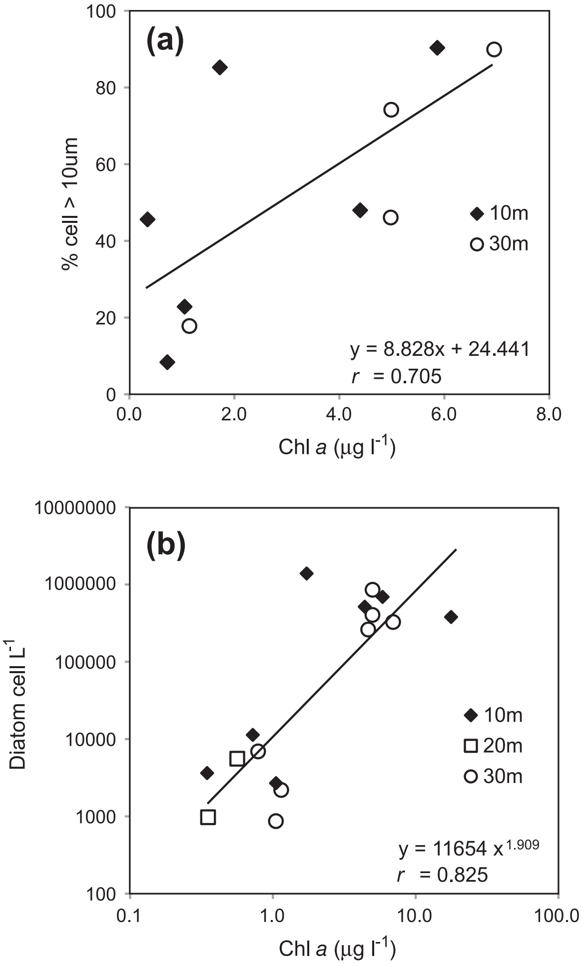

Fig. 6. Relationship between (a) Chl *a* ($\mu g\,l^{-1}$) and relative abundance of large phytoplankton (>10 µm), and (b) Chl *a* and diatom abundance (cell number l^{-1}).

2009). These results suggested that regional comparison of absolute value of zooplankton $\delta^{15}N$ based on samples taken at a time and/or a year might mislead us about the reason of its variation.

4.2. Interannual variation in Neocalanus $\delta^{15}N$

Because all three species showed coherent interannual variation within each region, with the exception of *N. cristatus* at Sta. P (Fig. 3), we postulated that the variation in *Neocalanus* $\delta^{15}N$ mirrored the yearly change in the regional environmental conditions, which influence annual nitrate availability and subsequently phytoplankton abundance.

However, the mechanism for this interannual variation differed between regions, which were classified roughly into the three regional groups: (1) OY and 180LineSA; (2) 180LineTN and TS and Off-Van; and (3) Sta. P (Fig. 8). For OY and 180LineSA, a cool–warm cycle of winter conditions and subsequent variation in primary production was suggested to determine the interannual variation in *Neocalanus* $\delta^{15}N$. In contrast, along 180LineTN and TS and Off-Van, the extent of transport of water with low nitrate concentrations was considered to be temporal variation in $\delta^{15}N$.

Our results show that *Neocalanus* $\delta^{15}N$ increased in years with cool, windy winters at OY and 180Line. Because cool, windy conditions would enhance nutrient availability within a mixed layer, and the nitrate levels of subsurface water (>200 m) do not isotopically differ or can even be reduced compared to that in the western subarctic NP gyre (Minagawa et al., 2001), isotopic fractionation is unlikely to be the cause of the increased phytoplankton and zooplankton $\delta^{15}N$.

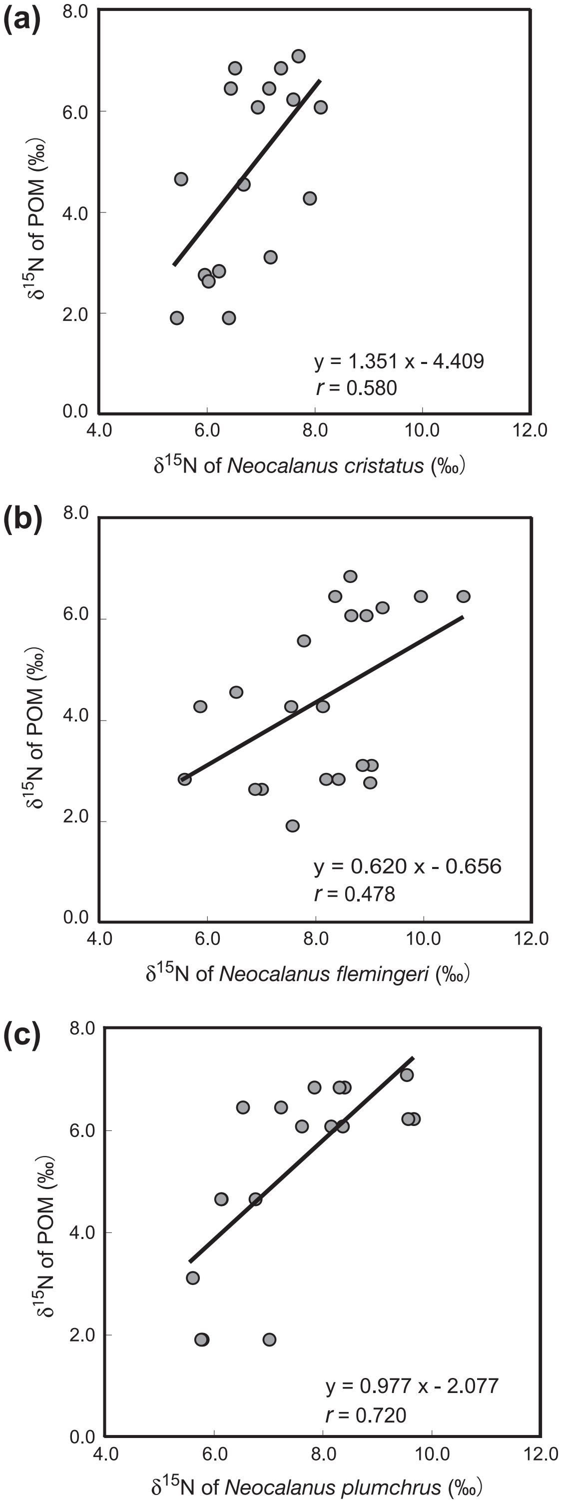

Fig. 7. Relationship between $\delta^{15}N$ (‰) of POM and that of *Neocalanus* species for (a) *N. cristatus*, (b) *N. flemingeri*, and (c) *N. plumchrus*. POM data are for 20- and 30-m depths, whereas *Neocalanus* were collected from 0 to 225 m. Data are for all sampling stations from March to July.

In a subarctic environment relatively rich in nutrients, light availability controls phytoplankton production (Polovina et al., 1995); consequently, a cold winter with deep mixing could reduce phytoplankton availability for *Neocalanus*. Indeed, both the winter

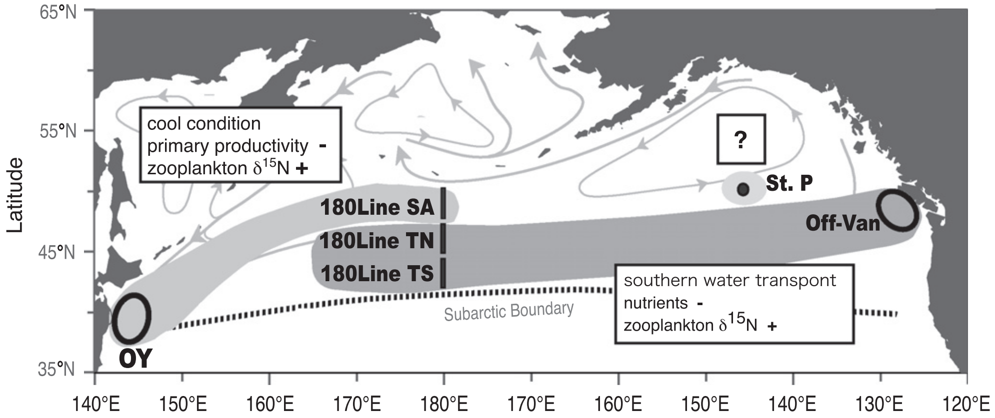

Fig. 8. Summary of the regional comparison of the mechanisms for the interannual variation in *Neocalanus* δ^{15}N.

and spring phytoplankton abundances were small in OY during the cool decade of the 1980s (Chiba et al., 2008). *Neocalanus* species are phytoplankton feeders that will feed on microzooplankton and other smaller zooplankton when phytoplankton availability is low (Kobari et al., 2003a). Therefore, in this region, it is plausible that the increased *Neocalanus* δ^{15}N indicated a switch in their feeding strategy to an omnivorous or carnivorous mode. In contrast, the low δ^{15}N in the years with warmer winters suggests that *Neocalanus* took advantage of enhanced phytoplankton production under favorable light availability due to increased stratification.

Along 180LineTN and TS, we detected that *Neocalanus* δ^{15}N was high in the years of strong southerly winds. Given that the 180LineTN and TS sites are located in the transition zone between the subarctic and subtropical fronts, southerly winds likely induce the intrusion of southern warm water with lower nitrate concentrations (Fig. 2b). Assuming negative correlations between latitudinal distribution of surface nitrate concentration and nitrate δ^{15}N in the mid to high latitude where nitrogen is a major source for phytoplankton production (Sigman et al., 2000), southern water advection is likely to result in increases in source water δ^{15}N. Low nitrate concentration and high nitrate ^{15}N could enhance phytoplankton uptake of the heavier isotope. Because the highest *Neocalanus* δ^{15}N value along 180LineTN and TS, i.e., c.a. 4.0–5.0 (Fig. 2b), was still in a low trophic level for omnivores and carnivores, the influence of a shift in *Neocalanus* feeding strategy on interannual variation in its δ^{15}N was considered small.

In Off-Van, *Neocalanus* δ^{15}N increased in years with strong westerly winds. A strong westerly enhances the North Pacific Current (NPC), the broad eastward flow that originates from the Kuroshio Extension in the central NP (Chelton and Davis, 1982). The NPC bifurcates into northward circulation, the Alaska Current as well as southward circulation, the California Current (Chelton and Davis, 1982) at approximately 45–50°N in the Off-Van region. The latitudinal position of bifurcation varies between years (Cummins and Freeland, 2007), and shifted northward to >50°N in 2002–2003 and southward to approximately 45°N in 2004–2005 (Batten and Freeland, 2007), roughly coinciding with years of strong and weak westerly winds, respectively (Fig. 4g). Batten and Freeland (2007) showed a distribution change in copepod communities in the Gulf of Alaska responding to the latitudinal shift of the bifurcation: more warm water species and less cold water species in the year of the north shift of bifurcation and vice versa. This indicates that enhanced circulation of the Alaska Current induced intrusion of southern water with low nitrate concentrations and high nitrate δ^{15}N to the Off-Van region, resulting in an increase in *Neocalanus* δ^{15}N through isotopic fractionation by phytoplankton along 180LineTN and TS. However, in Off-Van, the highest value of *Neocalanus* δ^{15}N reached 10–12‰, which is an equivalent level for carnivores in this region (Brodeur et al., 2002), suggesting that *Neocalanus* species may switch their feeding strategies to a more omnivorous or carnivorous mode under reduced phytoplankton abundance due to decreases in nutrient availability. Therefore, not only isotopic fractionation by phytoplankton but also behavioral responses of *Neocalanus* might cause the observed temporal variation in δ^{15}N.

We did not find a plausible explanation for the interannual change in *Neocalanus* δ^{15}N at Sta. P. This might be due to the limited duration of the time series, which may have been too short to compare climatic and environmental forcing, but is more likely a result of iron deficiency in this HNLC area. Phytoplankton is known to use NH_4 preferentially over NO_3 as a consequence of iron limitation, not because of NO_3 depletion (Frost, 1993); this differs considerably from the patterns at 180LineTN and TS, the other low Chl *a* regions observed in this study. Because NH_4 is regenerated within a mixed layer, nitrogen sources for phytoplankton at St. P are considered to be independent of the effects of seasonal vertical water mixing and stratification, which are largely affected by climatic forcing.

In addition, it is unclear why we observed interspecies differences in interannual variation in δ^{15}N only at Sta. P. *N. cristatus* vary temporally in a different manner than that of *N. flemingeri* and *N. plumchrus,* while the δ^{15}N values of all three species varied in a coherent manner in other regions, despite interspecies differences in life cycle timing and vertical habitat partitioning (Miller et al., 1984; Mackas et al., 1993; Kobari and Ikeda, 1999; Tsuda et al., 1999). Reviewing the life cycle strategy of *Neocalanus*, Kobari and Ikeda (2000) reported that species-specific timing of ontogenetic vertical migration and vertical distribution during the surface development period were similar in the Oyashio and St. P region, *e.g.*, a longer development period from early spring to summer and deeper distribution for *N. cristatus* compared to others.

This discrepancy may be derived from vertical hydrographic structure at St. P. A distinct permanent halocline is formed at 0–150 m deep in the Gulf of Alaska, above which *Neocalanus* species distribute with the near-surface dwellers *N. flemingeri* and *N. prumchrus* and the subsurface dweller *N. cristatus* (Mackas et al., 1993). As strong wind may induce shoaling of the halocline around the St. P area due to increases in Ekman pumping (Crawford et al., 2007), the vertical distribution range of *N. cristatus* may become shallower under this condition. The variation in δ^{15}N of *N. cristatus* in this study roughly coincided with the 100–150 m salinity anomaly, which indicates the extent of Ekman pumping: high δ^{15}N in years with a deeper halocline from the late 1990s to 2003, and low δ^{15}N with shallower the halocline seen in 2003–2004 (Crawford et al., 2007; Fig. 3g). As this species is known to feed on sinking aggregated particles (Dagg, 1993), shoaling and deepening of its distribution might affect quality and thus isotrophic composition of its food sources.

Although we detected no significant correlations between δ^{15}N variation and PDO in any regions on an interannual scale, we observed higher and lower δ^{15}N more frequently before and after the late 1980s, respectively, for OY, 180LineSA, and Off-Van (Fig. 3), roughly coinciding with the timing of the North Pacific Regime shift of 1988/89, when the PDO mode was reported to change (Bond et al., 2003). An intensified Aleutian Low enhanced the cyclonic subarctic circulation over the NP, resulting in cold and warm environments in the west and eastern subarctic NP, respectively, from the mid-1970s (Miller et al., 1994) to the 1988/1989 regime shift (Hare and Mantua, 2000). However, we observed a relatively higher δ^{15}N in both OY and Off-Van during these periods. As suggested in the previous section, this would occur because the mechanism for δ^{15}N variation differed between the eastern and western NP. The *Neocalanus* δ^{15}N mirrored the decline in phytoplankton production caused by a reduction in light availability due to cold conditions in the western NP, whereas in the eastern NP the strong subarctic circulation might intensify westerly and southern water transport with relatively oligotrophic water. In conclusion, the *Neocalanus* δ^{15}N reflected the changes in the lower trophic level ecosystem state, but with different mechanisms.

4.3. Seasonal nitrate consumption and plankton δ^{15}N in the Oyashio

As mentioned in the previous section, phytoplankton abundance was low during the cool period from the mid-1970s until the late 1980s in OY, whereas the wintertime abundance increased in the 1990s, which was thought to result from an increase in light availability in warmer, more stratified wintertime conditions (Chiba et al., 2008). However, the annual abundance remained low compared to that before the mid-1970s, because the spring abundance, which was approximately seven times larger than the wintertime abundance (Chiba et al., 2008), did not increase, presumably due to a reduction in the overall nutrient availability (Ono et al., 2002) under the more stratified conditions. Despite the decrease in total phytoplankton availability, the annual zooplankton biomass (Chiba et al., 2008) and the *Neocalanus* biomass (Tadokoro et al., 2005; Fig. 3a) increased markedly in the 1990s. *Neocalanus* species exhibit ontogenetic seasonal migration (Kobari and Ikeda, 2000) and so a consistent phytoplankton supply from early spring to summer is expected to be an important factor for their recruitment success, whereas an extensive spring bloom, such as that which occurs in the western NP (Kasai et al., 1997), and its peak abundance far exceeds the feeding demand of zooplankton (Tsuda and Sugisaki, 1994). Indeed, Chiba et al. (2004) reported that developmental timing of *N. flemingeri*, which develop within the surface layer from March to May, shifted earlier in the 1990s, implying favorable feeding conditions for this species during that period. Given these observations, Chiba et al. (2008) suggested that an increase in wintertime phytoplankton increased the survival of the early population of *Neocalanus*, driving their annual abundance in the 1990s.

In this study, the observed decline in *Neocalanus* δ^{15}N of approximately 3‰ in the 1990s was roughly equivalent to a change in one trophic level (Toda and Wada, 1990), suggesting a shift in feeding strategy from omnivore/carnivore to herbivore. This in turn indicates that *Neocalanus* indeed took advantage of the increased wintertime phytoplankton to increase recruitment success. Therefore, the results of this study support the hypothesized decadal-scale bottom-up control of *Neocalanus* biomass caused by a phenological shift in phytoplankton.

Based on the A-line observation, monthly variation in δ^{15}N of POM, which is presumably phytoplankton, and *Neocalanus* showed a clear positive correlation (Fig. 7). POM δ^{15}N increased gradually from March to July (Fig. 5a) in accordance with seasonal variation in nitrate availability within a mixed layer (Fig. 5b). Our results are consistent with a previous controlled ecosystem enclosure experiment that examined the relationship between nutrient concentration, primary production, and δ^{15}N throughout the course of a phytoplankton bloom (Nakatsuka et al., 1992). Our results suggest that *Neocalanus* δ^{15}N can be an indicator of upper water trophic conditions and phytoplankton abundance, and thus bottom-up control of secondary production.

However, we cannot dismiss another process of *Neocalanus* δ^{15}N variation; that is, the possibility of a switch in feeding behavior. We observed that Chl *a* peaked in April, which is when diatoms are considered dominant (Fig. 6). Indeed, a spring bloom is usually observed from late April to May in OY, and diatoms are the major phytoplankton species during the bloom period (Saito et al., 2002). Diatoms are an important food source for *Neocalanus* species when available (Kobari et al., 2003a), and it is possible that *Neocalanus* species gradually switched their feeding strategies from herbivorous to a more carnivorous mode after the bloom season.

Our results suggest that switching feeding strategies might be less important for *N. cristatus* compared to other species, which exhibited a small δ^{15}N range compared to POM δ^{15}N (Fig. 7a). This result is consistent previous knowledge that *N. cristatus* feed mainly on sinking aggregates rather than fresh phytoplankton (Dagg, 1993), and thus are supposed to be relatively less susceptible to fluctuations in surface phytoplankton availability. Conversely, the large δ^{15}N range of *N. flemingeri* (Fig. 7b) suggests that this species switched to a more omnivorous/carnivorous strategy according to phytoplankton availability. However, this is counterintuitive because *N. flemingeri* occurred in the surface layer during March–May, where it could utilize more phytoplankton as food resources compared to *N. plumchrus*, which occurred during May–July in OY. In addition, the mean δ^{15}N of *N. flemingeri* was highest among the three species at all sites except Off-Van (Fig. 2a). Thus, it may be necessary to consider species-specific metabolic rates, which differ with respect to ^{15}N enrichment within the bodies of each *Neocalanus* species (Rau et al., 2003). Indeed, Tsuda et al. (2001) reported a slow growth rate and prolonged recruitment period of *N. flemingeri* compared to the other species examined. These results should make us cautious when we interpret the trophic structure of a regional ecosystem based on δ^{15}N, particularly when considering the relationships among closely related species.

4.4. Conclusions

Our study demonstrates that δ^{15}N of *Neocalanus*, major secondary producers, could be a useful indicator for interannual variation in nutrient availability, phytoplankton productivity, and its influence on lower trophic level food web structure in the subarctic NP, at least in a qualitative way. We must consider that processes of change in the lower trophic levels indicated by zooplankton δ^{15}N differed between regions where light and nutrients are major controlling factors of phytoplankton growth, as seen in OY and 180LineSA versus 180LineTN, TS, and Off-Van, respectively (Fig. 8). We proposed two possible mechanisms for the regional variation in *Neocalanus* δ^{15}N: nutrient-controlled isotopic fractionation by phytoplankton and/or a shift in *Neocalanus* feeding strategy. Although we were unable to determine which mechanisms were most important, and the extent of their effects, based on the available dataset, it is possible that techniques based on amino acid-specific δ^{15}N (*e.g.*, Hannides et al., 2009) could help quantitatively determine changes in feeding strategy and trophic levels of zooplankton.

Numerous zooplankton time-series samples are available worldwide and some have been well preserved for more than 50 years (http://www.st.nmfs.noaa.gov/plankton/search/by_pi.html) and are available for analysis. Biological and chemical components of zooplankton can reveal accumulative information about regional environmental conditions over specific time periods even where frequent *in situ* observation is difficult. We expect that effective use of these zooplankton samples, including stable isotope analysis, through close domestic and international collaboration will yield improved opportunities for global comparison of how marine ecosystems respond to various climatic and anthropogenic forcing.

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References

Aberle, N., Malzahn, A.M., 2007. Interspecific and nutrient-dependent variations in stable isotope fractionation: experimental studies simulating pelagic multitrophic systems. Oecologia 154, 291–303.

Batten, S.D., Freeland, H.J., 2007. Plankton populations at the bifurcation of the North Pacific Current. Fisheries Oceanography 16, 536–546.

Batten, S.D., Welch, D.W., 2004. Changes in oceanic zooplankton populations in the north-east Pacific associated with the possible climatic regime shift of 1998/1999. Deep-Sea Research II 51, 863–873.

Beamish, R.J., Neville, C.E., Cass, A.J., 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Canadian Journal of Fisheries and Aquatic Sciences 54, 543–554.

Beaugrand, G., Ibanez, F., Lindley, J.A., Reid, P.C., 2002. Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. Marine Ecology Progress Series 232, 179–195.

Bode, A., Alvarez-Ossorio, M.T., Carrera, P., Lorenzo, J., 2004. Reconstruction of trophic pathways between plankton and the North Iberian sardine (*Sardina pilchardus*) using stable isotopes. Scientia Marina 68, 165–178.

Bond, N.A., Overland, J.E., Spillane, M., Stabeno, P., 2003. Recent shifts in the state of the North Pacific. Geophysical Research Letters 30. doi:10.1029/2003GL018597.

Brodeur, R.D., Frost, B.W., Hare, S.R., Francis, R.C., Ingraham Jr., W.J., 1996. Interannual variations in zooplankton biomass in the Gulf of Alaska and covariation with California Current zooplankton biomass. CalCOFI Report 37, 80–99.

Brodeur, R.D., Sugisaki, H., Hunt Jr., G.L., 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Marine Ecology Progress Series 233, 89–103.

Chelton, D.B., Davis, R.E., 1982. Monthly mean sea-level variability along the west coast of North America. Journal of Physical Oceanograpny 12, 757–784.

Chiba, S., Aita, N.M., Tadokoro, K., Saino, T., Sugisaki, H., Nakata, K., 2008. From climate regime shits to plankton phenology: synthesis of recent progress in retrospective studies of the western North Pacific. Progress in Oceanography 77, 112–126.

Chiba, S., Ono, T., Tadokoro, K., Midorikawa, T., Saino, T., 2004. Increased stratification and decreased lower trophic level productivity in the western subarctic North Pacific – a 30 years retrospective study. Journal of Oceanography 60, 149–162.

Chiba, S., Sugisaki, H., Nonaka, M., Saino, T., 2009. Geographical shift of zooplankton communities and decadal dynamics of the Kuroshio–Oyashio currents in the western North Pacific. Global Change Biology 15, 1846–1858.

Chiba, S., Tadokoro, K., Sugisaki, H., Saino, T., 2006. Effects of decadal climate change on zooplankton over the last 50 years in the western North Pacific. Global Change Biology 12, 907–920.

Cummins, P.F., Freeland, H.J., 2007. Variability of the North Pacific Current and its bifurcation. Progress in Oceanography 75, 253–265.

Crawford, W., Galbraith, J., Bolingbroke, N., 2007. Line P ocean tempreraturе and salinity, 1956–2005. Progress in Oceanography 75, 161–178.

Dagg, M., 1993. Sinking particles as a possible source of nutrition for the large calanoid copepod *Neocalanus cristatus* in the subarctic Pacific Ocean. Deep Sea Research I 40, 1431–1445.

Di Lorenzo, E., Schneider, N., Cobb, K.M., Chhak, K., Franks, P.J.S., Miller, A.J., McWilliams, J.C., Bograd, S.J., Arango, H., Curchister, E., Powell, T.M., Rivere, P., 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters 35, L08607. doi:10.1029/2007GL032838.

Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430, 881–884.

Frost, B.W., 1993. A modelling study of processes regulating plankton standing stock and production in the open subarctic Pacific Ocean. Progress in Oceanography 32, 17–56.

Gifford, D.J., 1993. Protozoa in the diets of *Neocalanus* spp. in the oceanic subarctic Pacific Ocean. Progress in Oceanography 32, 161–177.

Hanawa, K., Watanabe, T., Iwasaka, N., Suga, T., Toba, Y., 1988. Surface thermal conditions in the western North Pacific. Journal of Meteorological Society of Japan 66, 445–456.

Hannides, C.C.S., Popp, B.N., Landry, M.R., Graham, B.S., 2009. Quantification of zooplankton trophic position in the North Pacific Subtropical Gyre using stable nitrogen isotopes. Limnology and Oceanography 54, 50–61.

Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47, 103–145.

Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. Journal du conseil/Conseil permanent international pour l'exploration de la Mer 30, 3–15.

Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J.R., Yamaguchi, H., Walker, R.V., Myers, K.W., 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (Oncorhynchus spp.) in the central Gulf of Alaska in relation to climate events. Fisheries Oceanography 13 (3), 197–207.

Kasai, H., Saito, H., Yoshimori, A., Taguchi, S., 1997. Variability in timing and magnitude of spring bloom in the Oyashio region, the westerrn subarctic Pacific off Hokkaido, Japan. Fisheries Oceanography 6, 118–129.

Kasai, H., Saito, H., Kashiwai, M., Taneda, T., Kusaka, A., Kawasaki, Y., Kono, T., Taguchi, S., Tsuda, A., 2001. Seasonal and interannual variations in nutrients and plankton in the Oyashio region: A summary of a 10-years observation along A-line. Bulletin of Hokkaido National Fisheries Reserach Instition 65, 55–134.

Kline Jr., T.C., 2009. Characterization of carbon and nitrogen stable isotope gradients in the northern Gulf of Alaska using terminal feed stage copepodite-V *Neocalanus cristatus*. Deep-Sea Research II 56, 2537–2552.

Kobari, T., Ikeda, T., 1999. Vertical distribution, population structure and life cycle of *Neocalanus cristatus* (*Cristatus*: Copepoda) in the Oyashio region, with notes on its regional variations. Marine Biology 134, 683–696.

Kobari, T., Ikeda, T., 2000. Life cycle of *Neocalanus* species in the Oyashio region. Bulletin of Plankton Society of Japan 47, 129–135 (In Japanese with English abstract).

Kobari, T., Shinada, A., Tsuda, A., 2003a. Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific. Progress in Oceanography 57, 279–298.

Kobari, T., Ikeda, T., Kanno, Y., Shiga, N., Takagi, S., Azumaya, T., 2003b. Interannual variations in abundance and body size in *Neocalanus* copepods in the central North Pacific. Journal of Plankton research 25, 483–494.

Mackas, D.L., Goldblatt, R., Lewis, A.G., 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. Canadian Journal of Fisheries and Aquatic Science 55, 1878–1893.

Mackas, D.L., Peterson, W.T., Ohman, M.D., Lavaniegos, B.E., 2006. Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. Geophysical Research Letters 33, L22S07. doi:10.1029/2006GL027930.

Mackas, D.L., Peterson, W.T., Zamon, J.E., 2004. Comparisons of interannual biomass anomalies of zooplankton communities along the continental margins of British Columbia and Oregon. Deep-Sea Research II 51, 875–896.

Mackas, D.L., Sefton, H., Miller, C.B., Raich, A., 1993. Vertical habitat partitioning by large calanoid copepods in the oceanic subarctic Pacific during spring. Progress in Oceanography 32, 259–294.

Mantua, N.J., Hare, S.R., Zang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of American Meteorological Society 78, 1069–1079.

Miller, A.J., Cayan, D.R., Barnett, T.P., Graham, N.E., Oberhuber, J.M., 1994. The 1976–77 climate shift of the Pacific Ocean. Oceanography 7, 21–26.

Miller, A.J., Chei, F., Chiba, S., Moisan, J.R., Neilson, D.J., 2004. Decadal-scale climate and ecosystem interaction of the North Pacific Ocean. Journal of Oceanography 60, 163–188.

Miller, C.B., Clemons, M.J., 1988. Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. Progress in Oceanography 13, 201–243.

Miller, C.B., Frost, B.W., Batchelder, H.P., Clemons, M.J., Conway, R.E., 1984. Life histories of large grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the northeast Pacific. Progress in Oceanography 13, 201–243.

Minagawa, M., Ohashi, M., Kuramoto, T., Noda, N., 2001. δ^{15}N of PON and Nitrate as a clue to the origin and transformation of nitrogen in the subarctic North Pacific and its marginal sea. Journal of Oceanography 57, 285–300.

Minagawa, M., Yoshioka, T., 2005. Chikyu-Kagaku-Koza 5: Biogeochemistry. Baifukan, Tokyo, 215pp (In Japanese).

Mino, Y., Saino, T., Suzuki, K., Maranon, E., 2002. Isotopic composition of suspended particulate nitrogen ($\delta^{15}N_{sus}$) in surface waters of the Atlantic Ocean from 50°N to 50°S. Global Biogeochemical Cycles 16, 7-1–7-9.

Nakatsuka, T., Handa, N., Wada, E., Wong, S.C., 1992. The dynamic changes of stable isotopic ratios of carbon and nitrogen in suspended and sedimented particulate organic matter during a phytoplankton bloom. Journal of Marine Research 50, 267–296.

Odate, T., 1994. Plankton abundance and size structure in the northern North Pacific Ocean in early summer. Fisheries Oceanography 3, 267–278.

Ono, T., Tadokoro, K., Midorikawa, T., Nishioka, J., Saino, T., 2002. Multi-decadal decrease of net community production in western subarctic North Pacific. Geophysical Research Letters 29. doi:10.1029/2001GL014332.

Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Method for Seawater Analysis. Pergamon Press, Oxford, 173pp..

Perry, R.I., Batchelder, H.P., Mackas, D.L., Chiba, S., Durbin, E., Greve, W., Verheye, H.M., 2004. Identifying global synchronies in marine zooplankton populations: issues and opportunities. ICES Journal of Marine Science 61, 445–456.

Polovina, J.J., Mitchum, G.T., Evans, G.T., 1995. Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the central and North Pacific, 1960–88. Deep-Sea Research I 42, 1701–1716.

Rau, G.H., Ohman, M.D., Pierrot-Bults, A., 2003. Linking nitrogen dynamics to climate variability off central California: a 51 year record based on $^{15}N/^{14}N$ in CalCOFI zooplankton. Deep-Sea Research II 50, 2431–2447.

Saino, T., Hattori, A., 1987. Geographical variation of the water column distribution of suspended particulate organic nitrogen and its ^{15}N natural abundance in the Pacific and its marginal seas. Deep-Sea Research 34, 807–827.

Saito, H., Tsuda, A., Kasai, H., 2002. Nutrient and plankton dynamics in the Oyashio region of the western subarctic Pacific Ocean. Deep-Sea Research II 49, 5463–5486.

Sarmient, J.L., Gruber, N., 2006. Ocean Biogeochemical Dynamics. Princeton University Press, Princeton and Oxford, 503pp..

Satterfield IV, F.R., Finney, B.P., 2002. Stable isotope analysis of Pacific salmon: insight into trophic status and oceanographic conditions over the last 30 years. Progress in Oceanography 53, 231–246.

Sigman, D.M., Altabet, M.A., McCorkle, D.C., Francois, R., Fischer, G., 2000. The $\delta^{15}N$ of nitrate in the Southern Ocean: nitrogen cycling and circulation in the ocean interior. Journal of Geophysical Research 105, 19599–19614.

Sommer, F., Saage, A., Santer, B., Hansen, T., Sommer, U., 2005. Linking foraging strategies of marine calanoid copepods to patterns of nitrogen stable isotope signatures in a mesocosm study. Marine Ecology Progress Series 286, 99–106.

Sugimoto, T., Tadokoro, K., 1998. Interdecadal variations of plankton biomass and physical environment in the North Pacific. Fisheries Oceanography 7, 289–299.

Suzuki, R., Ishimaru, T., 1990. An improved method for the determination of phytoplankton chlorophyll using n,n-dimethylformamide. Journal of Oceanography 46, 190–194.

Tadokoro, K., Chiba, S., Ono, T., Midorikawa, T., Saino, T., 2005. Interannual variation in *Neocalanus* biomass in the Oyashio waters of the western North Pacific. Fisheries Oceanography 14, 210–222.

Thompson, D.W.J., Wallace, J.M., 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. Geophysical Research Letters 25, 1297–1300.

Toda, H., Wada, E., 1990. Use of $^{15}N/^{14}N$ rations to evaluate the food source of the mysid, *Neomysis intermedia* Czerniawsky, in a eutrophic lake in Japan. Hydrobiologia 194, 85–90.

Trenberth, K.E., 1984. Signal versus noise in the Southern Oscillation. Monthly Weather Review 112, 326–332.

Trenberth, K.E., Hurrell, J.W., 1994. Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9, 303–319.

Tsuda, A., Saito, H., Kasai, H., 1999. Life histories of *Neoclanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific. Marine Biology 135, 533–544.

Tsuda, A., Saito, H., Kasai, H., 2001. Life history strategies of subarctic copepods *Neocalanus flemingeri* and *N. Plumchrus*, especially concerning lipid accumulation patterns. Plankton Biology and Ecology 48, 52–58.

Tsuda, A., Sugisaki, H., 1994. In situ grazing rate of the copepod population in the western subarctic North Pacific during spring. Marine Biology 120, 203–210.

Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitteilungen Internationale Vereinigung Theoretische und Angewandte Limnologie 9, 1–38.

Welch, D.W., Parsons, T.R., 1993. $\delta^{13}C$–$\delta^{15}N$ values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* spp.). Fisheries Oceanography 2, 11–23.