Lipid-rich and protein-poor carbon allocation patterns of phytoplankton in the northern Chukchi Sea, 2011

Mi Sun Yun[a], Hui Tae Joo[a], Jung Woo Park[c], Jae Joong Kang[a], Sung-Ho Kang[b], Sang H. Lee[a,*]

[a] Department of Oceanography, Pusan National University, 2, Busandaehak-ro 63beon-gil, Geumjeong-gu, Busan 46241, Republic of Korea
[b] Division of Polar Ocean Sciences, Korea Polar Research Institute, 26 Songdomirae-ro, Yeonsu-gu, Incheon 21990, Republic of Korea
[c] Graduate School of Fisheries Sciences, Hokkaido University, Hakodate, Hokkaido 041-8611, Japan

ABSTRACT

The carbon allocations of phytoplankton into different photosynthetic end products (lipids, LMWM, polysaccharides, and proteins) were determined to understand physiological conditions of phytoplankton in the northern Chukchi Sea during the Korean Arctic expedition, 2011, using the ^{13}C isotope tracer technique. The carbon allocation rates of lipids, LMWM, polysaccharides, and proteins were 0.00009–$0.00062\,h^{-1}$, 0.00001–$0.00049\,h^{-1}$, 0.00001–$0.00025\,h^{-1}$, and 0.00001–$0.00062\,h^{-1}$ within the euphotic depths from surface to 1% light depths during our cruise period, respectively. Significant relationships between protein production rates and chlorophyll a concentrations (large and total) were found in this study. Moreover, we found a significant negative relationship between lipid production rates and ammonium concentrations. These relationships match well with the previous results for environmental/physiological conditions for phytoplankton growth. Overall, phytoplankton allocated more photosynthetic carbon into lipids ($42.5 \pm 17.7\%$) whereas relatively lower to proteins ($20.4 \pm 15.5\%$) in this study. The lipid-rich and protein-poor allocation patterns in this study suggest that phytoplankton in the northern Chukchi Sea were in a stationary growth phase under nutrient deficient condition based on biological and environmental conditions observed during our study period. Based on comparison with the previous studies in the northern Bering Sea and southern Chukchi Sea, we found that the photosynthetic carbon allocation patterns depending on physiological status of phytoplankton under the different growth and/or nutrient conditions could be largely vary at different regions in the Arctic Ocean. More intensive research on the physiological status of phytoplankton is further required to determine how phytoplankton response to the changing environmental conditions and consequently how they impact on higher trophic levels in marine ecosystems in the Arctic Ocean.

1. Introduction

Phytoplankton is the organism that responsible for the bulk of Arctic Ocean primary production (Arrigo et al., 2014). Since they constitute the base of the marine food web, the ecophysiological changes in phytoplankton have a direct influence on higher trophic levels through the short and efficient Arctic food web. According to Grebmeier et al. (2010), even small changes in primary production pathways can have large cascading effects on higher trophic organisms by altering organic carbon export, pelagic-benthic coupling, and benthic production and community structure.

In recent years, marine environmental changes caused by the drastic sea ice melting in the Arctic Ocean are leading to a notable change in phytoplankton community (Li et al., 2009; Grebmeier and Maslowski, 2014). Particularly, this change has been pronounced in the Pacific sector of the Arctic Ocean (e.g., Beaufort, Chukchi, East Siberian, and Laptev Seas) termed by Steele et al. (2010). For example, there was a large increase in annual primary production in the East Siberian Sea and Chukchi Sea resulted from increased open water area and longer ice-free season (Arrigo et al., 2008; Arrigo and van Dijken, 2011). Moreover, Yun et al. (2015) found that the occurrence of eddies with the recent loss of sea ice substantially could enhance local phytoplankton production and the contribution of large phytoplankton. In the Canada Basin, the increased freshwater content resulted in decreased primary production by controlling nutrient inventory in euphotic zone (Coupel et al., 2015). For the phytoplankton community, smaller phytoplankton could be increasing under the freshening and stratifying ocean condition (Li et al., 2009; Yun et al., 2014, 2016).

However, our understanding about physiological status of phytoplankton under the rapidly changing environmental conditions is still

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lacking in the Arctic Ocean. Previously, several studies observed the patterns of photosynthetic carbon incorporation into biochemical pools to try better understanding their physiological state in Arctic phytoplankton and ice algae (Smith et al., 1989, 1997; Mock and Gradinger, 2000; Lee et al., 2009; Joo et al., 2014). They reported on how Arctic phytoplankton response to variability in environmental factors such as irradiance and nutrient concentration. According to Scott (1980), the patterns of carbon allocation into each biochemical pool also have trophic implications in that the biochemical composition of phytoplankton eventually strongly affects herbivore assimilation efficiencies. Consequently, the physiological status of phytoplankton as a basic food source in the marine ecosystem could have an important effect on nutritional status of higher trophic levels (Scott, 1980; Lindqvist and Lignell, 1997). Therefore, it is important to monitor how recent physiological status of phytoplankton has been changed under the rapidly changing environmental conditions in the various regions of the Arctic Ocean. Here, we identified the physiological status of phytoplankton by determining the relative proportion of carbon allocation into the different photosynthetic end products (low-molecular weight metabolites (LMWM), lipids, polysaccharides, and proteins), since the photosynthetic carbon allocation patterns of natural populations can reflect rapid adjustments to the environmental condition and thus can be an useful index of the present cellular physiological state (Morris, 1981; Hitchcock, 1983; Priscu and Priscu, 1984). The aim of the present study was, therefore, to understand physiological status of phytoplankton in the northern Chukchi Sea, by determining carbon allocations into different photosynthetic end products. In addition, we compared the pattern of photosynthetic carbon allocation in the northern Chukchi Sea to those obtained from different regions in the Pacific sector of the Arctic Ocean. Finally, the major environmental factors affecting the composition of photosynthetic end products of phytoplankton in the region were evaluated in this study.

2. Materials and methods

2.1. Sampling

Samples were collected from 18 stations in the northern Chukchi Sea onboard Korean Research Icebreaker *ARAON* during 30th July to 19th August- 2011 (Fig. 1). Vertical profiles of water temperature, salinity, and density were obtained from downcast measurements using a Seabird SBE-911 + CTD profiler mounted on a rosette. Water samples for chemical and biological measurements were collected with the rosette sampler equipped with 20 L Niskin bottles at every CTD station.
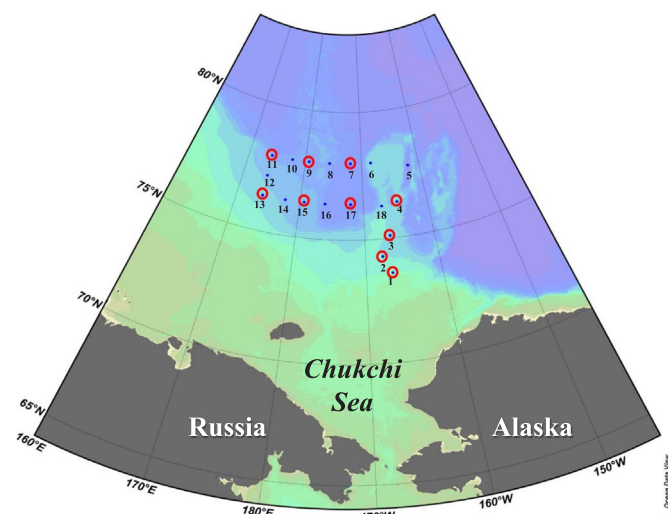

Fig. 1. Locations of sampling during the 2011 *ARAON* cruise in the northern Chukchi Sea. Red circles indicate stations for photosynthetic end products measurements.

Incident irradiance (photosynthetically active radiation (PAR), 400–700 nm) was continuously recorded at 15 min intervals during the cruise with a Li-190 surface PAR sensor (LICOR, USA) kept next to our incubator. The vertical PAR profile was obtained by using an underwater PAR sensor (LI-COR underwater 4π light sensor) lowered with CTD/rosette sampler. Ice cover (%) was obtained from visual observation determined by ice-navigators on ship-deck when the ship arrived at the productivity station. The bottom of the euphotic zone (Z_{eu}) in this study was defined as the depth receiving 1% of the surface PAR.

2.2. Chemical and biological measurements

Seawater samples for dissolved inorganic nutrient concentrations (nitrate, ammonium, phosphate, and silicate) were analyzed onboard immediately after collection, using an automated nutrient analyzer (SEAL, QuAAtro, UK) following the manufacturer's instruction. Water samples for measurement of total chlorophyll *a* concentration were filtered onto Whatman GF/F filters (24 mm). To obtain information on phytoplankton community composition in the study area, the size-fractionated chlorophyll *a* concentration was obtained at three light depths (100%, 30%, and 1% penetration of surface irradiance, PAR). The size-fractionated chlorophyll *a* concentration was determined samples passed sequentially through 20- and 5-µm Nuclepore filters (47 mm) and 0.7-µm Whatman GF/F filters (47 mm). Concentrations for total and size-fractionated chlorophyll *a* were determined using a Trilogy fluorometer (Turner Designs, USA) after 24 h extractions in the dark at 4 °C (Parsons et al., 1984).

2.3. Photosynthetic carbon allocation measurement of phytoplankton using stable ^{13}C

At selected 10 stations (see Fig. 1), the photosynthetic carbon allocations into different macromolecules as photosynthetic end products of phytoplankton were measured at three light depths (100%, 30%, and 1% penetration of surface irradiance, PAR) using a ^{13}C isotope tracer technique (Slawyk et al., 1977; Lee et al., 2009).

Water samples from the three light depths obtained the Niskin bottles were transferred to large polycarbonate incubation bottles (8.8 L) which were covered with screens (LEE filters) in order to simulate irradiance at the depths of sample collection. The isotope-enriched (99%) solution of $NaH^{13}CO_3$ was added to the bottles at concentrations of ~0.2 mM ($^{13}CO_2$) (Hama et al., 1983). The bottles were then incubated in a large incubator cooled with running surface seawater on deck under natural light conditions for approximately 4–7 h. After the incubation, the samples were terminated by filtration on to pre-combusted (450 °C) glass fiber filters (Whatman GF/F; diameter = 47 mm) and then immediately frozen at −80 °C until further mass spectrometric analysis.

Four macromolecular classes (LMWM, lipids, polysaccharides, and proteins) were extracted at the marine ecological laboratory of Pusan National University, Korea following the methods in Li et al. (1980) and Lee et al. (2009). To extract LMWM and lipids from phytoplankton on the filters, chloroform-methanol (2:1 v/v) solution was added in a test tube with small cut filters and ultrasonification was conducted for approximately 20–30 min. Then, the suspension was stored in a new test tube and further extraction was completed after three times repetition of same procedure. After approximately 1.5 mL distilled water was added to the solution in the tube, the mixture was shaken for 2–3 min and then set up for the separation of the chloroform-soluble phase (lipids) and the methanol-water soluble phase (LMWM). For further extractions of polysaccharides and proteins, the filters were resuspended in 5% trichloroacetic acid (TCA) solution and then heated at 95 °C for 20–30 min. The suspension was stored for TCA-soluble polysaccharides and the filters were kept for TCA-insoluble protein analysis after additional washing with 5% TCA solution to remove potential