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Marine Planktonic Ecosystem Dynamics in an Artificial Upwelling Area of Japan: Phytoplankton Production and Biomass Fate

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Abstract

Marine phytoplankton production as well as biomass is globally significant. This study hypothesized that a mild increase in nutrients concentrations (by a factor 1-2 higher) from artificial upwelling in oligotrophic water can alter phytoplankton dynamics (biomass, composition and size), and consequently, phytoplankton-derived particulate organic carbon flux. Primary production, carbon biomass of different planktonic groups, and organic carbon remineralization were examined by incubating seawater collected from two oceanographic stations in the vicinities of Ikitsuki Island, Japan, in 2004 and 2005. Station C, located near to and downstream of an artificial seamount that generates upwelling, had higher nutrient concentrations and biomass (Chl. *a* and carbon) than Station O-2, which was upstream and far from the seamount. Phytoplankton biomass and primary production rates remained higher during incubation for station C than for station O-2 in both 2004 and 2005. Phytoplankton composition also differed between the two stations. Picophytoplankton contributions to total biomass were smaller at station C than at station O-2 while those of micro- and nanophytoplankton were higher at station C. The results of this study indicate that even a small increase in nutrient availability in oligotrophic waters can alter productivity, biomass, and phytoplankton composition. Additionally, around 4.0% of net primary production was estimated to escape from grazers and remineralization, instead sinking into deep ocean layers in the form of less easily degraded particles. The difference in net primary productivity between Stns. C and O-2 gave an estimation of excess production at Stn. C resulting from upwelled nutrients. Owing to this 1.3 to 1.5 mg more carbon m^{-2} d^{-1} is likely to be exported at Stn. C compared to Stn. O-2

Key words: Artificial seamount, Nutrients, Primary production, Organic carbon remineralization, Excess production, Carbon sequestration

1. Introduction

Marine phytoplankton plays an important role in regulating the global carbon cycle (Beardall et al., 2009; Chisholm, 2000). These organisms contribute approximately 50% of the total global primary production (Beardall et al., 2009, Falkowski et al., 2007) and play a vital role in mitigating the amount of carbon dioxide (CO_2) in the atmosphere by fixing carbon that is then sequestered into the deep ocean via the biological pump (Falkowski et al., 2007). On average, 35% of carbon fixed by phytoplankton in the ocean is exported to the ocean interior (Falkowski et al., 1998). Many studies have recently shown that the amount of carbon exported depends on phytoplankton's production (Marañón et al., 2003), biomass (Roberts et al., 2003), composition (Boyd and Newton, 1999), and size (Smetacek, 1999).

The production of phytoplankton in the ocean can be enhanced by increasing nutrient availability in the euphotic zone (Lampitt et al., 2008; Matear and Elliott, 2004; Nishino et al., 2011). Upwelling of nutrient-rich deep water to the shallow layer is a natural source of nutrients for phytoplankton in the euphotic zone but it is slow and exhibits spatial and temporal variations. A number of researchers have proposed artificial fertilization of the ocean to enhance primary productivity, and hence, the biological pump (export of carbon) (Lampitt et al. 2008; Matear and Elliott, 2004). Others have suggested that the supply of nutrients in the euphotic zone can be increased by generating controlled (artificial) upwelling, with the deployment of ocean pipes below the surface layer (Lovelock and Rapley, 2007; White et al., 2010), leading to net carbon sequestration (Karl and Letelier, 2008). Nutrients can also be supplied to the euphotic zone by artificial upwelling using manmade marine structures (seamounts) (Casareto et al., 2006; Magi et al., 2005). Magi et al. (2005, 2006) showed that a seamount established in the vicinity of Ikitsuki Island, Japan (33° 28′ 40″ N, 129° 25′ 29″ E), naturally upwelled bottom water with the help of

tidal currents. This upwelled water was then transported by the Tsushima Current (a branch of the Kuroshio Current), resulting in a small increase in nutrient concentrations downstream of the seamount compared to upstream. The present study wanted to know whether such a mild increase in nutrient concentrations (by a factor 1-2 higher) caused by artificial upwelling may have implications for plankton ecosystem dynamics (primary production, phytoplankton biomass, heterotrophic metabolism, and food web structure) and the fate and flux of carbon.

The present research hypothesized that a mild increase in nutrient concentrations caused by artificial upwelling will i) increase phytoplankton biomass and production, ii) alter phytoplankton composition and size, iii) change the balance between autotrophs and heterotrophs, and iv) have implications in the export flux of carbon via the biological pump. These hypotheses were tested by comparing Station (Stn.) C and Stn. O-2 located downstream (near the seamount influenced area) and upstream (far from the seamount influenced area), respectively.

2. Materials and Methods

2.1. Study site, field observations, and seawater sampling

This research was carried out in cooperation with the Nagasaki Prefecture. Field observations were conducted on board the research vessel *Tsurumaru*, (which belongs to the Laboratory of Fisheries Experimental Station of Nagasaki Prefecture), in areas around an artificial marine structure or seamount located northwest of Kyushu Island, near Ikitsuki Island, Nagasaki Prefecture, Kyushu, Japan (33° 28′ 40″ N, 129° 25′ 29″ E) (Fig 1). The seamount was constructed as a permanent structure to generate upwelling in these regions. The construction started in 1997 and finished in 2000, using 4860 concrete blocks (2 m x 2 m in size) made of cement and fly ash. The seamount is 12 m high, 120 m long, 60 m wide, and is set up at a depth

of 80 m. The area where the artificial seamount was constructed and stations were studied is under the administration of the Nagasaki Prefecture of Japan; therefore, no specific permissions were required for this research. This research did not involve endangered or protected species.

Field observation methods are described in detail in Magi et al. (2005). In brief physical parameters were measured using a fixed mooring system with a current meter and a thermistor chain fixed about 500 m from the seamount. In addition, data were collected from a ship-based Acoustic Doppler Current Profiler (ADCP) with Differential Global Positioning System (DGPS), a weather-measurement system (WS-40) (Davis Instruments) on the roof of the Nagasaki Prefecture Fisheries Agency, and a tide level sensor (RML-10) (RIGO) at the Ikitsuki Fisheries Port. Data from ADCP and DGPS were collected at fixed time to check the status of upwelling along 2 transect lines each 2 km long, one on each side of the structure parallel to the main currents and at 50° angles with respect to the main axis of the seamount. Salinity and temperature vertical profiles were measured using a salinity, temperature, and depth meter (STD) (Alec Electronics) and light vertical profiles were measured using a multi-sensor (AAQ1183 series, Alec Electronics) at Stns. C, A, B, and O-2, in May 2004; and at Stns. F, E, D, C and A (downstream and east-northeast of the seamount) and Stns. B, O and G (upstream and west-southwest of the seamount) in September 2004; and at Stns. C and O-2 in July, August and October 2005. Total inorganic carbon (TIC) was measured at Stns. C and O-2 in October 2005 only. Nutrients were measured at Stns. C, A, B, O-2, in May 2004; and at Stns. F, E, D, C, A, B, O and G in September 2004; and at Stns. C and O-2, in July, August and October 2005. Chlorophyll *a* (Chl. *a*) vertical profiles were measured using a multi-sensor (AAQ1183 series, Alec Electronics) at Stns. C, A, B, and O-2 in May 2004; and at Stns. F, E, D, C, A, B, O and G in September 2004; and at Stns. C and O-2 in October 2005. Seawater for measuring vertical

profiles of TIC was collected using Niskin bottles. Seawater from Niskin bottles was dispensed into 100 ml brown bottles using a silicon tube, and preserved until analysis by adding mercury chloride ($HgCl_2$) in a final concentration of 0.5% (volume/volume) of a 50% saturated solution. For nutrients, seawater was collected at several depths in the euphotic and aphotic zones using Niskin bottles, dispensed into 50 ml acid-cleaned polyethylene bottles, and kept frozen until analysis. At least three replicates of TIC, nutrients and Chl. *a* were taken from different depths at each station during field survey carried out at different times.

2.2. Incubation experiments

Seawater for incubation was collected using 20-liter Niskin Bottles from Stns. C and O-2 at 2, 7, 18, 26, and 53 m (corresponding to 100%, 50%, 20%, 10%, and 1%, respectively, of surface incident irradiance in the water column) in May 2004, and from 2, 10, 20, 30, 40, and 50 m (corresponding to 100%, 50%, 20%, 10%, 5%, and 1%, respectively, of surface incident irradiance in the water column) in October 2005. Seawater from each depth was then dispensed from Niskin bottle into acid-cleaned 20-liter polycarbonate Nalgene bottles and transported under dark conditions to the laboratory. For more precision, nutrients and Chl. *a* samples were also taken from the waters collected for incubation experiments. Initial samples for chemical (Chl. *a*) and biological parameters were taken from 20-liter Nalgene bottle for each station and depths. For initial nutrients samples, seawater was dispensed directly from Niskin bottles into 50 ml acid cleaned polyethylene bottles. At least three replicates of nutrients and Chl. *a* were taken from different depths at each station for incubation experiments.

Incubations were done in 2.2-liter Nalgene bottles suspended in water baths of circulating tap water outside the Fisheries Experimental Station of Nagasaki Prefecture, Japan at in situ light

intensities corresponding to sampled depths by covering the bottles with mesh screens of different transparencies. The temperature of the water bath was adjusted to sea surface temperature: about 18–19 °C in May 2004 and 23–24 °C in October 2005. Light intensity and water temperature were monitored during incubations using in situ sensors (MDS-MkV/T and MDS-MkV/L, Alec Electronics).

To measure primary production rates, 2 ml of ^{13}C labeled sodium bicarbonate ($NaH^{13}CO_3$, 99.9% ^{13} C) prepared by adding 100 mg in 10 ml deionized water (purified using Chelax-100 to remove trace metals), was added to each liter of seawater in order to achieve a final ^{13}C concentration of around 11.5% (10.4 ^{13}C enrichment factor).

2.3. Incubation sampling

Biological and chemical characteristics of the incubated seawater were analyzed at 0 h, 12 h and 24 h. For Chl. *a*, 500 ml of water from each incubation bottle was filtered using 0.2 µm polycarbonate membrane filters, which were then stored at -20 °C until analysis. For ^{13}C isotope measurements of particulate matter, 500 ml of water from each incubation bottle was filtered using pre-combusted (at 500 °C) Whatman GF/F filters (47 mm), which were then stored at -20 °C until analysis.

To enumerate heterotrophic bacteria, picophytoplankton (<2 µm), heterotrophic and autotrophic nanoflagellates (HNF and ANF) (2-20 µm), duplicate samples from each incubation bottle were taken into sterilized 50 ml tubes, fixed by glutaraldehyde (1% final concentration) (Casareto et al., 2012), and kept cool until analysis. To enumerate and identify microplankton (phytoplankton and zooplankton), the remaining water in each incubation bottle was preserved in

buffered formalin at a final concentration of 4% and stored in the dark until analysis (Casareto et al., 2012; Niraula et al., 2007).

2.4. Degradation experiment

To determine the remineralization rate of phytoplankton-derived organic carbon, a degradation experiment was performed (parallel to the main incubation experiment) in 2004. Seawater was collected from 26 m (at 10% of incident light) from Stns. C and O-2 and dispensed into 20-liter Nalgene bottles. Samples were covered by mesh screen to filter light to 10% intensity and incubated in a water bath for 48 h to allow plankton growth, after which initial parameters were sampled. After sampling, the bottles were again incubated under dark conditions at a controlled temperature (20 °C) for about four months. Subsampling was periodically performed to measure particulate organic carbon (POC). Particulate organic carbon was collected onto pre-combusted (at 500 °C) Whatman GF/F filters (47 mm) and stored at -20 °C until measurement.

2.5. Measurements and Analysis

Dissolved inorganic nutrient concentrations (e.g., nitrite (NO_2^-), nitrite + nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), and silicic acid ($Si(OH)_4$)) were determined with a four-channel auto analyzer (TRAACS-2000: BRAN+LUEBBE) according to Hansen and Koroleff (1999). Concentrations of NO_3^- were determined by subtracting the values of NO_2^- from the values of $NO_3^- + NO_2^-$. Detection limits were 0.052 µM for $NO_3^- + NO_2^-$, 0.010 µM for NO_2^-, 0.020 µM for NH_4^+, 0.020 µM for PO_4^{3-}, and 0.307 µM for $Si(OH)_4$. Reproducibility (precision) of nutrient analysis was ± 0.2% for $NO_3^- + NO_2^-$, ± 0.5% for NO_2^-, ± 1.2% for NH_4^+, ± 0.8% for PO_4^{3-}, and ± 0.5% for $Si(OH)_4$. Dissolved inorganic nitrogen (DIN) was determined by adding

the values of NO_3^-, NO_2^-, and NH_4^+. Accuracy of method was tested using certificated reference materials (CSK standard solutions) distributed by Wako Co., and the accuracy was ±1% (1σ, n=10). Chlorophyll *a* was extracted from filters using N, N-dimethylformamide (DMF) (Suzuki and Ishimaru, 1990) and measured using a spectrofluorometer (RF-5300PC, Shimadzu Co.). Particulate matter with ^{13}C isotope measurements was determined using a mass spectrometer DELTA plus Advantage (Thermo-Finnigan Co.) equipped with EA1110. Primary production rates using ^{13}C as a tracer was determined according to Hama et al. (1993). Particulate organic carbon without ^{13}C enrichment was analyzed using an N/C analyzer (Sumi-Graph NC-90A). The analytical precision (standard deviation) for POC measurements was less than ±3%. Net primary production (NPP) was the production during 24 h incubations. Respiration (R) was calculated as the difference between 12 h production during the day and 24 h production: R = (12–24 h) × 2. Gross primary production (GPP) was calculated as the sum of NPP and R: GPP = NPP + R. The production to respiration ratio (P/R) was calculated by dividing GPP by R: GPP/R. Excess production caused by upwelled nutrients at Stn. C was calculated from the differences in the net primary production (NPP) between Stn. C and Stn. O-2: Excess Production = NPP (Stn. C) – NPP (Stn. O-2)

Total inorganic carbon was measured using the coulometric method (Johnson et al., 1987) using a CM5012 CO_2 Coulometer, UIC Company. The precision of the measurement was ±3 μmol kg^{-1} (1 σ , n=10). A certificated reference material (Bath 65) distributed by A. Dickson, University of California, San Diego was used to verify accuracy of method and it was ±6μmol kg^{-1} (1 σ , n=10).

Heterotrophic bacteria and picophytoplankton were collected on 0.2 µm black polycarbonate filters by filtering 10–15 ml aliquots stained with 4′,6-diamidino-2-phenylindole (DAPI). An epifluorescence microscope (Nikon-Eclipse) with a UV filter and a B filter was used to count heterotrophic bacteria and picophytoplankton, respectively. Heterotrophic and autotrophic nanoflagellates were collected on 0.8 µm black polycarbonate filters by filtering 30 ml aliquots stained with DAPI (Porter and Feig, 1980) and were counted under an epifluorescence microscope by using a B filter. Micro phytoplankton and micro zooplankton were counted and classified using an inverted microscope (Nikon, Bk-201) according to Chihara and Murano (1997).

The carbon biomasses of different plankton groups were also determined for both 2004 and 2005 samples. Bacteria and picoplankton carbon biomasses were calculated using a biovolume to biomass conversion factor: C $cell^{-1}$ in pg = 0.38 pg C μm^{-3} for bacteria (Lee and Fuhrman, 1987) and C $cell^{-1}$ in pg = 0.45 pg C μm^{-3} for picoplankton (Casareto et al., 2000). Carbon biomasses of diatoms and other protists plankton were calculated using the relationships given in Menden-Deuer and Lessard (2000): for diatoms, C $cell^{-1}$ in pg = $biovolume^{0.811} \times 0.288$ and for other phytoplankton and heterotrophic protists, C $cell^{-1}$ in pg = $biovolume^{0.819} \times 0.76$. Biovolume was determined by measuring the size of >30 individuals using an image analyzer fitted to a microscope and assuming the closest approximation of geometric shape. The carbon biomass of zooplankton (other than protists) was calculated according to Uye (1982).

3. Results

3.1. Field observations

3.1.1. Physico-chemical properties of the water column

The depth of the euphotic zone (1% of the surface light irradiance) measured at noon was about 53 to 50 m in both 2004 and 2005, respectively. Average seawater temperature and salinity varied in different months (Table 1). The vertical profiles of temperature and salinity (shown only for 2004 September, Fig. 2a and b) showed that stations downstream of the seamount (Stns. F, E, D, C and A) exhibited almost no vertical stratification and had lower ($p < 0.006$, *t*-test) temperatures than the upstream stations (Stns. B, O and G), and salinity overall also showed small fluctuations spatially (with depth and station)

3.1.2. Upwelling-influenced area

Harmonic analysis revealed that K1 (a diurnal current) and M2 (a semidiurnal current) dominated the study area. Data collected from ADCP along transect lines and vertical profiles of eco-intensity revealed internal waves and upwelling flow at the downstream side of the seamount. These data sets are shown in detail in a previous publication (Magi et al., 2005). The iso-echo intensity at 30 m to 60 m depths was around 7 m higher at the downstream side and especially higher (up to 15 m) when affected by strong tidal currents. These differences clearly demonstrate upwelling on the downstream side of the seamount.

3.1.3. Chemical parameters

Nutrient concentrations (DIN, silicate, and phosphate) varied spatially and temporally during field observations in 2004 and 2005 (Table 2). Concentrations of nutrients in 2004 were significantly higher at downstream stations than upstream in September ($p < 0.02$, *t*-test) and in May for DIN ($p < 0.05$, *t*-test) and silicate ($p < 0.05$, *t*-test) only. The same trend was seen in

2005 for both DIN and Silicate in August ($p < 0.02$, *t*-test) and in July ($P < 0.05$, *t*-test) and October ($p < 0.05$, *t*-test).

Figure 2c shows the vertical profile of Chl. *a* at both upstream and downstream stations for September 2004. Table 2 shows the integrated concentrations of Chl. *a* at different stations for both 2004 and 2005. Concentrations of Chl. *a* (Table 2) were higher at downstream stations than at upstream stations, however, the difference was significant only in 2004 September and 2005 October ($p < 0.05$, *t*-test). Maximal Chl. *a* concentrations were found from 30 m to 40 m deep.

At Stn. C, TIC fluctuated from the surface to the bottom, ranging from 1999 µM at the surface (0 m) to 2113 µM at bottom (77 m) Fig. 3. In contrast, TIC at Stn. O-2 increased with depth and ranged from 1984 $\mu mol \cdot L^{-1}$ at the surface (0 m) to 2129 µM at the bottom (76 m). Despite some fluctuations, there was no significant difference in TIC between Stns. C and O-2. The inventories (average integrated concentrations) of TIC were: from the surface to the bottom, 22717 $mmol \cdot m^{-2}$ for Stn. C and 22323 $mmol \cdot m^{-2}$ for Stn. O-2; from surface to 50 m (the euphotic zone), 20558 $mmol \cdot m^{-2}$ for Stn. C and 20381 $mmol \cdot m^{-2}$ for Stn. O-2; and from 50 m to the bottom (the aphotic zone), 28115 $mmol \cdot m^{-2}$ for Stn. C and 27179 $mmol \cdot m^{-2}$ for Stn. O-2.

3.2. Incubation experiment

3.2.1. Nutrients, Phytoplankton Biomass and Production

Initial concentrations of nutrients were higher at Stn. C compared to Stn. O-2 by a factor 1.0-2.0 higher for N, 1.2-1.3 for Si, and 1.2-1.6 for P (Fig. 4a and b), and the difference in nutrients concentration between Stns. C and O-2 was significant ($p < 0.02$, *t*-test) in both 2004 and 2005.

In 2004, the concentrations of Chl. *a* were higher ($p < 0.02$, t-test) at Stn. C than Stn. O-2. In 2005, also Chl. *a* were higher at St. C than St. O-2, but the difference was not statistically significant (Fig. 5). Phytoplankton carbon biomass was significantly higher ($p < 0.05$, t-test) at Stn. C than Stn. O-2 in both 2004 and 2005 (Fig. 6), consistent with nutrient concentrations.

Primary production rates were higher at Stn. C than Stn. O-2 for most depths in both 2004 and 2005 (Fig. 7). Time course data (over a 12-h period and 24-h period) on primary production allowed the calculation of R, GPP, and P/R in the euphotic zone for 2004 and 2005 (Table 3). The values of GPP, NPP, and R for both stations were higher ($p < 0.02$, *t*-test) in 2005 than in 2004. The difference between NPP at both stations revealed the excess production at Stn. C for both 2004 and 2005.

3.2.2. Heterotroph Biomass

The biomass of microzooplankton was higher ($p < 0.01$, *t*-test) at Stn. C than Stn. O-2 (Fig. 8). The biomass of heterotrophic nanoflagellates and picoflagellates was also higher (but not statistically significantly so) at Stn. C than Stn. O-2. Bacteria biomass was higher ($p < 0.04$, *t*-test) at Stn. O-2 than at Stn. C.

3.3. Degradation experiment

Particulate organic carbon decreased rapidly in the first 14 days indicating rapid decay or remineralization of initial POC (Fig. 9). Particulate organic carbon decreased slowly and at 90 days, an 88% decrease was observed in the seawater from both Stn. C and Stn. O-2. The rate of POC degradation at 90 days was 1.32 for Stn. C and 1.03 for Stn. O-2. After three months, ~12%

of the POC produced in the euphotic zone remained as a less easily degraded portion of total POC.

4. Discussion

Increased nutrient availability increases phytoplankton biomass (Agustí and Duarte, 2000; McAndrew et al., 2007; Niraula et al., 2005, 2007; Mahaffey et al. 2012) and community composition (Casareto et al., 2012; Niraula et al., 2007; Mahaffey et al. 2012). In this study, even a small increase in nutrient concentrations in oligotrophic waters produced these results. Picophytoplankton dominated at both stations in terms of biomass, however, the contribution of picophytoplankton to total phytoplankton biomass was smaller at Stn. C than at Stn. O-2, although the difference was significant ($p < 0.05$, *t*-test) only in 2004. In contrast, the contribution of micro- and nanophytoplankton (other than diatoms) was higher at Stn. C than at Stn. O-2 ($p > 0.03$, *t*-test) in both 2004 and 2005. Diatoms showed little or no difference in biomass between the two stations. Diatom growth is also limited by silica; they need ≥2 μM (Egge and Aksnes, 1992). Others show that diatom silica requirements vary and are higher in oligotrophic water than in eutrophic water (Brzezinski et al., 1997, 1998). Therefore, it is likely that the concentration of silica (which ranged from 2 to 4 μM) in the present incubation of oligotrophic seawater was insufficient for diatom growth.

Nutrient availability is also known to regulate the balance between autotrophs and heterotrophs in oligotrophic water (Duarte et al. 2000). Heterotrophic metabolism is always higher than autotrophic (Duarte et al., 2000) in oligotrophic water. Increased nutrient inputs leads to autotrophic metabolism dominance (Duarte et al., 2000; McAndrew et al., 2007), but with low nutrient inputs the balance remains unaltered (Duarte et al., 2000). The incubations in this study

also showed that a small increase in nutrient concentrations increased phytoplankton biomass but produced little or no change in the balance between autotrophs and heterotrophs for both Stns. C and O-2.

Biological production and consumption dynamics are important in determining carbon fluxes in the ocean (Casareto et al., 2012; del Giorgio and Duarte, 2002). A larger increase in photosynthetic carbon fixation than in respiration results in organic material export to the oceans' interior (Berelson, 2011; del Giorgio and Duarte, 2002; Falkowski, 1997; Williams 1998) and facilitates the diffusive drawdown of atmospheric CO_2 (Cermeno et al., 2008; Matear and McNeil, 2009). Nutrient availability can also temporally and spatially decouple gross primary production and respiration (McAndrew et al., 2007). Aristegui and Harrison (2002) reported that in upwelled waters, respiration is always significantly lower than photosynthesis (P:R > 1) and enhancements in photosynthesis are paralleled by increases in Chl. *a* but not in respiration. In this study, P:R was greater than 1 for both Stn. C and Stn. O-2. Moreover, the ratio was slightly higher at Stn. O-2 than Stn. C. Despite a higher P:R at Stn. O-2, phytoplankton carbon biomass, Chl. *a*, net primary production, gross primary productions and respiration were also higher at Stn. C than at Stn. O-2, indicating that enhancements in photosynthesis will increase both biomass and respiration.

The difference in net primary productivity between Stns. C and O-2 is an estimation of excess production at Stn. C resulting from upwelled nutrients (new nutrients). A number of studies show that excess primary production is exported to deep waters (Eppley, 1989; Eppley and Peterson, 1979; Roberts et al., 2003). Others show that the amount of carbon exported from the surface layer through sinking is determined by the size and composition of phytoplankton. Large phytoplankton, such as diatoms, sinks relatively rapidly, and therefore, is thought to

contribute more to the biological pump (Boyd and Newton, 1999; Boyd and Trull, 2007; Smetacek, 1999) than smaller phytoplankton. Other studies have shown that picoplankton also play an important role in export flux by forming aggregations (Richardson and Jackson, 2007), which have a high vertical settling velocity (Jackson et al., 2005). Richardson and Jackson (2007) showed that picoplankton contribution to export flux is proportional to their total net primary production.

In addition, the amount of carbon exported from the surface layer is determined by food web processes (Boyd and Trull, 2007; Casareto et al., 2012; Ducklow et al., 2001). Not all the primary production is exported through sinking. Around 67% of primary production is consumed by zooplankton through food web processes before being exported to deep water (Calbet and Landry, 2004).

Remineralization or degradation of organic matter is also a key factor determining the fate of carbon fixed in the surface layers (Casareto et al., 2006; De La Rocha and Passow, 2007; Elskens et al., 2008; Karl and Letelier, 2008). Much of photosynthetically fixed organic carbon is decomposed or remineralized in the euphotic zone, resulting in a small fraction of carbon that sinks to the ocean floor and becomes sequestered in deep-sea sediments (Buesseler et al., 2004; Elskens et al., 2008; Huesemann, 2008; Oschlies, 2009; Oschlies et al., 2010; Yool et al., 2009). Around 10–12% of net primary production reaches the deep layer after escaping remineralization (Buesseler, 1998; Elskens et al., 2008). The degradation experiment in this study also showed that 12% of POC was less easily degradable and had the potential to sink to the bottom layer (or ocean floor) by escaping remineralization. Given that the fraction of POC that can possibly escape remineralization is 12% and the fraction of phytoplankton carbon that can potentially escape from grazing is ~ 33% (after Calbet and Landry, 2004), it was estimated that around 4%

of net primary production has the potential to be exported in the bottom layer (Table 4). A similar estimation was made by Elskens et al (2008), who showed that from 17 to 23% of primary production is exportable, of which 6–13% sinks to a deeper layer (150 m) in the NW Pacific subarctic gyre. Further, excess production at Stn. C that resulted from artificial upwelling of nutrients implies that export flux of carbon would be 1.3 to 1.5 mg C $m^{-2} \cdot day^{-1}$ higher at Stn. C than at Stn. O-2 (Table 4).

In addition to nutrients, inorganic carbon (carbon dioxide) will also be upwelled by artificial or controlled upwelling (Oschlies et al., 2010; Shepherd et al., 2007; Yool et al., 2009). Therefore, despite primary production enhancement, the net oceanic uptake of CO_2 from the atmosphere associated with artificial upwelling is small (Oschlies et al., 2010; Shepherd et al., 2007; Yool et al., 2009).

In this study, TIC was comparable with previous report (Millero, 1992). The vertical profile of TIC and DIN at Stn. C showed that TIC fluctuated less with depth than DIN did. Dissolved inorganic nitrogen concentrations were much higher at the bottom than at the surface layer, leading to decreasing TIC/DIN with depth (Fig. 10). It is well known that most of the carbon and nutrients upwelled to the surface layer come from the degradation of sunken organic materials at the bottom layer.

The results of this study suggest the possibility of disproportionate degradation of sunken organic matter in the bottom layer, resulting in the release of more nutrients than carbon. Previous studies have also shown preferential removal (mineralization) of nitrogen compared to carbon in suspended matter (Burska et al., 2005) and in decaying particulate organic matter in both anaerobic and aerobic water (Kristensen and Blackburn, 1987). Therefore, it is likely that more nutrients than TIC were upwelled. Moreover, due to internal waves and vertical mixing in

the area around seamount (Magi et al., 2005), TIC remained almost similar from surface to bottom, but nutrients despite being released more than TIC remained low in surface due to planktonic uptake. The degradation experiment in this study indicates that not all organic matter is completely degraded. Some fraction of this sunken organic matter may still remain as less easily degraded material. This material may eventually be moved to an open ocean sub-surface layer by advection and diffusion for further sequestration at greater depths (Hales et al., 2005a, 2005b; Hales et al., 2006; Tsunogai et al., 1999).

Some previous studies have also shown that controlled upwelling generated with the deployment of ocean pipes below the surface layer will enhance primary productivity and the export of organic carbon to depths (Karl and Letelier, 2008; White et al., 2010). Others have shown that the magnitude of POC flux is subject to considerable inter-annual variability, making estimation of carbon export complex (Berelson, 2011; Buesseler et al., 2004) or unpredictable over short temporal scales (Lapoussiere et al., 2013). Furthermore, there may be many uncertainties and unintended consequences associated with the manipulating natural ecosystems (Cullen and Boyd, 2008; Powell, 2008). Letelier et al. (2008) suggest that controlled upwelling should be viewed as a tool to study the response of pelagic microbial assemblages to perturbations at different spatial and temporal scales.

5. Conclusions

A small increase in the concentration of nutrients (by a factor of 1-2) by artificial upwelling increased phytoplankton productivity and biomass, and altered composition of phytoplankton but produced little or no change in autotroph vs. heterotroph dynamics. This study shows that mild upwelling generated in relatively shallow areas could enhance the export of carbon (the carbon

flux) to bottom layer by increasing the amount of exportable carbon that can escape grazing and remineralization. The results of this study introduce new options for effective CO_2 sequestration by marine planktonic communities in the ocean via artificial upwelling in coastal or continental shelf areas. This upwelling only requires a manmade submarine structure and the natural energy from tidal currents (clean and environmentally friendly technology) and ensures that ecosystem productivity but not composition will be affected.

Acknowledgements

This study was supported by the research program of RITE (Research Institute of Innovate Technology for the Earth) under the fund from METI (Ministry of Economy, Trade and Industry). The authors express their sincere thanks to the staff of the Nagasaki Prefecture, Institute of Fisheries for their support in field observation, seawater sampling, and setting up the incubation experiments. The authors are also very much grateful to Dr. M. Magi of RITE for discussions and suggestions pertaining to this research.

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Figure Captions

Fig. 1: Position of stations in the vicinity of the artificial marine structure (seamount).

Fig. 2: Vertical profile of temperature, salinity and chlorophyll *a* at different stations in the vicinity of the seamount in September 2004.

A: Temperature B: Salinity C: Chlorophyll *a*

Fig. 3: Concentrations of TIC according to depth at Stns. C and O-2 in July 2005. Error bars represent standard deviations.

☐ Stn. C ○ Stn. O-2

Fig. 4: Initial concentrations of nutrients at different depths in 2004 (A) and 2005 (B) incubations. Error bars represent standard deviations.

☐ Stn. C ○ Stn. O-2

Fig 5: Integrated concentrations of Chl. *a* from the euphotic zone calculated from incubations in 2004 and 2005. Error bars represent standard deviations.

☐ Stn. C ■ Stn. O-2

Fig 6: Integrated phytoplankton carbon biomass from the euphotic zone at Stn. C and Stn. O-2 calculated from incubations in 2004 (A) and 2005 (B). Error bars represent standard deviations.

☐ Diatoms ▨ Other micro and nano phytoplankton ■ Pico phytoplankton

○ Total Phytoplankton

Fig 7: Primary production according to depth during 12 hours and 24 hours in 2004 and 2005. Error bars represent standard deviations.

A: Stn. C (2004) B: Stn. O-2 (2004) C: Stn. C (2005) D: Stn. O-2 (2005)

☐ 12 hours ○ 24 hours

Fig. 8: Integrated heterotrophic carbon biomass from the euphotic zone at Stns. C and O-2 calculated from incubations in 2004 (A) and 2005 (B). Error bars represent standard deviations.

☐ Micro zooplankton ▨ Bacteria

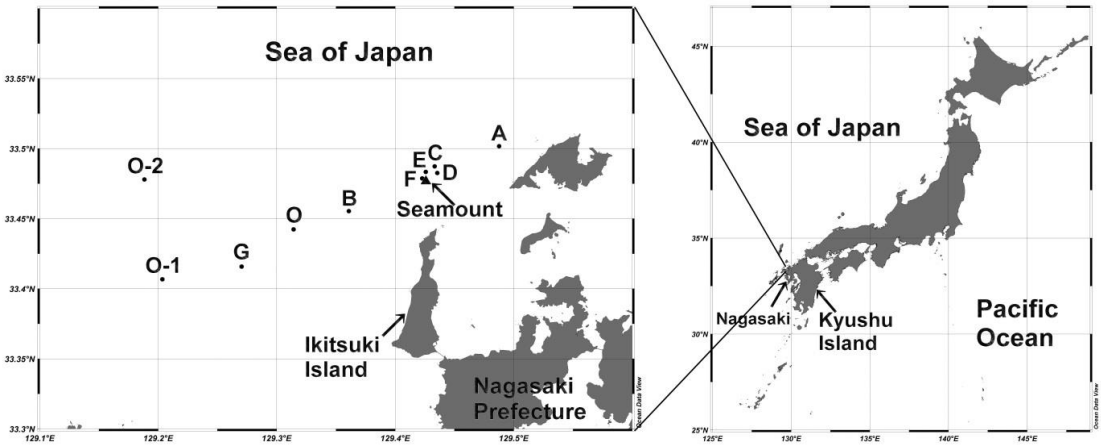
■ Heterotrophic pico- and nanoflagellates

Fig. 9: Temporal changes in POC during the degradation experiment in 2004. Error bars represent standard deviations.

☐ Stn. C ○ Stn. O-2

Fig. 10: Vertical profile of TIC, DIN and TIC/DIN ratio at Stn. C in July 2005.

☐ TIC (mM) ○ DIN (μM) △ TIC/DIN ratio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33.5°N
33.45°N
33.4°N
33.35°N
33.3°N
129.1°E
129.2°E
129.3°E
129.4°E
129.5°E
O-2
O-1
O
G
B
A
C
D
E
F
Seamount
Ikitsuki
Island
Nagasaki
Prefecture
Sea of Japan
45°N
40°N
35°N
30°N
25°N
125°E
130°E
135°E
140°E
145°E
Nagasaki
Kyushu
Island
Pacific
Ocean

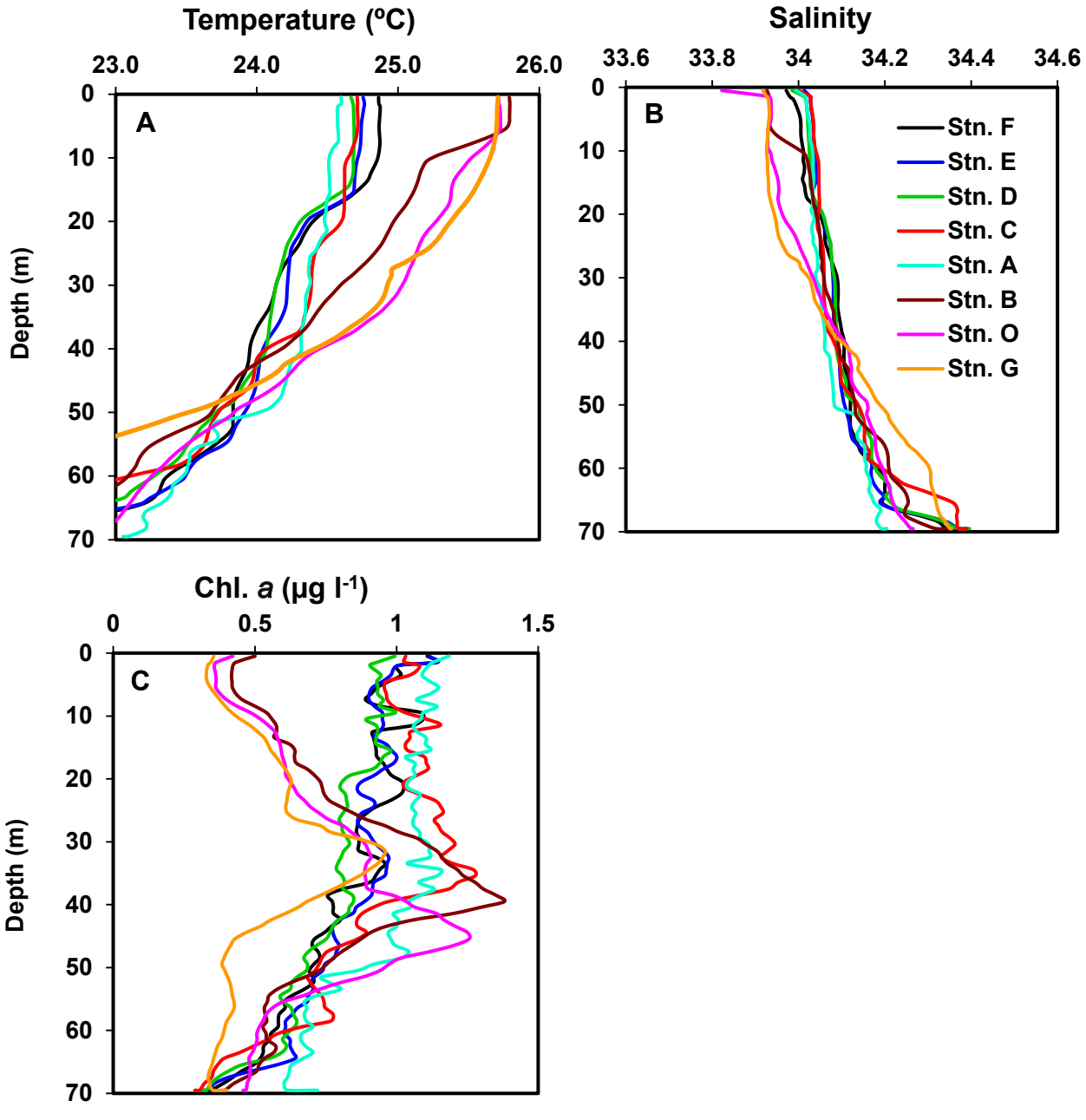

Fig. 2 (A, B and C): Casareto et al. 2016

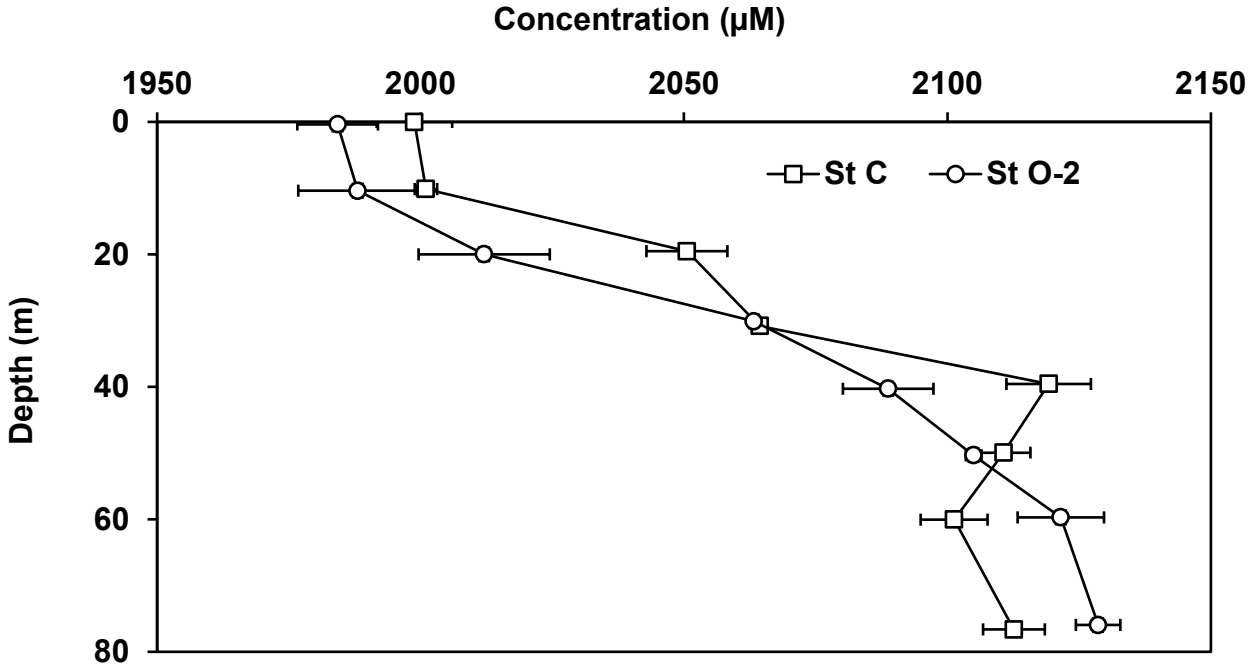

Fig. 3: Casareto et al. 2016

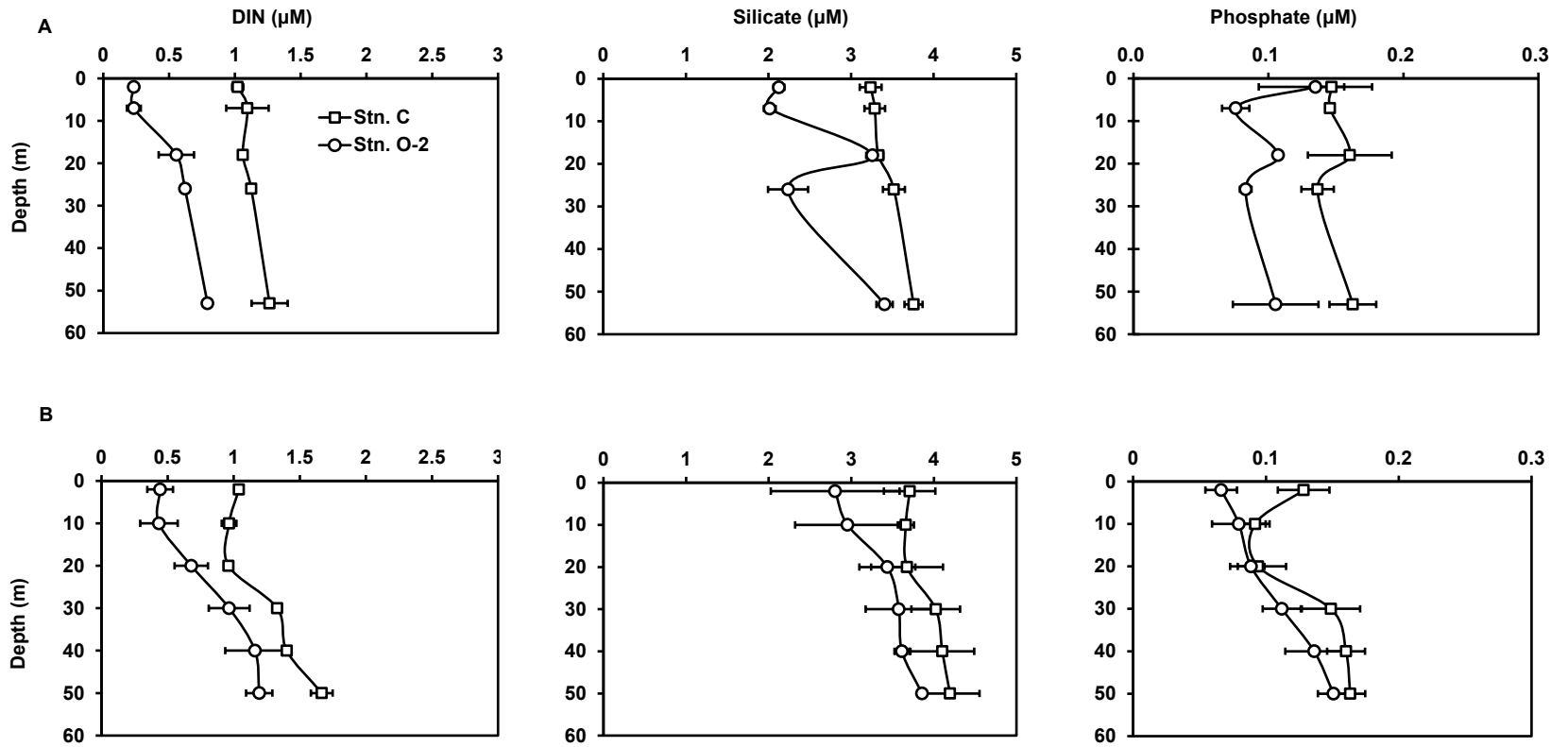

Fig. 4 (A & B): Casareto et al. 2016

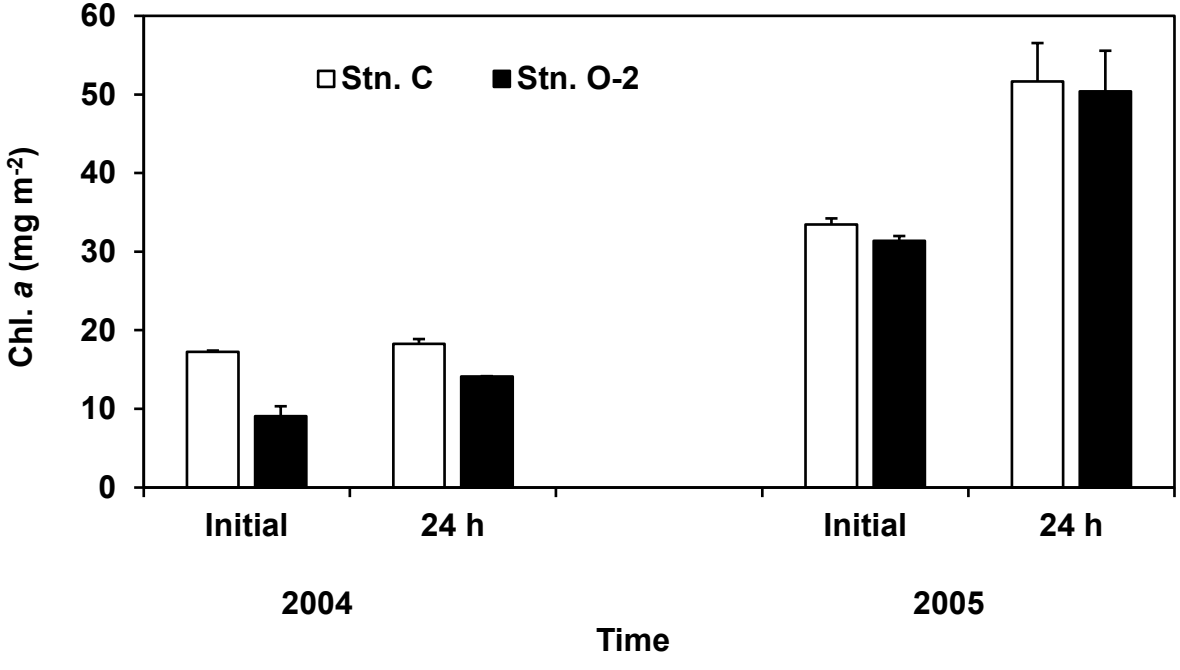

Fig. 5: Casareto et al. 2016

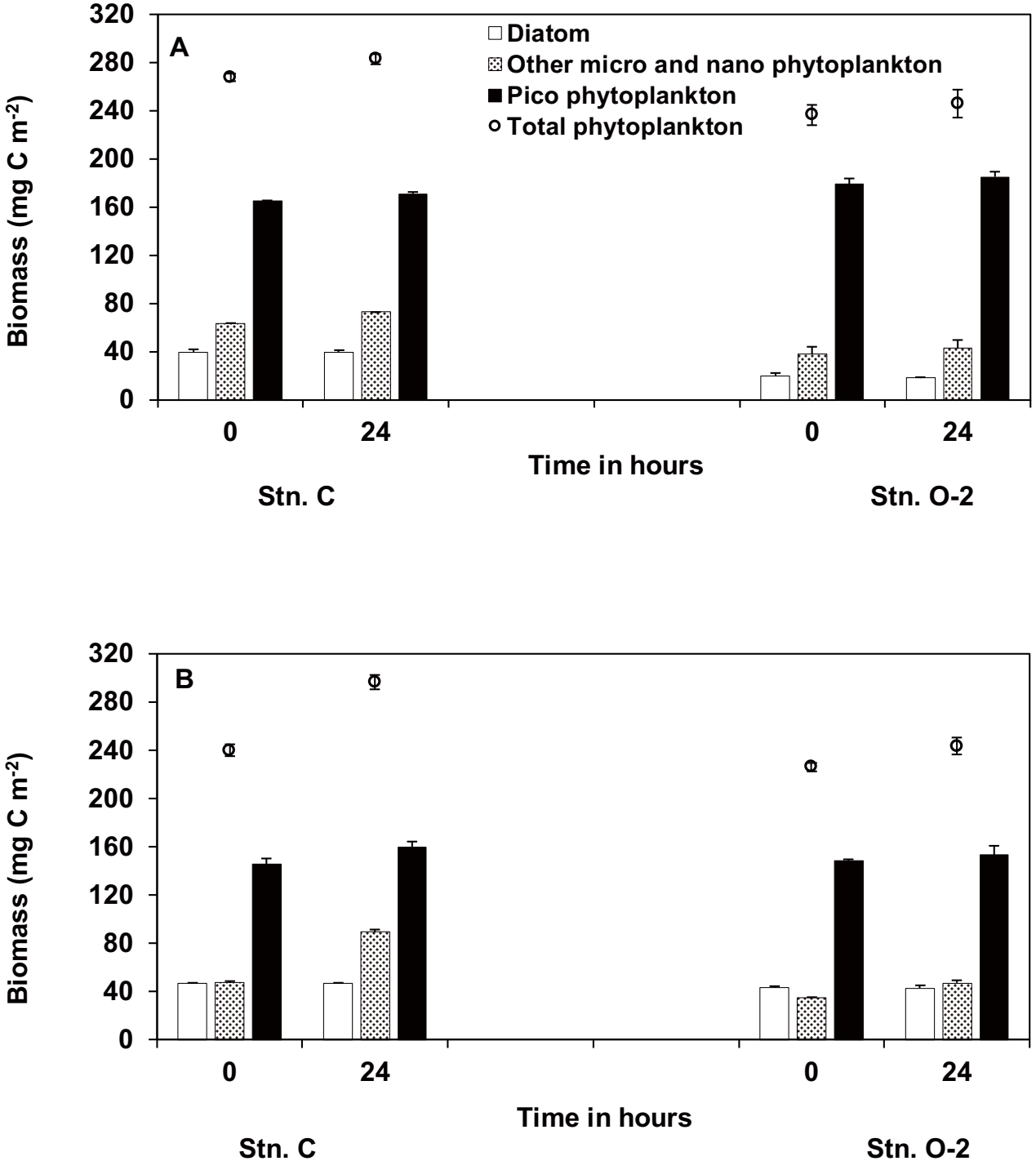

Fig. 6 (A and B): Casareto et al. 2016

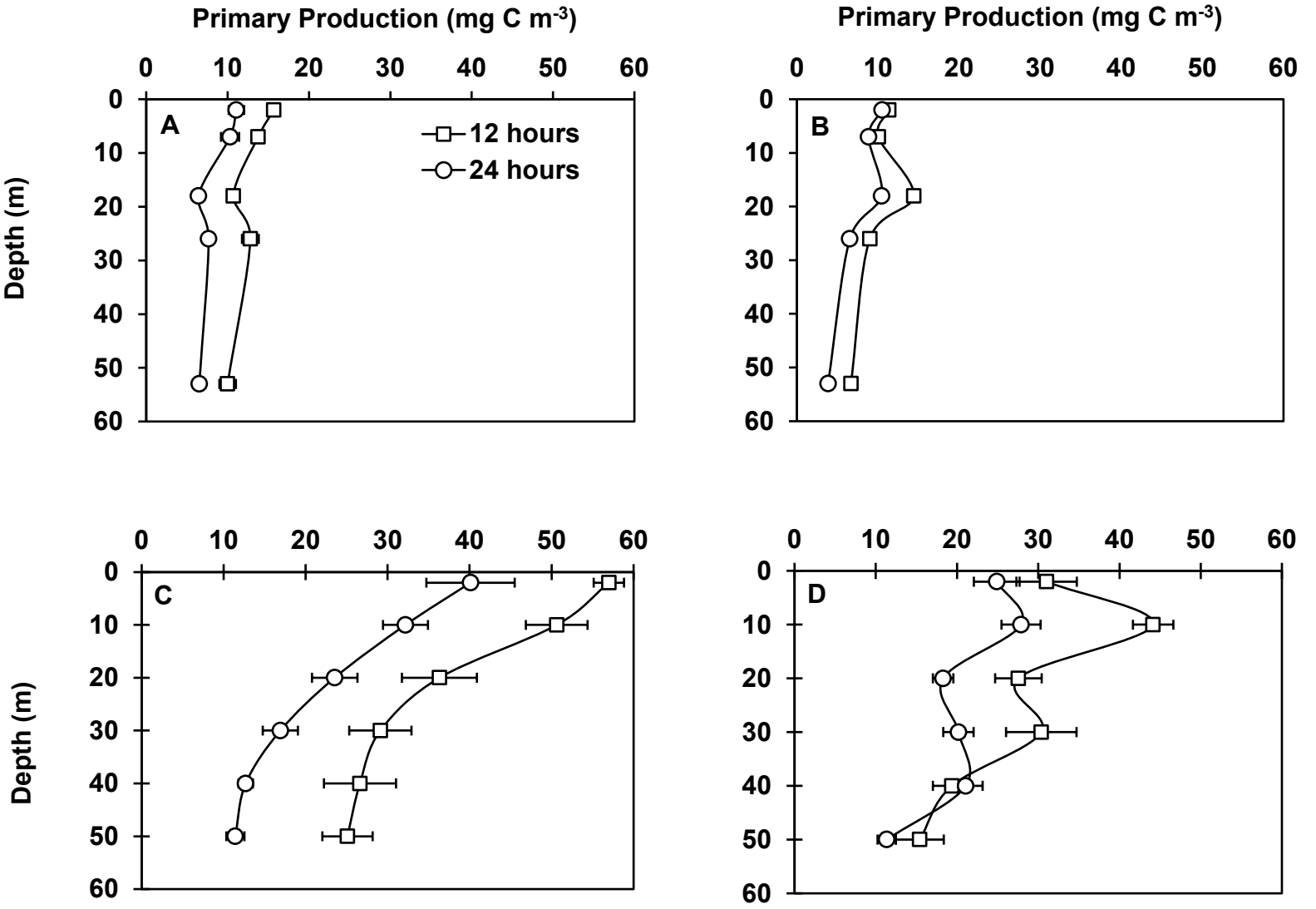

Fig 7. (A, B, C and D): Casareto et al. 2016

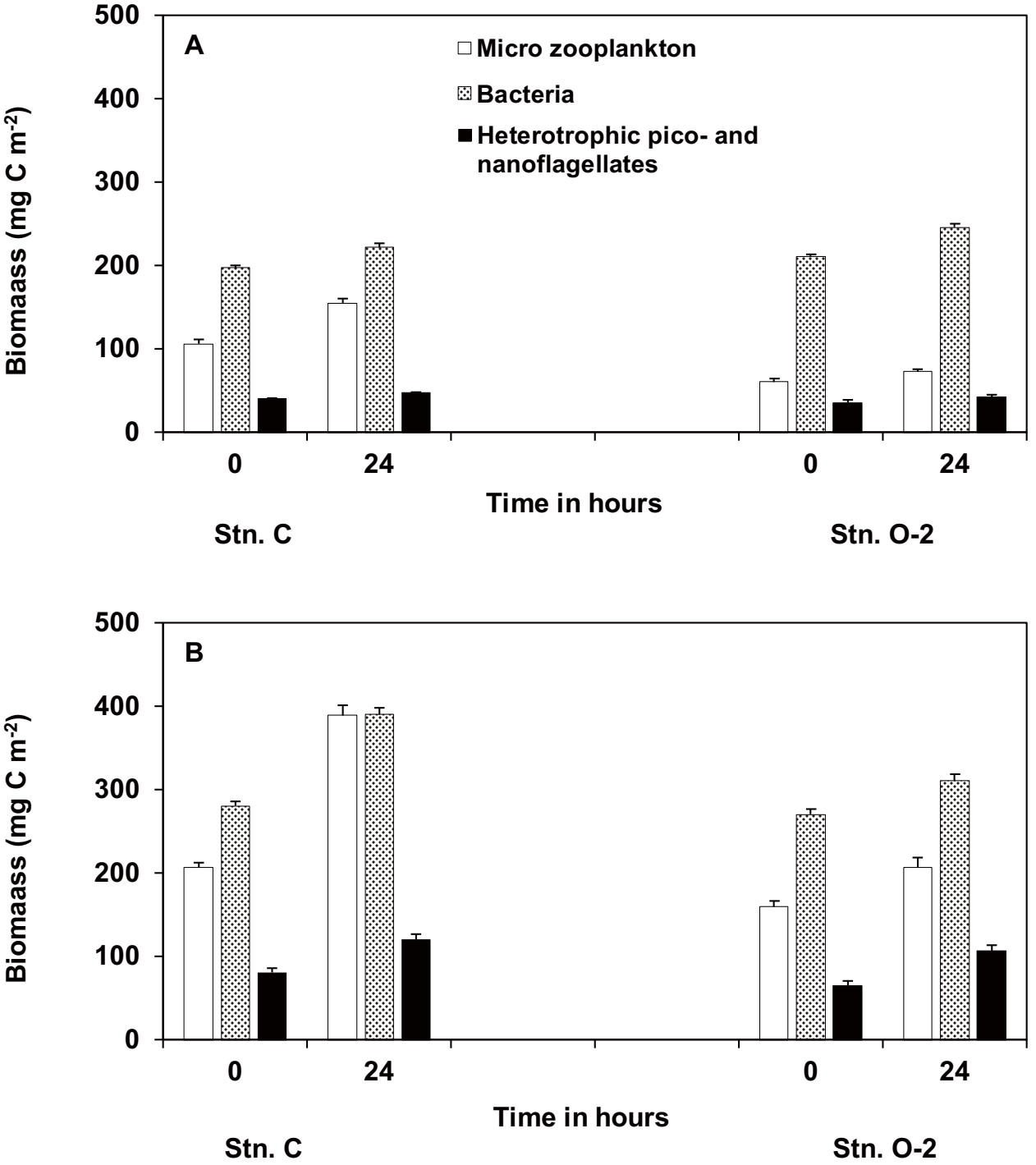

Fig. 8 (A and B): Casareto et al. 2016

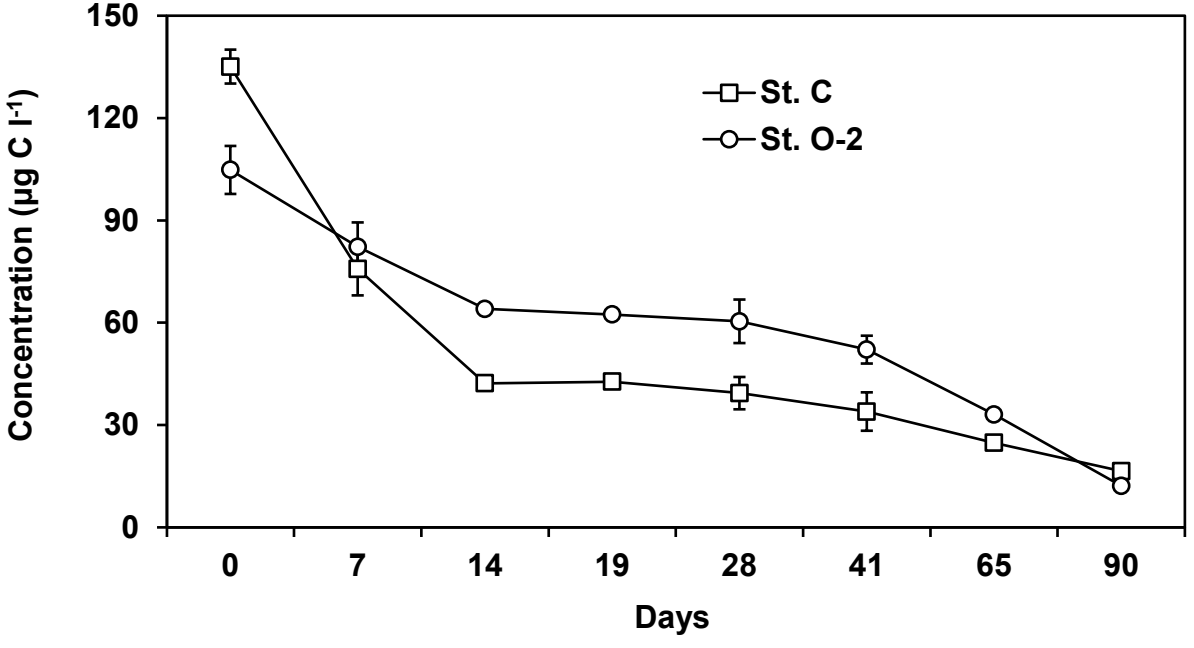

Fig. 9: Casareto et al. 2016

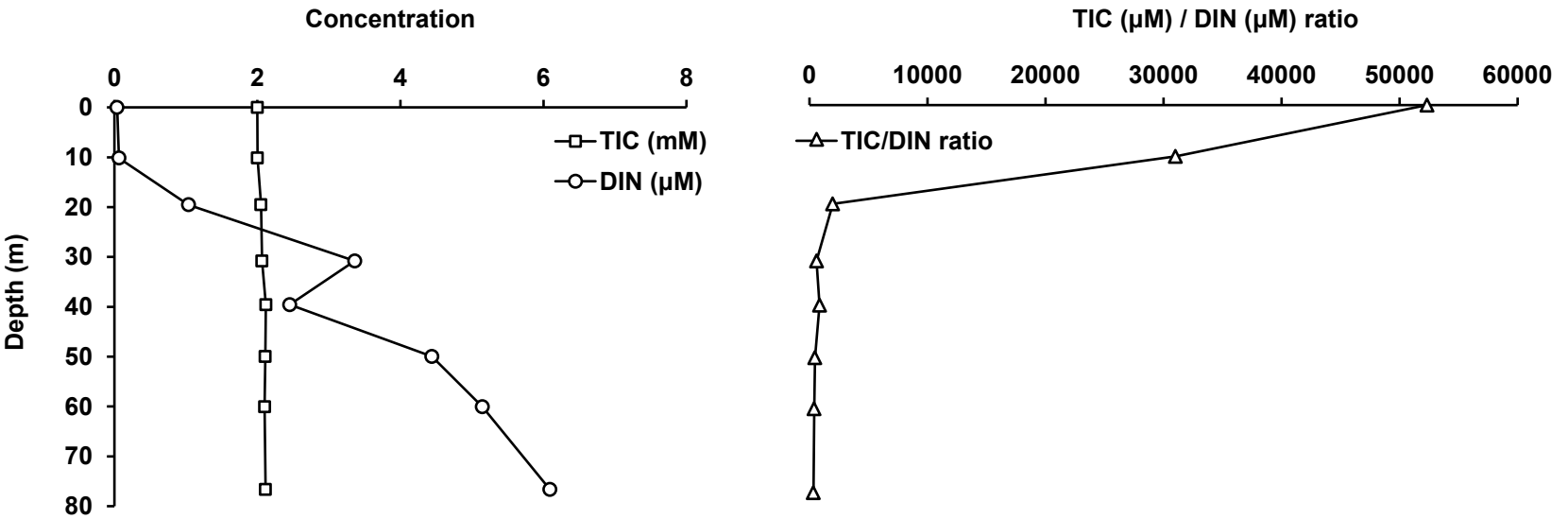

Fig. 10: Casareto et al. 2016

Table 1: Average seawater temperature and salinity at different stations in 2004 and 2005 ± represents standard deviations. n=3 for each depth

2004					
	May				
	Temperature (^{o}C)		Salinity		Observed depth up to
Stn. C	18.2	± 0.1	34.5	± 0.02	60 m
Stn. A	18.1	± 0.4	34.4	± 0.03	60 m
Stn. B	18.1	± 0.1	34.5	± 0.00	60 m
Stn. O-2	18.2	± 0.1	34.5	± 0.02	60 m
	September				
	Temperature (^{o}C)		Salinity		Observed depth up to
Stn. F	24.0	± 0.8	34.1	± 0.1	70 m
Stn. E	24.0	± 0.8	34.1	± 0.1	70 m
Stn. D	23.9	± 0.8	34.1	± 0.1	70 m
Stn. C	24.4	± 0.3	34.1	± 0.0	70 m
Stn. A	24.1	± 0.5	34.1	± 0.1	70 m
Stn. B	24.2	± 1.1	34.1	± 0.1	70 m
Stn. O	25.0	± 0.6	34.0	± 0.1	70 m
Stn. G	24.3	± 1.3	34.1	± 0.1	70 m
2005					
	July				
	Temperature (^{o}C)		Salinity		Observed depth up to
Stn. C	21.72	± 2.7	33.29	± 0.9	50 m
Stn. O-2	22.70	± 4.0	32.70	± 1.5	50 m
	August				
	Temperature (^{o}C)		Salinity		Observed depth up to
Stn. C	26.86	± 2.3	32.58	± 0.9	50 m
Stn. O-2	27.87	± 2.0	32.64	± 1.7	50 m
	October				
	Temperature (^{o}C)		Salinity		Observed depth up to
Stn. C	24.15	± 0.1	33.74	± 0.01	50 m
Stn. O-2	24.16	± 0.6	33.77	± 0.05	50 m

Table 2: Integrated concentrations of nutrients (mmol m^{-2}) and Chl. *a* (mg m^{-2}) at different stations in 2004 and 2005
± represents standard deviations.

2004											
	May										
	Nitrate		**DIN**		**Silicate**		**Phosphate**		**Chl. *a***		**Integration depth**
Stn. C	21.2	± 1.0	46.1	± 2.0	173.7	± 6.6	8.0	± 1.0	45.4	± 2.4	60 m
Stn. A	21.25	± 3	42	± 3	161	± 6	7.9	± 1	36.1	± 2.9	60 m
Stn. B	19.4	± 3.0	39.6	± 1.8	168.0	± 4.8	7.8	± 1.3	42.2	± 1.7	60 m
Stn. O-2	14.9	± 1.6	23.9	± 2.0	139.7	± 3.4	5.7	± 1.1	40.5	± 1.1	60 m
	September										
	Nitrate		**DIN**		**Silicate**		**Phosphate**		**Chl. *a***		**Integration depth**
Stn. F	118.4	± 3.9	138.7	± 4.6	310.5	± 7.8	11.4	± 1.5	55.8	± 3.0	70 m
Stn. E	111.8	± 3.5	130.4	± 4.3	296.5	± 6.5	11	± 2.2	57.1	± 2.9	70 m
Stn. D	130.7	± 4.9	151.4	± 7.3	328.9	± 8.3	12.5	± 1.9	53.3	± 1.8	70 m
Stn. C	99.7	± 1.6	116.3	± 3.2	300.3	± 6.7	10.7	± 2.0	63.1	± 2.9	70 m
Stn. A	89.3	± 2.8	112.0	± 2.9	301.3	± 5.9	10.5	± 1.7	66.5	± 3.9	70 m
Stn. B	76.1	± 3.3	88.6	± 2.5	274.8	± 4.0	9.19	± 2.0	51.7	± 1.4	70 m
Stn. O	36.0	± 2.3	46.3	± 2.3	214.8	± 5.7	6.46	± 1.1	49.3	± 2.0	70 m
Stn. G	78.5	± 2.5	98.1	± 2.6	273.6	± 3.9	11.1	± 1.0	36.6	± 2.9	70 m
2005											
	July										
	Nitrate		**DIN**		**Silicate**		**Phosphate**		**Chl. *a***		**Integration depth**
Stn. C	84.57	± 1.7	98.27	± 1.3	382.4	± 5.7	7.87	± 1.0	not taken		50 m
Stn. O-2	81.69	± 1.6	91.69	± 1.7	352.2	± 7.7	6.98	± 1.1	not taken		50 m
	August										
	Nitrate		**DIN**		**Silicate**		**Phosphate**		**Chl. *a***		**Integration depth**
Stn. C	16.77	± 1.5	38.53	1.9	169.5	± 3.6	3.04	± 0.9	not taken		50 m
Stn. O-2	4.71	± 1.2	11.49	1.7	145.6	± 3.1	4.47	± 0.8	not taken		50 m
	October										
	Nitrate		**DIN**		**Silicate**		**Phosphate**		**Chl. *a***		**Integration depth**
Stn. C	29.76	± 1.4	55.19	± 2.0	204.1	± 4.2	6.19	± 0.8	38.6	± 0.7	50 m
Stn. O-2	29.69	± 1.0	52.87	± 2.0	184.0	± 4.4	6.75	± 0.7	34.2	± 0.8	50 m

Table 3: Integrated primary production and respiration and estimation of excess production. ± represents standard deviations.

	Stn. C 2004	Stn. O-2 2004	Stn. C 2005	Stn. O-2 2005
Gross Primary Production (mg C m^{-2} day^{-1})	**440 ± 10.8**	**396 ± 15.9**	**1945 ± 118.0**	**1355 ± 119.5**
Net primary Production (mg C m^{-2} day^{-1})	**394 ± 13.0**	**362 ± 12.1**	**1082 ± 84.6**	**1045 ± 94.5**
Respiration (mg C m^{-2} day^{-1})	**46 ± 2.2**	**34 ± 3.8**	**863 ± 33.4**	**311 ± 25.0**
P/R ratio	**9.6 ± 0.7**	**11.6 ± 0.8**	**2.3 ± 0.10**	**4.4 ± 0.1**
Excess production (mg C m^{-2} day^{-1})	**32 ± 0.9**		**38 ± 9.9**	

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Table 4: Estimated fate of carbon in the upwelling area

	Values	Units	Remarks
Percent of phytoplankton carbon escaping heterotrophs	33	%	From Calbet and Landry, 2004
Percent of phytoplankton carbon escaping remineralization	12	%	This study (degradation experiment)
Sinking or exportable carbon	3.96	%	This study (12 % of 33)
Excess production in 2004 and 2005	32 and 38	mg C m^{-2} day^{-1}	This study (difference between the net primary production between Stn.C and Stn. O-2)
Amount of excess carbon that can potentially sink at bottom region of Stn. C compared to Stn.O-2	1.3 and 1.5	mg C m^{-2} day^{-1}	This study (32 x 3.96/100 and 38 x 3.96/100)
	4.6 and 5.5	mg CO_2 m^{-2} day^{-1}	This study (1.3 x (44/12) and 1.5 x (44/12)