Quantitative microbial ecology off the northern Antarctic Peninsula

Antarctic microbial ecology

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Dissertation for the degree doctor philosophiae (dr.philos)

at the University of Bergen

June, 2010

Scientific environment

The work for this thesis was carried out:

1. Using the facilities of the Polar Research Program, Marine Biology Research Division, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, 92093-0202, USA.

2. Aboard *R/V Yuzhmorgeologiya* that was chartered by the United States Antarctic Marine Living Resources Program, NOAA, National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA 92037.

3. Aboard *ARSV Laurence M. Gould* (LMG0402) sponsored by the United States National Science Foundation (NSF) from February 15 to March 15, 2004.

Acknowledgements

Dr. Osmund Holm-Hansen (Scripps Institution of Oceanography) got me interested in Antarctic microbiology nearly 30 years ago, obtained much of the financial support for my current research, and has always provided intellectual jousting of ideas that often resulted with our numerous papers together. He deserves the greatest appreciation that I can give. I also thank those in the AMLR program, especially Drs. Roger Hewitt, Christian S. Reiss, and Rennie Holt (Southwest Fisheries Science Center, La Jolla), for the opportunities that such a program can provide through its "ecosystem approach" to ecology. Dr. Christian S. Reiss and both Drs. Mati Kahru and B. Greg Mitchell from Scripps Institution of Oceanography were my co-authors in several publications, and obviously contributed to my focus on details of the relationships between hydrography and phytoplankton ecology. In addition, Professors Tron Frede Thingstad, Ian Dundas, and Gjert Knudsen at the University of Bergen and Professor Egil Sakshaug at the Norwegian University of Science and Technology, Trondheim, were of tremendous help during my years in Bergen and have my everlasting gratitude. Professor Egil Sakshaug also involved me with Barents Sea ecology through Pro Mare, in which I participated over several years while in Norway. Professor John Burks introduced me to landscape ecology through his advanced statistical ecology course at the University of Bergen that has made a lasting impression on how I interpret ecological data. Thanks are also extended to friends and colleagues who made up the Department of Microbiology (and Plant Physiology) at the University of Bergen during my graduate studies. I lastly thank Dr. Osmund Holm-Hansen, and Professors Egil Sakshaug, Tron Frede Thingstad, and David Karl (University of Hawaii) for their reviews, comments, and suggestions that improved my thesis.

Foreword

The US Antarctic Marine Living Resources (AMLR) program has conducted oceanic surveys during each austral summer in the South Shetland Islands (Antarctica) region since 1990. The area that is surveyed is located between the northern Antarctic Peninsula and the central Drake Passage, and encompasses vastly different ecosystems. The Drake Passage includes both the eastern edge of a large high-nutrient, low-chlorophyll (HNLC) region and the western edge of the Scotia Sea, which is among the most productive pelagic areas of the Southern Ocean. To the south of the AMLR survey area lies the Weddell Sea, a source of nutrient-rich water that empties into those constrained by the Antarctic Circumpolar Current to the north. Typically, two survey cruises are made each year, in mid-January to mid-February and mid-February to mid-March, in which ~100 regular stations are visited during each cruise. For each station, samples are obtained to measure, among others, the hydrographical properties and chlorophyll concentrations of the water column. Less frequently, samples are obtained for macro- and micronutrients, photosynthetic pigments, primary productivity, etc. These hydrographic, chemical, biological and optical data have been compiled into a relational database, containing data from >3,000 stations (1990-2008), that has been essential to the current understanding of the ecosystem for the South Shetland Islands area as illustrated by the papers included in this thesis.

My thesis consists of a set of six related papers that provide a quantitative description of microbial (phytoplankton) ecology for waters of the South Shetland Islands area. Each paper deals with a different aspect of this ecosystem, but when placed in context with the others provides an understanding of ecological principles that can be examined using gradient analyses. My thesis incorporates the application of quantitative methods to explain much spatial and temporal variability for phytoplankton biomass as observed in the South Shetland Islands area during austral summer. I show that, in waters surrounding the South Shetland Islands, a co-limited

control of phytoplankton by iron and mixed layer depth results with variability in chlorophyll concentration having a unimodal distribution across the salinity gradient. However, the taxonomic composition of the phytoplankton communities also changes across the salinity gradient, being likely more an expression of differing community grazing strategies between biogeochemical provinces than simply a change in biomass.

Abstract

The waters surrounding the South Shetland Islands, Antarctica, comprise a coastal/oceanic ecosystem that is iron-fertilized naturally from shelf sources of Weddell Sea origin. My thesis incorporates data from an 18-year time series of hydrographic, chemical and phytoplankton studies carried out during austral summer by the US Antarctic Marine Living Resources program. I show that the South Shetland Islands area is bordered by two contrasting high-nutrient, low-chlorophyll (HNLC) regions, and has an area of phytoplankton blooms that extends eastward from the shelves and shelf breaks surrounding the islands into the central Scotia Sea. As a consequence of low iron concentration, the HNLC region in the northwest sector has low surface chlorophyll concentrations but has a deep chlorophyll maximum (DCM) below the upper mixed layer. The DCM is a result of enhanced production due to elevated iron concentrations in the ferrocline, even though low ambient irradiance (hence light controlled photosynthetic rates) occurs there. The HNLC region in the southeast sector is abundant in nutrients, including iron, but has low chlorophyll concentrations resulting from deeply mixed surface waters to provide low mean ambient irradiances.

The phytoplankton blooms in the central and northeast sectors occur where both HNLC sources overlap to result with surface waters having high iron concentrations and shallow mixed layers. This mixing between sources of water is described qualitatively in terms of a salinity gradient, across which the variability in chlorophyll concentration has a unimodal distribution. Maximal concentrations of chlorophyll occur at salinity ~34, and they vary among years as a function of the upper mixed layer depth that is influenced by sea surface temperature. In turn, sea surface temperature appears associated with the atmospheric climate having a global connection through the El Niño Southern Oscillation. The two HNLC areas constitute different biogeochemical provinces, and the phytoplankton community size-class composition changes between them. This change is hypothesized as a result of size-

selective vs. non-selective grazing strategies of the different zooplankton assemblages that reside in each of the two provinces.

List of Papers

[1]Hewes, C.D. 2009. Cell-size of Antarctic phytoplankton as a biogeochemical condition. Antarc. Sci., 21(5): 457-470. doi:10.1017/arcS0954102009990125.

[2]Hewes, C.D., C.S. Reiss, M. Kahru, B.G. Mitchell, and O. Holm-Hansen. 2008. Control of phytoplankton biomass by dilution and mixing depth in the western Weddell-Scotia Confluence. Mar. Ecol. Prog. Ser., 366: 15-29.

[3]Hewes, C.D., C.S. Reiss, and O. Holm-Hansen. 2009. A quantitative analysis of sources for summertime phytoplankton variability over 18 years in the South Shetland Islands (Antarctica) region. Deep-Sea Res. I, 56: 1230-1241.

[4]Holm-Hansen, O. and C.D. Hewes. 2004. Deep chlorophyll-a maxima (DCMs) in Antarctic waters: I, Relationships between DCMs and the physical, chemical, and optical conditions in the upper water column. Polar Biol. 27: 699-710.

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Contents

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Background

The Southern Ocean, having no geographical features to describe its northern boundary, is politically defined as those waters lying between 60 °S to the Antarctic Continent. Sverdrup et al. (1942) discussed that major oceanic fronts could be used to delineate this northern boundary and suggested the Subtropical Front, although waters lying south of the Polar Front are often considered (see **Paper #1**). The Southern Ocean is an oceanic system of relative hydrographic simplicity - the Antarctic Circumpolar Current (ACC) contains the bulk of its waters and flows in an easterly direction (Fig. 3, **Paper #1**). The Southern Ocean also includes two large bays that define the Weddell and Ross Seas (Fig. 2, **Paper #1**) that as well have a generally clockwise circulation (Fig. 3, **Paper #1**). The ACC is the largest unimpeded oceanic circulation of our planet, and with the exception of deflection caused by the Antarctic Peninsula, flows clockwise largely driven by the winds that provide its other name – the "West Wind Drift". The Southern Ocean also contains the largest high-nutrient, low-chlorophyll (HNLC) areas of any ocean (Chisholm and Morel, 1991), in which nitrate concentrations are generally high (>10 µM) thus not consumed by phytoplankton, and a condition often referred to as the "Antarctic Paradox".

A survey of the literature (**Paper #1**) indicates that HNLC regions of the Southern Ocean are located predominately over deep basins (Fig. 2, **Paper #1**), where minimal iron enrichment of surface waters from either coastal sediments or upwelling processes occurs (Table 1 in **Paper #1**). Many of these HNLC waters contain a deep chlorophyll-a (Chl-a) maximum (DCM) located below the upper mixed layer (UML), and are at depths where light and iron are sufficient to support elevated primary production (also see **Paper #2**). Surface waters overlying or downstream of topographical seamounts/ridges in the Southern Ocean correspond with elevated Chl-a in the UML and do not have a DCM (**Paper #1**). The enrichment of Fe in pelagic

surface waters necessary to elevate Chl-a concentration is thought to be the result of upwelling processes (de Baar and de Jong, 2001; de Baar et al., 1990; 1995; Measures and Vick, 2001; Watson, 2001; Hiscock et al., 2003). The most pronounced areas of elevated Chl-a concentrations in the pelagic Southern Ocean are the Polar Frontal region (lying downstream of South Georgia and over the Southwest Indian Ridge), the Kerguelen/Crozet Plateaus, the Pacific Antarctic Ridge, the Southeast Indian Ridge, and the Scotia Sea (**Paper #1**). These collective observations are initial evidence that both UML depth (determining light regime) and iron are the principal controlling factors of primary production in the pelagic Southern Ocean (see de Baar et al., 2005).

The central Scotia Sea combined with areas to the west and north of South Georgia have higher integrated Chl-a than surrounding waters (Holm-Hansen et al., 2004a; 2004b; Kahru et al., 2007), and is among the largest productive pelagic areas in the Southern Ocean (see Fig. 2, **Paper #1**). Maximal concentrations are reached mid-summer (January), and decline by the austral fall (Holm-Hansen et al., 2004a). In contrast, very low Chl-a concentrations are observed for HNLC waters to the west in the Drake Passage, where maximal concentrations occur by early December and decline to minimum values by March. In the central Scotia Sea, considerable interleaving and mixing of water masses is found at depth, but surface waters appear to be a mixture of the Antarctic Surface Water (AASW) and coastal waters originating from Bransfield Strait and the Weddell Sea (Holm-Hansen et al., 2004a).

Although upwelling of deep iron-rich waters may be evoked to explain the high productivity in the Scotia Sea (i.e., de Baar et al., 1995), extensive horizontal mixing of surface waters by eddy activity might also transport biomass-limiting nutrients (e.g., iron and silicic acid) over great distances and across frontal zones (Strass et al., 2002; Kahru et al., 2007). The interannual variability of cyclonic (upwelling) eddy activity corresponds with elevated Chl-a concentration during spring blooms in the eastern Scotia Sea around South Georgia (Kahru et al., 2007). (Anti-) cyclonic eddies can impart a (de-) stabilizing effect in surface water promoting (downwelling) upwelling that (deepens) shoals the UML, as well as modulating the vertical transport of deep

nutrient sources (away from) into surface waters. It is possible that such eddy activity is responsible for the interleaving of water masses as observed below the UML in the eastern/ central Scotia Sea (e.g., Holm-Hansen et al., 2004a).

Yet, the seasonal plume of elevated Chl-a that extends between the Antarctic Peninsula and South Georgia (Fig.2, **Paper #1**) also suggests a natural iron-fertilization originating from continental sources (coastal regions of the South Shetland Islands, Bransfield Strait, the South Scotia Ridge, and the Weddell Sea) that is transported eastward by prevailing currents (**Paper #1**). Regardless of mechanisms for iron fertilization, since UML depth was found uncorrelated with Chl-a concentration in the Scotia Sea (Holm-Hansen et al., 2004a), iron availability might set an upper limit to the primary productivity that could occur in the central and eastern regions. The mechanism(s) supplying iron for fertilization to regions of the Scotia Sea remains controversial, as well as, do those conditions that prevent phytoplankton from consuming all available nitrate (the "Antarctic Paradox"). This could define most of the Southern Ocean, even productive areas, as "HNLC" waters, although in this thesis "HNLC" is considered as waters with less than ~0.5 mg Chl-a m^{-3}. However, the hydrographic and chemical properties that control the spatial and temporal distributions of microbial populations around the western boarder of the Scotia Sea are now somewhat understood (**Papers #2-#5**), and may provide clues to processes regulating primary production in other areas of the Southern Ocean.

Toward a quantitative microbial ecology of the South Shetland Islands (SSI) area

The US Antarctic Marine Living Resources (AMLR) program conducts its annual ecosystem survey at the western edge of the Scotia Sea (Lipsky, 2007). The composition of water masses within the water column varies considerably within the SSI area, as well as, do properties of the surface layer as is reflected in nutrient (nitrate, phosphate and silicic acid) and Chl-a concentrations (Holm-Hansen et al., 1997; **Paper #3**). The pelagic waters in the northwestern portion of the program's survey grid generally have very low Chl-a concentrations (<0.2 mg m^{-3}) in the UML (~50 m) during summer. A DCM occurs in the pycnocline at ~50-100 m, with peak

Chl-a concentrations at ~75 m that often are double those at the surface (**Paper #2**). DCMs likely develop by late austral spring after phytoplankton biomass in the UML has declined upon the depletion of available iron that was supplied from vertical mixing during winter. The very low Chl-a concentration in surface waters during austral summer results with a photic zone that extends into the pycnocline. In combination with presumably elevated iron concentrations in the pycnocline, photosynthetic rates and, subsequently, phytoplankton biomass (in terms of Chl-a) increase**.** The formation of the DCM is the result of increased net primary production at depth (evidenced by elevated O_2 concentrations), and not from a passive sinking of cells from the UML, or by the subduction of Chl-a from rich coastal waters. Importantly, no significant differences in photosynthetic rates occur between communities from iron-controlled and iron-replete environments in the SSI, so that differences in primary productivity are reflected largely by Chl-a concentration (i.e., biomass) rather than growth rate at a given irradiance (**Paper #2**).

In the AMLR survey area, summertime phytoplankton blooms are most often found in the northeastern pelagic waters north of Elephant Island, as well as, over the shelf and shelf-break areas surrounding the SSI. Optimum conditions for phytoplankton blooming result from horizontal mixing of surface waters between two areas of contrasting HNLC properties (**Paper #3**). Property/property plots and changes in trace metal and nutrient concentrations across isopycnal surfaces show that horizontal mixing of source waters, not upwelling from depth, is responsible for elevated iron concentrations found in the UML. The source of iron is high-salinity Weddell Sea Shelf Water (WSSW), but these waters are weakly stratified and have a deeply mixed surface layer leading to low Chl-a concentrations (**Papers #3, #4**). The depth of the UML is critical for the development of phytoplankton biomass in nutrient-replete waters (Sverdrup, 1953), with photosynthetic growth regulated by the shoaling of the UML that determines the mean irradiance to which a mixed-layer population is exposed (Mitchell and Holm-Hansen, 1991; Nelson and Smith, 1991). The most stratified waters of the SSI region are from low-salinity AASW found in the Drake

Passage ACC, but these contain low concentrations of iron that also result with low Chl-a concentrations (see also **Paper #2**).

The horizontal mixing of surface waters occurs between two HNLC sources that have a large difference in salinity, therefore the salinity gradient is a measure of the extent that one HNLC property has mixed conservatively with the other (**Papers #3, #4**). The response of phytoplankton to different conditions that control productivity results as a unimodal distribution of Chl-a variability across the salinity gradient. At low (high) surface salinities, Fe is scarce (abundant) and the UML is shallow (deep) resulting in low Chl-a concentrations that defines a specific HNLC area, being of AASW (WSSW) source(s). The salinity optimum for maximum Chl-a concentrations occurs at ~34, and represents the phytoplankton community response to shoaled UML depths (increased availability of incident irradiance) and adequate iron concentrations. Since the response pattern of Chl-a concentration to horizontal mixing in the SSI area is unimodal across salinity, the mechanisms controlling inter-annual variability and community structure can be examined in a quantitative manner using gradient analyses (i.e., **Papers #4, #6)**.

Eighteen years of hydrographic and phytoplankton data show that phytoplankton blooms ($>\sim 1$ mg Chl-a m^{-3}) at intermediate salinities of ~34 during summer have inter-annual variability correlated with the seasonal mean sea surface temperature that modulates depth of the UML (**Paper #4**). It is the depth of the UML, not iron concentration, found to regulate the magnitude of blooms in waters of the SSI, with depth of the UML a function of sea surface temperature (**Papers #4, #5**). However, even though maximal Chl-a occurs at a salinity of ~34, the mean UML Chl-a, as well as the mean UML salinity, for the AMLR survey area has a large inter-annual variability (**Paper #5**). Therefore, the outflow of the Weddell Sea and inflow of the ACC into the SSI area varies among years to influence the horizontal distribution of surface salinity and surface Chl-a, while maximal Chl-a concentrations occur at a salinity optimum of ~34 independent of location.

It is most likely that atmospheric climate regulates sea surface temperature that modulates UML depth, since the co-variability of temperature and UML depth was independent of salinity (**Papers #4, #5**). Although the frequency and severity of storms in the Southern Ocean might influence UML depth through a deep vertical mixing with pycnocline waters (Sakshaug et al., 1991), this process (as well as that of upwelling) would result with changes in UML temperature corresponding with changes in salinity. The inter-annual variability for UML salinity and temperature in the SSI area were not correlated (**Paper #5**), so that variability in UML temperature at salinity ~34 must reflect the net heat flux from incident solar irradiance that would be the only source of heat independent of conservative mixing between different water sources (**Paper #4**). Thus, climate has an impact upon UML depth through surface water temperature that modifies density, and as a consequence, influences the development of phytoplankton blooms in the SSI area. Ocean/atmosphere teleconnections were found to loosely correspond with water column properties in the SSI area (**Paper #5**). A deepening (shoaling) of the UML during El Niño (La Niña), being likely the result of lower (warmer) temperatures for the UML, limited (enhanced) bloom conditions. The marine food web in the SSI area is based primarily on phytoplankton productivity, and thereby this ecosystem becomes linked to patterns in global climate and its future change.

Yet, un-amended water from the SSI area can be incubated to grow its own phytoplankton to concentrations of 10-30 mg Chl-a m^{-3} within 1-2 weeks under conditions of low to moderate irradiance (Sakshaug and Holm-Hansen, 1986; Helbling et al., 1991; Holm-Hansen et al., 1999; Hopkinson et al., 2007). Similarly, blooms in localities adjacent to the SSI area can reach Chl-a concentrations that strip surface waters of macronutrients (Holm-Hansen et al., 1989). These are much higher phytoplankton biomasses than found on average in the high-productive waters of the SSI area (**Papers #4, #5**). Therefore, although light and iron are the critical bottom-up factors controlling gross primary productivity, it becomes apparent that other factors, such as grazing, are involved to control the magnitude of phytoplankton blooms in the SSI area. Grazing can influence the phytoplankton community structure through the

type of feeding strategy that would be different between protists and large zooplankton (Hewes et al., 1985; 1990), with both bottom-up (i.e., light and nutrients) and top-down (i.e., grazing) factors structuring the Antarctic phytoplankton community (Smith and Lancelot, 2004; Hoffmann et al., 2006). Specialized food web communities might also occupy different biogeochemical provinces of the Southern Ocean (Smetacek et al., 2004), and although the type of food available could determine the consumer species, grazing strategy might determine the taxonomic composition of a community. Such hypotheses can be tested in the SSI area (**Paper #6**) because Chl-a concentration has a unimodal distribution in variability across the salinity gradient that describes conditions between two dissimilar biogeochemical provinces (i.e., the light- vs. iron-controlled HNLC environments).

The Antarctic microbial food web consists of protozoan grazers (Hewes et al., 1985) that represent ~30% of total eucaryotic microbial biomass (Hewes et al., 1990; Becquevort, 1997) and consume 20-80% of daily primary productivity (Becquevort, 1997; Hall and Safi, 2001; Selph et al., 2001; Froneman et al., 2004). The Chl-a size-class composition of the phytoplankton community relates to different taxa, both autotrophic and heterotrophic, within a microbial population that changes with the Chl-a concentration (Hewes et al., 1990). Biota growing as natural cultures in un-ammended water from the SSI area develops such that the microplankton (>20 μm) Chl-a size-class increases at a rate faster than the nanoplankton (2-20 μm) Chl-a size-class (Helbling et al., 1991; Holm-Hansen et al., 1999; Hopkinson et al., 2007). Such cultures are incubated without large zooplankton (e.g., copepods, krill, or salp) and the results are strong evidence that grazing by protists is a selection process leading toward larger phytoplankton cell-size as predicted by Hewes et al. (1985), formalized by Thingstad and Sakshaug (1990), and developed further by Thingstad (1998).

Historically, the SSI area and Scotia Sea are well known for their high biomass of Antarctic krill, *Euphausia superba* (Marr, 1962; Everson and Miller, 1994; Hofmann et al., 1998; Atkinson et al., 2004; Loeb, 2007; Murphy et al., 2007), being the primary zooplankton in productive summertime waters of the Southern Ocean. The Antarctic

krill is >50 % efficient at filtering cells larger than ~6 μm diameters (McClatchie and Boyd, 1983; Boyd et al., 1984; Morris, 1984), but has a selective grazing strategy by choosing diatoms over *Phaeocystis* independent of the cell-size (Haberman et al., 2003). Moreover, Antarctic krill seem to avoid some types of ciliates (Boyd et al., 1984), yet are known to consume tintinnids, and also heterotrophic dinoflagellates, etc. (Hopkins et al., 1993a; 1993b; Perissinotto et al., 1997), being an important component of their summertime diet (Schmidt et al., 2006). In contrast, *Salpa thompsoni* is a dominant zooplankter found in the unproductive Drake Passage ACC (Pakhomov et al., 2002; Loeb, 2007) with a grazing strategy that is non-selective as occurs by passing water through a fine-meshed feeding net (Le Fèvre et al., 1998). Therefore, assuming a size-classed population of phytoplankton taxa growing at different rates, the introduction of protozoan, salp, or krill in different biomass propportions would influence the size-class distribution of the phytoplankton population in another way with relation to their unique grazing strategies over some given time.

Accordingly, the cell-size of phytoplankton communities during summertime in the SSI area increases from high- to low-salinity waters (**Paper #6**). Yet, small nanoplankton of the 2-5 μm size-class are most important to the composition of phytoplankton blooms in light-controlled environments, while the microplankton are the most important size-class in presumably iron-controlled Drake Passage ACC waters. These community compositions are contrary to an expected "nanoplankton dominating blue waters and microplankton dominating blooms" paradigm (i.e., Hewes et al., 1985), which seems paradoxical. However, this may be evidence that grazing strategies, hence food webs, are different in light and iron-controlled biogeochemical provinces, as suggested by Smetacek et al. (2004).

My hypothesis to explain the paradox for phytoplankton-size composition (**Paper #6**) is that selective grazing of microbial microplankton by Antarctic krill (and associated zooplankton assemblage) in productive regions of the SSI not only reduces the biomass of microplankton, but also has an impact on the protists that graze on

nanoplankton. Selective grazing pressure should cascade downward in the microbial food web by elevating the biomass of the least grazed phytoplankton (i.e., Hewes et al., 1985; Thingstad and Sakshaug, 1990; Thingstad, 1998). In this case for the SSI area, nanoplankton of the 2-5 μm size-class would be the largest size-class least impacted by selective grazing from a krill-dominant assemblage and otherwise mostly consumed by large protists that are also grazed by krill. This contrasts with low-productive, iron-controlled Drake Passage ACC waters that might be non-selectively grazed by the salp (and associated zooplankton assemblage; i.e., Pakhomov et al., 2002; Smetacek et al., 2004). Non-selective grazing would tend to maintain a microbial trophodynamic such that large cell-size provides survivorship from protist grazing. Even though large phytoplankton might have a slower *gross* rate of growth than small cells under iron-stressed conditions (Timmermans et al., 2001; 2004), an environment of non-selective zooplankton grazing would provide that large cell-size reduces the impact of microbial predation thereby increasing *net* growth rate of large-sized phytoplankton cells. That the composition of microplankton Chl-a increases for un-amended natural cultures inoculated from low-iron waters of the SSI area (Hopkinson et al., 2007) is evidence that large cells can achieve higher net growth than small-cells under iron-controlled conditions. A higher *net* growth of large-sized cells could lead towards their dominance in the microbial community as observed (**Paper #6**) and ultimately become a nutrient sink (including iron in the iron-controlled environment).

For the SSI area, the mechanisms that control phytoplankton biomass appear to occur in a hierarchal manner, such that bottom-up factors primarily influence the variability of total phytoplankton biomass, while grazing introduces an additional variability (a deviation from potential biomass) that leads to a labile phytoplankton community size-class structure. This notion is similar to a line of logic followed by Thingstad (1998) for modeling of microbial food webs, i.e. "Nutrient content determines the carrying capacity of the whole food web, the size selectivity of predators determines how the nutrient content is distributed between size classes of osmotrophs and phagotrophs …". The variability of Chl-a concentration has a unimodal distribution across the

salinity gradient for the SSI area, with salinity being an index for the blending between waters of contrasting HNLC conditions (**Papers #3, #4**). The "carrying capacity of the whole food web" on the inter-annual scale is reflected by the variability for maximal Chl-a concentrations at salinity ~34 for each year that corresponded with UML depth (i.e., the control by light; **Paper #4**). Yet, even though the Chl-a concentration for each size-class generally increased with total Chl-a concentration, the unimodal distribution for variability of total Chl-a concentration occurred mostly independent of the change in community size-class structure (Fig. 4 in **Paper #6**, with noted exceptions). Therefore, grazing for an entire community would be size-selective that leads toward a dominance of the least impacted taxa (i.e., the 2-5 µm size-class in light-controlled waters of the SSI area), while the magnitude of biomass for phytoplankton, although not reaching its potential from limiting nutrient because of grazing, fluctuates primarily as a function of UML depth.

Salinity is the gradient delimiting iron- versus light-controlled environments in surface waters of the SSI area that structures variability in the phytoplankton productivity as a unimodal response to co-limiting conditions thus regulating its biomass (**Papers #3, #4**). A succession of taxa through size-class occurs across this salinity gradient (**Paper #6**) that is likely both a function of light and iron availability, as well as, the assemblages of grazers that consume phytoplankton. Biological conditions for the SSI area can be described in terms of the salinity gradient in a consistent manner (**Paper #4**) which make it unique, and it is unlikely that many other ecosystems in the Southern Ocean can be described similarly (see **Paper #1**). Although low-iron HNLC conditions exist throughout the Southern Ocean, including the AMLR survey area (**Paper #2**), much of the iron that fertilizes the high-productive pelagic regions of the Southern Ocean is thought as occurring through upwelling (**Paper #1**). The SSI area therefore is distinguished from these other areas because iron-fertilization occurs through horizontal mixing and not upwelling (**Paper #3**). The SSI area lends itself as a natural laboratory because of its predictable iron-fertilization (**Paper #4**) combined with variable depths of the surface-layer (**Papers #3, #4, #5**), as well as containing an HNLC area where a DCM is found (**Paper #2**). Ecosystem dynamics therefore

become easier to understand for this area than in many other areas, especially because contrasting HNLC environments are in close proximity (**Papers #2, #3**), and comparable hydrographical and biological properties of the water column recur among years (**Papers #4, #5**). These conditions structure the microbial community composition for the SSI area that is also recurrent among years (**Paper #6**). However, there is still great variability in the horizontal and temporal distribution of phytoplankton that has not been, or even attempted to be, examined in my thesis. Undoubtedly, the SSI ecosystem will be understood in even greater detail over the next years. These new details, placed in context to a variability across the salinity gradient, may provide that the dynamic connections between climate, hydrography, chemistry, optics, and biology be eventually coupled into broad ecological models.

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