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Limiting factors of phytoplankton communities along the Ogasawara transect in North Western Pacific Ocean

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Abstract: In order to clarify the dynamics of oligotrophic ecosystems at the Subsurface Chlorophyll *a* Maximum (SCM), we investigated the distribution of phytoplankton and availability of nutrients in the euphotic layer along the Ogasawara transect (North-West Pacific Ocean). Depending on the distribution of underwater light and microphytoplankton communities a gradient between oceanic and coastal stations around Chichijima Island was identified. The vicinity of island is marked by lack of clear maximum peak of Chl. *a* and higher values of inorganic nutrients which pointed out a possible effect of island on this oligotrophic area. In contrast, significant SCMs reaching 5 times the Chl. *a* concentration at the surface were measured at the offshore stations. The SCM is located under the thermocline (60 to 68 m), the organisms mainly dominated by diatoms community were exposed to low light condition (4 to 1% of surface irradiance) and were associated with nutriclines (0.35 to 1.15 μM of nitrogen and 0.03 to 0.07 μM of PO_4^{3-}). Changes in the nutrient potential limitation were detected at the SCM. In the epipelagic layer of offshore stations, Si:N:P stoichiometries values mainly oscillated between phosphorus and nitrogen potential limitation. However, nitrogen suddenly shifted to a phosphorus potential limiting factor at the SCM. If this result can be confirmed by complementary studies, it adds evidence that regeneration or predation mechanisms and availability of phosphorus mainly control the growth of phytoplankton in this oligotrophic area.

Keywords: *Chlorophyll a, light, nutrient, N-W Pacific, oligotrophy, phytoplankton*

1. Introduction

According to recent projections, a decline of primary production associated with an extension of oligotrophic areas was reported in the Pacific Ocean. (LOPEZ-URRUTIA *et al.*, 2006; BEHRENFELD *et al.*, 2006). In this framework, identification and quantification of relationships between primary producers and oligotrophic conditions must be addressed in order to better understand the climate forcing and the ecological response.

In this low production area, previous investigations described usual subsurface Chlorophyll *a* maximum (SCM) close to the bottom of euphotic layer (EPPLEY *et al.*, 1988; FURUYA and MARUMO 1983, FURUYA 1990). The SCM takes large part of primary production in the Pacific Ocean where 90% of Chl. *a* concentration of sunlit zone can be located in this layer. Formation of SCM is a complex phenomenon links to photoacclimation mechanisms as well as nutrient availability and requirements of phytoplanktons (HENSE and BECKMANN, 2008). Irrespective of hypothesis about its development, the SCM remains currently unclear in

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the North Pacific Subtropical Gyre, (NPSG) (Lu *et al*., 2010).

Although the NPSG is a well documented area, few are known concerning the distribution of light, nutrients and phytoplanktons near the Bonin Islands and especially near the Chichijima Island (Taguchi, 1975). Thus, this cruise provides an interesting opportunity to detect the variability of oligotrophic conditions surrounding the island. In this report, we investigate parameters leading the distribution of phytoplankton in oligotrophic area. Special attentions will be focused on the SCM layer in order to identify the potential limiting factor depending on the environmental conditions.

2. Materials and methods

The Chichijima observations took place from November 18th to 21st 2009. The 12 sampling stations are located between the Chichijima harbor and the Tokyo Bay (Fig. 1). By using Niskin bottles, phytoplankton were sampled at three levels (surface, SCM, depth of 1% light intensity) and putted into 500 ml clean polyethylene bottles. To prevent grazing processes, Lugol's solution was immediately added. For each sampling point, 1 liter of sea water was enumerated onshore according to the Utermöhl method and references listed in the Hasle study, (1978).

Chlorophyll *a* and phaeopigment were measured on the basis of the fluorometer method (Suzuki and Ishimaru, 1990). During this cruise, 3 different filters were used: Whatman® nucleopore filters ~0.2 μm, glass microfiber filters, GF/D ~2.7 μm and paper filters N°1 ~ 11 μm. After sampling with Niskin bottle, 200 ml of seawater was filtrated through each filter type by lower vacuum pressure (<100 mm of Hg). Then, filters were immersed into N,N-dimethylformamide, (DMF) -containing tube, and stored in dark condition at 4℃. Analyses were made using a Turner Designs Fluorometer previously calibrated with pure Chl. *a* pigment.

The light parameters have been monitored using the Profiling Reflectance Radiometer, Instrument (PRR 600) Biospherical Instrument®. The PRR 600 simultaneously measures, Photosynthetically Active Radiation (PAR), down-

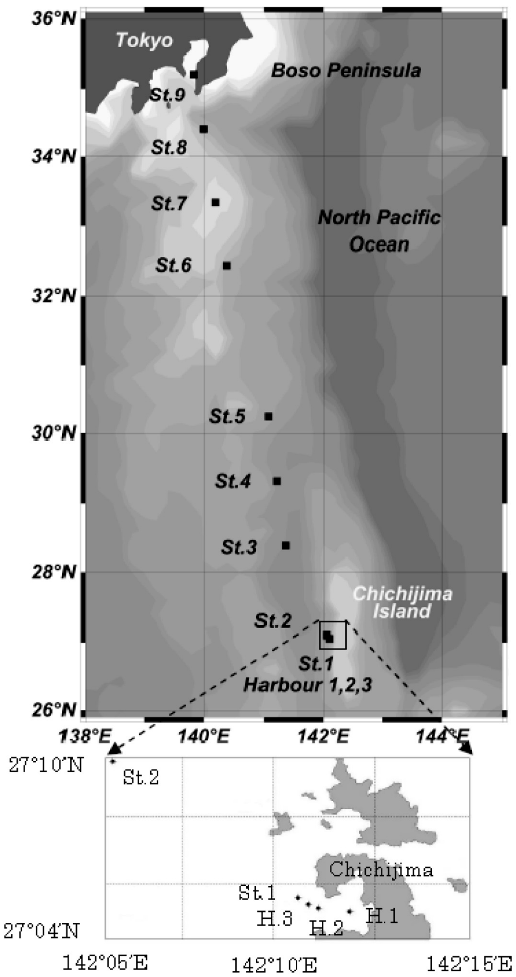

Fig. 1. Sampling stations in the North Western Pacific along the Ogasawara transect from Chichijima Island to Boso Peninsula.

welling irradiance and upwelling radiance with 10nm bandpass filters centered at 412, 443, 490, 510, 555, and 665 nm as a function of pressure, where pressure is used as a proxy for depth.

Inorganic nutrients, (NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, Si $(OH)_4$), were measured at each sampling point. Nutrient samples were collected by Niskin bottles, immediately putted into cleaned plastic tube and stored kept out of the light, in a freezer compartment. Analyses of inorganic nutrients were performed by using an autoanalyzer (AACS III). NH_4^+ was measured according to Kanda method (1995). PO_4^{3-} by the method of MURPHY and RIDLEY study (1962) and others nutrients (NO_3^-, NO_2^-, Si $(OH)_4$) by methods listed in HANSEN and KOROLEFF study, (1999). By using nutrient concentrations, different types of stoichiometries were used to identify the potential limiting factors. The Redfield and Brzezinski ratios have been calculated on the basis of following stoichiometries (BRZEZINSKI, 1985) :

Si : N : P = 15 : 16 : 1

In addition to this previous calculation another nutrient ratio was estimated (JUSTIC *et al.*, 1995). Three types of potential limitation can be evidenced according to the following assessments:

(a) P limitation, $[PO_4^{3-}] < 0.1\,\mu mol.L^{-1}$, $[Si(OH)_4]:[PO_4^{3-}] > 22$ and $[DIN]:[PO_4^{3-}] > 22$,
(b) N limitation, $[DIN] < 1\ \mu mol.L^{-1}$, $[DIN]:[PO_4^{3-}] < 10$ and $[Si(OH)_4]:[DIN] > 1$,
(c) Si limitation, $[Si(OH)_4] < 1\ \mu mol.L^{-1}$, $[Si(OH)_4]:[PO_4^{3-}] < 10$ and $[Si(OH)_4]:[DIN] < 1$.
Where $[DIN] = [NO_3^-] + [NO_2^-] + [NH_4^+]$,

In contrast to the REDFIELD and BRZEZINSKI stoichiometries, JUSTIC *et al.* took into account the nutrient uptake kinetics. In view to limit bias due in part to all chemical compounds in the calculation method, threshold criterions for each nutrient were added according to DORTCH and WHITLEDGE (1992).

3. Results

3–1 Biological measurements

During the cruise, we identified 157 species including 62 diatoms, 51 dinoflagellates, 21 tintinnid species and 23 others types (copepods, radiolarians). Concentration of diatoms and dinoflagellate organisms remained relatively weak at the surface between Chichijima Island and the station 5, (respectively ~22,750 orgs.m^{-3}, ~33,250 orgs.m^{-3}). From station 6, abundance of diatoms showed a gradual increase and reached a maximum value near the station 9 in Tokyo Bay (~520,000 orgs.m^{-3}) (Fig. 2). The spatial distribution of diatoms and dinoflagellates presented a specific pattern along the transect. On the basis of our measurements, diatoms dominated all types of microphytoplanktons at the surface of St. 4, from St.6 to St.9, maximum of Chl. *a* and bottom of euphotic layer. In contrast, our results suggested that dinoflagellates were dominant at the surface around the Chichijima Island. In the dinoflagellates community, the *Ceratium* genus appeared to be the most abundant especially the species *C. furca, C. lineatum*, and *C. pentagonum*.

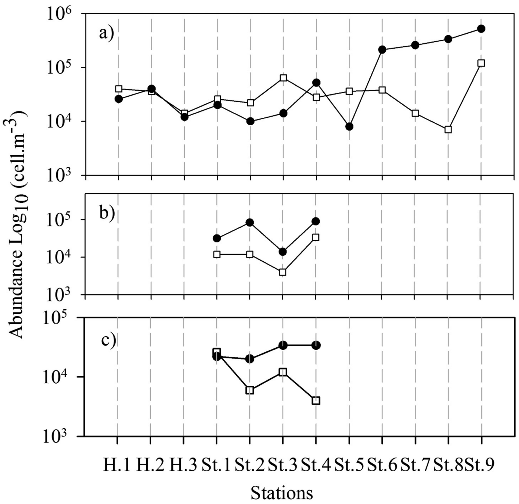

Fig. 2. Variability of diatoms (black circle) and dinoflagellates pool (white square) at three different depth levels along the Chichijima cruise. Graph a) shows the concentration at the surface, b) at the maximum of Chl. *a* and c) at 1% of incident light or at 100 meters for the station 4.

Although abundance are lower than dinoflagellates, some diatoms species like *Rhizosolenia pungens, Cerataulina pelagica* and *Pseudonitzschia* spp. were recorded especially at the SCM and at 1% of light intensity. Phytoplankton species enumerated from the stations 6 to Tokyo Bay showed that the *Chaetoceros* genus appeared to dominate the microphytoplankton community in particular with the species *C. curvisetus* and *C. laciniosum*. Concerning the zooplankton enumerations, the higher concentration of copepods and tintinnids were recorded at the SCM.

In the euphotic layer, the Chl. *a* concentration measured between the Chichijima Island and the station 5 ranged from 0.02mg.m^{-3} to 0.58mg.m^{-3}. Similar to the increase of

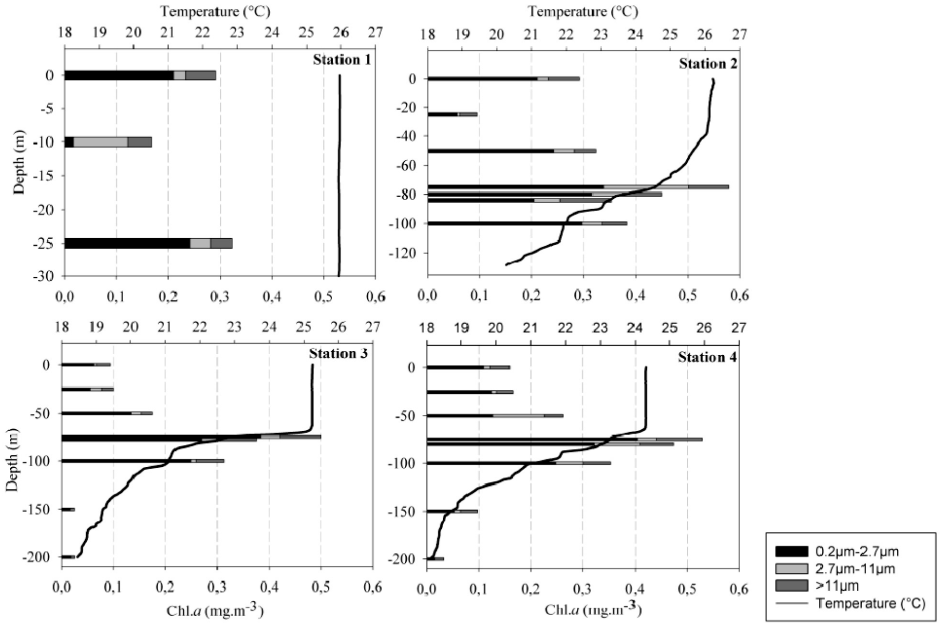

Fig. 3. Vertical profiles of Chl. *a* and temperature recorded at stations around Chichijima Island. Chlorophyll *a* (mg.m^{-3}) for different size classes is also shown. The black line is temperature in ℃.

abundance of diatoms mentioned above, the concentration of Chl. *a* recorded at the surface increased from station 6 to the Tokyo Bay (0.60 mg.m^{-3} to 2.29 mg.m^{-3}). Concentrations of Chl. *a* recorded from the station 6 to Tokyo Bay were significantly different from other stations measured in the subtropical gyre (p-value<0.05). On the basis of filter set results, the smallest fraction (0.2 μm to 2.7 μm) fixed the higher concentration of Chl. *a* in 91% of cases (Fig. 3).

3–2 Bio-optical environment

The SCMs were detected between 69m and 86m at the stations 2, 3, 4 and 5 (Fig. 4). These significant SCMs were located under a marked thermocline and just upper the nutriclines. At these stations, limits of euphotic layer were intrinsically linked to the maximum of Chl. *a*. However, no clear peak of Chl. *a* was recorded at the stations H.1 and 1 located in the Chichijima's bay where the light reached the bottom of seawater column with respectively 5% and 3% of relative incident light.

At the stations 2 and 5, the relative PAR was ranged from 1 to 4% at the center of the SCM. The bottom of the high chlorophyll layer received 0.1 to 4% of relative light intensity while the top was exposed to 1 to 20%. Similarly to attenuation coefficient curve, (data not show),

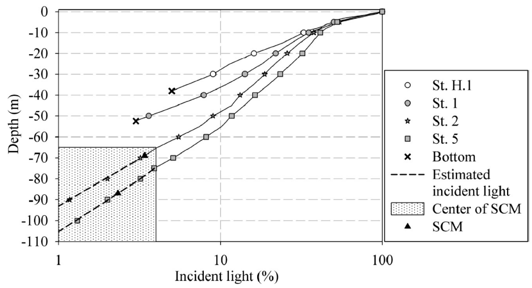

Fig. 4. Vertical profiles of incident PAR (%) from the coastal station H.1 to the offshore station 5. The intermediary stations (1, 2) were respectively located at the mouth of the Chichijima Bay and nearby the island. The black cross is the bottom of seawater column and black triangle is the depth of SCM. The dot filled rectangle shows the layer where center of SCM were detected. The continuous line shows the measured points and the dotted line the estimated incident light.

Table 1. Classification of optical water type depending on the wavelength and Jerlov table.

	412	443	490	510	555	665
St. H1	IB	II	IB	IB	I	I
St. 1	IA	IA	I	I	IA	I
St. 2	IA	IA	IB	IA	IA	I
St. 5	I	I	I	I	I	I

a progressive separation of incident light profiles was evidenced between the station H.1 and the offshore station 5 (respectively 22.4% and 9% at 30m).

Results on the optical water type (JERLOV, 1968) were shown in the Table 1. Although the offshore station 5 was in the case I at each wavelength, a type II (443nm) was monitored at the coastal station H.1. Between these two kinds of stations the optical water type varied from case I to IB at the sampling stations 1 and 2.

3–3 Nutrients and potential limiting factors

Vertical profiles of inorganic nutrient concentration showed a low value in the shallower layer (Fig. 5). However, noticeable nitracline and phosphacline were recorded between 60m and 90m. In these nutriclines, peaks in ammonium (0.6–0.85 μM) and nitrite (0.1–0.15 μM) were measured at the SCM of offshore stations. By using the REDFIELD and BRZEZINSKI ratios, four types of potential limitations were identified. Thus, 2 potential nitrogen limitations (Si,P,N ; P,Si,N), a potential phosphorus limitation (Si,N,P), and to a lesser extent a potential silicon limitation (N,P,Si) were detected. During the cruise, the distribution of potential limiting factor appeared to indicate a clear nitrogen limitation at all stations. In contrast, the [DIN]:[PO_4^{3-}] stoichiometry identified few clear potential limitations due to the high concentration of ammonium and threshold criterions used. However, phosphorus potential limitations were detected at the SCM and an oscillation between phosphorus and nitrogen occurred in the upper layer (Fig. 6).

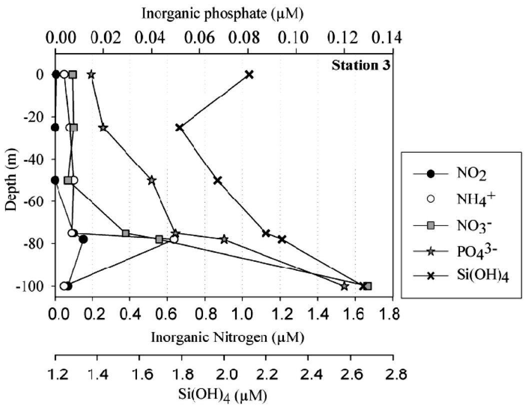

Fig. 5. Vertical distributions of concentration of inorganic nutrients at the St. 3. A primary nitrite maximum and a peak of ammonium were identified at the SCM.

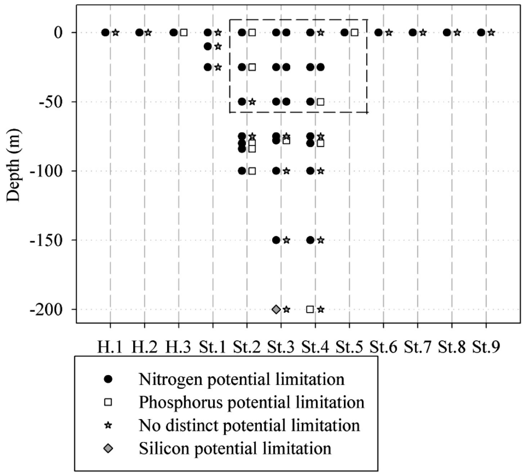

Fig. 6. Vertical distribution of potential limiting factor during the Chichijima cruise. At each depth, the REDFIELD and BRZEZINSKI stoichiometry is showed on the left side and the DIN:DIP on the right side. The black dotted rectangle point out the sampling point where the concentration measured were near the detection limit.

4. Discussion

4–1 Shifts in the phytoplankton communities depending on the environmental conditions

According to the results collected along the Ogasawara transect, our data set suggests a constant oligotrophic condition due to the low concentration of Chl. *a*, microphytoplankton and inorganic nutrients. However, two possible changes of environmental conditions depending on these parameters were identified. By using the one way analysis of variance test

(Kruskall-Wallis test) a significant difference of abundance of microphytoplankton (p-value < 0.05) was recorded between the St. 5 and the St.6. Difference of concentration was in part based on a shift of the dominant pool of microphytoplankton at the surface (dinoflagellate to diatom) and to drastic increase of abundance of the genus *Chaetoceros* spp.. Similarly, results on the Chl. *a* concentrations depending on the class sizes and nutrients appear to confirm this trend and define an area (St.6 to St.9) which was significantly different to the subtropical gyre (p-value<0.05). According to the location of stations and the sea surface temperature (Japan Oceanographic Data Center: (http://www1.kaiho.mlit.go.jp/jhd-E.html)), it's appeared that change was probably due to the Kuroshio's current conditions which differed from the Subtropical gyre area.

A second separation of data set was identified between the Chichijima Bay (H.1 to H.3) and the station St.1 to St.5. This change marked by the vicinity of island was reported on the microphytoplankton community and the distribution of light in the sea water column. According to previous report a decrease of concentration of microphytoplankton was monitored between St. H.1 and H.3 located at the mouth of the Chichijima Bay (TAGUCHI, 1975). In agreement with the TAGUCHI results, the concentration of dinoflagellates globally dominated the microphytoplankton species at the surface in the pool of stations surrounding the island and in the Chichijima Bay. However, dominant species enumerated in 1970 differed from this current study. For instance, abundance of *Peridinium* spp. were the dominant species enumerated around Chichijima Bay in 1970 but no occurrence was detected in our study. Moreover, even if the dominant species changed, no significant difference of total abundance of microphytoplankton was enumerated between the Chichijima Bay and the stations located in the Kuroshio counter current (St.1 to St.5).

Investigation of the relative light incidence condition provides a method to identify how the island modifies the surrounding area. In our data set, stations located at the mouth and in Chichijima Bay (St.1 and St. H.1) showed the higher light attenuation. Depending on the different wavelengths, variability of optical sea water types are consistent to the gradient observed but the seawater appeared more transparent than previously reported (SIMONOT and LE TREUT, 1986; EPPLEY *et al.*, 1988). Using JERLOV tables, optical water type near the absorption wavelength of Chl. *a* (665nm) did not change between the Chichijima Bay and the St. 5. In contrast, variability of different optical types is higher for the shorter wavelength and especially for maximum absorption of Chl. *a* spectrum (443nm). This classic significant absorption near the UV and declining to near zero between 650nm and 700nm is a characteristic of dissolved organic matter compound, CDOM (LOISELLE *et al.*, 2009).

The role of the inorganic particulate matter can also be putted in evidence due to the increase of upward radiance near the coastal area (data not show). In this oligotrophic condition the low light absorption coefficient associated with a greater backscattering process seemed to be a characteristic of higher turbidity near the Chichijima Island. This result involves that the reflective irradiance value due to shallow bottom is too low to modify the upward flux. As mentioned above, only 5% and 3% of incident light reached the bottom of sea water column. Thus, in contrast to the turbidity concentration, the reflective irradiance appears to be insignificant to drastically modify the upward flux of light.

Based on the optical properties, the higher nutrient concentration, CDOM and inorganic particulate matter can in part explain the lack of SCM in the Chichijima Bay. Similarly, lack of thermocline and pycnocline recorded between the station H.1 and St.1 highlighted that mixing condition was significant near the island and modify the shallow layer environment. Mixing conditions probably improved the nutrient availability in the upper layer and consequently, distribution of phytoplankton community was located in the entire sea water column. Our optical measurements were in line with the low concentration of phytoplankton enumerated during the cruise and suggested that the island modify the local distribution of microphytoplankton, but at a larger scale variability of abundance remains weakly detectable due in part to the globally constant oligotrophic condition.

4–2 Structure of SCM and limitation mechanisms

Distribution of phytoplankton has been monitored depending on the class sizes. By using filter set, our results suggested that small organisms (0.2 μm to 2.7 μm), played a significant role in the sea water column. Domination of small class size and concentration of Chl. *a* at the SCM reaching 5 times the concentration at the surface confirmed this ubiquitous phenomenon described in the NPSG (TAKAHASHI *et al.*, 1985; HENSE and BECKMANN, 2008).

Although this common structure is well documented, identification of potential limiting factor changed depending on the knowledge of seawater environment and methods used for nutrients measurement. CULLEN (1982) reported this issues regarding to biomass interpretation. In the Cullen study, location of SCM is drastically led by the nitrate availability, light and to lesser extent the temperature value which can change the chlorophyll concentration of cell by a factor 10. However, modification of Chl. *a* cell-content is also reinforced by the photoacclimation mechanisms which can inhibited 8 times the fluorescence in the upper layer (LOFTUS and SELIGER, 1975). In contrast to the high variability of Chl. *a* concentration in the sunlit zone, the low variability of microphytoplankton abundance between the surface and the other layers tends to show that a photoacclimation process occurred at the SCM.

As mentioned above, SCM is closely located at the boundary of the euphotic layer. This vicinity involves developing strategy, which according to previous reports, allow the growth of phytoplankton community under the arbitrary 1% of incident light (FALKOWSKY and OWENS, 1978; ANDERSON, 1979). The mobility of dinoflagellates organisms in the seawater column can be one favourable advantage contrasting to the slow migration of diatom species (JEPHSON and CARLSSON, 2009). Usually the dinoflagellates organisms swim upward in the morning and downward in the evening to respectively take advantage of optimal light and nutrient replete condition. In this study the domination of diatom measured in the night condition at the surface of station 4 tends to confirm this diel vertical migration. However, the lack of clear increase of dinoflagellate abundance at the bottom of sunlit pointed out the probable distribution in the shallow layer as previously described in experimental cultures (JEPHSON and CARLSSON, 2009).

Scavenging process at the SCM appears to be sizeable and can modify the relative fractioned size of Chl. *a*. Examination of large class size (>11 μm) suggested that an increase of the large size occurred under 1% of incident light. By using a microscope, our investigations revealed numerous particles at these depths mainly composed by fragments of the diatoms. Adsorption of organisms and scavenge of particles can in part explain the change of class size and the presence of Chl. *a* at these deep depth values. It should be noted that grazing pressure can explain the presence of particles at the SCM due to higher abundance of large phytoplankton predators (copepods and tintinnids) at these depths.

Grazing activity at the SCM initiate by large zooplanktons and heterotrophic bacterias was highlighted since the earliest report, (LE BORGNE, 1977; EPPLEY *et al.*, 1988; KUIPERS and WITTE, 2000). In this previous report, Le Borgne claimed that nutrient profiles can show the grazing activity due to the selective excretion of phosphate compared with the nitrate assimilation. According to the definition of LE BORGNE, our results showed the same difference between the profiles of phosphate and nitrate at the SCM. In addition, the peak of ammonium recorded at the SCM adds an evidence of regeneration of organic matter and a possible grazing activity (Fig. 5). However, due to the lack of measurement of grazing activity or picoplankton abundance in our study, discussion about the accumulation of Chl. *a* at the SCM layer remained difficult and especially to separate the photoacclimation mechanisms to sink of particles.

On the basis on the REDFIELD-BRZEZINSKI stoichiometries, identification of potential limiting factor of the area was investigated.

Variability of ratio can reflect the nutrient availability and their utilization by the plankton organisms. In our study distribution of REDFIELD and BRZEZINSKI ratios mainly shows a nitrogen potential limitation at each station. This result was consistent with previous meas urement which reported that (nitrate + nitrite): soluble reactive phosphorus, (SRP), was far below the REDFIELD stoichiometry in the western part of North Pacific Ocean (HASHIHAMA *et al.*, 2009). At the SCM, the DIN: [PO_4^{3-}] calculation seemed to be more suited for identification of the potential limiting factor due to the ammonium compound in the calculation process (JUSTIC *et al.*, 1995). In our study, the concentration of this compound appears to be significant in particular at the SCM where a peak has been recorded. The superimposition of these two indexes highlighted that the upper layer of euphotic layer oscillated between the nitrogen and phosphorus potential limitation probably due to the diazotrophy process (KARL *et al.*, 2001). However, specific pattern recorded at the SCM appears to be linked to the input of ammonium issue of the grazing activity and remineralisation mechanisms. This significant addition of ammonium and to lesser extent nitrite leads to change the nitrogen to phosphorus potential limitation at the SCM.

Finally, comparison of the depth of SCM and the light intensity tend to show two different features. The bio-optical parameters recorded in the Chichijima Bay indicated that phytoplankton communities can grow in the entire sea water column. In contrast, according to the previous studies, the SCM were systematically measured near the compensation depth for the stations located in the subtropical gyre (FURUYA, 1990). On the basis on our measurements, light intensity appears to control the access of nutrients in the gyre and allow in a stratified column to use the nutriments located under the thermocline.

5. Conclusions

Studies of some biological and physical parameters allow identification of three different oligotrophic areas in the Western part of the NPSG (Chichijima Island, the subtropical gyre, and the Kuroshio current). In these oligotrophic areas, the higher value of Chl. *a* concentration was recorded for the smallest fraction part (0.2 μm to 2.7 μm). The low concentration of microphytoplankton enumerated at each station around the Chichijima was dominated by the dinoflagellate species at the surface. The diatom pool is more dominant at the SCM and in the Kuroshio Current. Our measurements confirm that Chichijima Island appears to have specific feature in contrast to the Subtropical gyre area. In this oligotrophic location, the island seems to modify the optical properties of seawater, increase the concentration of nutrients which allowed utilisation over the entire seawater column by the phytoplankton organisms. Albeit complementary studies should be investigated, light availability and concentration of phosphorus under the thermocline appeared to be a key factor to support the growth of phytoplankton communities in the western part of NPSG.

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