Deep-Sea Research II 57 (2010) 1653–1664

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Primary productivity and its bio-optical modeling in the Oyashio region, NW Pacific during the spring bloom 2007

Tomonori Isada [a,*], Ai Hattori-Saito [a], Hiroaki Saito [b], Tsutomu Ikeda [c], Koji Suzuki [a,d]

[a] Graduate School of Environmental Science, Hokkaido University, North 10 West 5, Kita-ku, Sappro, Hokkaido 060-0810, Japan
[b] Tohoku National Fisheries Research Institute, Shinhama-cho 3-27-5, Shiogama, Miyagi 985-0001, Japan
[c] Faculty of Fisheries Science, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan
[d] Faculty of Environmental Earth Science, Hokkaido University, North 10 West 5, Kita-ku, Sappro, Hokkaido 060-0810, Japan

ARTICLE INFO

Article history:
Received 15 March 2010
Accepted 15 March 2010
Available online 20 March 2010

Topical issue on "Ecosystem Processes during the Oyashio Spring Bloom." The issue is compiled and guest-edited by the North Pacific Marine Science Organization (PICES).

Keywords:
Primary production
Phytoplankton
Absorption
Spring bloom
Oyashio
Ocean color remote sensing

ABSTRACT

Despite large diatom blooms occurring in the Oyashio region of the NW Pacific every spring, our knowledge of factors controlling primary productivity in the region during that season remains incomplete. Therefore, we investigated phytoplankton abundance, size structure, and primary productivity from April to June 2007. Significant changes were observed. Chlorophyll *a* (Chl *a*) concentrations in surface waters fluctuated between 0.37 and 17 mg m^{-3}. Micro-sized (>10 μm) phytoplankton dominated the phytoplankton community when Chl *a* was >1 mg m^{-3}. Depth-integrated daily primary production within the euphotic layer ranged between 328 and 3231 mg C m^{-2} d^{-1}. Higher values of the water-column light utilization index (Ψ) for phytoplankton photosynthesis were observed in May and June. Although no significant relationships were found between surface primary productivity and macronutrient concentrations or photosynthetically available radiation (PAR), surface primary productivity correlated significantly with Chl *a* concentration during April, indicating that algal productivity depended on phytoplankton biomass. Furthermore, significant linear relationships were found throughout the observations of phytoplankton absorption coefficient to surface primary productivity and of that coefficient to the optimum algal photosynthetic rate normalized by Chl *a* level (P^B_{opt}) in the water column. Modeling P^B_{opt} with the empirical equations of Behrenfeld and Falkowski (1997) or Kameda and Ishizaka (2005) did not accurately reproduce *in situ* P^B_{opt}. These results suggest that the phytoplankton absorption properties could become useful indicators for estimating primary productivity in the Oyashio region during spring.

1. Introduction

Annual primary production by phytoplankton accounts for approximately half of the global total (Field et al., 1998; Behrenfeld et al., 2001). In the Oyashio region of the northwest Pacific, massive phytoplankton blooms mainly consisting of diatoms occur every spring (Kasai et al., 1997, 1998; Saito et al., 1998). As a result, seasonal biological drawdown of pCO_2 in surface waters of the region is the greatest in the world's oceans (Takahashi et al., 2002). Despite the significance of phytoplankton productivity in the Oyashio region during spring, few *in situ* primary productivity data have been available (Shiomoto et al., 1994, 1998; Furuya et al., 1998; Kasai, 2000; Isada et al., 2009).

Recently, ocean-color remote sensing has become a powerful tool for identifying spatial and temporal variability of surface phytoplankton biomass in terms of chlorophyll (Chl) *a* concentration (O'Reilly et al., 1998, 2000) and phytoplankton functional types (see Nair et al., 2008; McClain, 2009). Primary productivity can also be estimated with algorithms using bio-physical parameters such as surface Chl *a* concentration, sea-surface temperature (SST), and photosynthetically available radiation (PAR) derived from satellite sensors (e.g., Longhurst et al., 1995; Antoine et al., 1996; Behrenfeld and Falkowski, 1997; Carr et al., 2006). One of the simplest models commonly used is the Vertically Generalized Production Model (VGPM) proposed by Behrenfeld and Falkowski (1997). This model estimates daily primary production in the euphotic layer from surface Chl *a* concentration, PAR, day length, euphotic depth, and optimum photosynthetic rate (P^B_{opt}) of phytoplankton in the water column. However, since it is difficult to determine the physiological status of phytoplankton from remote sensing, estimation of primary productivity in this model largely depends on an empirical

* Corresponding author. Current address: Faculty of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan.
Tel.: +81 138 40 5618; fax: +81 138 40 8844.
E-mail address: t-isada@salmon.fish.hokudai.ac.jp (T. Isada).

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doi:10.1016/j.dsr2.2010.03.009

relationship between SST and P^B_{opt}, represented by a seventh order polynomial function of SST. It should be noted that this model could produce significant over- or under-estimates of primary productivity at local scales (Siegel et al., 2001; Campbell et al., 2002; Behrenfeld et al., 2002), because this model was basically constructed for general estimates of primary productivity at a global scale (Behrenfeld and Falkowski, 1997). Therefore, a local algorithm should be established for accurate estimates (Platt and Sathyendranath, 1988). Recently, Bouman et al. (2005) suggested that the Chl *a*-specific absorptive characteristics of phytoplankton on the Scotian Shelf were well correlated with the maximum photosynthetic rate (P^B_m) of phytoplankton. Furthermore, Marra et al. (2007) also showed that phytoplankton absorption is well correlated with primary productivity in the surface ocean. These results suggested the possibility of more direct estimates of primary productivity from satellite sensors, provided the absorption coefficients of phytoplankton can be well reproduced by remote sensing (IOCCG, 2006). However, the model of Behrenfeld and Falkowski (1997) and the relationship between phytoplankton absorption and primary productivity have not yet been validated in the Oyashio region.

In this study, we investigated temporal changes in primary productivity of phytoplankton, together with bio-optical and hydrographic parameters, in the Oyashio region from April to June 2007, as part of the two projects: Oceanic Eco-dynamics Comparison in the subarctic Pacific (OECOS) and Blooming Plankton Succession Study in the Oyashio Marine Ecosystem (BLOSSOM). The purposes of this study are (1) to characterize the primary productivity of phytoplankton in the Oyashio region during spring, and (2) to validate the bio-optical models of Behrenfeld and Falkowski (1997) and Marra et al. (2007) for generating precise estimates of primary productivity in the study area using ocean color remote sensing.

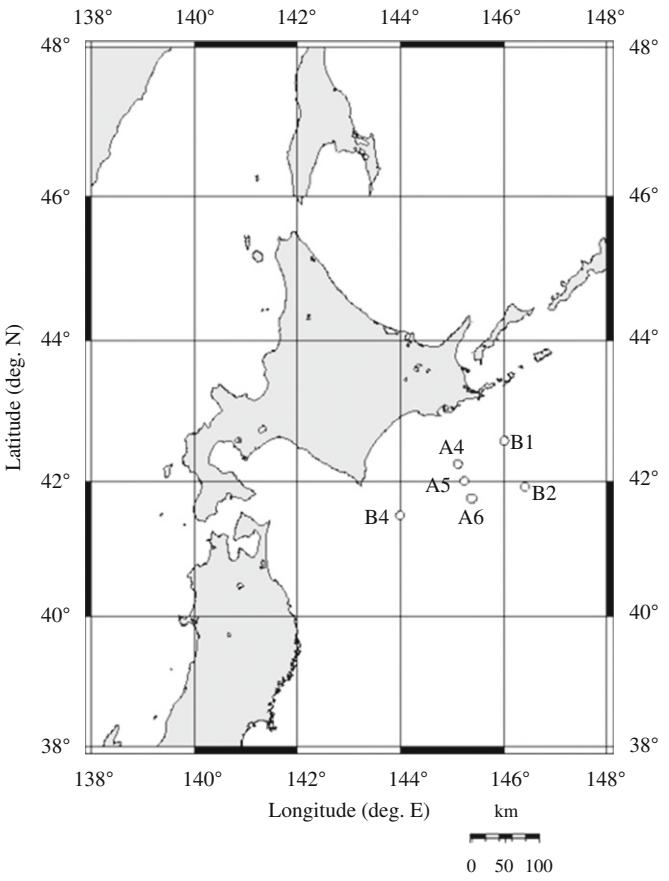

Fig. 1. Location of sampling stations along the *A-Line* and *B-Line* monitoring stations in the NW Pacific.

2. Methods

OECOS was conducted at Stations (Stn) A5 (42°00′N, 145°15′E) and A6 (42°45′N, 145°22.5′E) (Fig. 1) of the monitoring '*A-Line*' in the northwest Pacific Ocean from 5 April to 3 May 2007 on board the R/V '*Hakuho Maru*' of JAMSTEC, Japan. BLOSSOM was carried out at four sampling stations (Fig. 1: Stns A4, B1, B2 and B4) along the monitoring *A-Line* and *B-Line* during 9–21 May (WK0705) and 4–14 June 2007 (WK0706) on board the FR/V '*Wakataka Maru*' of the Fisheries Research Agency, Japan. Prior to sampling, vertical profiles of photosynthetic available radiation (PAR, 400–700 nm) and spectra of the downward PAR were obtained with profiling reflectance radiometers (Biospherical Instruments Inc.): MER2040/2041 during OECOS and PRR600/610 during BLOSSOM. Incident PAR above the sea surface was continuously measured on deck with a PAR sensor (ML-020 P, EKO Instruments Co., Ltd.), averaged every 10 minutes and recorded in a data logger. During OECOS, samples were collected from the surface (2–5 m) and 5 optical depths in the water column (i.e. 60, 30, 10, 5 and 1% light depths relative to the sea surface where light intensity was defined as 100%) at noon (11:00–12:00) by using a CTD carousel multi-sampler system (CTD-CMS) with acid-cleaned Niskin bottles. At Stn A6 on 12 April during OECOS, water samples were collected from the surface only without in-water optical measurements. During BLOSSOM, samples were collected from 5 m and four optical depths (i.e. relative 30, 10, 5 and 1% light depths) from early morning until noon using a CTD-CMS with acid-cleaned Niskin bottles. Nutrients (nitrate plus nitrite, hereafter, denoted as nitrate), phosphate and silicate) were determined with BRAN+LUEBBE auto-analyzers (TRACCS 800 and 1000) following the manufacturer's protocol.

2.1. Phytoplankton specific absorption coefficient

Duplicate water samples (300–500 ml) were filtered onto Whatman GF/F filters (25 mm in diameter) under gentle vacuum. The filters were immediately covered with aluminum foil and frozen (−80 °C) until analysis on land. The absorption coefficient of phytoplankton, $a_{ph}(\lambda)$ (m^{-1}), was measured with a spectrophotometer (MPS-2450, Shimadzu) equipped with an end-on type photomultiplier tube. The measurements were carried out according to the glass-fiber filter technique of Kishino et al. (1985). The particulate matter on the filter was soaked in NaClO solution (1% final concentration) to bleach phytoplankton pigments according to Tassan and Ferrari (1995). The absorption spectra of the bleached filters were measured to obtain the optical densities of detritus. The optical density of the phytoplankton was obtained by subtracting the optical density of the detritus from that of the total particles. Measured optical densities of particulate matter were corrected for the path length amplification effect using the equation of Cleveland and Weidemann (1993).

2.2. Phytoplankton pigments and size-fractionated chlorophyll a

For phytoplankton pigment analysis using high-performance liquid chromatography (HPLC), water samples (250–1000 ml) were filtered onto Whatman GF/F filters (25 mm diameter) under gentle vacuum (< 100 mm Hg), folded, blotted with a filter paper, and frozen (−80 °C). Pigments were extracted in 3 ml of *N,N*-dimethylformamide (DMF) in an amber glass vial with sonication. The details of the pigment analysis are described in Suzuki et al. (2005).