We reported a complete seasonality of biological productivity at lower trophic level and elucidate the environmental drivers in the western Hokkaido coast, Ishikari Bay from September, 2006 to December, 2007. In the high biomass period, average phytoplankton biomass and productivity were 6.92 µg L\(^{-1}\) and 36.12 µg C L\(^{-1}\) d\(^{-1}\), respectively. Water column salinity profile suggests bottom nutrient upwelling especially in summer-autumn when autotrophic production was at a maximum. Micro-size fraction accounted for >80% of the total contributions to phytoplankton biomass and productivity. Strong correlation of POC with Chl \(a\) \((r = 0.875; P < 0.001; n = 16)\) suggests that living phytoplankton in POC may outweigh detrital and bacteria biomass. Stoichiometry of inorganic nutrients revealed a seasonal low (13) and high (25) DIN: PO\(_4\) ratio, and a seasonal low (30) and high (37) Si:PO\(_4\) ratio, suggesting that phytoplankton growth was possibly limited by nitrate and phosphate. Diatoms, Dinoflagellates, Prymnesiophytes, and Chrysophytes were the dominant alga groups in spring, summer-autumn and high biomass period. We conclude that wind-driven convection may still be a significant source of nutrients input in this oligotrophic coastal system, and hypothesize that zooplankton grazing might be a crucial factor in controlling the Chl \(a\) biomass, especially in spring.

Keywords: Time series observation, nutrients, Chlorophyll \(a\), primary production, Ishikari Bay.

1.0 INTRODUCTION

Coastal monitoring studies have received enormous attention across the world in the last two decades due to higher vulnerability of coastal systems to natural and anthropogenic influence than the open ocean. Studies at local and regional levels have focused on water quality and pollution problems arising largely from human activities. In contrast, open coastal areas are generally not very sensitive to pollution due to the short water retention times that usually characterize such systems \([1]\). As a result, a biological productivity study at lower trophic level is considered important in coastal resource production. Phytoplankton is primary food for zooplankton, which in turn is food for fish through food web in marine ecosystem. The variations of phytoplankton strongly relate to the sea resources and these changes are partly depended upon some marine environmental conditions such as current, wind, light, sea temperature, and nutrients.
Marine primary productivity is a key metric of ecosystem health and carbon cycling, and is commonly a function of plant biomass, incident solar flux, and a scaling parameter that accounts for variations in algal physiology. Long-term monitoring of primary productivity is important because it is one of the essential parameters needed for the understanding of marine ecosystems and biogeochemistry. Phytoplankton biomass and primary productivity data have been extensively accumulated in the subarctic North Pacific by time series observation study. In the western subarctic North Pacific, primary productivity and phytoplankton structure have been measured at various locations and seasons [2]. However, the shortage of autumnal and winter observations in the western North Pacific, and lack of time-series site for the western subarctic North Pacific has been reported as the bane for lack of understanding of complete seasonality of biological productivity in these systems [3].

Consequently, the time-series observations at station KNOT (44°N, 155°E) gave important information about seasonal changes of chemical, biological productivity and its community structure in the western subarctic North Pacific. However, in coastal systems around the western subarctic North Pacific, there is still dearth of documented information. Thus, this times series observation was conducted as part of our study on the dynamics of primary production processes in Ishikari Bay, subarctic oligotrophic system with characteristic spatial and temporal variations in its physical, chemical and biological components. Seasonal change in riverine nutrients and distribution of chlorophyll a at 26 grided sampling stations in Ishikari Bay has been reported [4]. In this study, we aim to elucidate other environmental drivers of biological productivity at lower trophic level and to capture a complete seasonal process at a rim station with high accessibility for frequent sampling, homogeneously stable with time and outside influence of riverine nutrient flux. To achieve this, a bi-weekly and monthly time-series study was carried out at a location (43°N, 141°E) in Ishikari Bay off Otaru coast in Hokkaido, Japan during the period of September 2006 - December 2007. Here, we present a complete seasonality in the biological productivity at lower trophic level and related changes of several biogeochemical parameters (dissolved inorganic carbon (DIC), dissolved inorganic nitrogen (DIN) hydrogen ion concentration (pH), dissolved oxygen (DO), phosphate (PO₄), nitrate (NO₃), silicic acid (Si(OH)₄), particulate organic carbon (POC), particulate organic nitrogen (PON), dissolved organic carbon (DOC), and dissolved organic nitrogen (DON).

Figure 1: Map of study area indicating the time series station at 43°N, 141°E in the western Hokkaido coast, Ishikari Bay, Japan.

2.0 MATERIALS AND METHOD

2.1 Study area and sampling

This time series observation was conducted at 43° 11.4’ N, 141° 2.3’ E in Ishikari Bay off Otaru coast (~about 30 km from Ishikari River mouth and ca. 17 m depth) in western Hokkaido, Japan (Figure 1) Sixteen samplings were conducted bi-weekly or monthly starting from September 2006 to December 2007, except in June and November 2007. Water samples were collected at surface (~1 m depth) and bottom (~15 m depth) in acid cleaned 10 L cowboys and 5 L Niskin bottle suspended on a Kevlar line (Fitzwater et al., 1982). Physical parameters (temperature, salinity, PAR, and depth) were measured in-situ by deploying CTD profiler and PAR sensor before mid-day.

Biogeochemical parameters (dissolved inorganic carbon (DIC), dissolved inorganic nitrogen (DIN) hydrogen ion concentration (pH), dissolved oxygen (DO), phosphate (PO₄), nitrate (NO₃), silicate (Si(OH)₄), particulate organic carbon (POC), particulate organic nitrogen (PON), dissolved organic carbon (DOC), and dissolved organic nitrogen (DON).
carbon (DOC), and dissolved organic nitrogen (DON)) were measured in the laboratory. Phytoplankton biomass (Chlorophyll $a$), $^{13}$C primary production, phytoplankton growth rate ($\mu$), and Phytoplankton photopigments (chlorophylls and carotenoids) were determined to provide measures of the relative abundance of different algal groups. Photopigments were identified and quantified using high performance liquid chromatography (HPLC).

2.2 Nutrients
Water samples for nutrient analysis was Sub-samples for nutrients ($\text{NO}_3^-$, $\text{NH}_4^+$, $\text{PO}_4^-$, and $\text{Si(OH)}_4$) from surface and bottom were filtered using a 0.45 $\mu$m GF/F filter and collected in 5 mL spit tubes, and stored frozen at -30 °C until analysis in the laboratory [5]. Concentrations of the dissolved inorganic nutrients were determined using a continuous flow nutrient analyzer (BRAN + LUEBBE, QuAAtro).

2.3 Phytoplankton biomass and Primary Productivity
Phytoplankton biomass (Chl $a$) was measured for total and size fractionated Chl $a$. 150 ml of water were filtered, respectively, through Whatman GF/F (25 mm diameter, nominal pore size 0.7 $\mu$m), and 2 and 10 $\mu$m pore size Whatman Nucleopore polycarbonate filters using parallel filtration under low vacuum pressure (< 250 mg Hg) or gravity. After filtration, Chlorophyll $a$ was immediately extracted by immersing the filter in $N$, $N$-dimethylformamide [6], and preserved at -30°C until on shore analysis by fluorometry. Chlorophyll $a$ concentrations were determined using HITACHI F2000 fluorescence spectrophotometer, according to the method of Parsons [5].

Primary production was determined from $^{13}$C-NaHCO$_3$ uptake using a clean sampling technique [7]. $^{13}$C labeled NaHCO$_3$ was used as a tracer for inorganic $^{13}$C [8]. An aliquot of $^{13}$C NaHCO$_3$ (99 at% $^{13}$C; Shoko Corporation Limited, Japan) solution (0.2 mM) was spiked to samples, which was equivalent to about 10% of the total inorganic carbon in the seawater. Seawater samples were obtained for total and $>10$ $\mu$m size primary productivity. One bottle was used for zero-time and two bottles for 24 h in-situ incubation. Zero-time samples were filtered through 25 mm Whatman GF/F filters, pre-combusted at 450 °C for 4–5 h, under gentle aspiration (<100mm Hg vacuum), and the filtered samples were immediately frozen and stored at -30 °C until isotope analysis on shore. The incubated samples also were filtered similarly to the zero-time sample. The filters were freeze-dried, and then inorganic carbon was removed by an acid treatment in a HCl vapor bath for 4–5 h. Finally, the filters were completely dried in a freeze dryer. The isotopic ratios of $^{13}$C to $^{12}$C were determined by a combined system of EA1112 Elemental Analyzer and DELTA V Confl Mass Spectrometer. Primary productivity was calculated according to the equation described by Hama [8].

2.4 Phytoplankton growth rate ($\mu$)
We estimated phytoplankton growth rate ($\mu$) by dividing chlorophyll $a$ (Chl $a$)-normalized photosynthesis ($P^B$) by the phytoplankton carbon (C) to Chl $a$ ratio (C: Chl $a$) yields an estimate of phytoplankton $\mu$. According to Marañón [9], an estimate of $\mu$ (d$^{-1}$) attainable by a phytoplankton assemblage can be calculated as

$$\mu = \frac{P^B}{C: \text{Chl } a} \quad \text{…………(1)}$$

where $P^B$ is the photosynthesis rate per unit Chl $a$ (mg C [mg Chl $a$]$^{-1}$ d$^{-1}$) and C: Chl $a$ is the carbon (POC) to Chl $a$ ratio (mg C [mg Chl $a$]$^{-1}$).

2.5 DOC and DON
Sub-sample for DOC and DON analysis was filtered through 0.45 $\mu$m Whatman GF/F® filter and filtrate collected into acid clean precombusted glass bottles. The filtrate was dispensed into glass ampoules that were sealed subsequently and frozen at -30 °C until analysis. DOC concentration was measured by high-temperature catalytic oxidation method using a Shimazu TOC-5000A Total Organic Carbon analyzer. DON concentration was determined by subtracting the value of dissolved inorganic nitrogen (DIN), that is, nitrate, nitrite and ammonium concentration from the value of total dissolved nitrogen (TDN) concentration detected by a YANACO ECL-880US NOx analyzer for sample from the outlet of the TOC analyzer. EDTA was used as a standard substance.
2.6 **POC and PON**

Particulate organic carbon (POC) and nitrogen (PON) samples (500 mL) are filtered onto precombusted Whatman GF/F glass fiber filters (25 mm nominal pore size 0.7 µm) under low vacuum pressure (<100 mm Hg) or gravity. Samples are frozen until analysis, then thawed, dried, fumed with concentrated HCl for 6 hrs, and redried. Particulate organic carbon and nitrogen retained by the filters was determined by CHN analysis (FISONS, NA 1500).

2.7 **Statistical Analysis**

Two scales (season and biomass) were applied to classify and analyse data obtained from this study. The 16 occasions during September 2006 – December 2007 were divided into four seasons, spring (March – May), summer (July – August), autumn (September – November) and winter (December – February). Sampling was not conducted in June and November 2007. Using the biomass scale, Chl a data was used in classifying the entire data sets into: High (> 1.0 µg L⁻¹) and Low (<1.0 µg L⁻¹) biomass. Physical, chemical and biological data were classified accordingly and compared for variability using a one-way analysis of variance (ANOVA), whereas, Duncan multiple range test was used for separation of means. Pearson Product Moment Correlations coefficient was used to evaluate relations between variables.

3.0 **RESULTS**

3.1 **Environmental variables**

Fluctuations were identified and quantified, using seasonal and biomass scales, in some physical, biogeochemical and biological variables during September 2006 – December 2007. Surface temperature ranged from 3.77 to 23.13°C with lower values in winter and spring, and maximum value in summer, corresponding with the high biomass period. Salinity values were nearly homogenous across the sampling period with a narrow range of 31.00 ~ 33.65. Vertical profile of temperature across the sampling period was homogenous (Fig. 2a), whereas, salinity profile showed intermittent mixing of bottom waters to the surface especially in summer- autumn (Fig. 2b), evidencing water column vertical mixing. Temperature values were significantly different ($P < 0.001$) with seasons and biomass periods; salinity values were not significantly different ($P > 0.05$). Dissolved oxygen concentration in surface ranged between 5.27 and 7.37 ml L⁻¹, with higher concentration (> 6.40 ml L⁻¹) during winter and spring seasons, and in low biomass period. Seasonal pH values were the highest in summer (8.04 ± 0.22) and in High biomass (8.02 ± 0.19) period. Although, dissolved oxygen concentration was not significantly different ($P > 0.05$) in the High and Low biomass period but across the seasons, the variation was highly significant ($P < 0.001$). In contrast, there was significant variation ($P < 0.05$) in pH values in High and Low biomass period with no significant difference ($P > 0.05$) across seasons.

Suspended particulate matter (SPM) ranged from 1.40 to 19.40 mg L⁻¹. Highest values were observed in spring (7.25 ± 8.20 mg L⁻¹) and autumn (6.80 ± 5.71 mg L⁻¹), corresponding to High biomass period. Surface water photosynthetically active radiation (PAR) minimum and maximum values were 1.6 and
19.2 µmol m⁻² s⁻¹, respectively. PAR was the highest in summer (2130 µmol m⁻² s⁻¹ unit) and lowest in winter (829.46 ± 599.34). Although SPM and PAR were not significantly different in the High and Low biomass period (P >0.05), there was an increase in SPM and PAR values from Low to High biomass period. DIC concentration was fairly homogeneous across seasons and biomass periods. DIC values were not significantly different (P>0.05) with seasons and biomass periods.

3.2 Nutrient concentration and relative ratio
Nutrients concentrations (DIN, PO₄, Si(OH)₄) were statistically significant (P < 0.05) with season and in classified High and Low biomass periods, whereas, nutrients ratios (N:P, Si:P, Si:N) were not statistically significant (P >0.05) with season and biomass period.

Dissolved inorganic nitrogen (DIN: NH₄⁺ + NO₃⁻) concentrations during the sampling period ranged between 0.0 and 29.6 µM (Fig. 3e); the highest values were in winter and spring, diminishing through the summer and High biomass period. Across the season, percentage contribution of NO₃⁻ (4.3 µM) to DIN (8.1 µM) was highest in spring (53%) and closely followed in autumn (47%). The relative maximum of DIN in winter was due to high NH₄⁺ concentration (24.5 µM) in January (Fig. 3b and e). Aside from this peak, NH₄⁺ concentration was not significantly different (P > 0.05) across the sampling period.

Dissolved inorganic phosphate (PO₄³⁻) varied between 0.04 µM in July (summer) and 1.02 µM in January (winter) (Fig 3c). It also decreased from 0.44 µM in Low to 0.14 µM in High biomass period. Like other nutrients, silicic acid concentration peaked in winter, followed by spring and an abrupt decrease in summer (from 22.1 to 1.0 µM in September) (Fig. 3d). In the High biomass period, N:P ratio was close to the 16:1, optimal algal growth ratio as indicated by the Redfield ratio [9]. Seasonal patterns of the Si:P ratios were similar to the N:P ratios. The Si:P ratios were largely >16:1 across sampling seasons and biomass periods. The Si:N ratios varied seasonally and were largely above 1:1 across season and biomass periods.

In Figure 4, molar quotients between the concentrations of potentially limiting nutrients are defined in logarithmic plot (log N:P vs. log Si:N) by the Si:N=1, N:P=16 and Si:P=16 lines. The atomic N:P, Si:P and Si:N at the time series location in Ishikari Bay exhibited seasonal variations in stoichiometric nutrient limitation (Fig. 4). DIN appears to be most limiting nutrient with N:P molar ratio of <16 in the High biomass period. N:P molar ratios were largely >16 in the Low biomass period, except in March when ratio dropped to 7. In this study, silicate was not considered potentially limiting as Si:N molar ratios were often >1, except in January (0.7).
Figure 4: Si:N:P molar ratio limiting trends in High and Low biomass periods (b) at 43°N, 141°E location in the Ishikari Bay during the time series observation. Diagonal line: aggregated ratio (Si:N:P = 16:16:1).

3.3 Phytoplankton biomass (Chl a)

Total and micro-sized Chl a concentration peaked at the onset of this study in September, 2006 and in September, 2007, whereas, pico-sized Chl a peaked only at the onset (Fig. 5). Nano-sized fraction peaked in October, 2006 and September, 2007.

Micro-sized phytoplankton dominated and accounted for a significant proportion in spring (71.4%), summer (97.6%) and autumn (67.3%) seasons and during the High biomass events (84.2%) as compared to the nanoplankton and picoplankton fraction, which had almost equal proportion during the Low biomass periods. On average, the contribution to the total Chl-a of three phytoplankton size classes revealed the dominance of microphytoplankton. Total and micro-size fraction biomass contribution in both summer and autumn accounted for > 60% of the observed “High” biomass period.

Figure 5: Temporal variation of total and size fractionated Chl a (a), total Chlorophyll a concentration at 43°N, 141°E during the time series observation in Ishikari Bay.

Total Chl-a was significantly related to the micro-phytoplankton contribution (r = 0.990, P < 0.0001, n =16) and nano-phytoplankton contribution (r = 0.760, P < 0.001). No significant relationship was found with pico-

size fraction (Not shown). Chl a concentrations were not significantly different (P > 0.05) across seasons using a one-way ANOVA, justifying the biomass classification used, which exhibited a highly significant difference (P < 0.001) in this study.

3.4 Primary productivity and photosynthetic parameters

The mean annual cycle of primary productivity is similar to that of Chlorophyll-a, with highest production from summer to autumn, peaking at 543.8 µg C L⁻¹ d⁻¹ in September, 2007. Minimum values of 2.79 µg C L⁻¹ d⁻¹ occur in winter (January). Although, carbon assimilation (¹³C Uptake) closely followed the same temporal trend as Chl a in this study, but did not show a clear peak at the onset. Total and micro-sized primary production showed clear peaks in April, 2006 and September, 2007. The combination of Pico + Nano size fraction only peaked in September, 2007 (Fig. 6).

Generally, micro-sized primary production contributed >50% to the total primary production across seasons and biomass period. The micro-sized fraction dominated and accounted for a significant proportion in winter (50.3%), spring (70.7%), summer (85.5%) and autumn (67.0%) seasons and during High (85.2%) and Low (51.2%) biomass period. Also, the micro-sized primary production in spring, summer and autumn accounted for > 60% of the production in the High biomass period.

Figure 6: Temporal variation of total and size fractionated primary production (a), total primary production at 43°N, 141°E during the time series observation in Ishikari Bay.

Total primary production significantly relates to the micro-sized primary production (r = 0.995; P < 0.0001; n = 16) and the Pico + Nano-sized fraction (r = 0.929; P < 0.0001; n = 16). Similar to Chl a, primary production values were not significantly different (P > 0.05) across seasons using a one-way
ANOVA, but exhibited a highly significant difference \((P < 0.005)\) across biomass period. Assimilation index-Chlorophyll \(a\) (Chl \(a\))—normalized photosynthesis \((P_{\text{B}})\) showed significant seasonal variation \((P < 0.05)\) with a maximum \(P_{\text{B}}\) value in summer \((47.7 \, \mu g \, C \, \mu g^{-1}\text{Chl } a \, d^{-1})\) and a minimum in winter \((9.7 \, \mu g \, C \, \mu g^{-1}\text{Chl } a \, d^{-1})\). No significant variation \((P > 0.05)\) in biomass period.

Phytoplankton growth rate, \(\mu\) was highly significant \((P < 0.001)\) with biomass period, whereas, there was no significant variation \((P > 0.05)\) across season. In this study maximum phytoplankton growth rate \((\mu)\) was attained in summer \((0.58 \, d^{-1})\) and in the High biomass period \((0.44 \, d^{-1})\).

### 3.5 POC: Chl \(a\) ratio

Particulate carbon/Chl \(a\) ratio was lower in summer season, with the observed minimum \((38.8)\) occurring in September, 2006. The living phytoplankton carbon concentration estimated from POC:Chl \(a\) ratio \((73)\) and the total POC values, is in the range of 309-762 \(µg\) C L\(^{-1}\) \((mean = 436.1 \, \mu g \, l^{-1})\) in the period of High biomass. POC was significantly related to Chl \(a\) \((r = 0.875; \, P < 0.001; \, n = 16)\)

### 3.6 Dissolved and particulate organic matter

Particulate organic carbon was significantly related to particulate organic nitrogen \((r = 0.987; \, P < 0.001; \, n = 15)\) (Fig. 7). No significant relationship was found between DOC and DON. The POC:PON ratio of the High biomass period was 6.6, slightly lower than the ratio of 8.0 for the Low biomass period. In Low biomass period, all observed ratios were above the Redfield ratio while those in the High biomass period were closer to the C:N of 6.6 line. DOC:DON ratios were ~ 3 and 15 times higher than the Redfield C:N ratio line \((6.6)\) in the High and Low biomass period, respectively. While POC and PON concentrations were significantly different \((P < 0.001)\) in the biomass period, there were no significant variations with season. Also, DOC and DON were not significantly different \((P > 0.05)\) with season, but only DON was significantly different \((P < 0.005)\) across biomass periods. Low POC:PON ratios indicate that the particulate organic matter is nitrogen-enriched and typical of living material rather than detritus.

![Figure 7: Relationships of particulate organic carbon and nitrogen, and dissolved organic carbon and nitrogen. Dark thick Redfield ratio line in High and Low biomass period at 43°N, 141°E during time series observation in Ishikari Bay](attachment:figure7.png)

### 3.7 Phytoplankton community structure

Fucoxanthin phytopigment was conspicuously dominant in spring, suggesting Diatoms, Prymnesiophytes, and Chrysophytes as possible algal groups. In summer and autumn fucoxanthin dominated followed by diadinoxanthin, suggesting Diatoms, Dinoflagellates, Prymnesiophytes, and Chrysophytes as possible alga group. Thus, phytoplankton community was dominated by diatom especially in autumn, spring and summer seasons, and in the High biomass period.

### 4.0 DISCUSSION

This study provides a complete seasonality of biological productivity and environmental drivers in the western Hokkaido coast, Ishikari Bay. The seasonal variation of biological productivity at lower trophic level at this time series
station was very complex and driven by a variety of physical, chemical and biological factors. When temperature was highest in autumn (18.7°C), summer (21.5°C) and high biomass (18.5°C) period, there was direct corresponding increase in autotrophic production. Temperature was positively related to the micro-sized fraction of Chl \( a \) \( (r =0.730; \ P < 0.001; \ n = 16) \) and production \( (r =0.606; \ P < 0.01; \ n = 16) \) which dominated and accounted for > 80% of the total autotrophic production in this study.

Nutrients concentrations (DIN, PO\(_4\), Si(OH)\(_4\)) were statistically significant \( (P < 0.05) \) with season and biomass periods, whereas, nutrients ratios (N:P, Si:P, Si:N) were not statistically significant \( (P >0.05) \) with season and biomass period. However, according to reference [10], deviations from Redfield ratios are considered as an index of the potentially limiting factor. In a further study, references [11] and [12] suggested that stoichiometric limitation was determined according the following criteria: (1) P limitation, if Si:PO\(_4\) >22 and DIN:PO\(_4\) >22, (2) N limitation, if DIN:PO\(_4\) <10 and Si:DIN >1, (3) Si limitation, if Si:PO\(_4\) < 10 and Si:DIN <1. The stoichiometric ratio is an indication of suggested limitation; and probable limitation is assessed if the nutrient concentration is under a threshold limiting nutrient uptake. References [11] and [12] estimated threshold values of 2, 1 and 0.1 \( \mu \)M for Si, DIN, and PO\(_4\) respectively. In this study, the data of inorganic nutrients revealed a seasonal low (13) and high (25) DIN: PO\(_4\) ratio, and a seasonal low (30) and high (37) Si:PO\(_4\) ratio, suggesting that phytoplankton growth was possibly limited by nitrate and phosphate. Although, ambient concentration of PO\(_4\) was generally > 0.1 \( \mu \)M, except in summer when values were lower (0.04 – 0.06, range), summer-autumn seasons dominated and accounted for > 60% of total phytoplankton biomass and production in high biomass period. Thus, the phosphate physiology may be of importance to the dynamics of phytoplankton in the Hokkaido western coastal waters of the Ishikari Bay. Ratios of Si:N might also be important in structuring phytoplankton communities. Whereas diatom blooms tend to occur at Si:N ratios around or, >1, most harmful species (e.g., flagellates or dinoflagellates) bloom at lower ratios [13]. The Si:N ratios at our time series station were highly variable, as high as 67. In all observations Si:N ratio was > 1, except in January when value was 0.67. According to the above criteria, silicic acid was never limiting condition at the time series station investigated and phosphate was the principal factor limiting phytoplanktonic growth. Nutrient ratios indicated that stoichiometric N limitation dominated in the High biomass period corresponding largely to autumn and summer seasons. The low nitrate and ammonium concentrations in surface waters especially in the High biomass period may be explained by phytoplankton uptake and not by low-nutrient upwelling.

Chl \( a \) biomass and primary production were highest in summer-autumn due to thermohaline stratification, high nutrients, temperature, and light availability. However, in winter, wind mixing, rapid flushing, reduced irradiance and low temperatures resulted in low phytoplankton biomass and production. Despite some decreases in vertical mixing and an increase in light and temperature, the classical spring bloom of temperate areas was not observed at this time series station. Therefore, we hypothesize that in addition to tidal and wind mixing, zooplankton grazing might be a crucial factor in controlling the Chl \( a \) biomass, particularly in spring, during the initial stage of algal blooms when phytoplankton start to response to the increasing light, temperature and nutrient influx from tidal mixing and bottom upwelling.

According to reference [14], the primary factors that affect the abundance and distribution of Chl \( a \) and primary production levels in the coastal zone are the physical forces that transport not only phytoplankton but also nutrients to the euphotic zone (i.e. upwelling fronts). In this study, vertical mixing of bottom waters to the surface as suggested by salinity profile (Fig. 3) evidences the influence of bottom nutrients upwelling, especially in summer-autumn season when autotrophic production was at maximum. Moreso, water column maximum depth of ~ 17 m at the time series station may aid efficient transfer of nutrient from bottom to surface water. Also, elevated levels of primary production and Chl \( a \) have been reported along the coast of central Chile during upwelling events [15]. Along the western Hokkaido, prior to summer-autumn
season, a typhoon event which may result in water column vertical mixing is peculiar. These events have been considered responsible for the patches of phytoplankton-rich biomass in coastal waters [16].

Furthermore, it should be noted that in our biomass classification, High (or Low) phytoplankton biomass period does not necessarily indicate high (or low) absolute growth rates. Low biomass can be due to either low absolute growth (regulated by bottom–up factors such as nutrients or light), or elevated growth balanced by high rates of grazing or other losses [17] [18] [19]. The high productivity seems to have been induced by a new nutrients supply associated with upwelling into the sub-surface layers during the seasonal stratification periods in Ishikari Bay. Also, since temperature directly corresponds with the high productivity period faster regeneration of nitrogen may be accelerated. Determining whether phytoplankton are growing at rates proximal to their theoretical maximum is critical to predict the responses of the planktonic ecosystem to potential changes in nutrient supply to the upper oligotrophic ocean [9]. Thus, the growth rate (µ) of phytoplankton must be known because this rate sets an upper limit to the heterotrophic biomass that can be sustained by a given amount of photoautotrophic biomass [20]. Average phytoplankton growth rate (µ) in High and Low biomass periods were 0.44 d⁻¹ and 0.09 d⁻¹, respectively. Reported rates from the oligotrophic subtropical gyres range from average values of ~ 0.2–0.3 d⁻¹ [19] [21] to average values near [22] [23] or well above 1 d⁻¹ [24]. Strong correlation of POC with Chl a (r = 0.875) in this study suggest that living phytoplankton in POC far outweighed detrital and bacteria biomass.

Diatoms were the dominant group of phytoplankton found in spring, summer autumn and in the High biomass period. It has been shown previously that diatoms are the predominant phytoplankton group in estuaries [25] [26]. Throughout the seasonal cycle they were responsible for the observed phytoplankton biomass and productivity in spring, and summer-autumn.

Lastly, the annual cycle of mixing and irradiance drives a strong annual cycle of production in many oceanic ecosystems [27] [28]. The amplitudes of biological productivity seasonal cycles are reduced in this study (i.e. phytoplankton biomass and productivity were not significantly different seasonally), justifying our use of biomass in classification. In the absence of stronger mechanism of nutrient input in this oligotrophic system, we conclude that wind-driven convection may still be a significant source of nutrients. This further reveals the distinct seasonal variation of biological productivity in an oligotrophic subarctic coastal system of the Ishikari Bay.

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