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Primary productivity at the time-series stations in the northwestern Pacific Ocean: is the subtropical station unproductive?

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Abstract A comparative study of primary productivity in the northwestern Pacific Ocean was conducted at time-series stations K2 and S1 in the nutrient-rich subarctic gyre and oligotrophic subtropical gyre, respectively. The estimated annual means of net primary production (NPP) at the two stations were virtually identical: 292 mg C m^{-2} day^{-1} at K2 and 303 mg C m^{-2} day^{-1} at S1, whereas the annual mean of gross primary production (GPP) at S1 was 1.5 times that at K2. NPP was very much limited by the supply of nutrients, typified by nitrate at S1, although it was enhanced during winter due to mitigation of nutrient limitation. The NPP/GPP ratios were remarkably lower at S1 during the spring-to-autumn time interval than in winter. The reduced NPP/GPP ratio means that photosynthetically assimilated carbon was lost at a higher rate via respiration and extracellular release of dissolved organic carbon (DOC). The carbon loss (difference between GPP and NPP) was higher at S1 than at K2, probably because of the enhanced respiration due to the relatively high temperature throughout the year, as well as the enhanced DOC release by nutrient limitation. The released DOC should be accounted for as primary production, because it contributes to oceanic biogeochemistry in a manner similar to the photosynthesized compounds. Consequently, total primary production, the sum of NPP and DOC release, was higher at S1 than at K2.

1 Introduction

Subtropical ocean gyres at low and mid-latitudes are relatively poor in surface chlorophyll *a* (chl-*a*) and are sometimes referred to as "ocean deserts," because the oligotrophic subtropical ocean has often been considered an analog of terrestrial deserts, with little biomass and very low primary productivity (e.g., Irwin and Oliver 2009). Nevertheless, Emerson et al. (1997) estimated that the vertical transport of organic carbon in these gyres may be responsible for up to half that of the global ocean, because such vast provinces occupy ~60 % of the ocean surface. In contrast, subarctic ocean gyres at high latitudes are enriched into the euphotic zone via winter mixing to the intermediate water, especially in the North Pacific Ocean, as a result of deep-water circulation. Although this province has been characterized as a high-nutrient, low-chlorophyll region (Harrison et al. 1999), the vertical transport of organic carbon is more efficient and shows a higher rate than that of the subtropical ocean (Honda 2003; Buesseler et al. 2007). Both types of ocean gyre play an important role in carbon cycling, but the factors controlling primary productivity should be different in response to the respective oceanic environments. To enhance our understanding

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of primary productivity in both subtropical and subarctic gyres, a comparative shipboard time-series study was performed.

A time-series study in a subarctic gyre is being conducted at station OSP, which is located in the northeastern Pacific. For subtropical gyres, time-series programs such as the Hawaii Ocean Time-series (HOT) and the Bermuda Atlantic Time-series Study (BATS) are being conducted in the North Pacific Ocean and the North Atlantic Ocean, respectively. Unfortunately, it is difficult to compare primary productivity directly across gyres, because the primary production estimates are not based on the same incubation duration. Shorter, daytime-only incubations conducted in the HOT (Karl et al. 1996) and BATS (Steinberg et al. 2001) time series exhibit higher primary production than 24-h incubations at OSP (Boyd and Harrison 1999), because 24-h incubations include night-time losses of carbon via respiration (Chavez et al. 2011). The K2S1 project (Honda et al. 2016) enables a direct comparison of primary productivity between the established stations in the subarctic (K2; 47°N, 160°E) and subtropical (S1; 30°N, 145°E) gyres of the northwestern Pacific Ocean, because observational experiments are being conducted with the same methods in both gyres.

Subarctic station K2 is located at the center of the western Pacific subarctic gyre (Fig. 1), and the time series was established as a successor to the station KNOT time series (1998–2000) after the end of the observations at KNOT (44°N, 155°E). At the K2 station, nutrients are not fully consumed in the euphotic zone throughout the year (Wakita et al. 2010, 2013). Primary production shows clear seasonality and is enhanced from spring to early summer in the northwestern Pacific (Shiomoto 2000; Imai et al. 2002), as is apparent from the remarkable diatom blooms that occur during that time (Obayashi et al. 2001).

Subtropical station S1 was established south of the Kuroshio Extension in 2010, and it is located within the recirculation gyre (Fig. 1). South of the Kuroshio Extension, the surface mixed layer deepens in winter, and subtropical mode water is formed (Bingham 1992). Anthropogenic CO_2 is accumulated in association with the formation of subtropical mode water (Kouketsu et al. 2013), and primary productivity in the subsurface seems to be affected through upward transport of nutrients from the nutrient-rich subtropical mode water (Sukigara et al. 2011).

Phytoplankton are typically light-limited at higher latitudes and nutrient-limited at low and mid latitudes. Researchers have argued that primary productivity may be increased in the sunlit surface waters at higher latitudes and decreased by the reduced nutrient input (though light availability will be increased) at low and mid latitudes due to the enhanced stratification as a result of climate warming (Sarmiento et al. 2004; Behrenfeld et al. 2006; Doney 2006; Steinacher et al. 2010). Marine ecosystems will be directly affected by climate change, experiencing concurrent shifts in temperature, circulation, stratification, nutrient input, oxygen content, and ocean acidification (Doney et al. 2012). Time-series stations K2 and S1 are also expected to
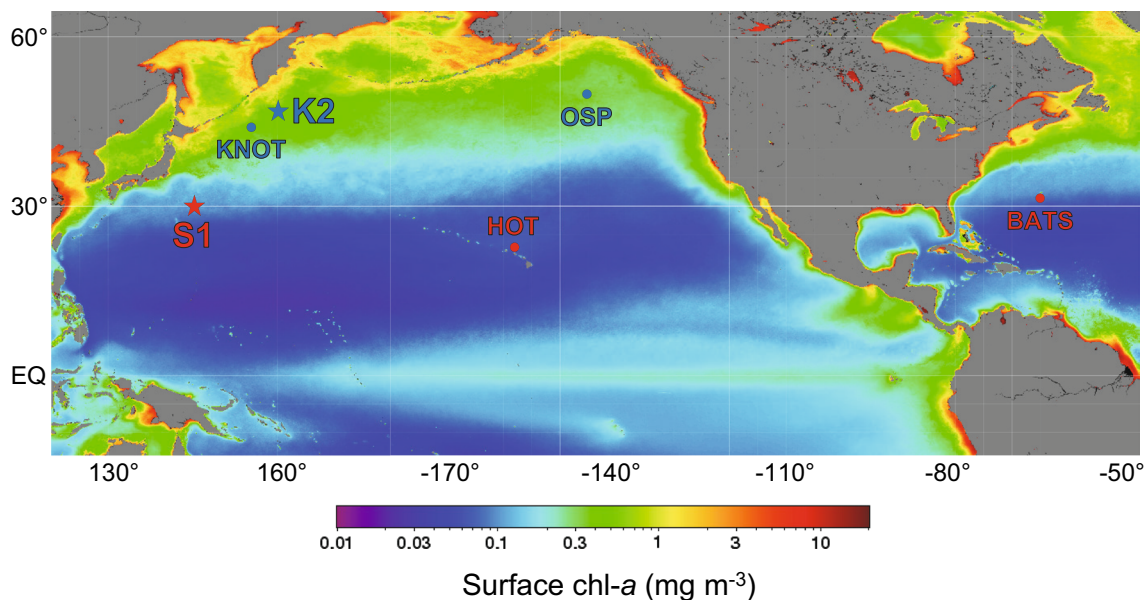

Fig. 1 Composite of surface chlorophyll *a* (chl-*a*) measured by the Aqua MODIS satellite sensor from 2002 to 2015 (level-3, 4-km data; http://oceancolor.gsfc.nasa.gov/cms/). The locations of subarctic and subtropical time-series stations discussed in this paper are indicated by *blue* and *red* symbols, respectively

be important stations for assessing the impacts of climate change on marine ecosystems.

Ishida et al. (2009) reported that the ratio of the biomass of large phytoplankton such as diatoms to the entire phytoplankton biomass tends to progressively temporally decrease in the subarctic gyre of the northwestern Pacific. If most of the phytoplankton community consists of small phytoplankton rather than large diatoms, the particulate organic carbon (POC) flux may be relatively low at K2. In addition, a progression of ocean acidification has also recently been reported at K2 (Wakita et al. 2013). Although S1 is definitely situated in low-chlorophyll water on a full year basis (Fig. 1), nutrients are supplied to the euphotic zone by diapycnal mixing in the thermocline during winter (Wakita et al. 2016). This fact implies that S1 is far from being an ocean desert, at least during winter, but there is concern that very low productivity areas such as the ocean deserts may expand due to climate warming (McClain et al. 2004; Polovina et al. 2008). These predictions suggest that oceanic desertification will be advanced at S1 as a consequence of increased stratification. In addition, the size structure of the phytoplankton community may change to small organisms as a result of nutrient deficiency, and such a transition could reduce the vertical transport of POC (Bopp et al. 2005; Marinov et al. 2010).

Shipboard observations at stations K2 and S1 have been conducted simultaneously since 2010 in all seasons as a part of the K2S1 project. The estimate of photosynthesis based on the incorporation of isotopically labeled inorganic carbon into POC during a 24-h incubation is generally considered a measure of net primary production (NPP), including associated respiratory loss of carbon (Falkowski and Raven 1997). This metric of NPP, in which only what is retained on filters is considered as POC, does not include the production of dissolved organic carbon (DOC) that is newly released as photosynthate by phytoplankton. However, DOC is an important link in marine ecosystems between phytoplankton and bacterial production via the microbial food web (Ducklow 2000). Concurrent measurements of photosynthesis based on the rate of oxygen evolution into the water provide an estimate of gross primary production (GPP). The ratio of NPP to GPP represents the fraction of photosynthetically fixed POC that is neither respired nor released as DOC by the phytoplankton. A relatively high NPP/GPP ratio indicates a productive ecosystem in which a large percentage of GPP goes into biomass (Dickson et al. 2001).

The aim of this study was to evaluate the seasonal variations of primary productivity, including both POC and DOC production, by comparing two estimates of photosynthesis, NPP and GPP. These findings will advance our understanding of biogeochemical cycles and facilitate predictions of their changes at both the K2 and S1 stations in the northwestern Pacific.

2 Materials and methods

2.1 Hydrographic observations and sample collection

Hydrographic observations were made from the R/V *Mirai* at the subarctic time-series station K2 between 2005 and 2013 and the subtropical time-series station S1 between 2010 and 2013. The scientific shipboard observations between 2010 and 2013 were conducted as a part of the K2S1 project (Honda et al. 2016). The seasons of the year were defined as follows: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). Four K2S1 cruises conducted during 2010–2011 were designed to focus in particular on the carbon budget: MR10-06 (autumn), MR11-02 (winter), MR11-03 (spring), and MR11-05 (summer) (Honda et al. 2016). Water samples were collected with Teflon-coated, acid-cleaned Niskin-X bottles suspended from a conductivity-temperature-depth profiler system, with the exception of surface samples, which were collected with a plastic bucket. Nutrient analyses were performed on board by using a TrAAcs 800 system (Bran + Luebbe, Norderstedt, Germany) or a QuATtro 2-HR (BL TEC K.K., Tokyo, Japan). The detection limit of nitrate was estimated as 0.03 µmol kg^{-1}.

2.2 Phytoplankton biomass

Phytoplankton biomass in terms of chl-*a* was measured on board by using a Turner fluorometer (model 10-AU, Turner Designs, Inc., Sunnyvale, CA, US) and the conventional acidification fluorometric method of Holm-Hansen et al. (1965). Particles in 0.5-L water samples were filtered onto a GF/F filter, and chl-*a* was immediately extracted in *N,N*-dimethylformamide in darkness at −20 °C for 24 h (Suzuki and Ishimaru 1990).

Phytoplankton taxa, determined by using the chemotaxonomy program CHEMTAX (Mackey et al. 1996) from the concentrations of biomarker pigments measured by high-performance liquid chromatography, were identified at K2 (Fujiki et al. 2014) and S1 (Fujiki et al. 2016). To estimate the phytoplankton biomass present as POC, carbon-based phytoplankton biomass was computed based on the following carbon/chl-*a* ratios (g g^{-1}) for the various phytoplankton taxa: 39 for diatoms, 34 for dinoflagellates, 65 for prymnesiophytes (including pelagophytes and cryptophytes in this study), 93 for cyanobacteria, 99 for green algae (applied to chlorophytes and

prasinophytes in this study), and 125 for prochlorophytes (Sathyendranath et al. 2009).

2.3 Net primary production

NPP denotes the organic carbon that has been produced by photosynthetic processes within a specified time period (Falkowski and Raven 1997). Here, it was estimated based on the incorporation of ^{13}C-labeled inorganic carbon into POC during a 24-h incubation from dawn to the next dawn. Incubations were conducted either in situ or on-deck using water from eight depths that were selected at appropriate intervals between light levels of ~100 and 0.5 % of photosynthetically active radiation (PAR) at the surface. After the incubation, the water samples were filtered through a pre-combusted GF/F filter, and inorganic carbon was removed by fuming with HCl. The ^{13}C content of the particulate fraction was measured with an automatic nitrogen and carbon analyzer mass spectrometer (SerCon, Ltd., UK) based on the method of Hama et al. (1983). For more details of experimental and analytical conditions, see Matsumoto et al. (2014). Water-column-integrated values of NPP were computed between the surface and the 0.1 % light depth.

2.4 Gross primary production in terms of oxygen

GPP is the total amount of electron equivalents originating from the photochemical oxidation of water (Falkowski and Raven 1997), which is equivalent to gross photosynthesis. Therefore, gross oxygen production (GOP), which is the rate of oxygen evolution over a diel cycle, was equated to GPP in terms of oxygen. GOP was measured by three methods in this study, two of which involved bottle incubations while the third was an optical technique. Incubations were conducted on-deck at eight simulated depths in the same manner as NPP.

2.4.1 Light- and dark-bottle technique

Transparent (light) and opaque (dark) glass bottles were incubated in parallel from dawn to the next dawn (24 h). The concentrations of dissolved oxygen were measured in triplicate by the automated Winkler titration technique immediately after incubation. GOP was calculated as the difference between the oxygen concentrations in the light and dark bottles at the end of the incubation. In this study, the results from surface incubations were excluded from the analysis because they were highly variable from one vertical profile to another. The surface rates were therefore extrapolated from data obtained beneath the surface. We estimated GOP by this technique during the MR10-06, MR11-02, MR11-03, and MR11-05 cruises, with the exception of S1 on the MR10-06 cruise.

2.4.2 ^{18}O-labeled oxygen technique

To determine whether respiration was greater in the light than in the dark, we estimated GOP using an alternative technique based on the H$_2^{18}$O method (Bender et al. 1987). Prior to incubation, water in a duplicate light bottle was spiked with ^{18}O-labeled water and incubated for 24 h together with the light and dark bottles. To determine the initial concentration and isotopic composition of the oxygen, some aliquots of water from the same depth were also collected. After incubation, 50 mL of water from each bottle was syphoned into a 300-mL vacuum flask to strip the oxygen and other dissolved gases from the liquid phase. Oxygen and argon were extracted chromatographically from the vacuum flask in an on-shore laboratory, and then the isotopic composition of the oxygen was determined with a dual-inlet, isotope ratio mass spectrometer (Delta Plus, Thermo Fisher, Inc., Waltham, MA, US). Another 2-mL aliquot of water from each bottle was collected for the determination of the oxygen isotopic composition of the water. GOP was computed from the initial and final isotopic compositions of the dissolved oxygen, as well as from the dissolved oxygen concentration and oxygen isotopic composition of the incubated water based on the method of Bender et al. (1999). In principle, this technique accounts for the amount of oxygen consumed by photorespiration and the Mehler reaction in light. The expectation is therefore that GOP is estimated with better accuracy by the H$_2^{18}$O method than by the oxygen light- and dark-bottle method (Bender et al. 1987). The surface data were treated in the same manner in the ^{18}O and light- and dark-bottle techniques. We estimated GOP by the ^{18}O technique on the MR11-02, MR11-03, MR11-05, and MR12-02 cruises.

2.4.3 Fast repetition rate fluorometry technique

A fast repetition rate (FRR) fluorometer (Kimoto Electric Co., Ltd., Osaka, Japan) with attached irradiance and depth sensors was lowered from the ship into the water to a depth of 200 m at S1 in autumn during the MR10-06 cruise. FRR fluorometry measures the rate of gross electron transfer, which should be related to GOP (Suggett et al. 2001). Because an FRR fluorometer measures an instantaneous rate without incubation when the equipment is deployed into the water, the data from casts conducted several times between predawn and dusk were integrated over time to obtain a daily rate. Details of GOP estimation by the use of FRR fluorometry were provided by Fujiki et al. (2008). The FRR fluorometry technique was adopted to estimate GOP only at S1 during cruise MR10-06, because of a lack of available GOP data from incubation techniques at that station. Suggett et al. (2003) noted that there is better agreement in the estimation of GOP between FRR fluorometry

and the $H_2^{18}O$ method for coccoid picophytoplankton than for larger, ovoid/cylindrical phytoplankton. The predominance of *Prochlorococcus*, which is the smallest coccoid picophytoplankton, was confirmed during cruise MR10-06 at S1 (Fujiki et al. 2016).

2.5 Gross primary production in terms of carbon assimilation

Estimates of GOP by the light- and dark-bottle and ^{18}O-labeled oxygen techniques should give different results due to photorespiration and the Mehler reaction (Laws et al. 2000). However, we have confirmed that there was no significant difference between the two estimates (paired *t* test), probably because the surface rates, which were expected to represent light-saturated conditions, were excluded from the water-column integration in this study. We therefore averaged these two rates to estimate GOP rates during each cruise. GOP can be converted to gross carbon assimilation (=GPP) by dividing by the photosynthetic quotient (PQ), which is the molar ratio of oxygen evolved during the light reactions of photosynthesis to carbon assimilated. The value of PQ typically lies in the range of 1.1–1.4, depending on the source of nitrogen, and increases stoichiometrically with the proportion of nitrogen uptake accounted for by nitrate when the formation of the major carbon macromolecules is considered (Laws 1991). Previous work has typically assumed a PQ of 1.4 (Marra and Barber 2004), and we tested PQs of 1.1 and 1.4 for converting GOP to carbon-based GPP in this study. Water-column-integrated values of GPP were computed in the same manner as NPP.

3 Results

3.1 Regional differences in biomass and net and gross primary production

Sea surface temperature (SST) was consistently less than 10 °C at K2, but it was over 18 °C at S1. The differences of the average water temperature within the euphotic zone were 15–16 °C between K2 and S1 in each cruise, whereas the seasonal variations were less than 5 °C at both stations. The depth-integrated chl-*a* was highest during summer at K2 (Fig. 2a) and during winter at S1 (Fig. 2b). The seasonality of depth-integrated chl-*a* was less apparent at K2 compared with that at S1. The annual mean chl-*a* was higher at K2 than at S1, but the carbon-based biomass computed on the basis of taxonomic composition was not significantly different between the two stations (Table 1). The depth-integrated NPP was highest during summer at K2 (Fig. 2a) and during winter at S1 (Fig. 2b). The seasonal variations of NPP were significant at both stations
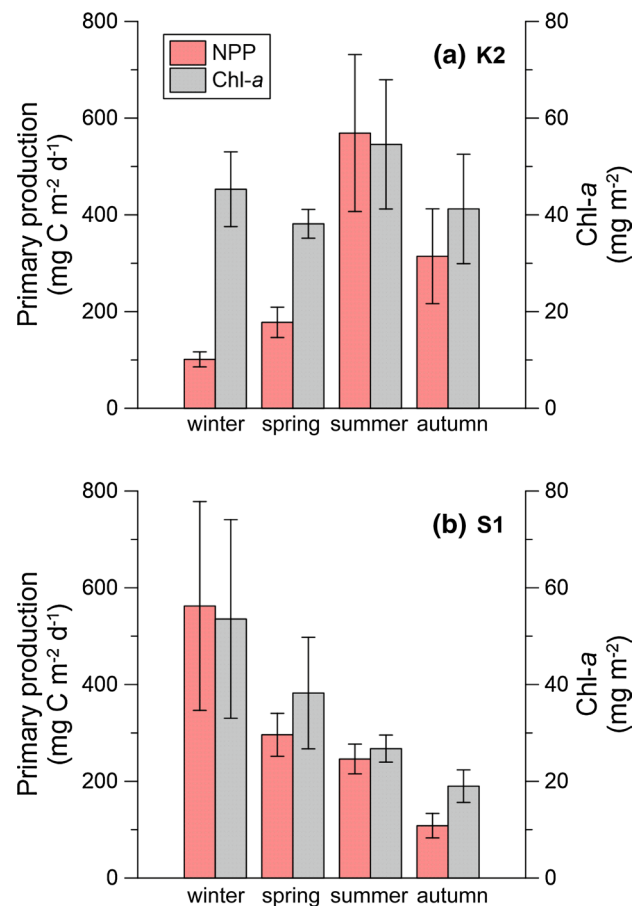

Fig. 2 Seasonal means and standard deviations of depth-integrated net primary production (NPP) and chl-*a* at **a** K2 and **b** S1. Seasonal data from shipboard observations between 2005 and 2013 were used at K2 and between 2010 and 2013 at S1. The data are available at http://ebcrpa.jamstec.go.jp/k2s1/en/index.html

(Kruskal–Wallis test, $p < 0.01$). At S1, NPP decreased from winter to autumn and the seasonality was quite similar to that of chl-*a*. At K2, however, the seasonality of NPP was more distinct than that of chl-*a*, because there was a large decrease of NPP in winter.

The annual mean GPP was 536 mg C m^{-2} day^{-1} at K2 and 825 mg C m^{-2} day^{-1} at S1, estimated with a PQ of 1.4 (Table 1). Seasonal variations of both GPP and NPP were similar, but at S1, the GPP was about 1.5 times that at K2. Because the annual means of carbon biomass and NPP were both similar at S1 and K2 (Table 1), this difference of GPP implied a higher loss of photosynthetically assimilated carbon that did not go into biomass as POC at S1. At K2, the NPP/GPP ratios were higher than 0.5, and they exceeded 0.6 during summer (Fig. 3a). At S1, the NPP/GPP ratio exceeded 0.6 during winter, but declined to less than 0.4 during the other seasons (Fig. 3b).

To further explore the variability of the NPP/GPP ratio, we estimated the relationship between GPP and NPP as

Table 1 Biomass and primary production at stations K2 and S1

Stn	Cruise code	Month/year	PAR (mol photons m^{-2} day^{-1})	Temperature (°C)		Chl-a (mg m^{-2})	Biomass (mg C m^{-2})	NPP (mg C m^{-2} day^{-1})	GPP[b]	
				SST	Euphotic				(PQ = 1.1)	(PQ = 1.4)
K2	MR10-06	Oct/2010	10	8.6	5.8	30.9	2442	248	599	471
	MR11-02	Feb/2011	11	1.9	1.8	40.6	2550	125	289	227
	MR11-03	Apr/2011	21	1.8	1.5	35.1	2450	200	446	351
	MR11-05	Jul/2011	23	6.7	4.6	59.9	3714	689	1395	1096
	MR12-02	Jun/2012	23	5.2	3.6	51.2	3047	570	1023	804
	Annual mean									
		(Oct 2010–Jul 2011)[c]	16	4.8	3.4	41.6	2789	315	682	536
		(Sep 2005–Jul 2013)[d]				42.1		292		
S1	MR10-06	Nov/2010	16	25.2	21.5	18.6	1846	108	504	396
	MR11-02	Feb/2011	21	18.6	18.3	72.5	4972	847	1640	1289
	MR11-03	Apr/2011	25	19.5	18.4	35.9	2825	296	1078	847
	MR11-05	Jul/2011	42	27.2	20.8	24.6	2242	224	977	768
	MR12-02	Jun/2012	35	23.4	18.8	25.5	2188	243	872	685
	Annual mean									
		(Nov 2010–Jul 2011)[c]	26	22.6	19.7	37.9	2971	369	1050	825
		(Jan 2010–Jul 2013)[d]				34.4		303		

Data (excluding PAR and SST) are averaged for each cruise within the euphotic zone

PAR photosynthetically active radiation, *SST* sea surface temperature, *NPP* net primary production, *GPP* gross primary production, *PQ* photosynthetic quotient

[a] Averaged gross oxygen production by incubation techniques based on the light- and dark-bottle method and ^{18}O-labeled oxygen were applied to the estimation, but fast repetition rate fluorometry was applied for the data during the MR10-06 cruise at S1

[b] Periods of data for intensive cruises of the K2S1 project

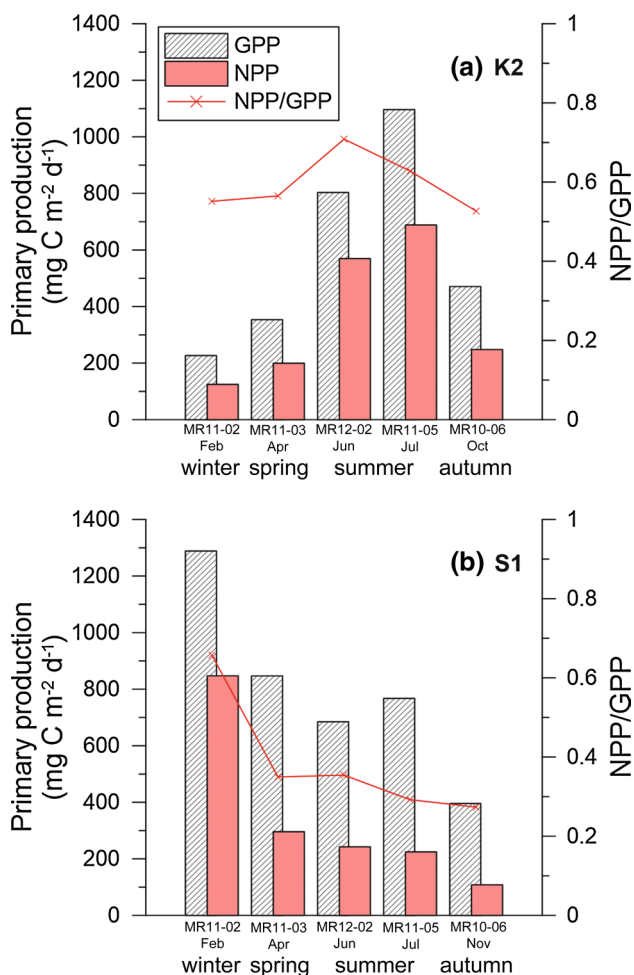[c] Periods of data available at the respective stations

Fig. 3 Depth-integrated gross primary production (GPP), net primary production (NPP), and the NPP/GPP ratio at **a** K2 and **b** S1 between 2010 and 2012. Cruises were conducted twice in summer and once in each other season. GPP was computed based on a PQ of 1.4
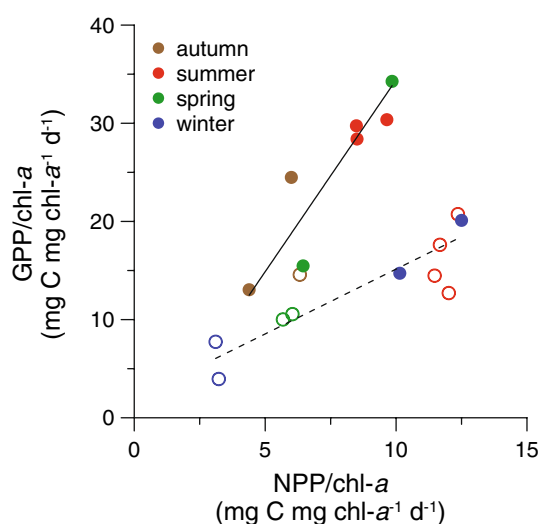

Fig. 4 Relationships between the chl-a-specific rates of gross primary production (GPP) and net primary production (NPP) at K2 and S1. GPP was computed based on a PQ of 1.4. *Dashed* and *solid lines* are model II geometric mean regression lines. *Open* and *solid symbols*, as well as *dashed* and *solid lines*, correspond to K2 and S1, respectively (K2: $y = 1.3x + 1.9$, $r^2 = 0.71$; S1: $y = 3.9x - 4.7$, $r^2 = 0.83$). The winter data at S1 were excluded from the regression and correlation analysis
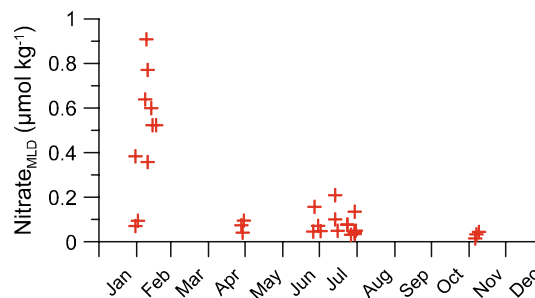

Fig. 5 Seasonal variation of averaged nitrate in the mixed layer depth (MLD) at S1

chl-a-specific rates to clarify the ratio independent of variations in chl-a biomass at both stations (Fig. 4). The chl-a-specific rates of GPP, which were computed based on a PQ of 1.4, were higher at S1 than at K2. The chl-a-specific rates of GPP increased significantly as a function of the chl-a-specific rates of NPP at both stations. The slope of the regression line was 1.3 ($p < 0.01$) at K2 and 3.9 ($p < 0.01$) at S1. However, winter values at S1 were excluded from the regression analysis because they were extreme outliers from the S1 regression line, and such outliers were very close to the K2 regression line.

3.2 Increased nitrate availability during winter at S1

High primary production during winter was confirmed at S1 (Fig. 2b). Although nitrate availability was quite low during other seasons, the surface mixed layer contained available nitrate at concentrations up to ~1 µmol kg^{-1} during winter

(Fig. 5), as a result of winter mixing. Shipboard measurements were conducted twice during winter at S1: in 2010 (MR10-01) and 2011 (MR11-02). A nitrate concentration less than 0.1 µmol kg^{-1} was occasionally found in the surface mixed layer during the MR10-01 cruise, even in winter (Fig. 5).

The nitracline depth, which is defined as the shallowest depth of >0.1 µmol kg^{-1} nitrate, deepened during spring because of phytoplankton consumption of nitrate and a reduction in the supply of nitrate associated with the development of stratification at S1 (Fig. 6). A significant negative correlation ($p < 0.01$) was found between NPP and the nitracline depth, with the exception of outliers during the winter of MR11-02 (Fig. 6). This correlation is consistent
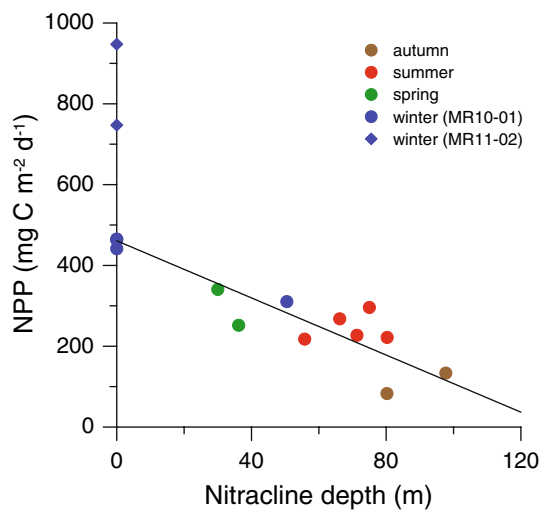
Fig. 6 Linear regression of net primary production (NPP) on the nitracline depth at S1. The solid line denotes model II geometric mean regression ($y = -3.54x + 461$, $r^2 = 0.81$). Data collected during cruise MR11-02 were not included in the calculation of the regression equation

with the assumption that NPP was basically limited by the supply of nutrients, typified by nitrate at S1. In addition, the outliers imply that nitrate was no longer a factor that limited NPP in the winter of 2011 during cruise MR11-02.

The values of NPP and chl-*a* during MR11-02 were nearly double the values during MR10-01 (data not shown); consequently, the standard deviations of the winter values were large (Fig. 2b). On the one hand, if we used all data obtained by discrete measurements between 2010 and 2013, the annual mean NPP at S1 would decrease by about 20 % relative to the means from intensive observation cruises only. On the other hand, the annual mean NPP at K2 did not differ between 2010–2011 and 2005–2013. Regardless of the time interval used in the calculations, the annual mean NPP was not lower at S1 than at K2 (Table 1).

4 Discussion

4.1 Comparison of primary production among gyres

Based on the distributions of surface chl-*a* (Fig. 1), we had expected that the subtropical gyre was a less productive region than the subarctic gyre. In reality, there was little difference in the annual mean NPP and phytoplankton carbon biomass between the two stations in the gyres (Table 1). Thus, primary production was lower than expected in the subarctic gyre, higher than expected in the subtropical gyre, or both.

Annual primary production was estimated to be 106 g C m^{-2} year^{-1} at K2 (Matsumoto et al. 2014), which is

comparable with the estimate of 90 g C m^{-2} year^{-1} at KNOT, located southeast of K2 (Imai et al. 2002). However, these values are smaller than the estimates of 140–215 g C m^{-2} year^{-1} at station OSP, which is located in the subarctic gyre in the northeastern Pacific (Harrison et al. 1999). Therefore, it has been suggested that primary production is relatively low in the subarctic gyre of the northwestern Pacific Ocean. Matsumoto et al. (2014) noted that this may be attributed to low light availability (for further discussion, see "Sect. 4.2").

Time-series programs such as HOT and BATS in oligotrophic subtropical gyres have reported remarkable seasonality and high production rates (range: 154–898 mg C m^{-2} day^{-1}, average: 436 mg C m^{-2} day^{-1} at HOT; range: 49–1041 mg C m^{-2} day^{-1}, average: 441 mg C m^{-2} day^{-1} at BATS) (Chavez et al. 2011; Church et al. 2013). Such results indicate that primary production at S1 (range: 108–847 mg C m^{-2} day^{-1}, average: 303 mg C m^{-2} day^{-1}) is not excessively high in the subtropical ocean (Table 1). Although our estimates appear to be lower than those of HOT and BATS, they are actually likely comparable because daytime incubation overestimates primary production by at least 15 % compared to that of 24-h incubation due to the carbon loss via respiration during the night (Karl et al. 1996). Our findings indicate that the annual NPP was comparable between the subarctic and subtropical gyres in the northwestern Pacific Ocean, although it might be lower than that of the subarctic gyre in the northeastern Pacific.

4.2 Factors controlling net primary production at the respective stations

Nutrient concentrations are high in the euphotic zone throughout the year at K2 (Wakita et al. 2010, 2013), but iron limitation causes high-nutrient, low-chlorophyll conditions by effectively controlling primary productivity in the subarctic gyre (Boyd and Harrison 1999; Harrison et al. 1999). In addition, greater control of primary productivity by light has been reported at K2 (Matsumoto et al. 2014), although such a relationship was not previously recognized in the northeastern Pacific (Welschmeyer et al. 1993; Boyd and Harrison 1999; Harrison et al. 1999). At K2, primary productivity was depressed during winter and spring in response to the reduced light availability caused by deep mixing, and it was depressed even in summer due to attenuation of sunlight by dense sea fog, which occurs frequently during summer in the region (Matsumoto et al. 2014). As a result, the estimated NPP was lower at subarctic station K2 than at subarctic station OSP in the northeastern Pacific (Harrison et al. 1999; Matsumoto et al. 2014). This was not exactly what we had expected prior to this study. Although relatively high POC transport to the deep sea has been

reported in the northwestern Pacific subarctic gyre (Honda 2003), that high transport seemed to result from efficient vertical transport via aggregation of diatoms (Honda and Watanabe 2010) rather than from high productivity.

Subtropical station S1 is located in an apparently oligotrophic region (Fig. 1). Indeed, we found that nitrate availability at S1 was remarkably reduced within the surface mixed layer during the stratified season from spring through autumn (Fig. 5). Based on our standard analytical methods, both nitrate and phosphate seemed to be unavailable during the stratified season at S1 (Wakita et al. 2016), but based on a high-sensitivity analysis in this region, Hashihama et al. (2009) reported that the depletion of phosphate was greater. Phosphate deficiency seems to be a consequence of nitrogen fixation, which is expected to be an important nutrient source in the oligotrophic subtropical ocean (Karl et al. 1997). However, it is unlikely that nitrogen fixation will last for a long period at S1, because it depends on iron and phosphorus availability (Sohm et al. 2011). Nitrogen fixation had only a limited effect on primary productivity, because primary production was significantly regulated during such stratified seasons as compared to that of winter (Fig. 2). Moreover, a previous study indicated that nitrogen fixation was not remarkable at this latitude in the northwestern Pacific during winter, while nitrate assimilation increased (Shiozaki et al. 2009). In fact, microscopy and flow cytometry suggest that the population of diazotrophs is quite small compared with that of other phytoplankton at S1 throughout the year (data not shown). Thus, the enhancement of primary productivity at S1 seemed to be due simply to mitigation of a nutrient deficiency by deep mixing during winter (Fig. 5).

Although winter mixing supplies nutrients into the euphotic zone at S1, the nutrient supply may not be continuous during winter, because apparent nitrate limitation was observed within the sunlit layer during MR10-01 (Fig. 6). Even so, the intermittent supply of nutrients resulted in enhancement of NPP, at least during MR11-02, and the annual NPP was very similar at S1 and K2 (Table 1). The NPP/GPP ratios were remarkably higher in winter during cruise MR11-02 at S1 and during summer at K2 (Fig. 3) than the ratios of 0.4–0.6 that have commonly been reported in the ocean (Kiddon et al. 1995; Bender et al. 1999; Laws et al. 2000; Hashimoto et al. 2005), implying that photosynthetically assimilated carbon is incorporated into biomass efficiently at these times and places. Relatively higher POC transport was reported during winter at S1 (Honda et al. 2015), apparently due to the increased carbon biomass (Table 1). Through direct comparison with a subarctic station, the observations of the K2S1 project indicate that station S1 in the northwestern Pacific subtropical gyre is clearly not an ocean desert, in contrast to the traditional expectation.

4.3 Why is gross primary production greater at the subtropical station than the subarctic station?

The close correlation between NPP and the nitracline depth (Fig. 6) suggests that NPP at S1 is very much nitrate-limited. Although nutrient input may occur via mesoscale eddies (McGillicuddy et al. 1998), typhoons (Lin 2012), and atmospheric deposition (Duce et al. 2008), the nitracline depth increases from spring to autumn (Fig. 6). Thus, such sporadic nutrient inputs were not enough to satisfy the requirement of phytoplankton. Hence, primary productivity at S1 was probably supported mainly by recycled nutrients during the spring-to-autumn time interval. The proportion of production based on recycled nutrients was probably higher at S1 than at K2. If phytoplankton use ammonium or nitrate as a nitrogen source, the PQ should be 1.1 or 1.4, respectively (Laws 1991). This implies that the PQ was probably closer to 1.1 than to 1.4 at S1. Although the annual mean GPP at S1 was 1.5 times that at K2, the GPP estimated at S1 in terms of carbon would be even higher if the PQ were assumed to be 1.1 (Table 1).

The higher temperatures at S1 may also have enhanced NPP, because the light-saturated photosynthetic rate would be expected to increase by a factor of ~2 for a 10 °C rise in temperature if it were not constrained by nutrient limitation (Davison 1991). The average temperature in the euphotic zone was about 15–16 °C higher at S1 than at K2 (Table 1), presumably due to the higher insolation at S1 throughout the year (Table 1). We hypothesize that the higher temperature and insolation at S1 caused NPP to increase when photosynthetic rates were not strictly constrained by nutrient limitation, as was the case during winter. It is commonly assumed that metabolic rates increase exponentially with temperature (e.g., Eppley 1972; Smith and Kemp 1995). According to studies in various aquatic systems, the expected factor by which metabolic rates increase in response to a 10 °C rise in temperature, which is represented as the temperature coefficient (Q_{10}), is close to 2 for phytoplankton (Eppley 1972) and zooplankton (Ikeda et al. 2001). The high GPP at S1 may be largely due to the increase of algal respiration with increasing temperature. This hypothesis seems to explain the fact that the GPP at S1 is 1.5 times the GPP at K2, because a 15–16 °C increase of temperature would be expected to increase algal respiration by a factor of 3 if the Q_{10} is 2.

However, assuming that the difference in GPP between the two stations is due solely to algal respiration leads to a contradiction. The NPP/GPP ratios estimated during the spring-to-autumn time interval at S1 (Fig. 3) were relatively low compared to the commonly observed ratios of 0.4–0.6 ("Sect. 4.2"). As an exponential increase of algal respiration with temperature has been found in nature (Smith and Kemp 1995), algal respiration was probably

enhanced at S1 compared to K2 by the comparatively high temperatures at S1. The lower NPP/GPP ratio during the spring-to-autumn time interval implies that the loss of photosynthetically assimilated carbon was greater at S1 during that time. In contrast, the NPP/GPP ratio was remarkably high during winter at S1 (Fig. 3), implying that POC was produced efficiently. The chl-*a*-specific rates of GPP and NPP during winter were excluded from the correlation between the two at S1 because the relationship was consistent with the corresponding relationship at K2 (Fig. 4). Thus, algal respiration may have been reduced during winter at S1 to a rate equivalent to that at K2. But why would it have been so reduced during winter, given the fact that the seasonal variation of temperature was small (Table 1)? The answer, we hypothesize, is that algal respiration was not in fact greatly reduced during winter, but rather, that relatively large amounts of DOC were released during the spring-to-autumn time interval, and production of DOC would have contributed to GPP along with algal respiration at S1.

4.4 Enhanced dissolved organic carbon release under oligotrophic conditions

According to Fogg (1983), phytoplankton typically release DOC equivalent to 5–40 % of fixed carbon. Typically, extracellular release of DOC by phytoplankton is attributed to two mechanisms: an overflow mechanism, which is related to the photosynthetic rate, and passive diffusion, which is related to the phytoplankton biomass (see review by Carlson 2002). Phytoplankton actively release photosynthesized compounds under conditions of macronutrient limitation via the former mechanism because there is a limited requirement for compounds that contain neither nitrogen nor phosphorus (Fogg 1983). The latter mechanism is associated with diffusion of low-molecular-weight compounds across the cell membrane at a rate proportional to the difference between intracellular and extracellular concentrations (Bjørnsen 1988).

The fraction of photosynthetic production released as DOC is highly variable and depends on the community structure, light intensity, degree of nutrient deficiency, and temperature (see review by Carlson 2002). The slopes of the regression lines relating GPP and NPP were 3.9 at S1 and 1.3 at K2 (Fig. 4). Thus, the rate of carbon loss in terms of respiratory loss and DOC release increased more rapidly with increasing NPP at S1. If the increase of carbon loss was due to both algal respiration and DOC release, then the surplus DOC associated with the increase of photosynthesis as light and temperature increased was likely released by the overflow mechanism under nitrate-limited conditions at S1. Moreover, although diatoms were most abundant during the MR11-02 cruise in winter at S1, the smallest phytoplankton taxon, *Prochlorococcus*, was most abundant during the summer-to-autumn time interval at S1 (Fujiki et al. 2016). Because relatively small cells have a higher surface-to-volume ratio than large cells, DOC release is also expected to be enhanced via passive diffusion during summer and autumn (Bjørnsen 1988). In contrast, the enhanced diatom growth would reduce the impact of passive diffusion, and the overflow mechanism would not be maintained by the excessive nutrients during winter. It is expected to reduce the DOC release instead of the enhanced carbon uptake during the winter at S1, and this resulted in the higher NPP/GPP ratio (Fig. 3).

The percentage of extracellular release of DOC (PER), which equals DOC production expressed as a percentage of the sum of DOC and POC production, has been estimated to equal 13 % when averaged over all ocean basins (Baines and Pace 1991). However, Marañón et al. (2004) reported that PER is 19 % when integrated over depth, because PER increases with depth. A greater supply of nutrients and predominance of relatively large diatoms would be expected to reduce the PER. According to Malinsky-Rushansky and Legrand (1996), the PER of relatively large cells is only 4–5 %, but that of picoeukaryotes is 29 %. Teira et al. (2001) measured DOC and POC production on the basis of ^{14}C incubations in the Atlantic Ocean, and the PER increased in oligotrophic waters where picophytoplankton

Table 2 Released dissolved organic carbon (DOC; mg C m^{-2} day^{-1}) in the euphotic zone at stations K2 and S1 calculated as 5 or 30 % of the sum of DOC and particulate organic carbon (POC) production

Cruise code	Month/year	K2		S1	
		5 % PER[a]	30 % PER	5 % PER	30 % PER
MR10-06	Oct–Nov/2010	13	106	6	46
MR11-02	Feb/2011	7	54	45	363
MR11-03	Apr/2011	11	86	16	127
MR11-05	Jul/2011	36	295	12	96
MR12-02	Jun/2012	30	244	13	104

[a] *PER* percentage of extracellular release of DOC: the DOC production expressed as a percentage of the sum of DOC and POC production

were abundant. The PER was 4–9 % in the upwelling region and 11–42 % in the oligotrophic region (Teira et al. 2001). There is also a wide range of PER in the Pacific Ocean. A PER range of 8–40 % was reported in the field at a variety of coastal and open ocean sites, but rates are higher in oligotrophic waters (see Table II in the review by Carlson 2002).

We estimated the released DOC based on PERs of 5 and 30 % (Table 2). According to the previous findings, we considered PERs of 5 and 30 % to be appropriate for representing eutrophic and oligotrophic waters, respectively. The released DOC decreased from 363 to 45 mg C m^{-2} day^{-1} during winter at S1, when the PER was assumed to be 5 % (not 30 %). If this assumption is correct, it may explain why the relationship between the chl-a-specific rates of GPP and NPP overlapped with the K2 regression line during winter at S1 (Fig. 4). The fact that the average concentration of DOC in the surface mixed layer was remarkably low during winter at S1 (Wakita et al. 2016) supports the hypothesis that the DOC release was relatively small during winter at S1. The relative importance of the two DOC release mechanisms is still unclear, but an increase of DOC release would increase the estimated GPP at the oligotrophic subtropical station. If the PER were assumed to be 5 % at eutrophic K2 and 30 % (oligotrophic from spring to autumn) and 5 % (eutrophic in winter) at S1, the annual mean release of DOC would have been 17 mg C m^{-2} day^{-1} at K2 and 79 mg C m^{-2} day^{-1} at S1 for the intensive cruises of the K2S1 project (Table 3). In that case, the annual mean total primary production (i.e., the sum of POC and DOC production) would have been estimated to be higher at S1 than at K2 (Table 3).

5 Conclusions

Contrary to the traditional expectation that a subarctic gyre is relatively productive compared to a subtropical gyre, this study revealed that there was no great difference in the annual means of phytoplankton biomass and NPP between stations in the two types of gyres. The similarity of NPP at the two stations reflected the fact that annual NPP was lower than expected at subarctic station K2 and higher than expected at subtropical station S1. At K2, an increase of NPP during summer was associated with a diatom bloom, but annual NPP was kept relatively low due to the relatively low availability of light and iron. At S1, NPP was markedly enhanced as a result of nutrients supplied via winter mixing.

The increase of respiration rates attributable to the high temperatures at S1 created a relatively large gap between GPP and NPP, but the gap was further increased by the enhancement of DOC release under the nutrient-limited conditions at this station. The implication is that the annual mean of total primary production, after subtracting respiratory losses, was higher at S1 than at K2. Subtropical station S1 is more productive than subarctic station K2 as a result of greater DOC release. Nutrient limitation decreases NPP but increases DOC production; it seems unlikely that S1 will simply become less productive as a result of greater stratification due to global warming. Instead, it is likely that the microbial food web will be stimulated by an increase in DOC production.

Table 3 Annual mean primary production estimated as particulate organic carbon (POC), dissolved organic carbon (DOC), and total at stations K2 and S1

Station	Primary production (mg C m^{-2} day^{-1})			Data periods
	POC[a]	DOC[b]	Total[c]	
K2	315	17	332	(Nov 2010–Jul 2011)[d]
	292	15	307	(Sep 2005–Jul 2013)[e]
S1	369	79	448	(Nov 2010–Jul 2011)[d]
	303	77	380	(Jan 2010–Jul 2013)[e]

[a] Data are estimated as NPP retained on filters

[b] Data are estimated based on percentages of extracellular release of DOC (PERs) of 5 % (K2 and S1 during winter) and 30 % (S1 from spring to autumn)

[c] Data are estimated as the sum of POC and DOC production

[d] Periods of data for intensive cruises of the K2S1 project

[e] Periods of data available at the respective stations

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