



## Research Article

# Seasonal variations of size-fractionated chlorophyll *a* and primary production in the coastal area of Hokkaido in the Okhotsk Sea



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## Abstract

The size structure of phytoplankton has a significant influence on the marine ecosystem and fishery production. To elucidate which size of phytoplankton make up the majority of the primary producer community, size-fractionated chlorophyll *a* and primary production were investigated in the coastal area of Hokkaido in the Okhotsk Sea, which has high fishery production. Large ( $> 10 \mu\text{m}$ ) phytoplankton accounted for approximately 80% of biomass and production in the spring bloom, approximately 40–75% in summer and autumn, but only approximately 20% in winter. Nutrient limitation possibly led to the lower contributions of large phytoplankton to biomass and production in summer and autumn. The size structure of chlorophyll *a* reflected that of primary production. Large phytoplankton were considered the main producers throughout the year, except winter. However, there was no significant difference in the chlorophyll *a*-specific primary production among the three sizes (large:  $> 10 \mu\text{m}$ ; medium:  $2\text{--}10 \mu\text{m}$ ; small:  $< 2 \mu\text{m}$ ) in any season, implying the same growth rates in the three sizes. The lower contribution of large phytoplankton in winter may have been due to an intense copepod grazing. Large phytoplankton are likely to be the main primary producers throughout the year, leading to high fishery production in the study area.

**Keywords** Size fractionation · Primary production · Chlorophyll *a* · Chlorophyll *a*-specific primary production · Large phytoplankton · Coastal area of Hokkaido in the Okhotsk Sea

## 1 Introduction

The size structure of a phytoplankton community influences its food web structure, the ecosystem's biomass and production [1–4], and hence, fishery production. It is well known that the concentration of nutrients in an ecosystem significantly affects the size structure of the phytoplankton community. It has been reported from field surveys that large phytoplankton dominate under nutrient-rich conditions, whereas small phytoplankton dominate under oligotrophic conditions [2, 5–12]. The supply of nutrients to the upper layers is also important for controlling the size structure of the phytoplankton community [9, 10, 13]. Ecosystems dominated by large phytoplankton have

fewer trophic levels than those dominated by small ones [3]. When the trophic level increases by one, the biomass becomes one-tenth [3, 14, 15]. Therefore, ecosystems, in which large phytoplankton make up the bulk of main primary producers, can maintain a higher fishery production than that of the systems with small phytoplankton. Accordingly, it is important to determine which phytoplankton size is the main component of the total primary producers.

Our study area is located in the southwestern part of the Okhotsk Sea and has prosperous fisheries [16–18]. In the study area, the Soya Warm Current, a warm current, flows from late spring to late autumn, and the East Sakhalin Current, a cold current, flows from late autumn to spring of the

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following year; moreover, the area is occupied with drift ice during the mid-winter period [19–21]. The changes in the marine environment according to season are remarkably pronounced in this area, and they include variations in environmental factors such as temperature, nutrients, and light, which affect phytoplankton production and biomass [18, 19, 21–26].

According to the summary of Shiomoto et al. [18], the water temperature rises from around 0 °C in early spring toward summer, reaching a maximum water temperature of around 20 °C. After that water temperature decreases again in the winter. Nutrient concentrations are high in early spring, but become extremely low throughout the phytoplankton spring bloom, remaining low until late autumn and rising again in early winter. For example, nitrate, which is considered to be the limiting nutrient for phytoplankton in spring bloom, decreases from ca. 15  $\mu\text{mol/L}$  to almost depleted condition through the spring bloom and reaches ca. 2  $\mu\text{mol/L}$  in early winter. These remarkable environmental changes should result in marked seasonal changes in primary producers.

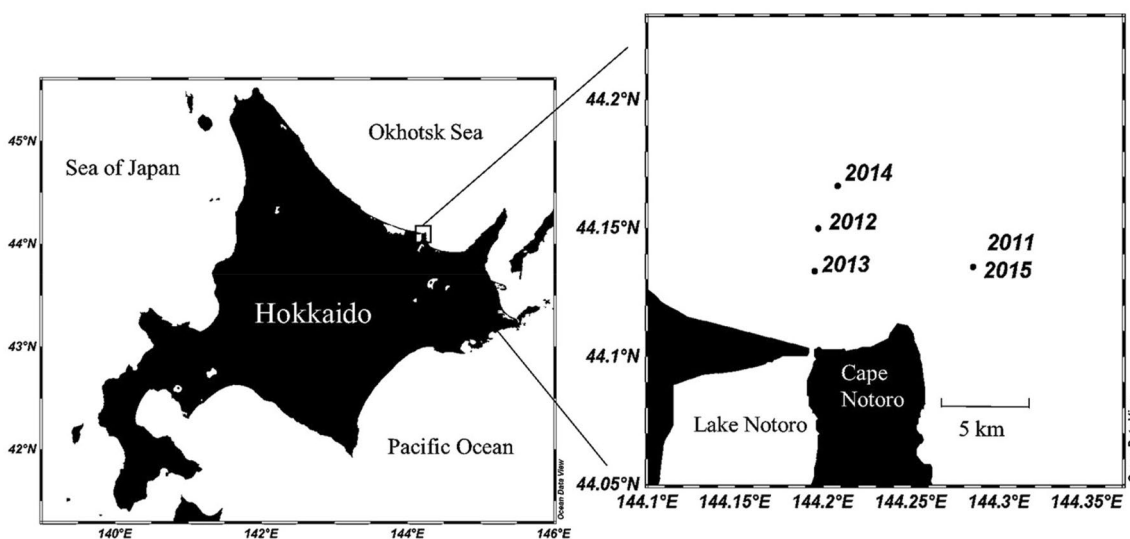
A previous study about the size structure of phytoplankton standing stock (chlorophyll *a* concentration) in this area has been conducted. The spring bloom by diatoms occurs in April, and the chlorophyll *a* concentration, which is below 1  $\mu\text{g/L}$  in early spring, reaches a maximum of 30  $\mu\text{g/L}$  [18]. After spring bloom, chlorophyll *a* concentration is around 1  $\mu\text{g/L}$  until winter. Spring blooms are dominated by large ( $> 10 \mu\text{m}$ ) phytoplankton, which continues until late autumn. Smaller ( $< 10 \mu\text{m}$ ) phytoplankton dominate in winter. However, size-fractionated primary production has not yet been measured. The standing stock

of phytoplankton is determined by the difference between production and loss, implying that chlorophyll *a* size structure does not necessarily reflect the main primary producers. Therefore, to determine which phytoplankton size make up the majority of the primary producer community, we measured the seasonal variations in size-fractionated primary production as well as size-fractionated chlorophyll *a* in the coastal area of Hokkaido in the Okhotsk Sea.

## 2 Materials and methods

This study was conducted in the coastal area of Hokkaido, Okhotsk Sea, during a cruise of the “Wakashio Maru” of the Abashiri Fishery Cooperative in the period of April–December (avoiding drift ice period) 2011–2015 (Fig. 1). During the 5 year study period, surveys were conducted 4 times in August and December; 5 times in October; 6 times in April, June, and November; 7 times in May; 8 times in September; and 9 times in July. The survey area is a scallop aquaculture ground with water depth of approximately 60 m. Surface water samples were collected at 0800–1200 h using an acid-cleaned plastic bucket. Water temperature and salinity at the surface were measured using a digital thermometer (SN3000, NETSUKEN) and salinometer (Model 5, Tsurumi Seiki), respectively. Nutrient concentrations were measured with a BLTEC Auto Analyzer SWAAT after storing the samples at  $-70 \text{ }^\circ\text{C}$ .

The chlorophyll *a* (Chl *a*) concentrations of total and size-fractionated samples were measured fluorometrically using a Turner Designs 10-AU fluorometer according to Welschmeyer [27]. The water samples (200 mL)



**Fig. 1** Location of the sampling stations along the coastal area of Hokkaido in the Okhotsk Sea. The numbers represent the years of each investigation. The water depth of the stations was approximately 60 m

were filtered through Nuclepore filters with pore sizes of 10 and 2  $\mu\text{m}$ , and the filtrate was re-filtered through Whatman GF/F filters (approximately 0.7  $\mu\text{m}$  pore size). Size fractions of < 2 and < 10  $\mu\text{m}$  were collected. In addition, 200 mL water samples were directly filtered using Whatman GF/F filters (total). Chl *a* was extracted with N, N-dimethylformamide [28]. Calibration of the fluorometer was performed using a commercially available Chl *a* standard (MERK). Chl *a* concentrations for the < 2- $\mu\text{m}$  size fraction (small) and the total sample were obtained directly and those for the 2–10- $\mu\text{m}$  (medium) and the > 10- $\mu\text{m}$  (large) size fractions were obtained from the differences between the < 10 and < 2- $\mu\text{m}$  size fractions and between the total and < 10- $\mu\text{m}$  size fractions, respectively.

Primary production was measured by the simulated in situ method using the  $^{13}\text{C}$  uptake technique [29]. The samples (2 L) were dispensed into two 2-L polycarbonate bottles and enriched with  $^{13}\text{C}$ - $\text{NaHCO}_3$  (98 atom%  $^{13}\text{C}$ ; Isotec) to approximately 10% of the total inorganic carbon in ambient water within 3–4 h of sample collection. The samples were placed in a water tank installed on the roof of the Tokyo University of Agriculture building and incubated under sunlight for 24 h at the same water temperature as that in which the samples were collected. Dark bottle uptake is similar to the zero-time blank in the  $^{13}\text{C}$  technique [30], and thus, no dark bottles were not used. Photon fluxes [photosynthetically available radiation (PAR) 400–700 nm] were monitored every 5 min with a quantum sensor (LI-190R, Li-Cor) during the incubation.

Following incubation, the seawater samples in bottles were immediately supplied to the size-fractionation operation. The procedure used for size-fractionation was the same as that used for Chl *a*. The Whatman GF/F filters used for measuring primary production were pre-combusted at 450  $^\circ\text{C}$  for 4 h. Before the isotope analysis, the filters were treated with HCl fumes for 4 h to remove inorganic carbon and completely dried in a vacuum desiccator. The isotopic ratios of  $^{13}\text{C}$  to  $^{12}\text{C}$  and particulate organic carbon contents were determined using a mass spectrometer (ANCA SL or INTEGRA 2CN, CerCon). The total inorganic carbon in the water was measured using an infrared analyser (TOC 5000, Shimadzu). Primary production was calculated according to the equation described by Hama et al. [29], and the values of the two polycarbonate bottles were averaged. Primary production for the < 2- $\mu\text{m}$  (small), 2–10- $\mu\text{m}$  (medium), and > 10- $\mu\text{m}$  (large) size fractions were obtained from the same procedure as that for Chl *a*.

Principal component analysis (PCA) was carried out to investigate how the environmental factors (light, water temperature, salinity, nutrients) are related to the size structure of phytoplankton biomass and production. PCA was performed using Excel Statistics 2012 for Windows®

(SSRI Co., Ltd., Japan). Statistical significance was determined at  $p < 0.05$ .

## 3 Results

### 3.1 Physical and chemical environments

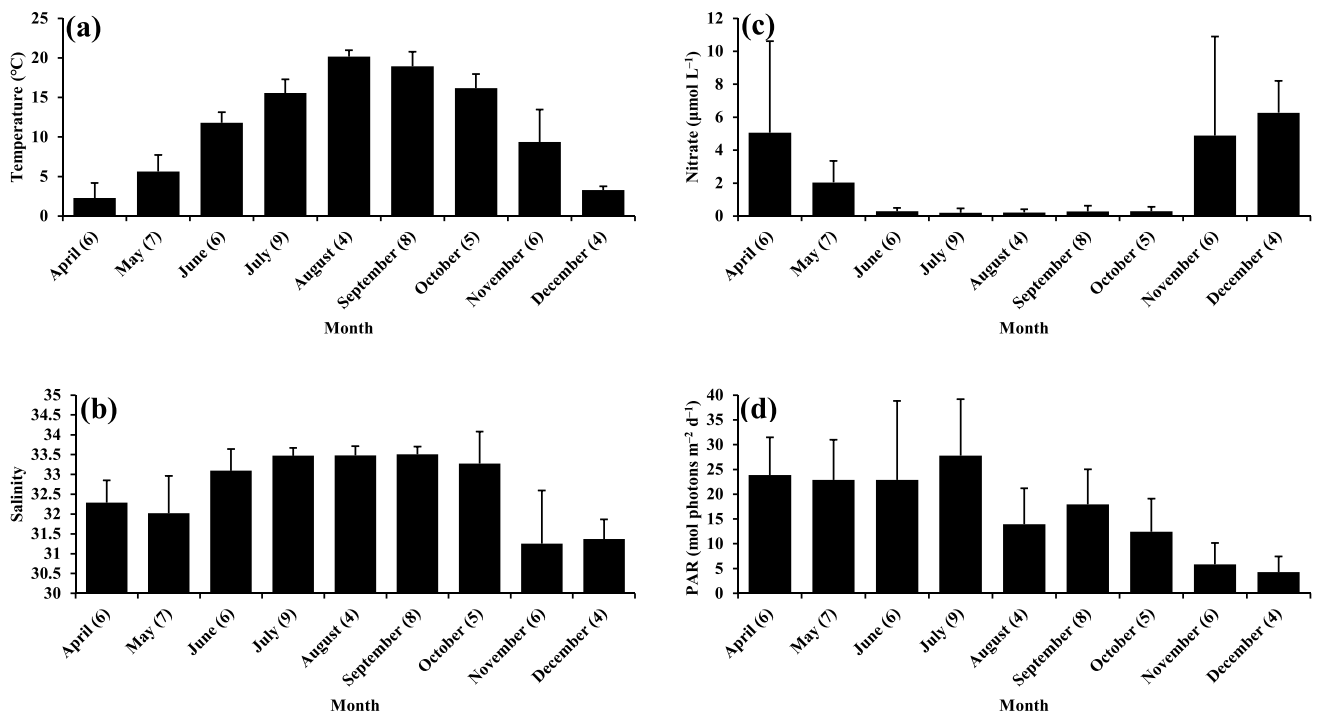
Water temperature increased from April–August and decreased from September onward (Fig. 2a). The minimum value of the year was approximately 2  $^\circ\text{C}$  in April, and the maximum value was approximately 20  $^\circ\text{C}$  in August. Water temperatures over 10  $^\circ\text{C}$  were observed between June and October. Salinity was approximately 32.0 in April and May, between 33.0 and 33.5 in June–October, and approximately 31.3 in November and December (Fig. 2b). The influences of the East Sakhalin Current (temperature: < 7  $^\circ\text{C}$ ; salinity: < 32.0) [21] and the Soya Warm Current (temperature: 7–20  $^\circ\text{C}$ ; salinity: 33.6–33.4) [21] were strongly observed in April–May and June–October, respectively. November and December were again affected by the East Sakhalin Current.

Nitrate concentrations were 2–6  $\mu\text{mol L}^{-1}$  in April, May, November, and December, and approximately 0.3  $\mu\text{mol L}^{-1}$  in June–October (Fig. 2c). Nitrate concentrations were relatively high from early winter to the next spring, influenced by the East Sakhalin Current, and were nearly depleted from early summer to late autumn because of the Soya Warm Current. The PAR during incubation was approximately 23 mol photons  $\text{m}^{-2} \text{d}^{-1}$  in April and May, 12–28 mol photons  $\text{m}^{-2} \text{d}^{-1}$  in June–October, and approximately 5 mol photons  $\text{m}^{-2} \text{d}^{-1}$  in November and December (Fig. 2d); the PAR was significantly lower in winter compared to the other seasons.

### 3.2 Chlorophyll *a*

The maximum mean value of total Chl *a* throughout the year was 5.0  $\text{mg m}^{-3}$  in April (Fig. 3a). The maximum value measured over the five years was 8.4  $\text{mg m}^{-3}$  on April 1, 2015. These observations indicate that the spring bloom in the survey area occurred in April. From May–December, the monthly mean values were between 0.7 and 2  $\text{mg m}^{-3}$ . There were no significant differences among the total Chl *a* concentrations in each month, except for in April (Kruskal–Wallis test,  $p > 0.05$ ).

Large (> 10  $\mu\text{m}$ ) phytoplankton were dominant in April, accounting for 84% of the total Chl *a* concentration (Fig. 3b). They were also dominant between May and October, but the proportion was lower (42–74%). In November and December, the proportions of medium and small phytoplankton were high, at approximately 35% and 45%, respectively. Combined, both size classes accounted for



**Fig. 2** Seasonal variations in the mean and standard deviation of the temperature **a**, salinity **b**, nitrate **c**, and photosynthetically available radiation (PAR) during incubation **d**. The mean values and

standard deviations for each month were calculated using all data obtained in the 5-year study. The numbers in parentheses represent the number of data sets

approximately 80% of the total phytoplankton. The proportion of large phytoplankton was low, accounting for approximately 20%.

### 3.3 Primary production

The maximum mean value of total primary production throughout the year was found in April, similar to the total Chl *a* concentration, and it was 62 mg C m<sup>-3</sup> d<sup>-1</sup> (Fig. 4a). The maximum value measured over the five years was 123 mg C m<sup>-3</sup> d<sup>-1</sup> on April 1, 2015. These results support the occurrence of the spring bloom in April. From May–November, the mean values were of 20–45 mg C m<sup>-3</sup> d<sup>-1</sup>; the value in December was approximately 6 mg C m<sup>-3</sup> d<sup>-1</sup>, which was less than one-third of the mean values of the other months. There was no significant difference in the primary production from May to November (Kruskal–Wallis test, *p* > 0.05), whereas a significant difference was obtained by including the results for December (Kruskal–Wallis test, *p* < 0.05). The seasonal variation in total primary production was the same as that for the total Chl *a* concentration, except for the low value in December.

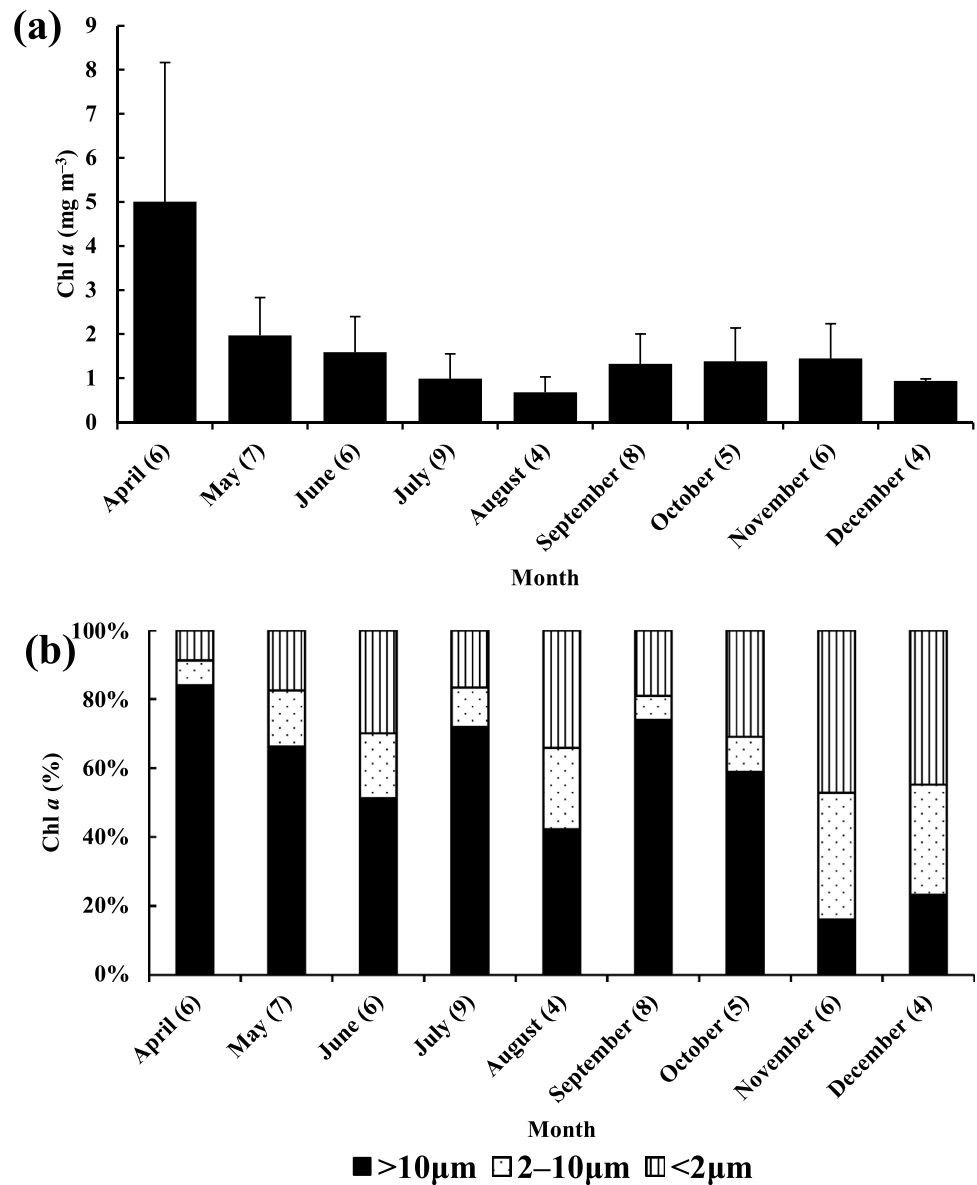
Large phytoplankton were dominant in terms of the total primary production in April, accounting for 82% (Fig. 4b). They were also dominant from May–October, but the proportion was 48 to 66%. In November and

December, the proportions of medium and small phytoplankton were high, accounting for 52% and 35% in November and 41% and 31% in December, respectively. Both sizes accounted for approximately 80% of the average for November and December. The proportion of large phytoplankton was low, accounting for 13% in November and 28% in December. The seasonal variation in the size structure of primary production was the same as that of the total Chl *a* concentration, showing that the size structure of Chl *a* reflected that of primary production.

### 3.4 Chlorophyll *a*-specific primary production

Primary production is affected not only by light but also by phytoplankton biomass. The light-saturated production divided by Chl *a* concentration is called the assimilation number, which represents the maximum specific growth rate [31, 32]. Since there was no guarantee that the primary production obtained in this study was light-saturated, the primary production divided by Chl *a* concentration is herein referred as the Chl *a*-specific primary production, considered an index of the specific growth rate. The values of Chl *a*-specific primary production were higher for all phytoplankton sizes from June–October (summer and autumn) and lower in April and May (spring) and November and December (winter) (Fig. 5). For all sizes,

**Fig. 3** Seasonal variations in the mean and standard deviation of the total chlorophyll *a* concentration **a** and the mean size structure of chlorophyll *a* concentration **b**. The mean values and standard deviations for each month were calculated using all data obtained in the 5-year study. The numbers in parentheses represent the number of data sets



the values of Chl *a*-specific primary production were significantly higher in summer and autumn than in spring and winter (Mann–Whitney U test,  $p < 0.05$ ). There was no significant difference in the values between spring and winter for medium and small phytoplankton (Mann–Whitney U test,  $p > 0.05$ ); however, for large phytoplankton, the Chl *a*-specific primary production was significantly higher in spring than in winter (Mann–Whitney U test,  $p < 0.05$ ). Higher values were found in the Soya Warm Current water, whereas the lower values were found in the East Sakhalin Current water.

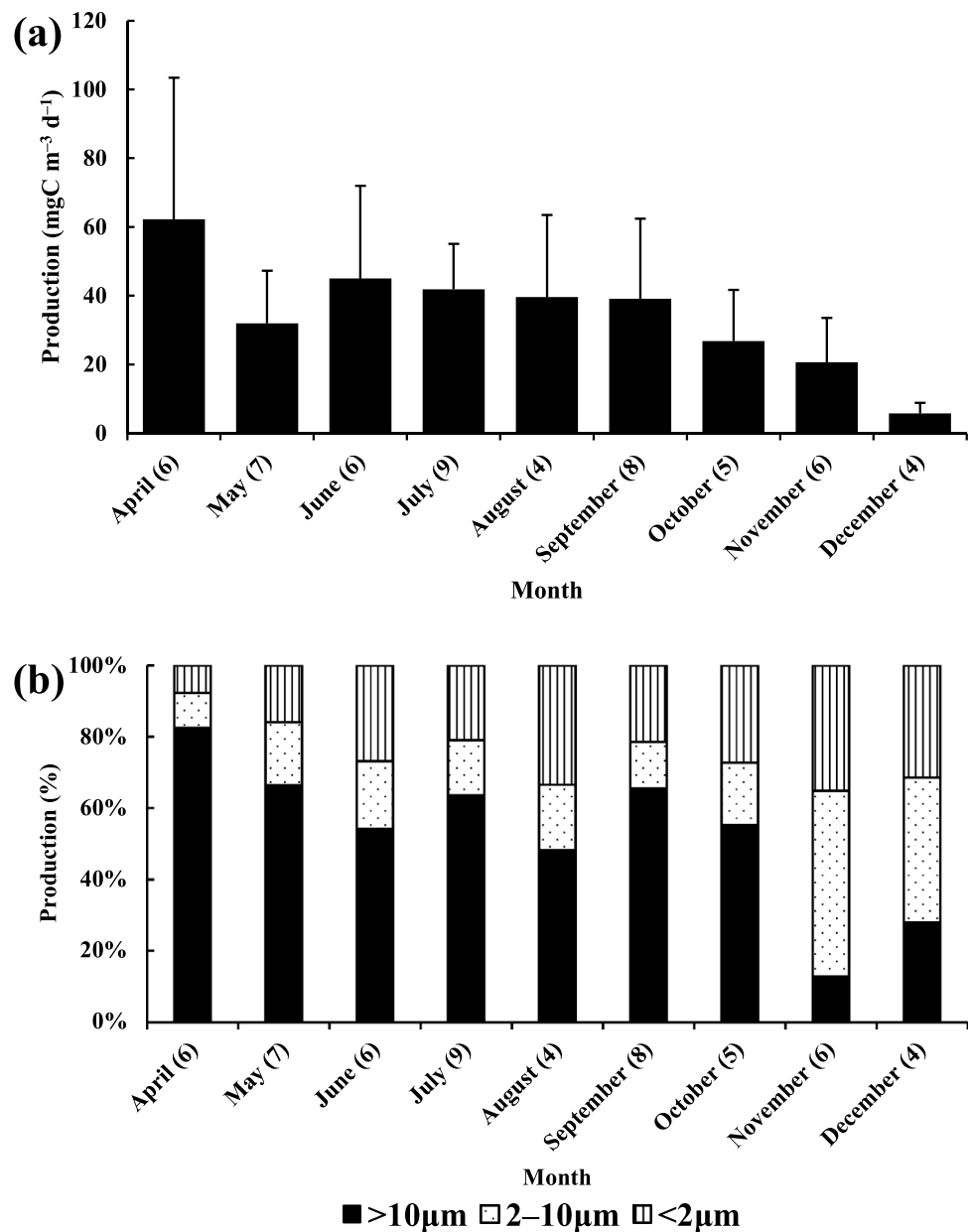
There were no significant differences in the Chl *a*-specific primary production among the three sizes in all seasons (April–December), spring (April and May), summer and autumn (June–October), and winter (November and December) (Kruskal–Wallis test,  $p > 0.05$ ; Fig. 6a, b, c, d).

However, the average values and the median of the Chl *a*-specific primary production were the highest in the medium phytoplankton (Fig. 6).

### 3.5 Relationship between phytoplankton size structure and environmental factors

The PCA ordination for 14 variables explained 73.8% of data variability in the first two axes (Fig. 7). From the PCA ordination diagram (Fig. 7), the first principal component was found to have positive correlations with the nutrients and the percentage contributions of small and medium phytoplankton to Chl *a* and primary production. In contrast, negative correlations were found with light, water temperature, salinity, and the percentage contributions of large phytoplankton to Chl *a* and primary

**Fig. 4** Seasonal variations in the mean and standard deviation of the total primary production **a** and the mean size structure of primary production **b**. The mean values and standard deviations for each month were calculated using all data obtained in the 5-year study. The numbers in parentheses represent the number of data sets

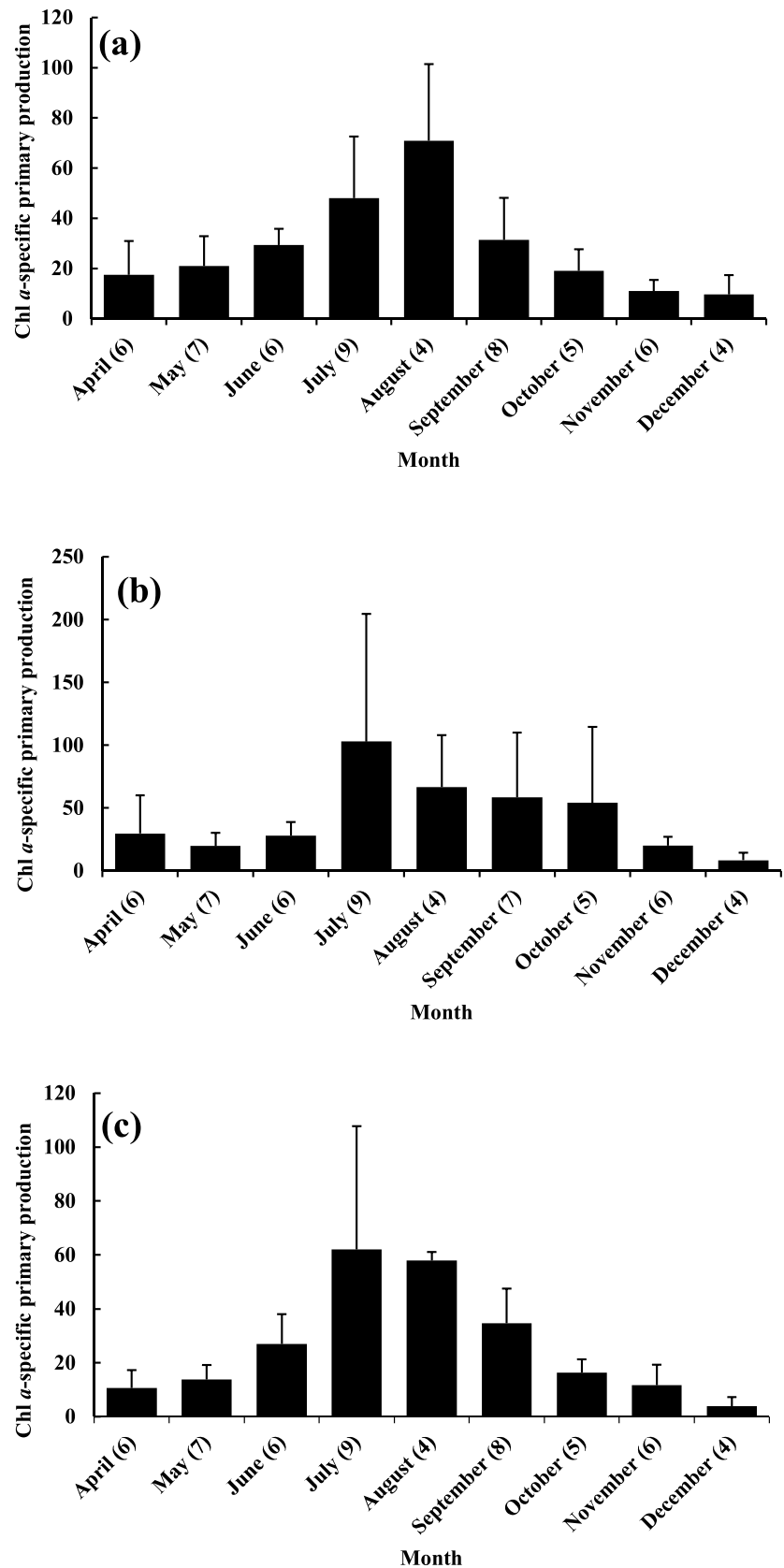


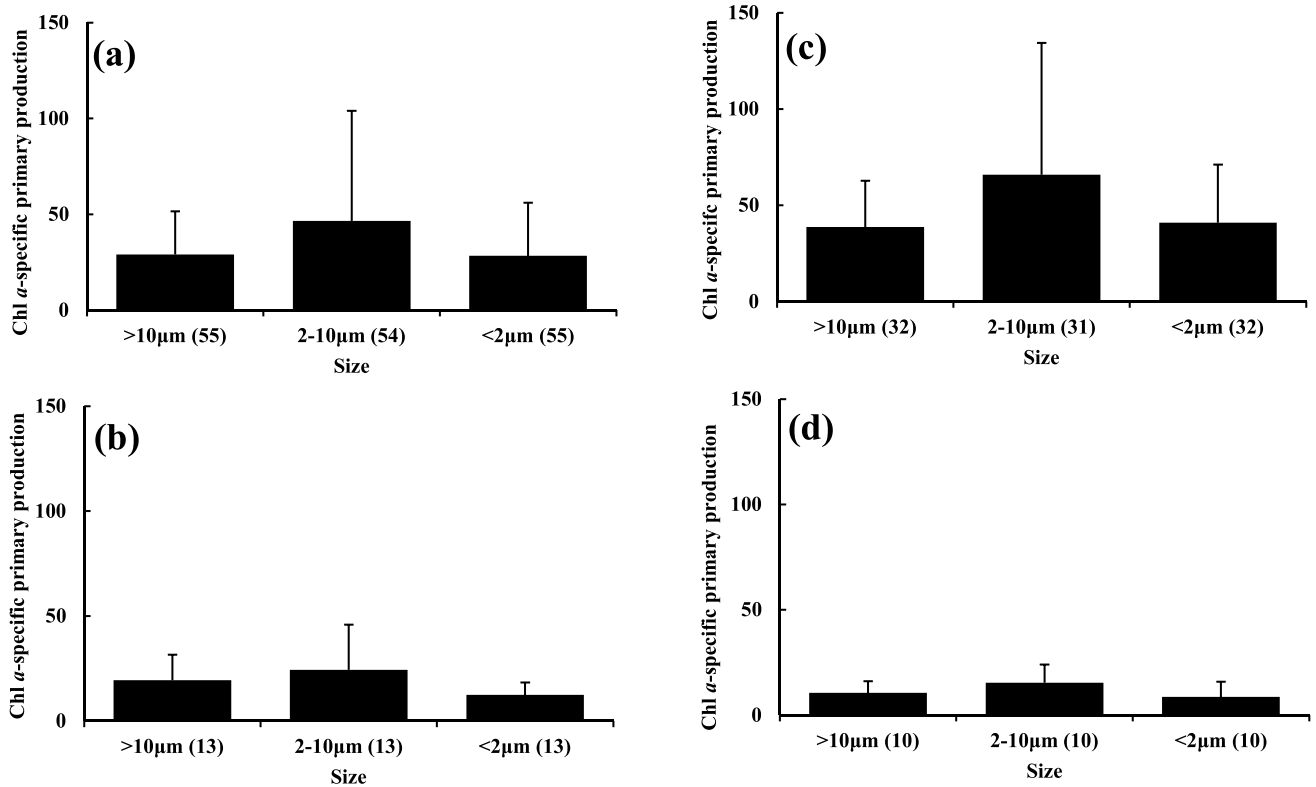
production. These facts indicate that water mass change between warm water (the Soya Warm Current water) and cold water (the Eastern Sakhalin Current water) in the survey area is the first principal component. In relation to the second principal component, positive correlations were found with light, nutrients, and the percentage contributions of large phytoplankton to Chl *a* and primary production. Negative correlations were found with water temperature, salinity, and the percentage contributions of small and medium phytoplankton to Chl *a* and primary production. These show that the spring bloom is the second principal component.

#### 4 Discussion

This study was performed using only surface samples. There is no guarantee that the seasonal changes of Chl *a* and primary production at the surface reflect those in the entire water column; accordingly, it is necessary to confirm this. According to Shiomoto et al. [18], a survey of Chl *a* in the entire water column showed high values (10–30 µg/L) in the spring bloom (April), followed by low values (ca. 1 µg/L) up to December. In the size structure of Chl *a*, large phytoplankton occupied a high proportion

**Fig. 5** Seasonal variations in the mean and standard deviation of the chlorophyll *a*-specific primary production ( $\text{mgC mgChl } a^{-1} \text{ d}^{-1}$ ) of the large ( $> 10 \mu\text{m}$ ) **a**, medium ( $2\text{--}10 \mu\text{m}$ ) **b**, and small ( $< 2 \mu\text{m}$ ) **c** phytoplankton. The mean values and standard deviations for each month were calculated using all data obtained in the 5-year study. The numbers in parentheses represent the number of data sets

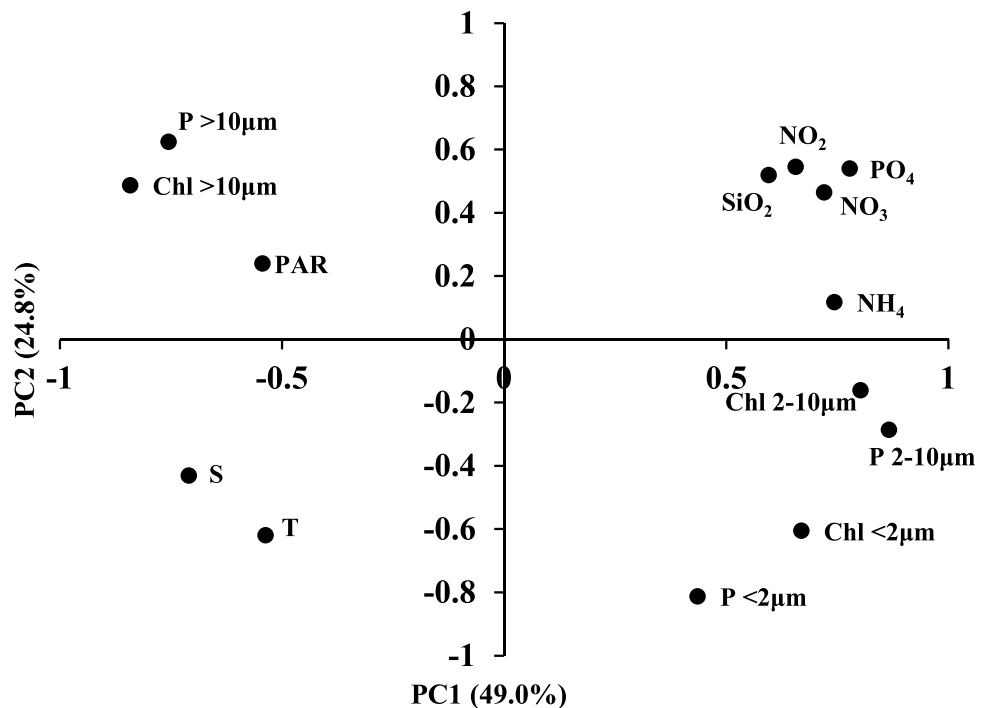




**Fig. 6** Comparison of the mean and standard deviation of the chlorophyll *a*-specific primary production ( $\text{mgC mgChl } a^{-1} \text{ d}^{-1}$ ) among large ( $> 10 \mu\text{m}$ ), medium ( $2\text{--}10 \mu\text{m}$ ), and small ( $< 2 \mu\text{m}$ ) phytoplankton in all seasons (April–December) **a**, spring (April and May) **b**,

summer and autumn (June–October) **c**, and winter (November and December) **d**. The numbers in parentheses represent the number of data sets

**Fig. 7** Principal components analysis (PCA) ordination diagram for the percentage contributions of large ( $> 10 \mu\text{m}$ ), medium ( $2\text{--}10 \mu\text{m}$ ), and small ( $< 2 \mu\text{m}$ ) phytoplankton to Chl *a* and primary production, and environmental factors (light, water temperature, salinity, and nutrients). PAR: light; T: water temperature; S: salinity; Chl: chlorophyll *a*; P: primary production





in spring (ca. 70%) and also a relatively high proportion (ca. 40–70%) until late autumn. On the other hand, in winter, smaller phytoplankton (< 10  $\mu\text{m}$ ) accounted for a high proportion (ca. 75%). These results were in good agreement with the results seen in this study (Fig. 3). The seasonal variation of Chl *a* at the surface likely reflects that of the entire water column. This study also showed that seasonal variations in Chl *a* and primary production were in good agreement, showing that surface primary production may have reflected that of the entire water column.

There was no significant difference in the Chl *a*-specific primary production, an index of the growth rate, among the three sizes in any season (Fig. 6). Chl *a*-specific primary production and growth rate have been reported to be higher for small phytoplankton [33–37], but recent studies have pointed out that these values are highest for medium phytoplankton (6–10  $\mu\text{m}$ ) [38–40]. Moreover, no significant difference in Chl *a*-specific primary production was found among the different phytoplankton sizes in the subarctic region (water temperature: < 10  $^{\circ}\text{C}$ ) [41–43]. In the polar region, the difference in productivity was small between sizes [44]. The results of the present study showed that the Chl *a*-specific primary production was not significantly different among the three sizes in winter and spring when the water temperature was < 10  $^{\circ}\text{C}$ , which is consistent with previous findings [41–44]. Moreover, in summer and autumn, when the water temperature was 10–20  $^{\circ}\text{C}$ , no significant difference in the value was observed among the three sizes. No significant difference can be found among sizes throughout the year in the subarctic region, even at the high summer temperatures. In the subarctic region, further studies are needed to determine whether the Chl *a*-specific primary production varies among sizes.

The same Chl *a*-specific primary production implies that the growth rates are the same for all sizes. The larger the phytoplankton, the higher the carbon content per cell [45–47]. If nutrient concentration is sufficient for large phytoplankton and there are no losses from grazing or sedimentation [48, 49], large phytoplankton should dominate; this was observed in spring, summer, and autumn but not in winter (Figs. 3b, 4b), indicating that there may be severe limitations and many losses in winter but not in spring, summer, and autumn. Before the spring bloom, there was a high-nutrient condition (Fig. 2c). The lower respiratory loss resulting from the shallower mixed layer is considered to cause the spring bloom in the study area [18]. Kitamura et al. [50] and Nakagawa et al. [51] reported that copepods, which feed on large phytoplankton (e.g., [49]), are not abundant in spring bloom in this area. It is probable that there were no severe limitations or many losses in the spring bloom, and hence the spring bloom of the large phytoplankton occurred even though the Chl *a*-specific

primary production was lower than that in summer and autumn (Fig. 5).

This study showed that the change of water mass plays a significant role in the seasonal variation of the size structure of phytoplankton biomass and production in the study area (Fig. 7). Changes of water mass were observed in the early summer and early winter. We therefore discuss which phytoplankton size make up the largest proportion of the primary producers in summer and autumn and winter. In summer and autumn, large phytoplankton were main primary producers in the study area based on the results of Chl *a* (Fig. 3b) and primary production (Fig. 4b). Conversely, the nutrient concentrations were remarkably lower in summer and autumn (Fig. 2c). The findings on the relationship between the nutrient condition and phytoplankton size structure have shown that small phytoplankton dominate under nutrient-poor conditions, and large phytoplankton dominate under relatively high-nutrient conditions, regardless of the ocean type (open sea or coastal) [2, 5–12]. The result of this study, in which large phytoplankton dominated despite remarkably low nutrient concentrations, is contrary to the previous findings about the relationship between nutrient concentration and phytoplankton size structure. In other words, a paradox was found in summer and autumn.

In summer and autumn, Chl *a* concentrations of large phytoplankton were of 0.04–2.38  $\text{mg m}^{-3}$ , and the frequency of observations of > 1  $\text{mg m}^{-3}$  of Chl *a* for large phytoplankton was approximately 25% in all observations. Values > 1  $\text{mg m}^{-3}$  are found when > 1  $\mu\text{mol L}^{-1}$  of nitrate is available in the open sea [12]. All of nitrate concentrations were less than 1  $\mu\text{mol L}^{-1}$  in summer and autumn (Fig. 2c). These facts imply a nitrate supply from somewhere. However, the Chl *a* concentration and primary production were lower in summer and autumn than in the spring bloom (Figs. 3a, 4a). Furthermore, the percentage contribution of large phytoplankton to Chl *a* and primary production were 40–75% (Figs. 3b, 4b), which was lower than the contribution (approximately 80%) in the spring bloom. The lower Chl *a* concentration and primary production contributions in summer and autumn possibly reflected the limiting nutrient (nitrate). In contrast, the possible sources of nitrate remain unconfirmed. The cold belt, characterized by a lower temperature than that of its surroundings, is formed off the Soya Warm Current resulting from the flow of the current during summer and autumn, and it is the driver for upwelling of the lower water (e.g., [52–54]). Therefore, the cold belt is considered an important nutrient (nitrate) source for the study area, as pointed out by Mustapha et al. [55]. Accordingly, the flow of the Soya Warm Current along the coastal area of Hokkaido possibly played an important role in producing the dominance of large

phytoplankton (diatoms) in summer and autumn. An additional nutrient load may be the intrusion of intermediate cold water from the Okhotsk Sea [18, 25]. Finding a source of nutrient and estimating its supply are the first step to clarify the paradox in summer and autumn.

In winter, the smaller (medium and small) phytoplankton were considered the main primary producers based on the results of Chl *a* (Fig. 3b) and primary production (Fig. 4b). However, the nutrient concentration was relatively high in winter (Fig. 2c). A paradox, opposite to that in summer and autumn, was also found in winter. As in other seasons, no significant difference was found in the Chl *a*-specific primary production among the three sizes in winter (Fig. 6). Accordingly, there should have been many losses for large phytoplankton. Copepods were reported to be relatively abundant in winter [50, 51], which implies that there was a greater grazing loss by copepods on large phytoplankton in winter. However, it is well known that grazing by copepods is more significantly reduced than phytoplankton growth at low temperature, e.g., in winter [56].

In the survey area during the ice-free period, Nakagawa et al. [57] showed that grazing by copepods depends on the Chl *a* concentration of large phytoplankton; no relationship was found between grazing pressure and water temperature (2–12 °C) in their study. It is thus possible that the grazing impact by copepods on large phytoplankton produces the dominance of the smaller phytoplankton in winter. Furthermore, in Funka Bay, a coastal area of Hokkaido, the grazing pressure of small zooplankton was reported to be low in winter [58]. Although there is no information on grazing by small zooplankton in the study area, the Chl *a* concentrations of medium and small phytoplankton were relatively high in winter (mean  $\pm$  SD,  $n = 10$ ;  $0.44 \pm 0.24 \text{ mg m}^{-3}$  and  $0.58 \pm 0.44 \text{ mg m}^{-3}$  for medium and small phytoplankton, respectively) than in other seasons (mean  $\pm$  SD,  $n = 45$ ;  $0.21 \pm 0.18 \text{ mg m}^{-3}$  and  $0.32 \pm 0.17 \text{ mg m}^{-3}$  for medium and small phytoplankton, respectively), which suggests the possibility of low grazing impact by small zooplankton on smaller phytoplankton. Apparently, in winter, although the smaller ( $< 10 \mu\text{m}$ ) phytoplankton significantly contributed to standing stock and primary production of phytoplankton communities (Figs. 3b, 4b), large phytoplankton might actually be the main primary producers supporting the ecosystem. If this is correct, having large phytoplankton as the main primary producers throughout the year can be said to be one of the mechanisms that support the high fishery production in this area. It is necessary to clarify whether the high grazing of copepods causes the low contribution of large phytoplankton to phytoplankton community.

## 5 Conclusion

Large phytoplankton made up the highest proportion of primary producers in spring, and this was also seen in summer and autumn. Conversely, in winter, smaller (medium and small) phytoplankton were the main primary producers, which is considered an apparent phenomenon when compared to previously reported studies. Based on these observations, we can infer that large phytoplankton are the main primary producers throughout the year. This is a positive finding for elucidating the mechanism leading high fishery production in the study area because generally, and high fishery production is expected when large phytoplankton are the main primary producers.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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