

제 출 문

아문젠해 빙봉소멸과 연관된 미생물 생태/생지화학

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본 보고서를 “아문젠 빙봉소멸 속도와 해양변동 추세에 관한 연구(본과제명)”과
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탁과제명)”과제의 최종보고서로 제출합니다.

Microbial ecology and biogeochemistry associated with
sea-ice melting in the Amundsen Sea, Antarctica



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보고서 초록

요 약 문

위탁연구과제명	아문젠해 빙봉소멸과 연관된 미생물 생태/생지화학				
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요약(연구결과를 중심으로 개조식 500자 이내)				보고서 면수	77쪽
<ul style="list-style-type: none"> 아문젠 해 폴리나 지역에서 식물플랑크톤 대증식 발달시기에 따른 종속영양 박테리아 요인의 분포 차이를 파악하여, 수층 미생물 먹이망 및 생지화학적 탄소순환에서의 박테리아의 역할에 대해 규명하고자 함 식물플랑크톤 대증식 초기 시기(ANA04)에는 <i>Phaeocystis antarctica</i>가 우점하였고, Chl-a 및 일차생산이 높게 나타남. 반면, 대증식 중반 시기(ANA06)에는 규조류가 우점하였으며, Chl-a와 일차생산력이 낮게 나타남. 박테리아 개체수, 생산력 및 호흡률은 ANA04가 ANA06에 비해 높게 나타남 박테리아 생산력 대 일차생산력의 비도 ANA04에 비해 ANA06에 감소한 것으로 나타났으며, 이는 식물플랑크톤 우점종의 변화에 기인한 것으로 인식되며, 이러한 결과는 식물플랑크톤의 우점종 변화가 수층 내 미생물 먹이망 및 탄소순환에도 영향을 미칠 수 있음을 의미함 한편, 아문젠 해 폴리나, ice-shelf 및 sea-ice지역 퇴적물 내에서 차세대 염기서열 분석 방법을 통해 저층 미생물 군집 구조 및 조성을 조사한 결과, 다른 해양 퇴적 환경 및 다른 남극 폴리나에서 조사된 것과 차이를 보임. 수층 환경 내 <i>Phaeocystis</i>가 우점하는 아문젠해 퇴적물 내 가장 우점하는 미생물 군집은 일반적인 퇴적물 환경에서 우점하는 <i>Proteobacteria</i> 대신 <i>Planctomycetes</i>로 나타났다. <i>Phaeocystis</i>로부터 유래된 난분해성 유기물 분해와 밀접한 관련이 있는 것으로 사료됨. 본 연구 결과는 기후변화에 민감한 남극의 수층 환경 내에서 일차생산자의 군집 변이로부터 야기될 수 있는 생태 및 생지화학적 과정의 변화로 인한 저층으로 유입되는 유기물의 변화와 이에 반응하는 미생물 군집에 대한 유용한 정보를 제공할 것임 					
색인어 (각 5개 이상)	한글	아문젠 해, 폴리나, 박테리아 생산력, 박테리아 호흡율, 식물플랑크톤, 저층 미생물 군집, <i>Planctomycetes</i> , <i>Phaeocystis</i>			
	영어	Amundsen Sea, Polynya, bacterial production, bacterial respiration, phytoplankton, benthic microbial community, Planctomycetes, Phaeocystis			

I. 제 목

아문젠해 빙봉소멸과 연관된 미생물 생태/생지화학

II. 연구개발의 목적 및 필요성

최근의 온난화로 인해 빙하가 녹아내리는 속도가 가속화되는 남극해양에서 생지화학적 탄소순환을 보다 잘 이해하기 위해서는 미생물의 생물량과 대사활동 및 이를 조절하는 물리-화학-생물적 요인들에 대한 연구가 이루어져야 하며, 이들 군집 구조에 대한 이해가 필요하다. 본 연구는 남극 아문젠 해에서 식물플랑크톤 최대 대증식 시기에 다양한 미생물적 인자들을 측정하여 미생물이 극지기후변화에 따른 남극해의 CO₂ 저장기능에 미치는 생물적 영향에 대한 정보 및 이에 관여하는 미생물 군집 구조에 대한 정보를 획득하기 위함이며, 또한 퇴적환경 내 물질순환에 기여하는 미생물 군집에 대한 정보를 획득하기 위한 것이다.

III. 연구개발의 내용 및 범위

아문젠 해 해빙해역에서의 승선연구 중 2013년 12월 ~ 2014년 1월에 수행된 ANA04 크루즈와 2016년 1월 ~ 2016년 2월에 수행된 ANA06 크루즈를 통해 폴리나 정점에서 중속영양 박테리아의 개체수, 생산력, 그리고 호흡률을 조사하여 두 시기에 따른 박테리아 분포 차이를 확인하고, 박테리아와 식물플랑크톤 및 DOC 분포와의 상호작용을 밝혀내어, 아문젠 해 폴리나에서의 미생물 먹이망과 생지화학적 물질순환에 대한 박테리아의 역할을 규명하고자 하였다. 또한 2012년 1월 31일부터 3월 20일까지 진행된 아문젠해 해빙해역에서의 승선연구를 통해, 폴리나, ice-shelf 및 sea-ice 지역 퇴적물 내에서 미생물 군집 구조, 조성 및 다양성을 조사하여, 수직적 및 지역적 분포 특징을 밝혀내고, 생지화학적 물질순환에 중요한 기여를 하는 미생물 군집을 규명하고자 하였다.

IV. 연구개발결과

PART I 아문젠 해 폴리나에서 해빙후퇴에 따른 박테리아 대사반응 연구

ANA04(식물플랑크톤 대증식 초기)와 ANA06(대증식 중반)을 비교한 결과, ANA06에 표층수온이 ANA04에 비해 약 0.16°C 상승하였으며, 유광층 깊이가 감소함에 따라 Chl-a 농도 및 일차생산력이 감소하였다. 아문젠 해 폴리나 해역에서 박테리아 개체수, 생산력 및 호흡률을 조사한 결과, ANA04에 비해 ANA06에 모두 감소하여 나타났으며 이러한 결과는 Chl-a 농도 및 일차생산력 결과와도 일치하였다. 박테리아 생산력과 호흡률을 조절하는 요인을 파악하기 위해 Chl-a, 유색 용존 유기물(CDOM), DOC와의 상관관계를 조사한 결과, 박테리아 생산력은 Chl-a와 양의 상관관계를 보인 반면, 박테리아 호흡률은 상관관계를 갖는 요인이 나타나지 않았다. 세포당 박테리아 생산력 및 호흡률을 조절하는 요인을 파악한 결과, 세포

당 박테리아 생산력은 Chl-a와 강한 양의 상관관계를 보였으며, 세포당 박테리아 호흡률의 경우 DOC/DON 비와 양의 상관관계를 보였다. 박테리아 성장효율은 전반적으로 매우 낮았고, ANA04에 비해 ANA06에 더욱 감소하는 것으로 나타났으며 이는 박테리아가 사용하는 유기탄소의 대부분이 호흡을 통해 다시 CO₂로 재순환된다는 것을 의미하며, 이러한 박테리아 성장효율이 ANA06에 더욱 감소한 것은 미생물 먹이망을 통해 상위영양 단계로 전달되는 유기물의 양이 더욱 적어짐을 가리킨다. 박테리아 생산력 대 일차생산력의 비를 비교한 결과, ANA04에 비해 ANA06에 감소하는 것으로 나타났으며, 이러한 감소는 식물플랑크톤의 종조성 변화에 기인한 것으로 인식된다. Diatom의 침강속도가 *P. antarctica*에 비해 상대적으로 빠른 것을 고려했을 때, 박테리아 생산력 대 일차생산력 비의 감소는 일차생산으로부터 생성된 유기물이 박테리아에 의해 이용되는 비율보다 심해로 침강하는 비율이 더욱 증가할 가능성이 있음을 의미한다.

PART II 수층 내 *Phaeocystis antarctica*가 우점하는 아문젠 해 폴리나 퇴적물에서 독특하게 나타나는 미생물 군집 연구

지구 온난화로 인해 환경 변화가 급격히 진행되는 남극환경에서 저층 미생물 군집에 대한 정보는 제한적이다. 우리는 생지화학적 분석 및 유기물 분해율 측정과 함께 미생물의 16S rRNA gene의 차세대 염기서열 분석, 정량 PCR, 그리고 CARD-FISH를 수행하여 아문젠해 퇴적물에 분포하는 미생물 군집의 조성 및 다양성, 그리고 이를 조절하는 요인에 대해 알아 보았다. 폴리나에서 우점하는 미생물 그룹으로 검출된 *Planctomycetes*는 전체 미생물 군집에서 40%를 차지하였으며, *Thaumarchaeota*는 폴리나 이외의 지역에서 전체 군집의 51%를 차지하는 것으로 조사되었다. *Planctomycetes*의 높은 상대적 풍부도 (relative abundance in total microbial community)는 퇴적물 내 유기탄소 함량과 높은 상관관계를 보였으며, 이는 *Planctomycetes*가 주로 *Phaeocystis*의 대증식 및 수층 내 유기물 분해 결과 생성된 상대적으로 난분해성인 유기탄소를 이용하는 주요한 미생물 그룹임을 시사하였다. 본 연구 결과는 향후 일어날 수 있는 저층 미생물 군

집 변화는 기후 변화에 따른 *Phaeocystis*에서 규조류로의 플랑크톤 군집의 변화를 포함한 생태 및 생지화학적 과정의 변화로 인해 퇴적물로 공급되는 유기물의 양적 및 질적인 변화에 대한 가치 있는 과학적인 자료를 제공한다.

V. 연구개발결과의 활용계획

본 위탁과제를 통해 획득된 아문젠해 해빙역-폴리나에서의 미생물 생물량 및 생산력의 공간적 분포양상에 대한 정보는 온난화로 인한 해빙의 감소가 급격히 일어나는 극지에서 극지기후변화 및 CO₂ 저장기능에 대한 남극해의 기능 및 변화양상을 밝히는데 중요한 정보를 제공할 것이다.

S U M M A R Y

(영문 요약문)

I. Title

Microbial ecology and biogeochemistry associated with sea-ice melting in the Amundsen Sea, Antarctica

II. Purpose and Necessity of R&D

Long-term shifts in bacterial parameters have a potential to provide the best warning system for global environmental changes. Therefore, it is particularly important to measure bacterial abundance and metabolic rates and its physico-chemical and biological controls in polar ocean to better understand any shifts in biogeochemical carbon cycles. This study is to elucidate the role of bacteria in controlling the function of Southern Ocean as a CO₂ sink related to climatic changes.

III. Contents and Extent of R&D

We investigated distributional difference of bacterial abundance, production, and respiration of polynya zone between two Amundsen Sea Polynya expedition, ANA04 cruise (from December 2013 to January 2014) and ANA06 cruise (January to February 2016), and then identified interactions among the bacteria, phytoplankton and distribution of DOC concentration to elucidate the role of heterotrophic bacteria in microbial loop and biogeochemical carbon cycles. and during the Amundsen Sea polynya expedition from January 31 to March 20, 2012, we investigated the vertical and spatial distribution and shift of microbial communities in the sediments of the polynya, ice-shelf zone and sea-ice zone, and then elucidated ecologically importance of the microbial communities controlling for the biogeochemical cycles.

IV. R&D Results

PART I : Microbial ecology and biogeochemistry associated with sea-ice melting in the Amundsen Sea, Antarctica

Comparing ANA04 (early phytoplankton bloom) and ANA06 (mid bloom), surface seawater temperature of ANA06 increased by 0.16°C compared to ANA04, and Chl-a concentration and primary production decreased as decreasing of euphotic depth. Bacterial abundance, production rates, and respiration rates in the Amundsen Sea Polynya were reduced in ANA06 compared to ANA04. These results were consistent with decreasing of Chl-a concentration and primary production. We performed linear regression between bacterial parameters and chemical properties to identify the factors controlling bacterial production and respiration. The results showed a positive relationship between bacterial production and Chl-a, whereas no significant relationship was observed with bacterial respiration. Cell-specific

bacterial production and respiration were significantly correlated with Chl-a and ratio of DOC and DON, respectively. Bacterial growth efficiency was generally very low and was found to be more reduced in ANA06 compared to ANA04, which indicates that most of organic carbon consumed by bacteria respired back to CO₂ via respiration, and the reduced bacterial growth efficiency implied that the amount of organic carbon transported to higher trophic level through microbial loop was lessened. In addition, bacterial production to primary production ratio was decreased in ANA06 compared to ANA04, and this decrease might be attributed to the change in species composition of phytoplankton. Considering that the sinking rate of diatom is relatively faster than that of *P. antarctica*, indicating that decrease in bacterial production to primary production ratio could lead to increase the portion of organic carbon exported to the deep sea, and lessen the portion of organic carbon processed by bacteria.

PART II: A unique *Planctomycetes*-dominated microbial community in sediments underlying the *Phaeocystis antarctica*-dominated Amundsen Sea polynya, Antarctica

Characterization of benthic microbial communities is underrepresented in the Southern Ocean where environmental changes due to global warming are occurring rapidly. We performed high-throughput sequencing of 16S rRNA gene, quantitative PCR and CARD-FISH, in combination with biogeochemical analyses and metabolic rate measurements, to determine the composition, diversity and controls of major microbial communities in sediments of the Amundsen Sea polynya (ASP). A large fraction of the sequenced benthic microbial community (40% on average) in the polynya was uniquely affiliated with the phylum *Planctomycetes*, whereas *Thaumarchaeota* (51%) predominated in non-polynya areas. The existence of *Planctomycetes* was further demonstrated by CARD-FISH analysis using

newly designed probes targeting MSBL-9. Relative abundance of *Planctomyces* correlated significantly with organic carbon (C_{org}) content in the sediment, suggesting that *Planctomyces* constitute a major bacterial group utilizing relatively recalcitrant C_{org} produced primarily by *Phaeocystis* blooms. Our results suggest that any modifications in *Planctomyces*-dominated microbial communities provide valuable insight into changes in organic matter transport to the seafloor that may result from the variations in ecological and biogeochemical processes including the shift in planktonic communities from *Phaeocystis* to diatoms associated with climate changes in the future.

V. Application Plans of R&D Results

Spatial distribution on the bacterial abundance and production obtained along the sea-ice zone, polynya and ice shelf area will provide an information on the role of the Southern Ocean in controlling the carbon cycle and climatic change associated with the global warming in the Antarctic Ocean. The analysis of the abundance and composition of the prokaryotes in the sediment of the Amundsen provides new insights into the roles of prokaryotes in biogeochemical cycles in the Antarctic Ocean.

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제 1 장 서론

남극해는 지구 온난화에 민감하게 반응하는 곳으로 수층 내 높은 생물 생산력과 심층수의 형성으로 인해 전지구적 탄소 순환에 중요한 역할을 수행하고 있다(Sarmiento and Toggweiler 1984, Sarmiento and Le Quéré 1996, Le Quéré et al. 2007, Takahashi et al. 2009). 특히 남극 해 연안에 형성되는 폴리냐는(polynya)는 해빙으로 둘러싸인 지역에 생긴 해역으로서 주변에 비해 얼음 층의 두께가 상대적으로 얇기 때문에 기후변화에 따른 생태계 변화가 가장 먼저 포착되는 곳으로 인식된다(Smith and Barber 2007). 일반적으로 polynya에서는 표층의 양호한 광조건, 빙하 녹은 물의 공급으로 인해 철의 공급이 늘어나고, 성층화로 인해 수층이 안정되기 때문에 일차생산력이 높게 나타난다. 결국, polynya 수층 내 높은 생산력은 대기 중 이산화탄소를 격리 시키는 생물펌프를 강화시키는 원인이 되기도 한다.

하지만 일차생산자에 의해 전환된 유기탄소는 입자성 유기탄소의 형태로 저층으로 침강하는 동안 수층에서 분해되거나, 퇴적물 내에서 미생물에 의한 분해를 통해 상당부분 무기탄소로 전환되어 다시 수층으로 재순환된다. 이러한 미생물 호흡과정을 통한 무기탄소의 재순환은 생물펌프를 통한 대기로 부터의 탄소 격리(carbon sequestration)을 약화시키는 역할을 한다. 수층에서 미생물 호흡을 통한 유기물 분해 및 이산화탄소의 되먹임(feed back)은 온난화로 인한 극지의 수온 상승 시 더욱 증가되는 것으로 인식된다. 예로서, Kirchman et al. (2009)은 수온이 -1.8°C 에서 4°C 로 증가하면 박테리아 생산력(BP)과 일차생산력(PP)의 비율(BP/PP)이 증가하여, 수층으로의 CO_2 재순환이 증가할 수 있음을 보였다. 따라서 남극해 수층의 생산력 변화에 따른 수층에서 호흡에 의한 유기물 분해 및 이에 따른 무기탄소의 재순환 그리고 유기물 분해에 관여하는 미생물 군집에 대한 연구는 남극 폴리냐 해역에서 온난화에 따른 수층의 탄소순환을 이해하고, 탄소저장고로서의 극지해양의 역할을 평가하기 위해 필수적으로 수행되어야 할 연구 분야이다.

한편, 수층으로부터 퇴적물로 공급된 유기물은 종속영양미생물의 호흡 과정을 통해 무기탄소로 재순환되며, 이 과정에 무기 질소 영양염(NH_4^+ , NO_3^-), 인산염

(PO_4^{3-})과 같은 영양염이 함께 배출되기도 한다. 수층으로부터 표층 퇴적물로 공급된 유기물은 대부분 호기성 미생물 군에 의해 분해되게 된다. 하지만 유기물 공급이 높은 퇴적환경에서는 표층 수 mm 이내에서 산소가 고갈되기 때문에 산소 대신 다양한 전자 수용체 (질산염, 산화망간, 산화철, 황산염)를 이용하는 미생물 군들의 호흡 작용으로 인해 표층 수 cm 이내에서 다양한 원소들의 수직적 분포가 결정되기도 한다. 즉, 퇴적물 내 미생물 군집 분포는 유입되는 유기물의 종류와 양, 그리고 전자 수용체의 존재에 영향을 받으며, 결국 퇴적물 내 미생물 군집 구조를 파악하는 것은 탄소 및 원소들의 거동 이해하는데 필수적인 연구분야이다.

서남극의 로스해와 베링하우젠해 사이에 위치한 아문젠해는 전지구적 기후 변화에 빠르게 반응하는 지역이다(Rignot et al. 2008; Stammerjohn et al. 2012). 아문젠해에는 하계(11월과 2월 사이)동안 규모가 큰 폴리나가 형성된다(Arrigo and van Dijken 2003). 아문젠해 폴리나에서는 단위면적당 일차 생산력이 $\sim 220 \text{ g C m}^{-2}\text{y}^{-1}$ (Lee et al. 2012; Kim et al. 2014a)으로 남극해 주변의 37 개 폴리나 가운데 가장 높게 나타나는 지역 중 한 곳으로 보고되었다(Arrigo et al. 2012). 하지만, 아문젠해 폴리나는 수층 내 높은 일차 생산력에도 불구하고, 수층에서 생성된 유기물의 대부분이 수층에서 분해되어 저층 퇴적물에 도달하는 양이 상대적으로 적어 퇴적물 내 유기탄소 함량은 0.7 - 1.0%로 보고되었으며, 이에 따라 총 유기물 분해율을 의미하는 산소소모율과 황산염 환원력이 매우 낮은 것으로 조사되었다(Kim et al. 2016). 한편, sea-ice가 분포하는 open sea의 수층 내 일차 생산력은 폴리나 해역보다 낮으며(Kim et al. 2014a), 수층 내 미생물 생산력(bacterial production) 또한 현저히 낮게 나타났다(Hyun et al. 2016). 이에 상응하여 퇴적물 내의 유기탄소 함량은 0.4 - 0.5%로 폴리나에 비해 더욱 낮게 나타났으며, 유기물 분해율 또한 폴리나 지역에서 보다 낮은 것으로 보고되었다(Kim et al. 2016). 이러한 아문젠해 폴리나 해역 퇴적물 내 미생물 군집 조성 및 다양성을 밝혀내고 이를 주변 해역과 비교하여 연구하는 일은 남극 폴리나 지역의 퇴적물 내 생지화학적 물질 순환을 이해하는데 필수적이다. 이전 연구를 통해 대조적인 퇴적물 지화학 특징을 지닌 것으로 밝혀진, 폴리나 및 주변 해역의 퇴적물에서 탈질산화에 관여하는 기능성 유전자의 정량 결과 폴리나 지역에서 더 높게 나타났으며, 혐기성 암모니아 산화(anaerobic ammonia oxidation, anammox)와 연

관된 미생물 그룹은 폴리나 지역에서 표층 3 cm 깊이까지 증가하는 양상으로 조사되었고, 외해지역에서는 4 cm 깊이 부근에서만 $10^5 \text{ copies cm}^{-3}$ 수준으로 검출되어 두 지역 내 서식하는 미생물 군집이 서로 다르게 분포하고 있음을 시사한 바 있다(Choi et al. 2016). 본 연구에서는 서로 다른 특징을 가진 남극 아문젠해역의 폴리나 지역과 폴리나가 아닌 지역에서 (1) 2016년도에 이루어진 아라온호 승선 연구 당시 수층 내 박테리아 생물량 및 호흡율과 일차생산력과의 상관관계를 분석하고자 하였다. 또한 (2) 수층 내 *Phaeocystis*가 하계 대증식을 일으키는 폴리나 저층 퇴적물 내 서식하는 미생물들의 16S rRNA gene의 다양성을 차세대 염기서열 분석 방법(next-generation sequencing)을 통하여 진정 세균(Bacteria) 및 고세균(Archaea) 군집의 수직적 및 지역적 분포를 묘사하고 서로 비교함으로써 생지화학적 물질순환에 기여하는 미생물 그룹을 밝혀내고자 한다.

제 2 장 국내외 기술개발 현황

현재까지 북극의 Northeast Water(NEW), North Water(NOW) 지역 그리고 남극의 Ross Sea Polynya (RSP)에서 수층의 박테리아 생태와 생물펌프의 기능과 관련한 미생물의 역할 등에 관한 연구가 진행되었으나(Ducklow and Yager 2006), 아문젠해의 polynya에서는 상대적으로 많은 연구가 이루어지지 않았다.

남극의 polynya 지역에서의 부유생태계 연구는: (1) 1994년 11월-12월과 1995년 12월- 1996년 1월에 수행된 미국의 Ross Sea Polynya Project (Smith and Gordon 1997), (2) 1996년-1998년 사이 Ross Sea에서의 해양-대기변동과 생태계 반응연구(Research on Ocean-Atmosphere Variability and Ecosystem Response in the Ross Sea; ROAVERRS) (Arrigo et al. 1999), (3) 1996년 10월-1997년 12월에 US JGOFS의 일환으로 수행된 남극환경과 남극해 과정연구(Antarctic Environment and Southern Ocean Process Study; AESOPS) (Smith et al. 2000a) 등이 있었다.

Amundsen Sea Polynya에서는 2007년에 스웨덴 연구팀에 의해 단기간의 현장 연구가 이루어진 이래, 2010년 12월에 미국과 스웨덴이 ASPIRE (Amundsen Sea Polynya International Research Expedition; <http://antarcticaspire.org/research>)를 국제공동 연구로 수행하였다. 현재까지 알려진 Amundsen Sea Polynya(ASP)는 단위면적 당 생산력이 가장 높고 식물플랑크톤 대증식 기간 동안 높은 클로로필의 농도를 나타내며, 일차생산력과 생물량의 연간변화(interannual variability)가 변화가 기존에 연구된 RSP보다 더 심한 곳으로 인식된다.

아문젠해 내 polynya에서 미생물의 생태에 관한 연구는 최근에 ASPIRE 팀에 의한 남극 아문젠해의 해양-생태연구에 대한 예비결과를 요약 논문이 게재된 바 있으며(Yager et al. 2012), 최근(2012년 2-3월)에 극지연구소의 아문젠 해역 탐사의 일환으로 남극해 하계대증식 후반부에 미생물 요인과 환경요인간의 심도 있는 연구가 이루어 졌다(Hyun et al 2016). 그 결과 아문젠 해역에서 폴리나 중심부에서 미생물 생태량 및 생산력이 가장 높게 나타났으며, 이는 일차생산력과 매우 밀접한 상관관계를 보였다. 또한 높은 수층 내 생산력을 지닌 아문젠 해역의 퇴적물 내 유기물 분해율 및 질소제거율에 대한 연구 결과도 보고되었다(Kim et al 2016, Choi et al. 2016). 폴리나 수층 내 높은 생산력에 비해 퇴적물 내 유기물 함량은 매우 낮게 나

타났으며, 유기물 분해율도 낮은 것으로 조사되어 수층에서 생산된 유기물의 대부분은 수층에서 분해되는 것으로 보고되었다. 한편, 폴리나 지역 및 외해 퇴적물내 탈질소화를 비교하여 본 결과 수층 내 일차 생산자에 의한 유기물 공급이 원활한 폴리나 해역의 퇴적물에서 질소 제거율에 대한 잠재력이 더 높은 것으로 나타났다.

본 보고서를 통해 정리된 아문젠해 폴리나에서의 박테리아 생물량 및 생산력 분포와 조절요인으로서 제시된 용존 유기탄소와의 상관관계에 대한 결과는 향후 다른 연구결과 (export flux, benthic mineralization, 수층의 pCO_2 등)와의 종합적인 분석을 통해 아문젠 해빙 해역내의 탄소순환 및 생물펌프의 기능을 이해하는데 핵심적인 정보를 제공할 것이다. 또한, 폴리나 해역과 외해 저층 퇴적물 내 서식하는 미생물 군집 구조를 서로 비교함으로써 수층 생산력과 저층 미생물 군집 구조간의 상관관계를 이해하고 원소 및 탄소 순환을 이해하기 위한 기초 자료를 제공할 것이다.

제 3 장 연구개발수행 내용 및 결과

PART I. 아문젠 해 폴리냐에서 해빙후퇴에 따른 박테리아 대사 반응 연구

제 1 절 서 론

중속영양 박테리아는 해양생태계 내 생지화학적 탄소순환 및 미생물 먹이망 과정에서 중요한 역할을 한다(Azam 1998; Kirchman 2000; Williams and del Giorgio 2005). 박테리아가 탄소순환에 기여하는 방법은 크게 두 가지로 나누어 볼 수 있는데, 하나는 박테리아 생산(bacterial production, BP)으로 용존 유기탄소(dissolved organic carbon, DOC)와 상위영양단계간의 중요한 에너지 전달(trophic link)과정이고(Azam et al. 1983), 다른 하나는 박테리아 호흡(bacterial respiration)으로 DOC를 용존 무기탄소(dissolved inorganic carbon, DIC)로 전환시키는 과정이다(Ducklow et al. 1986). 한편, 남극 연안은 다른 연안 생태계에 비해 육상 및 외부로부터의 공급되는 DOC의 양이 적기 때문에 DOC 농도가 낮으며, 이로 인해 박테리아는 궁극적으로 식물플랑크톤으로부터 공급되는 DOC에 의존하게 된다. 따라서 남극해의 생지화학적 탄소순환을 이해하기 위해서는 박테리아의 대사과정과 일차생산 및 DOC 분포와의 상관관계에 대해 파악할 필요가 있다.

남극해는 수층 생산력이 높고, 전세계 해양의 CO₂ 흡수의 20%가 남극해에서 이루어지고 있어 전지구적 탄소 순환에 중요한 역할을 수행하는 해역이다(Arrigo et al. 2008, Takahashi et al. 2009). 특히, 아문젠해 폴리냐 (Amundsen Sea Polynya, ASP)는 단위면적 당 생산력이 ~220 g C m⁻² y⁻¹으로 남극에서 가장 높게 나타나는 지역으로 보고되었다(Lee et al. 2012; Kim et al. 2014). 또한, ASP의 일차생산력과 생물량의 연간변화(interannual variability)가 기존에 연구된 로스해 폴리냐(Ross Sea Polynya, RSP)보다 더 심한 곳으로 인식 된다(<http://antarcticaspire.org/research>). 이러한 폴리냐 수층 내 높은 생산력은 대기 중 CO₂를 격리 시키는 생물펌프를 강화시키는 원인이 되기도 한다. 하지만 일차생산자에 의해 전환된 유기탄소는 입자성

유기탄소의 형태로 저층으로 침강하는 동안 수층에서 미생물에 의한 분해(호흡)과정을 통해 상당부분 무기탄소로 전환되어 다시 수층으로 재순환된다. 이러한 미생물 호흡과정을 통한 무기탄소의 재순환은 생물펌프를 통한 대기로 부더의 탄소 격리(carbon sequestration)을 약화시키는 역할을 한다. 따라서 생산력이 높은 ASP에서의 탄소순환을 이해하기 위해서는 높은 일차생산이 미생물 활성과 일치하는지, 그리고 미생물이 ASP의 export flux에 어떤 영향을 미치는지에 대해 파악할 필요가 있다.

ASP의 일차생산은 대부분 규조류(diatom)과 *Phaeocystis antarctica*에 의해 일어나며, 이들의 대증식 시기 및 장소는 각각 다르게 나타난다. *P. antarctica*는 남극의 봄(11월~12월)에 폴리냐 중앙에서 대증식을 일으키며, diatom은 남극의 여름에 성장하며 주로 ice edge 근처에서 대증식을 일으킨다(Smith et al. 2010). *P. antarctica*는 diatom에 비해 낮은 광량에서도 광합성이 가능하여 diatom에 비해 상대적으로 혼합층의 깊이가 깊은 곳에서 우점하여 나타난다(Arrigo et al. 1999). 또한, *P. antarctica*가 diatom에 비해 약 2배의 CO₂를 흡수할 수 있고, 소형 동물플랑크톤에 의한 피식률이 적기 때문에(Yager et al. 2012) 두 식물플랑크톤의 상대적 기여도는 폴리냐의 생지화학 및 생태계에도 영향을 미친다. 식물플랑크톤 중마다 생성하는 DOM 화합물의 생화학 조성이 달라지는데, 예를들어 *P. antarctica*의 경우 박테리아가 쉽게 분해할 수 있는 불안정한 저분자 탄수화물로 이루어진 유기물을 생성한다(Osinga et al. 1997; Jense et al. 1999). 게다가, *Phaeocystis* 증식에 의해 분비되는 중합체는 박테리아가 이용하기 유리한 질소함량이 높은 유기물을 제공한다(Solomon et al. 2003). 따라서 아문젠 해에서 우점하는 식물플랑크톤 종의 전환에 따라 박테리아의 활성도 영향을 받게 된다(Delmont et al. 2014).

최근 서부 남극반도(western Antarctic Peninsula, WAP) 지역은 급격한 기후 온난화를 겪고 있으며, 아문젠 해에서도 대량의 빙상 손실이 지난 수 십년간 지속되어 왔다(Montes-Hugo et al. 2009; Jenkins et al. 2018). 식물플랑크톤 대증식의 시기 및 장소는 본질적으로 ice coverage와 바람의 강도 등과 같은 기후조건과 연관되어 있기 때문에(Saba et al. 2014), 이러한 기후변화로 인한 일차생산의 변동은 중속영양 미생물의 활성 및 생지화학적 탄소순환에도 영향을 미칠 것이다. 따라서 수층의 생산력 변화에 따른 미생물의 유기물 분해 및 무기탄소의 재순환에 대한 연구는 아문젠 해 빙역에서 온난화에 따른 수층의 탄소순환을 이해하고, 탄소저장고로서의 극지해양의 역할을 평가하기 위해 필수적으로 수행되어야 할 연구 분야이다.

본 연구에서는 남극 아문젠 해역의 폴리나 지역에서 식물플랑크톤의 대증식 시기 및 우점종의 차이에 따라 수층 내 박테리아 생물량 및 호흡율과 일차생산력 및 용존 유기탄소 농도분포와의 연관관계 분석하고자 하였다.

제 2 절 연구지역 및 연구방법

1. 연구지역 및 시료채집

아문젠 해는 벨링스하우젠 해와 로스 해 사이에 위치해 있으며, 아문젠 해 폴리나(Amundsen Sea Polynya, ASP)는 남극해 37개 폴리나 중에서도 생산력이 높은 폴리나 중 하나이다(Arrigo and van Dijken 2003). 여기서 폴리나(polynya)는 sea-ice coverage가 표면적의 10%이하인 곳을 의미하며, 폴리나의 형성 시기와 지속시간이 아문젠 해의 일차생산 변화에 영향을 미친다. Arrigo et al.(2012)의 연구에 의하면, ASP는 보통 10월(초봄)에 형성되기 시작하여 2월(늦여름)에 면적이 최대로 확장되었다가 서서히 감소하여 3월에는 ASP전체가 다시 sea-ice로 뒤덮이게 된다. 이에 따라 ASP의 일차생산력은 12월~1월 초에 최대로 나타났다가 1월 중순부터 식물플랑크톤 대증식이 감소하면서 일차생산력 또한 감소하는 것으로 나타났다(Arrigo et al. 2012).

본 연구에서는 남극해 하계기간 동안 아라온 호 승선연구를 통해 아문젠 해 폴리나(polynya)에서 초기 대증식 시기(2014년 1월 초, ANA04 크루즈)와 대증식 중반(2016년 1월 중순-1월 말, ANA06 크루즈)에 조사를 수행하였다. 초기 대증식 시기(1월 초)에 5개 polynya정점(Stns 10, 13, 14, 19, 27)과 대증식 중기(1월 중순-1월 말)에 8개의 polynya정점(Stns 8, 10, 12, 14, 16, 32, 33, 36)에서 조사를 수행하였다(Fig. I-1). 대증식 초기에 해당하는 ANA04에는 일차생산이 높고, *P. antarctica*가 우점하는 것으로 나타났으며(Lee et al. 2016), 대증식 중반 시기에 해당하는 ANA06에는 폴리나가 더욱 확장되었고, diatom이 우점하는 것으로 나타났다. 따라서, 본 연구에서는 대증식 시기에 따른 식물플랑크톤과 박테리아의 상호관계에 대한 차이를 파악하고자 한다.

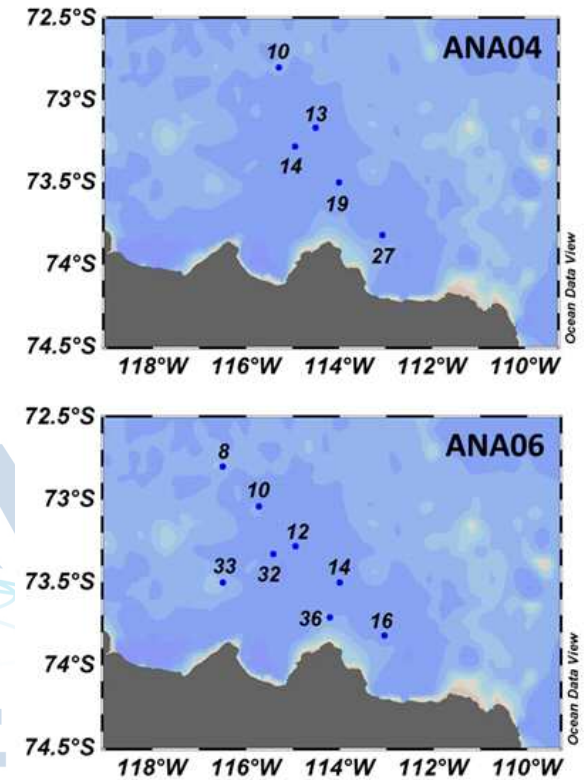


Fig. I-1 Sampling stations in the Amundsen Sea Polynya in ANA04 and ANA06.

2. 연구재료 및 방법

가. 물리-화학요인 분석

수온, 염분 및 밀도는 CTD(SBE 911 Plus, Seabird Electronics)를 통해 측정하였으며, 수층 샘플은 생물, 화학적 분석을 위해 1, 10, 30, 40 - 50, 60, 75, 100m 깊이에서 니스킨 바틀을 이용하여 샘플링 하였다. 혼합층 깊이는 10m 깊이 기준치에 비해 밀도변화가 0.05 kg m⁻³를 초과하는 깊이로 정의하였다 (Venables and Moore 2010).

수층 엽록소-a는 해수시료를 GF/F로 여과한 후 90% 아세톤을 넣고 암소에서 24시간 동안 엽록소를 추출하여 fluorometer (Turner Designs model, 10-AU)를 이용하여 분석하였다(Parsons et al. 1984). 또한, 수중형광측정기(Sea Tech)를 사용하여 현장에서 엽록소-a의 수직 연속분포를 측정하여, 최종 엽록소-a(Chl-a)농도는 10-AU fluoro- meter로 측정된 엽록소-a와 수중형광측정기로 측정된 엽록소-a(flu)간의 선형 관계로부터 다음과 같이 계산되었다; ANA04: Chl-a = 0.160 × flu + 0.824 (r² = 0.81, n = 156), ANA06: Chl-a = 0.134 × flu + 0.175 (r² = 0.82, n = 140). 식물플랑크톤 세포의 탄소량은 탄소 대 Chl-a비율(C:Chl-a)을 50으로 사용하여 전환하였다 (Ducklow et al. 2000).

유색용존유기물(chromophoric dissolved organic matter, CDOM)은 해수시료를 주사기필터로 여과한 후 10 cm 석영셀을 사용하여 350-900 nm 스펙트럼 범위에서 spectrophotometer (Shimadzu UV-1800)로 측정하였고, 375 nm에서 측정된 흡광도를 이용하여 계산한 값(CDOM₍₃₇₅₎ m⁻¹)을 CDOM 농도로 판단하였다 (Kowalczyk et al. 2005).

$$CDOM_{(375)} = 2.303A/l$$

A: 흡광도(375 nm), l: 석영셀 길이(m)

나. 박테리아 요인

박테리아 세포수의 정량을 위해 채수한 해수를 글루타르 알데하이드 (gluteraldehyde)로 고정(최종농도 1%)한 후 실험실에서의 분석 때 까지 -20℃에

서 냉동 보관하였으며(Hyun and Yang, 2003), DAPI 염색 방법을 이용하여 미생물 세포를 염색한 후 형광현미경(Zeiss Axiophot)을 이용하여 계수 하였으며 (Porter and Feig, 1980), 세포의 탄소량은 세포 당 10 fg C를 사용하여 계산하였다(Fukuda et al. 1998). 박테리아 생산력은 thymidine이 박테리아 세포내로 흡수되는 양을 추적하여 계산하였으며(Fuhrman and Azam, 1980, 1982), thymidine 생성에 대한 세포증가량은 thymidine 1 mol 당 8.69×10¹⁷ 세포생산에 해당하는 전환상수(Ducklow et al. 1999)를 사용하였다. 군집 호흡률은 시간에 따른 용존산소의 감소율로 계산하며, 용존산소는 Labasque et al. (2004)에 따라 분석하였다. 해수 샘플을 300 ml BOD 병에 overflow 시켜 채수한 후, 해수순환이 이루어지는 암소에서 현상온도로 배양하였다. 각 샘플은 일정한 시간 간격에 따라 배양을 멈추고 고정시약(Man-ganese chloride solution, 2ml; alkaline iodide solution, 2ml)을 첨가한 후, 즉시 마개를 닫고 BOD병을 흔들어 준다. 분석시에 sulphuric acid 2ml를 첨가한 후, spectrophotometer (Shimadze, UV-1800)를 이용하여 466nm에서 5분 이내로 흡광도를 측정한다. 박테리아 호흡률은 군집 호흡률의 45%로 계산하였다(Robinson, 2008). 박테리아 성장효율(bacterial growth efficiency, BGE)은 박테리아 생산력과 호흡률을 사용하여 계산하였다; BGE = BP/(BP+BR).

제 3 절 연구결과 및 토의

1. 물리-화학요인

표층 100m 이내에서 수온, 염분 및 밀도는 ANA04에 각각 -1.77 ~ -0.08℃, 33.62 ~ 34.11 psu, 27.01 ~ 27.46 kg m⁻³, ANA06에 각각 -1.58 ~ 0.46℃, 33.32 ~ 34.14 psu, 26.76 ~ 27.47 kg m⁻³의 범위로 나타났다(Fig. I-2). 유광층 깊이(euphotic depth, EUP)는 ANA04에 11 ~ 14 m, ANA06에 15 ~ 20 m의 범위로 나타났으며, 표층 혼합층 깊이(mixed layer depth, MDL)는 ANA04에 24 ~ 63 m, ANA06에 12 ~ 64 m의 범위로 나타났다(Table I-1). 평균 MLD는 ANA04에 35.8 m, ANA06에 31.9 m로 큰 차이를 보이지 않았으나, MLD 내에서의 평균

수온, 염분, 밀도는 전반적으로 ANA04에 비해 ANA06에 증가하는 것으로 나타났다(Fig. I-2, Table I-1).

표층 100 m이내 Chl-a의 분포는 ANA04에 0.85 ~ 10.15 $\mu\text{g L}^{-1}$, ANA06에 0.18 ~ 3.90 $\mu\text{g L}^{-1}$ 의 범위로 나타났으며, ANA04(average $4.10 \pm 3.12 \mu\text{g L}^{-1}$)가 ANA06(average $0.95 \pm 0.84 \mu\text{g L}^{-1}$)에 비해 약 4배 높게 나타났다(Fig. I-3). CDOM의 농도 분포는 ANA04에 0.05 ~ 0.23 m^{-1} , ANA06에 0.02 ~ 0.28 m^{-1} 의 범위로 나타났으며, ANA04(average $0.15 \pm 0.06 \text{m}^{-1}$)가 ANA06(average $0.10 \pm 0.06 \text{m}^{-1}$)에 비해 1.5배 높게 나타났다(Fig. I-3). DOC의 농도 분포는 ANA04에 40.67 ~ 72.72 μM , ANA06에 41.64 ~ 53.27 μM 의 범위로 나타났으며, ANA04(average $50.24 \pm 8.09 \mu\text{M}$)가 ANA06(average $45.84 \pm 2.85 \mu\text{M}$)에 비해 약 1.1배 높게 나타났다(Fig. I-3).

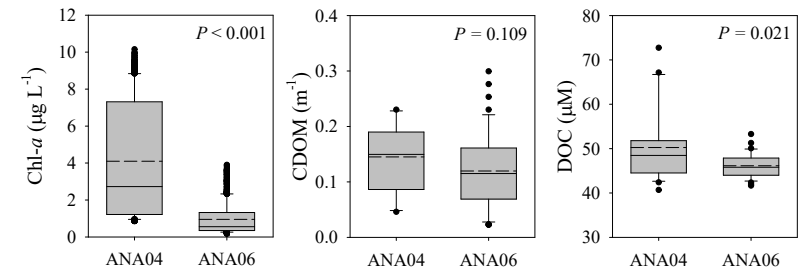


Fig. I-3 Chemical parameters (Chl-a, CDOM, DOC) in ASP (DOC data provided by KOPRI).

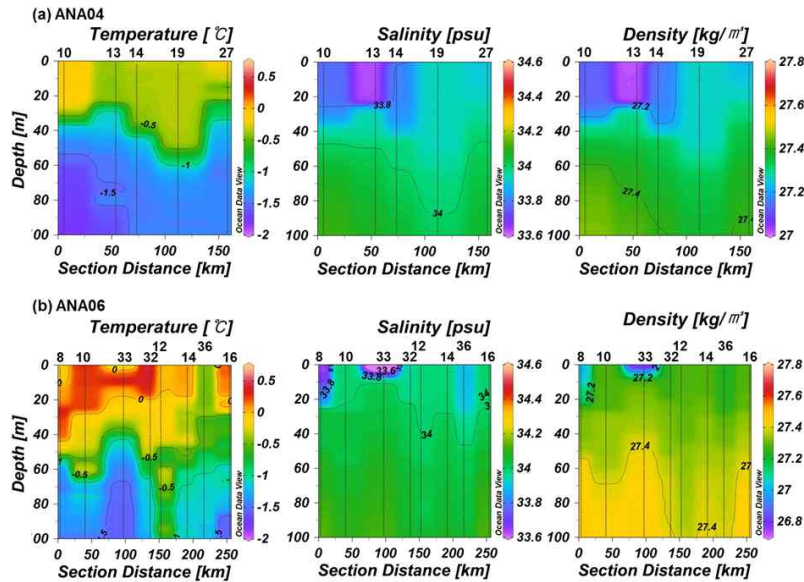
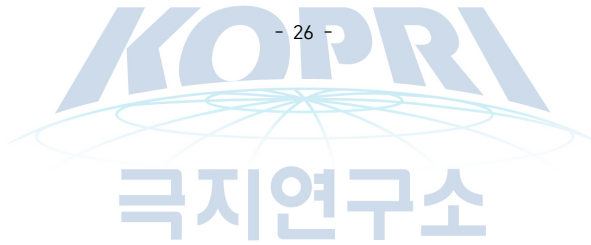


Fig. I-2. Physical parameters(temperature, salinity, and density) in the ASP in ANA04 (a) and ANA06 (b).

Table I-1. Oceanographic parameters in the surface water column in the Amundsen Sea Polynya

Cruise	Stn	Sampling date	Latitude (°S)	Longitude (°W)	Water depth (m)	Euphotic depth (m)	Mixed depth (m)	Temp. (°C)	Sal. (psu)	Den. (kg m ⁻³)	Chl-a (μg L ⁻¹)	CDOM (m ⁻¹)	DOC (μM)	DON (μM)
ANA04	10	5-Jan.	72.800	115.298	590	11	30	-0.08	33.78	27.13	9.54	0.207	51.9	4.06
	13	6-Jan.	73.170	113.500	711	-	25	-0.39	33.62	27.02	8.29	0.230	-	-
	14	6-Jan.	73.281	114.950	821	11	37	-0.28	33.81	27.16	9.17	0.138	51.8	5.24
	19	7-Jan.	73.500	114.001	704	14	63	-0.33	33.94	27.27	7.86	0.069	44.4	2.80
	27	10-Jan.	73.821	113.067	769	11	24	-0.13	33.90	27.23	7.10	0.184	50.9	8.75
ANA06	8	17-Jan.	72.800	116.501	625	-	12	-0.07	33.66	27.03	2.29	0.115	45.1	-
	10	17-Jan.	73.040	115.725	706	20	29	0.25	34.00	27.28	2.09	0.230	45.0	-
	12	18-Jan.	73.279	114.951	831	15	64	-0.02	33.99	27.29	1.95	0.069	47.0	2.39
	33	24-Jan.	73.500	116.500	369	-	22	0.22	33.67	27.02	1.06	-	-	-
	32	24-Jan.	73.328	115.421	916	-	23	0.44	33.97	27.25	1.26	-	46.9	6.40
	14	18-Jan.	73.500	114.000	709	-	45	0.08	33.99	27.29	1.23	0.092	49.3	4.27
	36	24-Jan.	73.711	114.216	565	15	30	-0.45	33.90	27.24	3.35	-	-	-
	16	19-Jan.	73.820	113.045	789	20	33	0.20	34.00	27.29	3.05	0.115	49.8	1.62

* Datas of DOC and DON provided by KOPRI



2. 박테리아 요인

박테리아 세포수(bacterial abundance, BA)는 ANA04에 $0.25 \sim 7.50 \times 10^8$ cells L⁻¹, ANA06에 $0.34 \sim 5.80 \times 10^8$ cells L⁻¹의 범위로 나타났으며, ANA04 (average $1.95 \pm 1.66 \times 10^8$ cells L⁻¹)와 ANA06 (average $1.49 \pm 0.96 \times 10^8$ cells L⁻¹)가 큰 차이를 보이지 않았다(Fig. I-4). 박테리아 생산력(bacterial production, BP)은 ANA04에 $0.12 \sim 6.13 \mu\text{g C L}^{-1} \text{d}^{-1}$, ANA06에 $0.08 \sim 1.24 \mu\text{g C L}^{-1} \text{d}^{-1}$ 의 범위로 나타났으며, ANA04 (average $1.41 \pm 1.50 \mu\text{g C L}^{-1} \text{d}^{-1}$)가 ANA06 (average $0.39 \pm 0.25 \mu\text{g C L}^{-1} \text{d}^{-1}$)에 비해 약 4배 높게 나타났다(Fig. I-4). 박테리아 호흡률(bacterial respiration, BR)은 ANA04에 $15.83 \sim 320.4 \mu\text{g C L}^{-1} \text{d}^{-1}$, ANA06에 $12.85 \sim 82.07 \mu\text{g C L}^{-1} \text{d}^{-1}$ 의 범위로 나타났으며, ANA04 (average $131.2 \pm 96.90 \mu\text{g C L}^{-1} \text{d}^{-1}$)가 ANA06 (average $43.15 \pm 20.63 \mu\text{g C L}^{-1} \text{d}^{-1}$)에 비해 약 3배 높게 나타났다(Fig. I-4). 박테리아 성장효율(bacterial growth efficiency, BGE)은 ANA04에 $0.002 \sim 0.086$, ANA06에 $0.003 \sim 0.013$ 의 범위로 나타났으며, ANA04 (average 0.016 ± 0.023)와 ANA06 (average 0.007 ± 0.003)가 유의한 차이를 보이지 않았다(Fig. I-4).

3. 박테리아 생산력 및 호흡률 조절요인

BP 및 BR과 Chl-a, CDOM, DOC 농도와의 상관관계를 Fig. I-5에 나타내었다. BP는 Chl-a와 양의 상관관계를 보였으나, CDOM, DOC와는 유의한 상관관계가 나타나지 않았다(Fig. I-5). 식물플랑크톤 대증식 시기에 따른 차이를 확인한 결과, 대증식 초기인 ANA04에는 CDOM과 DOC가 박테리아 생산력과 상관관계를 보이지 않았으나, 대증식 중반인 ANA06에는 양의 상관관계를 보였다(CDOM, $r^2=0.418$; DOC, $r^2 = 0.20$). 이는 대증식 초기인 ANA04에는 식물플랑크톤으로부터 공급되는 labile 유기물이 박테리아의 성장에 쓰이지만, 대증식 중반인 ANA06에는 labile 형태의 유기물의 양이 빠르게 감소하고, 미생물의 분해 또는 광분해를 거친 semi-labile 형태의 유기물이 박테리아의 성장에 쓰인 결과로 사료된다.

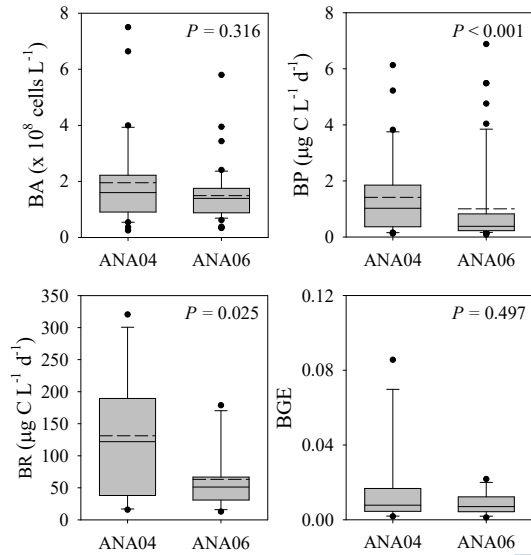


Fig. I-4. Bacterial parameters (BA, BP, BR, BGE) in ASP (solid line indicate median value and dotted line indicate average value).

반면에, BR은 Chl-a, CDOM, DOC와 모두 유의한 상관관계가 나타나지 않았다. Williams et al (2016)의 연구에서도 ASP에서 BR이 다른 요인들과 상관관계를 보이지 않았으며, 박테리아 탄소요구량의 약 91%가 호흡에 의해 사용되는 것으로 나타났다.

세포당 박테리아 생산력(cell-specific BP, BP_{sp})과 세포당 박테리아 호흡률(cell-specific BR, BR_{sp})의 조절요인을 확인한 결과, BP_{sp} 는 Chl-a와 강한 상관관계를 보였으며, BR_{sp} 은 DOC/DON 비와 강한 상관성을 보였다(Fig. I-6). 이러한 결과는 BP는 이용 가능한 유기물의 양에 직접적으로 반응하지만, BR은 이용 가능한 유기물의 양보다는 유기물의 질에 영향을 받는다는 것을 나타낸다.

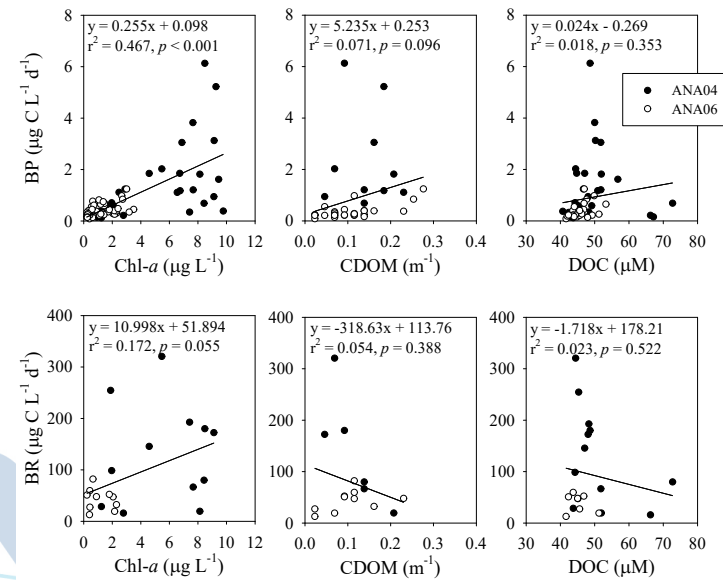


Fig. I-5. Relationship between Chl-a, CDOM, DOC and bacterial production (BP), respiration (BR)

식물플랑크톤과 박테리아의 연관성(coupling)을 파악하기 위해, 박테리아와 식물플랑크톤의 세포수와 생산력을 표층 혼합층 내에서 누적하여 비교하였다(Table I-2). Phytoplankton carbon biomass(Chl-C), bacterial carbon biomass(BCB), BP, 일차생산(primary production, PP) 모두 대증식 초기(ANA04)에 비해 대증식 중반인 ANA06에 감소한 것으로 나타났다. 이를 바탕으로 식물플랑크톤과 박테리아를 비교했을 때 BCB/Chl-C 비율은 두 시기 모두 매우 낮게(< 0.02) 나타났으며, 이렇게 낮은 BCB/Chl-C 비율은 원생동물에 의한 섭식으로 박테리아 현존량이 조절되기 때문이다.

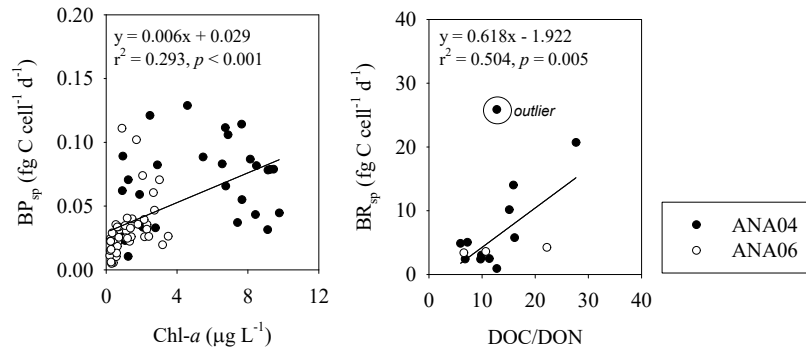


Fig. I-6. Relationship between cell-specific BP(BP_{sp}), BR(BR_{sp}) and Chl-a, DOC/DON ratio.

Table I-2. Depth integrated (0~MLD) inventories of phytoplankton and bacterial parameters (phytoplankton carbon biomass, Chl-C; bacterial carbon biomass, BCB; primary production, PP; bacterial production, BP), and BCB/Chl-C ratio and BP/PP ratio.

Cruise	Stn	Chl-C (mg C m ⁻²)	BCB (mg C m ⁻²)	BCB/Chl-C	PP (mg C m ⁻²)	BP (mg C m ⁻²)	BP/PP
ANA04	10	11240	56	0.005	892	38	0.04
	13	9199	82	0.009	-	62	-
	14	15438	120	0.008	1213	34	0.05
	19	19375	170	0.009	655	131	0.20
	27	7105	68	0.010	921	72	0.08
	AVE.	12471	99	0.008	920	73	0.09
	SD.	4937	46	0.002	229	35	0.07
ANA06	8	1862	12	0.006	-	5	-
	10	2622	26	0.010	887	10	0.01
	12	4336	79	0.018	426	20	0.05
	33	1353	50	0.037	-	14	-
	32	1447	37	0.026	-	15	-
	14	2342	41	0.017	-	10	-
	36	5057	56	0.011	677	14	0.02
	16	4288	57	0.013	994	31	0.03
	AVE.	2913	45	0.017	746	20	0.05
	SD.	1445	21	0.010	251	10	0.02

반면, BP/PP 비율은 ANA04에 비해 ANA06에 약 3배 감소하는 것으로 나타났다(Fig. I-7, Table I-2). 일반적으로 극지방에서는 BP/PP 비율이 약 0.04로 낮게 나타나며, 이는 일차생산의 극히 일부분만이 박테리아에 의한 탄소소모에 사용됨을 의미한다. 본 연구에서도 ANA04의 St.19정점을 제외하면 BP/PP ratio가 대부분 0.04~0.08의 범위로 나타났다. 그러나, ANA06에 BP/PP 비율이 더욱 감소한 것은 일차생산이 미생물 먹이망(microbial loop)을 통해 상위영양단계로 전달되는 비율보다 biological pump에 의해 제거되는 비율이 더 많기 때문이며, 이러한 변화는 식물플랑크톤 우점종이 *P. antarctica*에서 diatom으로 전환된 것

과 연관이 있는 것으로 여겨진다. 실제로 DeJong et al. (2017)의 연구에 의하면, 로스해에서 *P. antarctica*가 우점한 정점에 비해 diatom이 우점한 정점에서의 export efficiency가 더 높게 나타났으며, 이러한 차이는 점액질 성분으로 이루어진 *P. antarctica*가 수층 내에서 콜로니를 형성하여 침강속도가 느린 반면, diatom은 규질 껍데기로 이루어져 있고, 동물플랑크톤의 섭식에 의해 fecal pellet으로 재형성되어 침강속도가 빠르기 때문이다. 이상의 결과들은 향후 기후변화로 인한 식물플랑크톤의 우점종 및 일차생산의 변화는 박테리아와 식물플랑크톤간의 관계에도 영향을 미치며 이는 향후 아문젠 해역에서의 먹이망에도 영향을 미칠 수 있음을 시사한다.

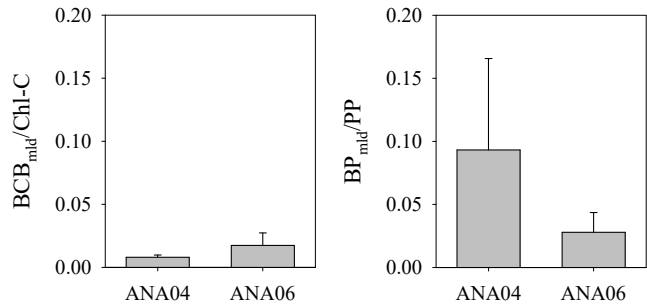


Fig. I-7. Bacterial carbon biomass : phytoplankton carbon biomass ratio (BCB/Chl-C) and bacterial production : primary production ratio (BP/PP).

PART II. 아문젠 폴리냐 저층 미생물 군집 연구

Title: A unique *Planctomycetes*-dominated microbial community in sediments underlying the *Phaeocystis antarctica*-dominated Amundsen Sea polynya, Antarctica

제 1 절 서 론

In marine surface sediments, microorganisms occur in enormous number (approximately 1.7×10^{28} cells worldwide) (Whitman et al. 1998) and extremely high diversity (Huber et al. 2007). They are notably involved in carbon, nitrogen and sulfur cycling on Earth (Canfield et al., 2005; Orcutt et al., 2011). Since microbial community composition, diversity, and metabolic activities are significantly influenced by environmental changes (Bertics and Ziebis 2009; Jorgensen et al. 2012; Nguyen and Landfald 2015), a characterization of microbial distribution can provide relevant information on the variations of environmental conditions in time and space (Schauer et al., 2010; Robador et al., 2016; Fuhrman et al. 2009). For the Southern Ocean (SO) where environmental changes due to global warming proceed rapidly, however, little is known about benthic microbial communities (Baldi et al. 2010; Ruff et al. 2014; Learman et al. 2016).

The SO plays a profound role in regulating the global carbon cycles, accounting for approximately 20–30% of CO₂ uptake in global ocean (Gruber et al. 2009, Takahashi et al. 2002, 2009). As the pCO₂ in the atmosphere increases (Petit et al. 1999), the role of the SO as an atmospheric C sink has received more attention. The coastal zone of the SO is typically characterized by the occurrence of polynyas, areas of seasonally recurring open water surrounded by sea-ice (Williams et al. 2007; Nihashi and Oshima 2015). Because of the combined effects of the enhanced light conditions and iron supply resulting from melting sea-ice, the polynyas are among the most productive marine ecosystems (Sedwick and DiTullio 1997; Smith and Gordon, 1997; Arrigo and van Dijken 2003; Montes-Hugo and Yuan 2012), and thus are regarded as

significant sink for atmospheric CO₂ (Miller and DiTullio 2007; Arrigo et al. 2008). Among the 37 known coastal polynyas around Antarctica, the Amundsen Sea polynya (ASP) is reported to be most productive (Arrigo and van Dijken, 2003; Arrigo et al. 2012) with a primary productivity (PP) per unit area (~ 220 g C m⁻² y⁻¹, Lee et al., 2012; Kim et al., 2014a). The prymnesiophyte *Phaeocystis antarctica* is predominant and responsible for the high primary productivity in the central polynya (Fig. II- 1B; Yager et al. 2012; Ducklow et al. 2015; Lee et al. 2016; Williams et al. 2016; Yang et al. 2016).

Due to the inflow of warm Circumpolar Deep Water (CDW), the glaciers near the Amundsen Sea are undergoing the highest rates of melting and thinning on the Antarctic continent (Rignot 2008; Jenkins et al. 2010; Jacobs et al. 2011). Consequently, as global warming progress, the heat flux intensity of the CDW may stimulate the ice-melting, which ultimately results in the changes in phytoplankton productivity and community composition (Deppeler and Davidson 2017), thereby regulating the function of the ASP in carbon sequestration (Thoma et al. 2008; Lee et al. 2017). The composition and metabolic activities of benthic microbial communities are ultimately determined by the quality and quantity of the organic matter supplied from the overlying water column (Franco et al. 2007). Therefore, given that the microbial communities quickly respond to environmental changes (Danovaro et al. 2000; Luria et al. 2016), quantitative and/or qualitative information on benthic microbial communities and their metabolic activities is pivotal for assessing the response of these ecosystems to the variations of water column productivity associated with climate change in the SO. In the Antarctic Ocean, the benthic microbial community have studied in several regions, including Mertz Glacier Polynyas, Ross Sea, Bellingshausen Sea, and Australian-Antarctic ridge (Bowman and McCuaig 2003; Baldi et al. 2010; Carr et al. 2013; Learman et al. 2016). In these studies, *Proteobacteria* were reported as a predominant bacterial group in the sediments of Antarctic Ocean and have been considered as a major C_{org} oxidizer. However, there is no information on the composition and diversity of the entire microbial communities in the sediments of the ASP, except for the microbial community associated with the N cycles (Choi et al. 2016).

The objectives of this study were: (1) to identify microbial communities in the sediments of the Amundsen Sea Polynya underlying the *Phaeocystis*-dominated water column, and (2) to elucidate major factors controlling the microbial communities with special emphasis on the organic carbon (C_{org}) content in sediments across the marginal ice zone (MIZ) – polynya - ice shelf of the Amundsen Sea polynya (ASP). We here report that the members of *Planctomycetes* represent the major bacterial group in the surface sediments of the ASP comprising 40% of the sequenced communities. Based on the significant positive correlation between the distribution of *Planctomycetes* and C_{org} content in the sediment, we further suggest that *Planctomycetes* are responsible for the mineralization of recalcitrant C_{org} originating mostly from *P. antarctica* bloom in the water column.

제 2 절 연구지역 및 연구방법

1. Study area

The Amundsen Sea is located in western Antarctica between the Ross Sea and Bellingshausen Sea (69°S–74°S; 100°W–135°W, Fig. II-1), and is characterized by a large polynya from November to February (Arrigo and van Dijken 2003). The Korean Amundsen Sea Expedition was conducted during the austral summer, from February 18 to March 7, 2012, aboard the Korean icebreaker research vessel RV Araon. Water depth ranged from 530 to 1,064 m, and temperature ranged from -1.8 to -1.1°C (Table II-1).

Sediment samples were collected using a box corer at four stations at three contrasting sites along the marginal ice zone (Stn 83) – polynya (Stn 10 and 17) – ice shelf site (Stn 19) (Table II- 1). *P. antarctica* was the major planktonic algae in this highly productive polynya area, whereas diatoms were more abundant in the relatively less-productive marginal ice zone (Stn 83) (Fig. II- 1B) (Yang et al. 2018). Subsamples for DNA extraction were taken from the center portion of the box corer using acryl

sub-core liners (6 cm i.d.). Cores were sliced at 1-cm intervals to a depth of 16 or 18 cm, and immediately frozen at -80°C .

Table II-1. Oceanographic parameters and sediment properties in the Amundsen Sea, February 10 – March 09, 2012.

Station	Polynya		Ice shelf zone	Sea-ice zone
	Stn 10	Stn 17	Stn 19	Stn 83
Latitude	73.250°S	73.496°S	74.202°S	71.699°S
Longitude	114.997°W	114.008°W	112.51°W	114.037°W
Water depth (m)	825	730	1064	530
Temp. ($^{\circ}\text{C}$) ^a	-1.1	-1.2	-1.5	-1.8
Salinity (psu) ^a	33.5	33.4	33.6	33.6
Sediment accumulation rate (cm y^{-1})	0.180	0.201	0.122	0.134
TOC (% dry wt.) (0–1 cm)	1.03	0.71	0.62	0.41
TN (% dry wt.) (0–1 cm)	0.15	0.1	0.08	0.07
OPD (cm)	1.8 ± 0.1	2.0 ± 0.2	3.6 ± 0.1	3.5 ± 0.3
Total oxygen uptake (mmol $\text{O}_2 \text{ m}^{-2} \text{ d}^{-1}$)	2.44	3.11	1.58	1.57
Denitrification (nmol $\text{N cm}^{-3} \text{ sed. d}^{-1}$) ^b	1.44 - 4.32	0.96 - 7.2	nd	nd
Sulfate reduction (mmol $\text{S m}^{-2} \text{ d}^{-1}$) ^c	0.07	0.06	0.05	0.04
Anammox (nmol $\text{N cm}^{-3} \text{ sed. d}^{-1}$) ^b	3.12 - 3.84	3.84 - 6.24	nd	nd

OPD: oxygen penetration depth

nd: not detected

^a Bottom water

^b Depth-integrated inventories of sulfate reduction down to 6 cm

^c Depth-integrated inventories of sulfate reduction down to 10 cm

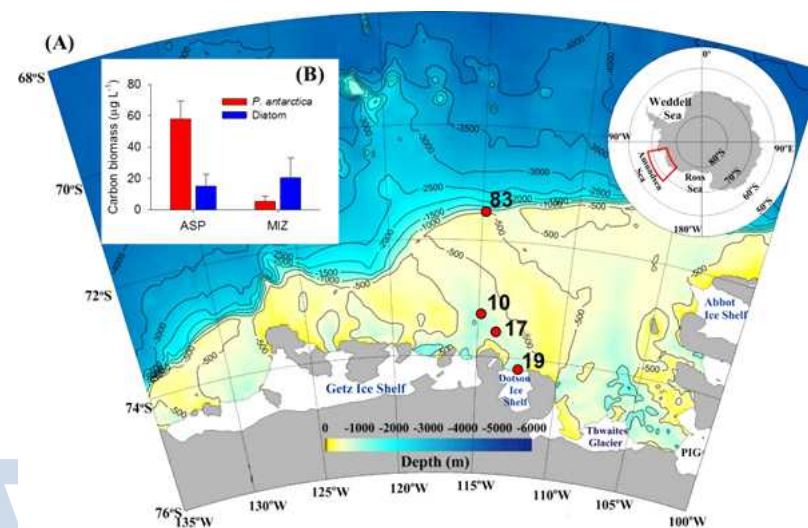


Fig. II-1. A map showing the sampling sites (panel A), and carbon biomass ($\mu\text{g L}^{-1}$) of the major phytoplankton groups (panel B) in the Amundsen Sea polynya during austral summer 2012. ASP and MIZ denote Amundsen Sea polynya and marginal ice zone, respectively.

2. DNA extraction, quantitative PCR, and pyrosequencing of 16S rRNA genes

Total genomic DNA was extracted from the different sediment layers using a PowerMax DNA Isolation kit (Mo Bio Laboratories, Carlsbad, CA, USA), following the manufacturer's instructions. Quantitative real-time polymerase chain reaction (qPCR) was used to determine the copy number of archaeal and bacterial 16S rRNA genes and archaeal *amoA* genes using a TaqMan assay and a SYBR Green I assay, respectively (Table II- 2). qPCR was used to determine the copy number of archaeal and bacterial 16S rRNA genes and archaeal *amoA* genes by a TaqMan assay and SYBR Green I assay, respectively. The PCR products from the 16S rRNA gene of *Escherichia coli* DH5 α and an environmental thaumarchaeotal 16S rRNA gene sequence amplified from natural sediment of the ASP were used as the standards for bacterial and archaeal quantification, respectively. TaqMan assay was performed using Premix Ex Taq™ (TaKaRa Co. Japan) with 20 μ M of the primers and 2.5 μ M of the probe. The TaqMan probes were modified at the 5' and 3' end with FAM reporter and Black Hole Quencher dye (Integrated DNA Technologies, Illinois, USA). Quantitative PCR was performed on an ABI 7500 Real-Time PCR System (Applied Biosystems, Foster City, CA, USA). The temperature profile for the TaqMan assay was composed of an initial incubation step for 2 min at 50°C (polymerase activation) followed by a 10 min pre-denaturation step at 95°C, 40 cycles of denaturation for 30 s at 95°C, and annealing and elongation for 1 min at 60°C. The calculated 16S rRNA gene copy numbers were converted to cell numbers using conversion factors of 1.5 for *Archaea* and 4.1 for *Bacteria*, following recommendations by Schippers et al. (2006). Q-PCR was also used to determine the abundance of archaeal *amoA* genes with SYBR Green I assays. Standards were purified plasmid DNAs from clones generated from archaeal *amoA* genes recovered from sediment sample of ASP. PCR conditions for *amoA* gene amplification are as described in the previous study (Moin et al 2005). SYBR Green assay was performed using TB Green™ Premix Ex Taq™ (TaKaRa Co., Japan) with 20 μ M of the primers. Quantitative PCR was performed on an ABI 7500 Real-Time PCR System (Applied Biosystems, Foster City, CA, USA). Samples were run in triplicate. SYBR

Green I Assays included a melting curve analysis to verify PCR specificity. Melting-curve peaks for the standards and samples amplified using the *amoA* gene-specific primers occurred at temperatures between 83.0 and 85.5°C. Every qPCR included a set of standards with concentrations ranging between 10² and 10⁷ fragment copies per μ L and a blank (where the sample was replaced with sterilized distilled water), both run in triplicate. All qPCRs had an R² above 0.99. The efficiencies of the archaeal *amoA* gene 98% (Standard curve: slope= -3.38) and that of 16S rRNA gene qPCRs were 97% (standard curve: slope = -3.4). We used automatic settings for determination of the threshold cycle line. Gene targets as well as probe and primer sequences used in this study are summarized in Table II- 2.

Table II-2. Primer and probe sequences used in quantitative PCR

Primer	Target gene	Sequence (5'-3')
349F	<i>Archaea</i> 16S rRNA	GYG CAS CAG KCG MGA AW
806R	<i>Archaea</i> 16S rRNA	GGA CTA CVS GGG TAT CTA AT
516F (probe)	<i>Archaea</i> 16S rRNA	TGY CAG CCG CCG CGG TAA HAC CVG C
331F	<i>Bacteria</i> 16S rRNA	TCC TAC GGG AGG CAG CAG T
797R	<i>Bacteria</i> 16S rRNA	GGA CTA CCA GGG TAT CTA ATC CTG TT
518R (probe)	<i>Bacteria</i> 16S rRNA	CGT ATT ACC GCG GCT GGC AC
<i>amoAF</i>	Archaeal <i>amoA</i>	STA ATG GTC TGG CTT AGA CG
<i>amoAR</i>	Archaeal <i>amoA</i>	GCG GCC ATC CAT CTG TAT GT

For each DNA sample, PCR amplification of the 16S rRNA genes was performed in triplicate using a primer set of Uni787F (Roesch *et al.*, 2007) and Uni1391R (Lane *et al.*, 1985) according to Jorgensen et al. (2012) (thermal cycler conditions: 95 °C for 15 min, then 25–30 cycles of 94 °C for 45 s, 53 °C for 45 s, 72 °C for 1 min followed by 72 °C for 7 min). Each reaction mixture contained 1X PCR buffer, 2 mM MgCl₂, 0.2 mM dNTPs, 5% dimethyl sulfoxide, 0.1% bovine serum albumin, 1.2 μ M primers, 2.5 units/ μ l DNA polymerase (Takara Bio, Shiga, Japan). After confirming PCR products by gel electrophoresis and UV illumination, PCR products from the triplicate

PCR reaction were pooled and purified using the QIAquick PCR Purification Kit (Qiagen). The purified products were quantified using the Quant-iT™ PicoGreen® dsDNA Assay Kit (Invitrogen). An equal DNA amount of the purified PCR products from each sample was pooled for pyrosequencing. Resulting amplicons were sequenced by Macrogen Corporation (Korea) using the 454 GS FLX+ system (Roche). Raw data were deposited in the National Center for Biotechnology Information Sequence Read Archive database under accession number SRX3405376. Raw flowgrams of pyrosequencing reads were filtered and de-noised by a PyroNoise algorithm (Quince et al. 2011) implemented in a MOTHUR pipeline (ver. 1.36.1) (Quince et al. 2009). Chimeric sequences were identified and removed by ChimeraSlayer. For each of the 48 sampled sediment layers at the polynya and non-polynya sites, we generated a 16S rRNA gene amplicon library, with one primer set covering the V5-V8 region of both bacterial and archaeal taxa (Jorgensen et al. 2012). A total of 132,914 pyrosequencing reads from 48 samples were qualified for further processing. The sequences were then clustered into operational taxonomic units (OTUs) that met the criteria of a 97% similarity threshold and a minimum cluster size of 2 using a QIIME pipeline (ver. 1.9.1) (Caporaso et al. 2010). Taxonomy for each OTU_{0.97} was assigned using the RDP classifier method (Wang et al 2007) with the Greengenes database (ver. 13_8) (McDonald et al. 2012). To avoid the effects of different sample sizes for estimating diversity, comparison sequences were randomly subsampled to the smallest library size (Kirchman et al 2010), which was 1,628 sequences in the present study. Chao1 estimates were created using QIIME software to assess diversity (Chao et al. 1984).

3. CARD-FISH analysis and probe design

Samples for catalyzed reporter deposition fluorescence in situ hybridization (CARD-FISH) were obtained from frozen sediment cores. Subsamples from depth layers 0-1 cm and 1-2 cm were fixed in 50% ethanol (final concentration) while thawing, diluted, ultrasonicated at 20% intensity, 20 cycles, 20s (Bandelin, Sonopuls HD 200, Germany) and filtered on a 0.22 µm pore size polycarbonate filter. CARD-FISH was

performed as previously described (Ishii et al., 2004) with the following modifications: cell walls were permeabilized with lysozyme (10 mg ml⁻¹) for 60 min at 37°C followed by achromopeptidase treatment (60 U ml⁻¹ in 0.01 M NaCl, 0.01 M Tris-HCl pH 8) for 30 min at 37°C. Endogenous peroxidases were inactivated with 30% H₂O₂ in methanol for 30 min at room temperature. Filters were finally embedded in 4,6_-diamidino-2-phenylindole (DAPI)-containing mounting medium and cells were counted in 20-100 independent microscopic fields of view using an epifluorescence microscope (Nikon Eclipse 50i).

As none of the two general probes for *Planctomycetes*, PLA46 (Neef et al. 1998) and EUB338-II (Daims et al., 1999), covers clade MSBL-9 (≥ 3 mismatches) probes for MSBL-9 were developed using the software package ARB and the implemented function 'probe design' (Ludwig et al. 2004) using SILVA database SSURefNR 132 (Quast et al. 2013). Probe MSBL-9-46 (GACTTGCATGTCTTAGCC) was used at 30% formamide together with competitor cMSBL-9-46 (GACTTGCATGTCTTAACC) to avoid unspecific binding of Verrucomicrobia having one mismatch to the probe. Probe MSBL-9-338 (GCAGCCCTCCGTGGAGGT) was used at 35% formamide concentration.

4. Geochemical characterization

Geochemical constituents (NH₄⁺, NO_x [NO₃⁻ + NO₂⁻], PO₄³⁻, and Fe²⁺) in the pore water, sediment accumulation rates, oxygen penetration depth (OPD), total oxygen uptake (TOU), sulfate reduction rates, and N₂ removal rates by denitrification and anaerobic ammonia oxidation (anammox) were adopted from the results reported by Kim et al. (2016) and Choi et al. (2016). Total organic carbon (TOC) and total nitrogen (TN) were analyzed with Elemental Analyzer (Carlo Erba, NA-1500) (Verardo et al., 1990). To measure total organic carbon (TOC) in the sediments, 5-10 mg of dried sediment in a silver capsule was treated with 6% H₂SO₄ for dissolution of carbonates. Treated-sediments were analyzed with Elemental Analyzer (Carlo Erba, NA-1500). To determine total nitrogen (TN), 10-15 mg of dried-sediment was placed in a tin capsule

and analyzed with Elemental Analyzer (Carlo Erba, NA-1500).

5. Statistical analyses

The significance of spatial differences of geochemical constituents was assessed using a Mann-Whitney U, and a significance level of 0.05 was used to determine a significant statistical difference. Relative abundance of microbial populations were tested using Kruskal-Wallis test.

The OTU table from QIIME and geochemical measurements were analyzed in R (v. 3.3.2) (R Core Team, 2016) with custom scripts and several packages including vegan (v. 2.4-2) and lme4 (v. 0.9-35). Exploratory data analysis was carried out for both microbial community and geochemical measurements data using non-metric multidimensional scaling (NMDS), diversity measures and hierarchical clustering analysis. Microbial community was analyzed at the OTU_{0.97} level as well as at phylum and order level. The compositional difference of microbial communities among stations was tested by MANOVA-like non-parametric tests (ANOSIM and PERMANOVA). The ordination of microbial communities was fitted with geochemical measurements by vector fitting. Constrained ordination models were constructed by redundancy analysis (RDA) in iterative fashion considering collinearity among constraining geochemical variables. The community structures were compared among stations, and between *Bacteria* and *Archaea* using Procrustes test on RDA ordination configuration and Mantel test.

제 3 절 연구결과 및 토의

1. Spatial variations of benthic microbial communities in the Amundsen Sea

The distribution of geochemical constituents and community structures showed distinct spatial variation between the polynya sites and non-polynya sites of the Amundsen Sea

(AS). Sediment accumulation rates in the polynya sites (Stns 10 and 17) were 1.5 times higher (0.180–0.201 cm y⁻¹) than in the ice self (0.134 cm y⁻¹) and marginal ice zone (0.122 cm y⁻¹). Contents of TOC, and TN were approximately 1.25 to 2.1 times higher at the polynya than at the ice shelf zone (Stn 19) and sea-ice zone (Stn 83) (Table II-1 and Fig. II-2) ($p < 0.001$). Accordingly, oxygen penetration depth (OPD) at the polynya sites (1.8–2.0 cm) was shallower than at the non-polynya sites (3.5–3.6 cm). Pore-water analysis revealed that the concentration of NO_x at the polynya sites decreased with depth from approximately 30 μM at the top to 8 μM at 3–5 cm depth interval, and then remained constant down to 10–20 cm depth (Fig. II-2). In contrast, NO_x concentration at the non-polynya sites (ice shelf and sea ice zone) was high (> 20 μM) at all depth range. NH₄⁺ concentration was higher at the polynya sites than at the non-polynya sites (Fig. II-2) ($p < 0.001$). Concentration of Fe²⁺ in the pore-water was low at all sites (< 10 μM), but the average concentration of dissolved Fe²⁺ was higher at the polynya sites (4.9 μM) than at the non-polynya sites (1.98 μM) ($p = 0.003$). Consequently, metabolic activities such as total oxygen uptake (TOU) rate and anaerobic respiration by sulfate reduction were consistently higher in the polynya sites with relatively higher C_{org} content compared to those measured at non-polynya site (Table II-1 and Fig. II-2) ($p = 0.002$).

The NMDS ordination configuration fitted with geochemical parameters showed that the microbial communities were segregated according to the polynyas and non-polynyas, driven by differences in geochemical constituents (NH₄⁺, Fe²⁺, and PO₄³⁻), TOC, TN, and sulfate reduction rate (Fig. II-5). Both archaeal and bacterial communities were quite distinctive between polynya sites and non-polynya sites ($P < 0.001$ from both PERMANOVA and ANOSIM) (Fig. II-3). Likewise, selected-orders covering 70% of total reads abundance nicely showed the distinctive microbial communities between polynyas and non-polynyas (Fig. II-3D). From the RDA analysis (Fig. II-4), the NO_x concentrations correlated with surface microbial communities at all stations. The C_{org} contents correlated with the microbial communities in surface sediments of Stn 10 and in intermediate depth of Stns 17 and 19, respectively. Microbial communities in Stn 83 were clearly unique compared to those in other sites. Archaeal communities were more

distinctive among stations, while bacterial communities were more similar overall. Compositional similarity at phyla level better reflects the ecological or geographic settings.

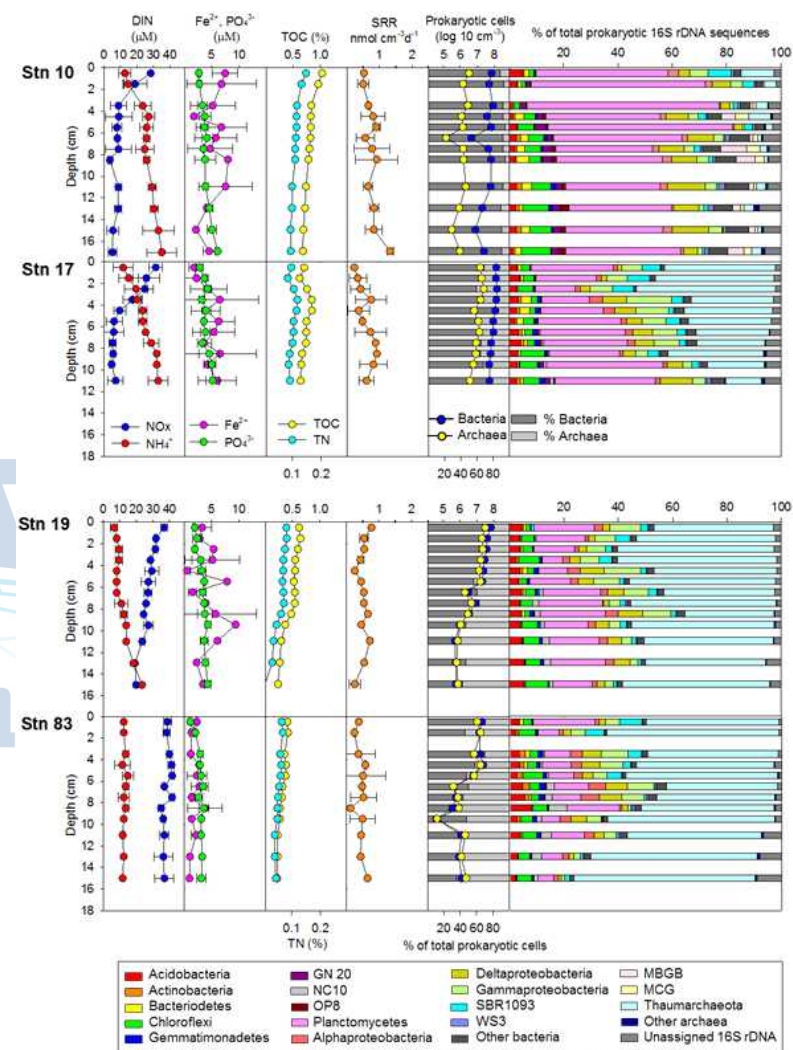


Fig. II-2. Distribution of geochemical constituents (NH_4^+ , NO_x , PO_4^{3-} , Fe^{2+}) in pore-water and TOC, TN, sulfate reduction rate (SRR), prokaryotic cell abundance based on Q-PCR, and relative abundance of major phyla in the sediment of the polynya sites (Stns 10 and 17) and non-polynya sites (Stns 19 and 83) of the Amundsen Sea.

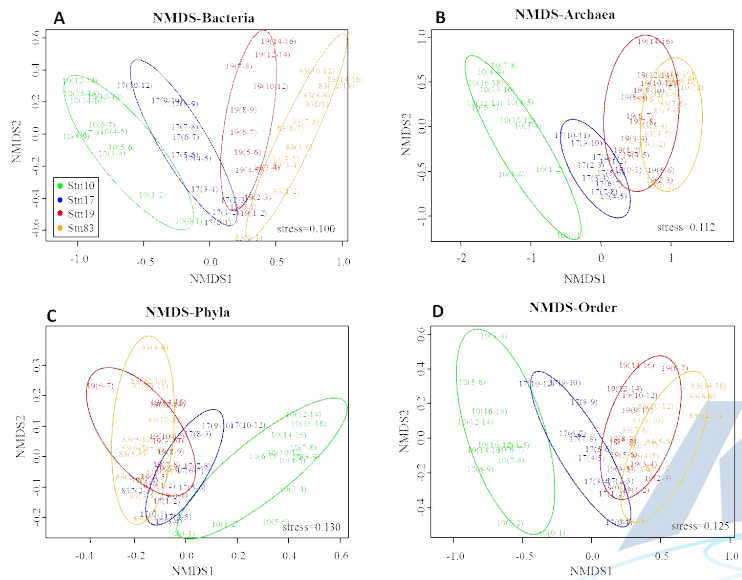


Fig. II-3. Non-metric multidimensional scaling (NMDS) ordination of the bacterial (A) and archaeal (B) communities based on the OTUs of 16S rRNA genes, and total prokaryotic communities at phyla level (C) and order level (D).

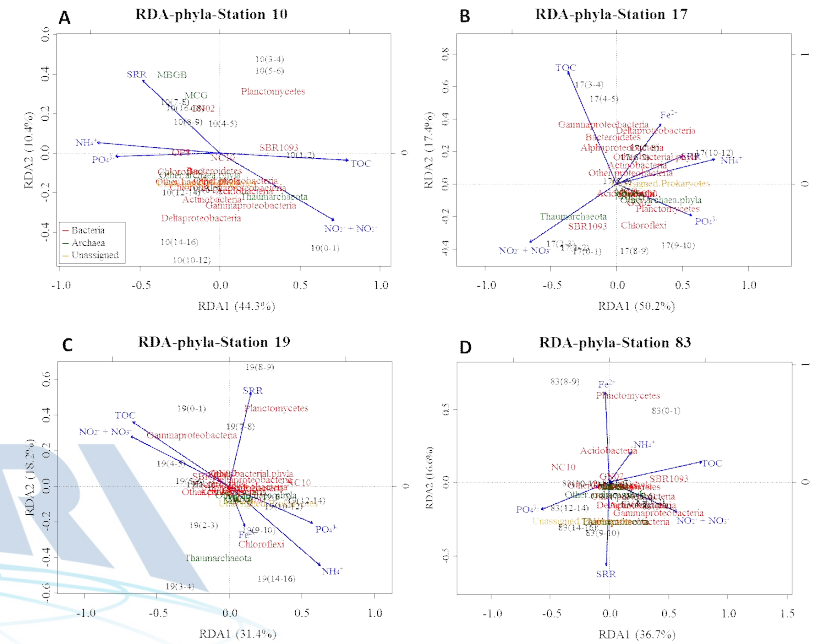


Fig. II-4. Redundancy analysis (RDA) models Stations 10 (A. adj. $R^2 = 0.262$, $P = 0.001$), 17 (B. adj. $R^2 = 0.382$, $P = 0.001$), 19 (C. adj. $R^2 = 0.262$, $P = 0.001$) and 83 (D. adj. $R^2 = 0.288$, $P = 0.001$) based on phyla level prokaryotic communities with selected significant environmental variables with minimum collinearity

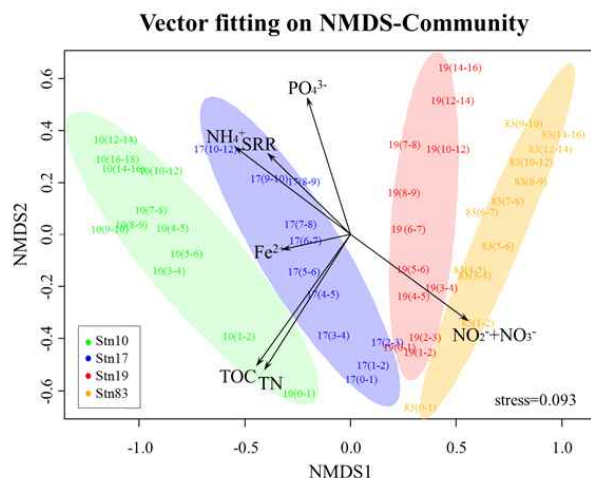


Fig. II-5. Prokaryotic community by 16S rRNA gene (NMDS ordination) showing the microbial communities segregated according to the polynya and non-polynya, driven by differences in nutrients (NH_4^+ , Fe^{2+} , and PO_4^{3-}), TOC, TN, and sulfate reduction rate.

In total, 9,852 reads were unique, with an average length of 601 bp. Chao1 indices are as high as average 1,909 in the 7–8 cm depth of Stn 17, and were lowest as 704 in 14–16 cm depth of Stn 83 (Table II- 3). Chao1 and observed $\text{OTU}_{0.97}$ count of the polynya sites and ice-shelf site were higher than those of the sea-ice zone. These two indices were estimated to be highest within the sub-oxic layers (3–8 cm depth) of all sites. The community compositions at the phylum level were dramatically different between sites (Figs II-2 and II-6). At the polynya site (Stn 10), the most dominant phyla were *Planctomycetes* (35–71%), *Proteobacteria* (4.8–22%), *Thaumarchaeota* (1.2–12.1%), and *Chloroflexi* (1.9–10.8%). Candidate Division GN02 (0.5–4.4%), Candidate Division SBR1093 (0.2–8.3%), *Acidobacteria* (1.2–5.0%), and *Bacteroidetes* (0.4–3.2%) were of minor abundance. At Stn 17, the proportion of *Planctomycetes* slightly decreased (14.8–43%), whereas the percentage of *Thaumarchaeota* (13–51%) appeared to be more abundant than those at Stn 10. Other phyla included *Proteobacteria* (10.6–31%), *Chloroflexi* (2.1–8.7%), Candidate Division SBR1093 (0.5–8.3%), and *Acidobacteria* (2.6–4.1%). The proportion of archaeal sequences prominently increased at Stns 19 and 83, which is consistent with the results of archaeal cell number estimated from 16S rRNA gene quantification by Q-PCR (Fig. II-2 and Table II-3). Relative abundance of *Thaumarchaeota* accounted for 41–59% and 41–67% at Stn 19 and Stn 83, respectively. *Proteobacteria* (4.1–27.8%), *Planctomycetes* (5.8–24%), *Chloroflexi* (1.6–8.1%), *Acidobacteria* (2–8%), and Candidate Division SBR1093 (0.3–8.1%) appeared in similar proportions at the both non-polynyas (Fig. II-2).

Total prokaryotic cell numbers determined by 16S rRNA gene Q-PCR ranged from 0.1×10^7 to 9.9×10^7 cells cm^{-3} per each sample, which showed no difference between the sites (Table II-3). Total prokaryotic abundances were higher in the surface sediments and decreased with depth at all sites (Fig. II-2). The proportion of bacterial cells to total prokaryotic cells was highest at Stn 10 (92%), and then decreased to 67% (Stn 17), 57% (Stn 19) and 48% on average (Stn 83). In contrast, archaeal proportion comprised 8% at Stn 10, and then gradually increased with distance further from Stn 10 to 33% (Stn 17), 43% (Stn 19) and 52% on average (Stn 83) (Table II-3).

Table II-3. Abundance of prokaryotes estimated by q-PCR based on 16S rRNA gene copy numbers and estimates of phylotype richness and coverage for the prokaryotic assemblages

Station	Depth (cm)	Prokaryotic abundance (cells cm ⁻³) [§]	No. of total reads	No. of OTUs*	Good's coverage	Chao1		
Polynya	Stn 10	0-1	1.89×10 ⁷ (88.5/11.5)	2397	805	66.4	1239	
		1-2	1.30×10 ⁷ (92.6/7.4)	3205	958	70.1	1317	
	3-4	2.25×10 ⁷ (91.8/8.2)	2580	876	66	1359		
	4-5	9.90×10 ⁶ (92.2/7.8)	2894	1014	65	1640		
	5-6	1.69×10 ⁷ (94.6/5.4)	2316	735	68.3	1200		
	6-7	1.16 ×10 ⁶ (91.9/8.1)	3041	1189	60.9	1816		
	7-8	1.17×10 ⁷ (91.7/8.3)	3049	1159	62	1801		
	8-9	1.70×10 ⁷ (94.1/5.9)	2973	1076	63.8	1561		
	10-12	1.64×10 ⁷ (91.7/8.3)	1857	809	56.4	1557		
	12-14	5.33×10 ⁶ (89.5/10.5)	1713	709	58.6	1392		
	14-16	2.05×10 ⁶ (89.9/10.1)	2414	959	60.3	1622		
	16-18	6.58×10 ⁶ (90.6/9.4)	3154	959	69.6	1348		
	Ice-shelf	Stn 17	0-1	4.67×10 ⁷ (68.5/31.5)	3156	861	72.7	1322
			1-2	4.89×10 ⁷ (63.2/36.8)	2589	767	70.4	1314
		2-3	5.93×10 ⁷ (59.3/40.7)	2743	716	73.9	1341	
		3-4	4.76×10 ⁷ (67.3/32.7)	2644	987	62.7	1666	
4-5		3.45×10 ⁷ (81.4/18.6)	1628	705	56.7	1415		
5-6		3.29×10 ⁷ (64.9/35.1)	3526	1186	66.4	1793		
6-7		3.53×10 ⁷ (61.9/38.1)	2844	1076	62.2	1784		
7-8		2.47×10 ⁷ (65.2/34.8)	2706	1080	60.1	1909		
8-9		2.31×10 ⁷ (64.3/35.7)	2378	792	66.7	1418		
9-10		1.79×10 ⁷ (68.0/32.0)	2398	872	63.6	1418		
10-12		1.66×10 ⁷ (78.3/21.7)	3103	1067	65.6	1601		
Sea-ice		Stn 19	0-1	9.90×10 ⁷ (68.5/31.5)	2530	849	66.4	1361
	1-2		6.03×10 ⁷ (66.5/33.5)	3002	831	72.3	1424	
	2-3	5.92×10 ⁷ (62.9/37.1)	5309	1153	78.3	1457		
	3-4	4.57×10 ⁷ (63.1/36.9)	3269	773	76.4	1326		
	4-5	3.82×10 ⁷ (64.2/35.8)	3154	977	69	1617		
	5-6	3.68×10 ⁷ (56.5/43.5)	4887	1142	76.6	1560		
	6-7	4.97×10 ⁶ (60.7/39.3)	3050	974	68.1	1609		
	7-8	1.29×10 ⁷ (63.0/37.0)	2387	608	74.5	991		
	8-9	6.31×10 ⁶ (54.3/45.7)	2306	818	64.5	1462		
	9-10	2.03×10 ⁶ (47.0/53.0)	2516	717	71.5	1239		
	10-12	1.25×10 ⁶ (40.7/59.3)	2961	743	74.9	1126		
	Sea-ice	Stn 83	0-1	3.09×10 ⁷ (66.1/33.9)	3402	803	76.4	1182
1-2			3.06×10 ⁷ (45.6/54.4)	3480	683	80.4	1125	
3-4		2.24×10 ⁷ (69.7/30.3)	2553	750	70.6	1243		
4-5		4.00×10 ⁷ (58.2/41.8)	2397	731	69.5	1229		
5-6		1.27×10 ⁷ (47.3/52.7)	2181	602	72.4	1194		
6-7		8.12×10 ⁵ (50.2/49.8)	2333	734	68.5	1179		
7-8		1.33×10 ⁶ (43.2/56.8)	1859	620	66.6	1277		
8-9		1.21×10 ⁶ (29.3/70.7)	2195	503	77.1	779		
9-10		8.51×10 ⁴ (47.6/52.4)	2121	505	76.2	735		
10-12		3.25×10 ⁶ (36.8/63.2)	2587	643	75.1	963		
12-14	2.06×10 ⁶ (42.3/57.7)	2618	508	80.6	781			
14-16	3.55×10 ⁶ (35.1/64.9)	3074	467	84.8	704			

§ Numbers in parenthesis indicates the percentage of bacteria or archaea of total prokaryotic cells based on 16S

rRNA gene copy quantification using Q-PCR

* Based on 97% similarity clustering

Good's coverage (%) = $[1 - (n/N)] \times 100$ (n, the number of OTUs; N, the total number of reads)

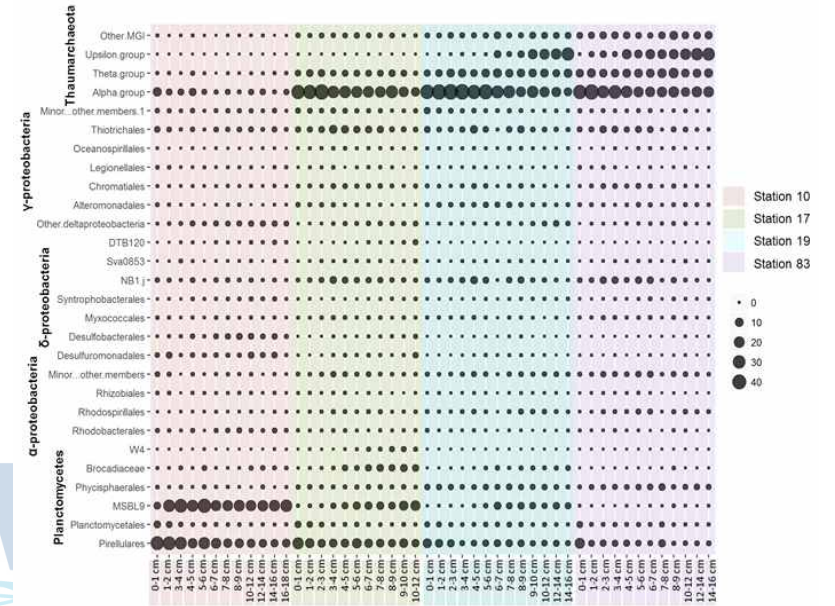


Fig. II-6. Relative abundance of major microbial 16S rRNA gene OTUs based on order level and uncultivated clades in the sediments of the ASP.

2. Sequence-abundant *Planctomycetes* and its visualization by CARD-FISH

One of the most prominent features revealed from the 16S rRNA gene pyrosequencing was that the members of *Planctomycetes* appeared to be the most abundant microbial members detected in the highly productive polynya sites, especially at Stn 10 (Fig. II-2). Many *Planctomycetes* have been found attached to sinking marine aggregates in water column (DeLong et al., 1993; Fuchsman et al., 2011, 2012). At ASP, however, they were not detected in the water column (Delmont et al., 2014; Kim et al., 2014b). Thus, the highly abundant *Planctomycetes* sequences in the ASP sediment are not supposed to be originated from water column, confirming the results by Probandt and coworkers who showed that *Planctomycetes* in subtidal, sandy sediments differed from those in the overlying water column (Probandt et al., 2017).

From the NGS result of 16S rRNA amplicons, the most abundant *Planctomycetes* in the total microbial communities were belonged to three clades, i.e. *Pirellula*-like group, candidate order MSBL-9 (Mediterranean Sea Braine Lake-9) (Pachiadaki et al., 2014), and *Candidatus* Brocadiaceae (Fig. II-7). The *Pirellula*-like group and the candidate order MSBL-9 were the two most dominant bacterial groups at Stn 10, comprising 34% and 32% of total 16S rRNA gene sequences, respectively (Figs. II-6 and II-7). In contrast, relative abundance of *Pirellula*-like group decreased to < 17%, and the candidate order MSBL-9 group was not discernible at Stn 83. *Candidatus* Brocadiaceae that is known to be capable of anaerobic ammonium oxidation (anammox) using nitrite as the electron acceptor (Schmid et al., 2003) was most abundantly detected at Stn 17 among the four sites, and appeared a maximum 9.2% of the total prokaryotic sequences at 9–10 cm depth (Figs. II-6 and II-7).

The *in situ* existence of *Planctomycetes* was demonstrated in the surface sediment layers of the polynya stations (Stns 10 and 17) as well as in sediments of the ice-shelf (Stn 19) and below sea-ice (Stn 83) by CARD-FISH using the general probe for *Planctomycetes* PLA46. Most sequences retrieved from the polynya sites, however, were affiliated with clade MSBL-9 of the class *Phycisphaera* (Figs. II-7 and II-8) which is neither covered by probe PLA46 nor by any of the general bacterial probes EUB338 I-III. Thus, we designed and tested two new probes for these target sites with a coverage of nearly 100% of clade MSBL-9 and named them MSBL-9-46 and MSBL-9-338. Both probes showed bright CARD-FISH signals in the AS sediments. Cells had the typical ovoid to elliptical morphology

(Fig. II-8, panels A to F). The applied formamide concentration of 30% for MSBL-9-46 and 35% for MSBL-9-338 will allow a combined use of these probes with PLA46 and EUB338 I-III in future experiments. In this study, we cannot provide *in situ* quantification of cell abundance because the sediments used for CARD-FISH were not pre-fixed immediately after sampling (Moter and Gobel 2000). However, the CARD-FISH images for the class *Planctomycetia* and the candidate order MSBL-9 (Fig. II-8) strongly support the extensive distribution of *Planctomycetes* in the AS sediments.

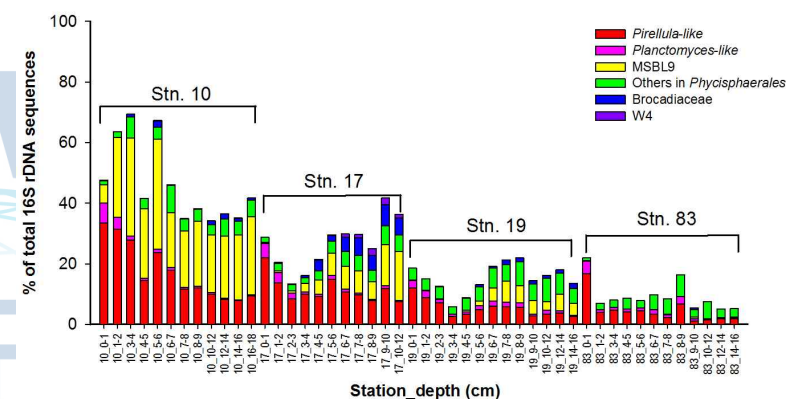


Fig. II-7. Relative abundance of major groups in the phylum *Planctomycetes* (based on order level) of the total 16S rRNA gene sequences at each sample

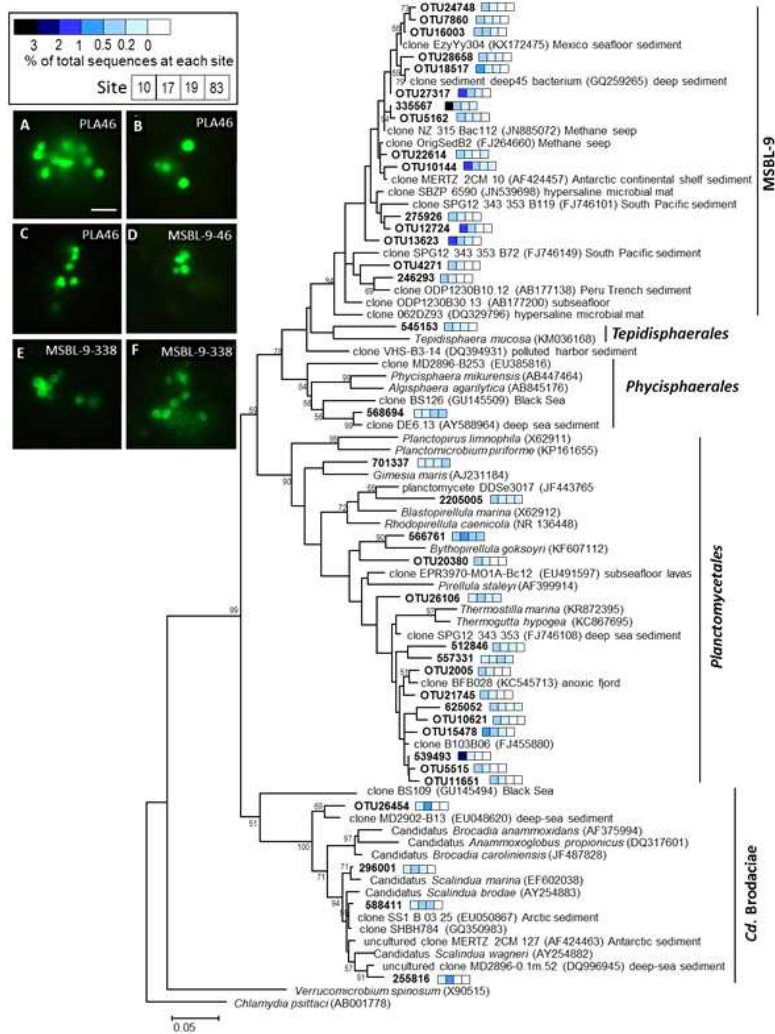


Fig. II-8. CARD-FISH images (panels A to F) and phylogenetic tree showing the distribution of the 16S rRNA genes sequences retrieved from the ASP sediments within the phylum *Planctomycetes*. The tree was constructed using the maximum-likelihood algorithm in MEGA 7.0. The color of the square bar represents the relative abundance of the sequences for each site (Stn 10, Stn17, Stn19, and Stn 83). Node support estimated using 1,000 bootstrap replicates. Bootstrap value above 50% is shown.

3. *Planctomycetes* are likely responsible for the C_{org} mineralization in the ASP sediments

Pirellula members in *Planctomycetes* have been often reported as heterotrophic bacteria degrading organic matter produced by macro- or micro algae (Glöckner et al. 2003; Morris et al. 2006; Bižić-Ionescu et al. 2015) while little information is available to speculate about the ecological role of the uncultured *Planctomycetes* (Fig. II-8). Most of the cultivated *Planctomycetes* have been known as aerobes or facultative aerobes (Schlesner et al. 2004). However, environmental sequences from *Planctomycetes* were often retrieved from anoxic zones, such as in methane hydrate-bearing sediment (Inagaki et al. 2006) and subsurface sea floor sediment (Jorgensen et al. 2012). Therefore, detection of these sequences in oxygen-depleted layers is not surprising (Fig. II-9).

In fine-grained marine sediments receiving high organic material input, *Delta-* and *Gamma*proteobacteria have been reported as the predominant bacterial group (Rooney-Varga et al. 1997; Bowman and McCuaig 2003; Bissett et al. 2006). Therefore, our results exhibiting high *Planctomycetes* abundance, comprising average 40% of total sequence (Fig. II-2), in the ASP sediments is intriguing. Major controls regulating the distribution of the *Planctomycetes* in the sediments remain unknown, largely because any culture-based studies are not available (Bauld and Staley 1976; Schlesner et al. 2004; Lee et al. 2013). However, our statistical analysis (Fig. II-6) revealed that relative abundance of *Planctomycetes* in the ASP showed a significant positive correlation with TOC contents and inorganic constituents (NH_4^+ , PO_4^{3-} and Fe^{2+}) presumably resulting from the C_{org} mineralization. It is well known that the *Phaeocystis* colony excretes mucous matrix containing both carboxylated and sulfated-heteropolysaccharides as main constituent (van Boekel 1992; Alderkamp et al. 2007). Based on metagenomic information from the Namibian and Oregon coastal upwelling system, Woebken et al. (2007) revealed that all marine planctomycetes genomes, except for *Candidatus* *Kuenenia stuttgartiensis*, possess a high number of sulfatase genes, which suggest marine *Planctomycetes* might be able to breakdown the recalcitrant sulfated heteropolysaccharides (Wegner et al. 2013; Probandt et al. 2017). In addition, since the *Phaeocystis* settles slowly (Collier et al. 2000, DeJong et al. 2017), most labile C_{org} produced by *P. antarctica* bloom are rapidly decomposed by heterotrophic bacteria in the water column before reaching the sediment of the ASP (Kirchman et al. 2001), and the organic materials

accumulated in the surface sediments of the deep ASP (> 700 m) would be intrinsically recalcitrant. Consequently, the high relative abundance of *Planctomycetes* in the center of the polynya (Stns 10 and 17) suggests that the members of *Planctomycetes* are a significant heterotrophic bacterial group utilizing recalcitrant organic materials originated from *Phaeocystis* bloom in the water column of the ASP. Recently, Probandt et al. (2017) also suggested that *Planctomycetes* play a key role for degradation of high molecular weight compounds and recalcitrant materials entering surface sediments from the water column of the Wadden Sea.

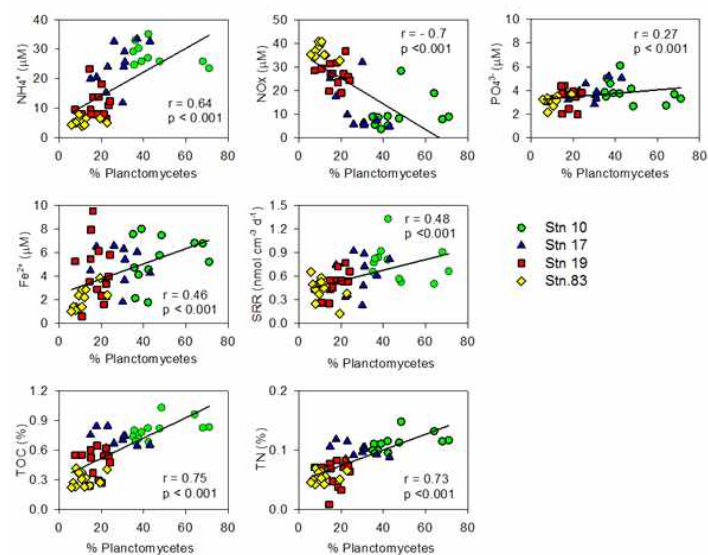


Fig. II-9. Correlations between the relative abundance of the planctomycetal 16S rRNA gene in total sequences and geochemical properties.

4. Spatial variability of *Proteobacteria*, *Chloroflexi*, and *Bacteroidetes*

Gammaproteobacteria and *Deltaproteobacteria* were the two most abundant groups within *Proteobacteria*, comprising 1–26% and 3–17% of total bacterial sequences, respectively (Fig. II-6). Relative abundance of *Proteobacteria* did not show significant spatial variations with sites (Kruskal-Wallis, $\chi^2(3) = 1.375$, $p = 0.711$). However, based on the class level, delta- and alphaproteobacterial compositions showed spatial variations (Fig. II-10). *Desulfobacterales* and *Desulfuromonadales* that have been well known as a typical sulfate- and sulfur (S^0)-reducing bacterial group in marine sediments appeared the most abundant in Stn 10 but were rarely detected in Stn 83. These results correspond with the previous biogeochemical study that sulfate reduction rates were higher in the polynya site (Stn 10) than those in the non-polynya site (Stn 83) (Kim et al. 2016). In contrast, the deltaproteobacterial sequences in the candidate order NB1-j appeared higher at Stn 19 and Stn 83, but showed low relative abundance at Stn 10 (Figs. II-6 and II-10). However, their ecological or physiological information in marine environment has not been known because they have only been observed as 16S rRNA gene in marine environments (Schauer et al. 2010; Zeng et al. 2011).

The subgroups in *Chloroflexi* appeared to be different between polynya and non-polynya. Major *Chloroflexi* in Stn 10 were affiliated with the class *Anaerolineae* (Fig. II-11). Although most members in class *Anaerolineae* consist of a huge number of environmental 16S rRNA gene sequences (Blazejak and Schippers 2010), their physiological insights are not known well because only a few cultivated bacteria in this class have been isolated (Yamada et al. 2006). In contrast, the sequences clustered in the class SAR202 and TK17 were more abundant at Stns 17, 19 and 83. Genomic studies suggested that the bacteria in SAR 202 clade oxidize relatively recalcitrant organic compounds in the deep-sea water column (Landry et al. 2017; Mehrshad et al. 2018). The sequences in the TK17 clade were affiliated with uncultured *Chloroflexi* sequences that were retrieved from various habitats, such as hydrocarbon-contaminated soil (Milton et al. 2010) and sponge tissue (Montalvo and Hill 2011). The members in *Bacteroidetes* that have been reported as a major organic matter decomposer in the sediments of the SO (Carr et al. 2013; Ruff et al. 2014; Learman et al. 2016) were substantially low with relative abundance less than 5% of total 16S rRNA gene sequences (Fig. II-2).

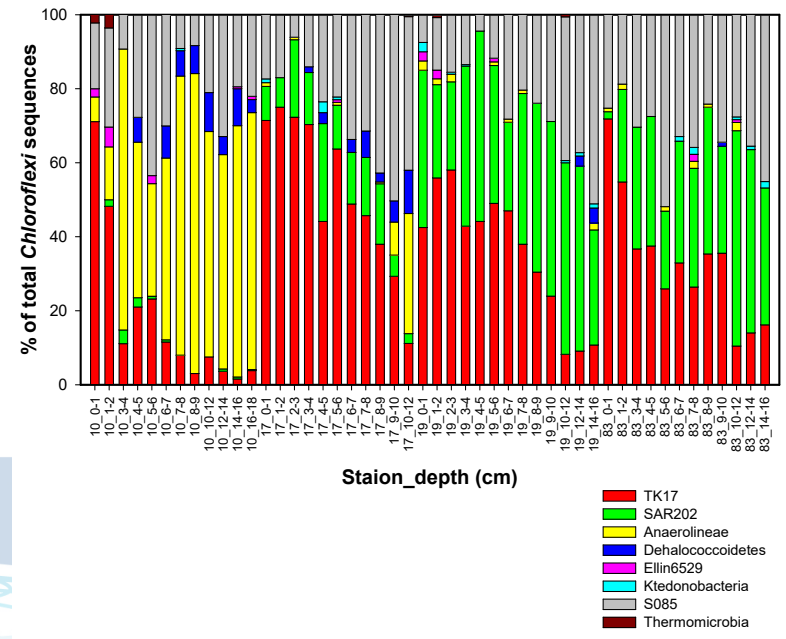
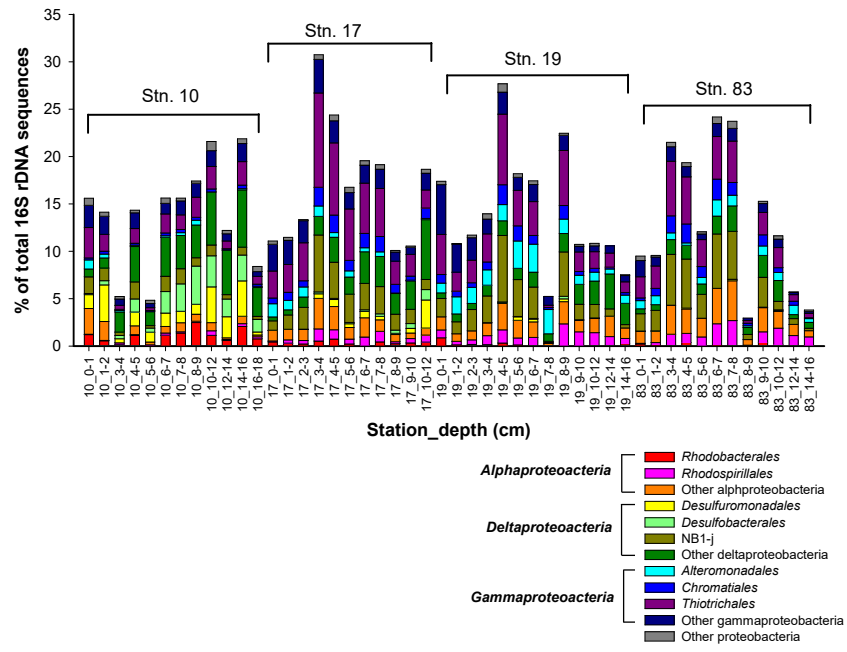


Fig. II-10. Relative abundance of major proteobacterial groups (based on order level) of the total 16S rRNA gene sequences at each sample

Fig. II-11. Relative abundance of major class groups in the total *Chloroflexi* sequences

5. High archaeal abundance in the marginal sea ice zone

One interesting finding revealed from Q-PCR analysis was that archaeal abundance occupied more than half (30–71%) of total prokaryotic abundances at the marginal ice zone (Stn 83) in which most archaeal 16S rRNA gene sequences were assigned to *Thaumarchaeota* (Table II-3 and Fig. II-2). The *Thaumarchaeota* (formerly known as MG-I) were a predominant microbial group in the sediments of AS except at Stn 10 (Fig. II-2). Most *Thaumarchaeota* sequences could be classified into three subgroups termed Alpha, Theta, and Upsilon (Durbin and Teske, 2010) (Fig. II-12). The *Thaumarchaeota* subgroup Alpha was dominant at top layers (0–5 cm) at all sites. The community composition of *Thaumarchaeota* subgroup changed gradually from top to bottom at the non-polynya sites (Fig. II-12). Relative abundance of archaeal sequences associated with Theta and Upsilon subgroup in *Thaumarchaeota* increased with increasing depth, especially at marginal sea ice zone (Stn 83). Except for the *Thaumarchaeota*, Marine Benthic Group B (MBGB) and Miscellaneous Crenarchaeotic Group (MCG), proposed as *Thorarchaeota* (Meng et al. 2014) and *Bathyarchaeota* (Rinke et al. 2013), respectively, that have been reported as putative heterotrophic microorganisms (Biddle et al. 2006; Jorgensen et al. 2012; He et al. 2016) were only detected at Stn 10 (~9.5% and ~5% of total sequences, respectively). Similarly, archaeal sequences related to the methane cycle were only detected in low abundance at Stn 10 (< 2% of the total sequences).

The members in *Thaumarchaeota* are known as major contributors for aerobic ammonia and nitrite oxidation in aquatic environments (Konneke et al. 2005). To examine the potential of sedimentary *Thaumarchaeota* to oxidize ammonia, we quantified the archaeal *amoA* gene that is known for a genetic marker for the ammonia oxidation. The depth profiles of archaeal *amoA* and 16S rRNA gene copy numbers were very similar to each other in the samples except for some layers (Fig. II-13), which imply that most archaeal members in all depth have a gene encoding ammonia monooxidase. Both proportion of archaeal cell abundance in total prokaryotic abundance (Fig. II-14A) and the relative abundance of *Thaumarchaeota* in total 16S rRNA gene sequences (Fig. II-15B) showed a negative correlation with TOC contents. Previously, the environmental members in *Thaumarchaeota* have been reported in oligotrophic marine sediments as an important chemolithotrophic

microbial assemblage (Inagaki et al. 2006; Durbin and Teske, 2011). Similarly, cultivated thaumarchaeal ammonia oxidizers have been shown to be adapted to oligotrophic conditions (Martens-Habbena et al. 2009; Prosser and Nicol 2012). Likewise, the metaproteomic data indicate that MGI are abundant and metabolically active at the surface water of west Antarctic ocean during the winter (Williams et al. 2012), and chemoautotrophic carbon fixation by *Thaumarchaeota* significantly contributed to bacterioplankton production during the Antarctic winter, accounting for up to 9% (Tolar et al. 2016). Therefore, we suggest that the predominant *Thaumarchaeota* in the sediments of non-polynya are a significant chemolithoautotrophic group, sustaining the oligotrophic benthic ecosystem.

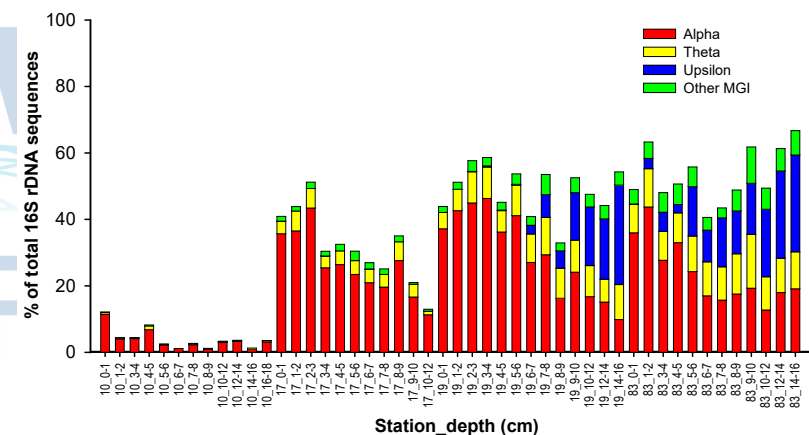


Fig. II-12. Relative abundance of thaumarchaeotal subgroups in the total 16S rDNA gene sequences at each sample.

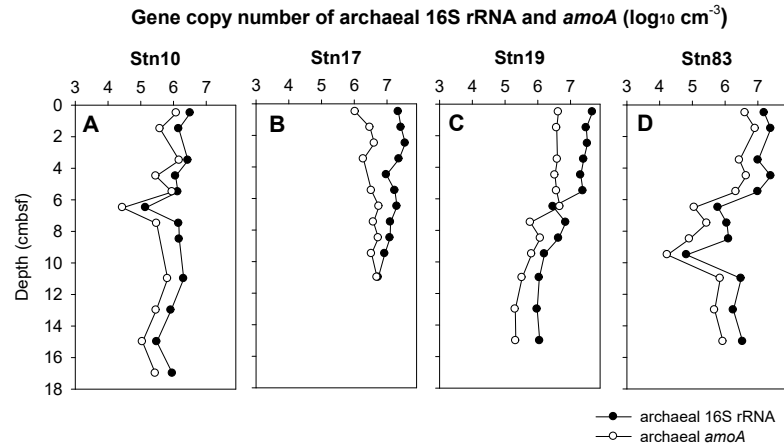


Fig. II-13. Depth profiles of the archaeal 16S rRNA gene and archaeal *amoA* gene in the sediments of the ASP

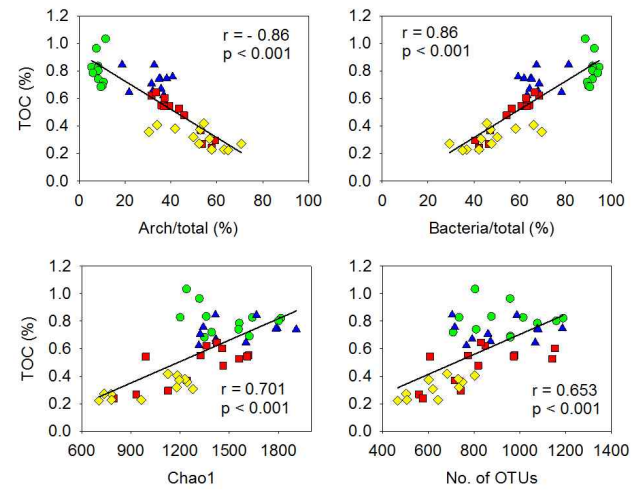


Fig. II-14. Significant correlations between microbial abundance (A and B) and diversity indices (C and D) between TOC content in the ASP sediments

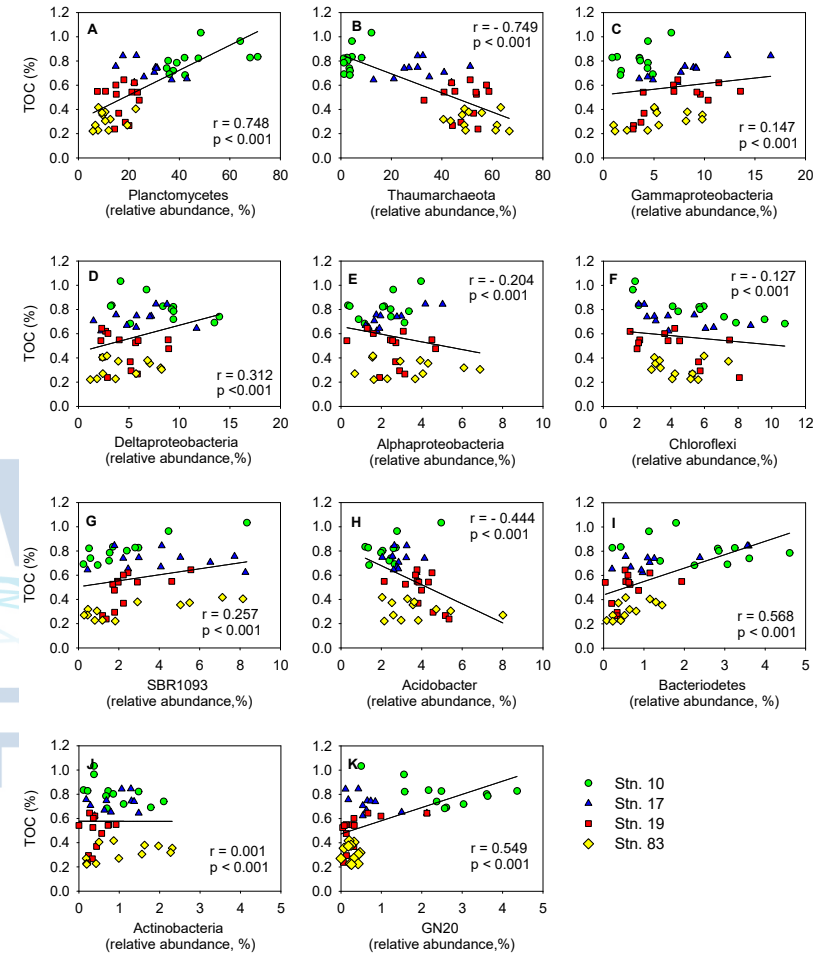


Fig. II-15. Linear regression between the relative abundance of individual taxa in the total prokaryotic 16S rRNA gene sequences and TOC contents in the ASP sediments

7. Implication of *Planctomycetes*-dominated communities in assessing ecosystem response to climate change

This study presents a unique distribution of the benthic microbial communities dominated by *Planctomycetes* in the ASP sediment underlying *Phaeocystis antarctica*-dominated water column. Since the structure and function of benthic microbial communities are largely controlled by the quantity and quality of the organic matter from water column (Danovaro et al. 2000; Bissett et al. 2006; Jamieson et al. 2013; Learman et al. 2017; Probandt et al. 2017), predominance of the *Planctomycetes* in the ASP sediment has a significant implication for the response of benthic ecosystems associated with the proposed shift in phytoplankton communities resulting from the climate changes in the water column (Arrigo et al. 1999; Tortell et al. 2008). The export flux of C_{org} formed by *Phaeocystis* bloom is twice slower than that formed by diatom bloom (DeJong et al. 2017), and thus the contribution of *P. antarctica* cells to total export below the photic zone dramatically declined (Reigstad and Wassmann 2007). In contrast, the organic materials that are produced by diatom possess relatively faster sinking rate and lower C:N ratio (i.e., relative more labile) compared to that of the *Phaeocystis* (Alderkamp et al. 2007; DeJong et al. 2017). Therefore, any transition in phytoplankton community, i.e., from *Phaeocystis* to diatom, would accumulate more labile organic matter in the benthic system of the SO, which ultimately affects the benthic microbial community composition. In the SO, like most coastal ecosystems, proteobacterial groups such as *Delta*- and *Gammaproteobacteria* have been known to occupy ecological niche as a primary mineralizers of the organic materials in the sediments (Bowman and McCuaig 2003; Baldi et al. 2010; Learman et al. 2016; Ruff et al. 2014). Therefore, microbial community structures dominated by *Planctomycetes* rather than *Proteobacteria* in the present study provides relevant baseline information in assessing and/or predicting the environmental changes associated with the climate changes in the Amundsen Sea where *Phaeocystis* consists of dominant phytoplankton composition.

제 4 장 연구개발목표 달성도 및 대외기여도

당해 연도(2018년도)에는 2013-2014년도와 2016년도의 승선연구를 통해 아문젠 해 폴리나 해역의 식물플랑크톤 대증식 시기(대증식 초기, 대증식 중반)에 따른 (1) 종속영양미생물의 생물량, 생산력 및 호흡율의 분포양상 및 (2) 박테리아 요인들의 조절요인으로서 식물플랑크톤으로부터 공급되는 유기물의 중요성에 대한 연구결과들을 획득하였다. 또한 2012년도 1-3월 사이의 승선연구를 통해 채취한 아문젠 해의 서로 다른 해양환경(sea-ice zone, polynya, ice shelf and offshore)내 퇴적물 내 미생물 군집 조성을 살펴보고, 아문젠해 퇴적물 내 미생물 군집은 다른 해양 환경과는 다른 특이한 군집분포를 보임을 밝혀냈다. 특히 폴리나 환경에서는 진정세균(*Bacteria*) 군집인 *Planctomycetes*가 원소 순환에 중요한 역할을 하는 미생물 군집으로 나타났으며, 폴리나가 아닌 지역에서는 고세균(*Archaea*)의 비율이 높아지고, *Thaumarchaeota*가 주요 고세균 구성원으로 검출됨에 따라 퇴적환경 내 고세균의 생태적 역할이 중요함을 보였다.

이상의 연구결과들은 향후 다른 분야 연구결과들과의 종합적인 분석 및 토의를 통해 기후변화 및 온난화에 따른 아문젠 해역에서의 탄소순환 및 생물펌프의 기능을 밝히고, 퇴적 환경 내 생지화학적 순환에 있어 중요한 역할을 수행하는 미생물 군집 조성을 밝혀냄으로써 아문젠해 퇴적 환경에서 물질순환 과정을 이해하는데 중요한 정보를 제공할 것이다.

제 5 장 연구개발결과의 활용계획

본 위탁과제를 통해 획득된 아문젠해 해빙역-폴리나에서의 미생물 생물량 및 생산력의 공간적 분포양상에 대한 정보는 수층의 물리-화학 및 다른 생물요인들에 대한 연구결과들과 더불어 아문젠해 폴리나를 중심으로 연안지역 부유생태계의 미세생물 먹이망 과정을 이해할 수 있는 기본정보를 제공할 것이다.

식물플랑크톤의 일차생산력 및 우점종의 변화와 함께 (1) 박테리아 생산력 및 호흡의 조절요인, (2) 수층 용존유기탄소의 시공간적 분포 그리고 (3) 박테리아 생산력 대 일차생산력의 비 등에 대한 정보는 탄소순환 및 침강플럭스를 조절하는 생물요인을 이해하는데 중요한 정보를 제공할 것이며, 이는 온난화로 인한 해빙의 감소가 급격히 일어나는 극지해양의 탄소순환과 기후변화에 대한 해양의 탄소소절기능을 이해할 수 있는 중요한 정보를 제공할 것이다. 또한, 기후 변화로 인해 예견되는 수층 일차 생산자의 조성 변화는 저층으로 공급되는 유기물의 양과 질의 변화를 초래할 수 있으므로, 유기물 분해경로를 이해하고 이에 관여하는 미생물 군집 구조를 이해하는 것은 향후 지구 온난화로 인한 해빙의 감소가 급격히 일어나는 극지해양의 탄소순환과 기후변화에 대한 해양의 탄소소절기능을 이해할 수 있는 중요한 정보를 제공할 것이다.

수층 내 일차 생산력이 높은 아문젠해 polynya 해역에서 수층 환경에서 중속영양 미생물 활성은 일차생산자에 의해 생성된 유기물에 매우 의존적이며, 수층에서 생성된 대부분의 유기물은 일부만이 저층으로 공급되고 대부분은 수층에서 분해되는 것으로 나타났다. 이러한 환경에서 수층 내 중속영양 미생물 군집을 파악하는 것은 탄소 순환을 이해하는데 필수적인 지식을 제공할 것이다.

또한, 본 위탁과제를 통해 축적된 연구결과들은 국내/외 학술대회 발표 및 학술지 게재를 통해, 극지연구의 중요성 및 대한민국의 극지 및 지구환경변화에 대한 연구역량 및 이해 노력을 제고할 수 있는 지표로 활용가능하다.

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