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MICROBIOLOGICAL OCEANOGRAPHY IN THE REGION WEST OF THE ANTARCTIC PENINSULA: MICROBIAL DYNAMICS, NITROGEN CYCLE AND CARBON FLUX

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Microorganisms are ubiquitous in Southern Ocean habitats and play a vital role in production and transformation of organic matter. Compared to other coastal and oceanic habitats, however, microbial processes in antarctic marine habitats are poorly understood. One major reason is the spatially and temporally variable nature of the habitat and the general inaccessibility of selected habitats (e.g., multi-year pack ice in austral winter). Despite these limitations, the region west of the Antarctic Peninsula is beginning to provide an opportunity for year-round field investigations. Progress to date has focused on the role of microorganisms in the biogeochemical cycling of carbon and associated elements, the regulation of bacterial populations and the relationships between primary production and particulate matter export from the euphotic zone. The emergent patterns of carbon and energy flow and of microbial population inter-actions comprise a prospectus and a challenge for future studies in this region.

1. INTRODUCTION

Microorganisms, defined here as organisms with a diameter of approximately 150 μm or less, are ubiquitous in the world ocean. In most marine environments they generally comprise the greatest biomass (i.e., g C m^{-3}) of living organisms. This large and diverse assemblage includes all three major phylogenetic domains: *Archaea*, *Bacteria* and *Eucarya* [*Olsen et al.*, 1994], and virus particles.

In the sea, microorganisms are largely responsible for the production and decomposition of organic matter, for the uptake and regeneration of inorganic nutrients and for the control of the chemical redox state. One unique characteristic of microorganisms is their ability to use a variety of carbon and energy sources during metabolism. Photoautotrophs use sunlight as their energy source and dissolved inorganic carbon (DIC) as their carbon source. Photoautotrophic marine microorganisms are responsible for a major portion of the organic matter and oxygen production on earth. All other groups of marine micro-organisms rely directly or indirectly upon the chemical energy produced during photosynthesis. Although most microorganisms are free-living, certain groups exist in symbiotic associations either with microbes or metazoans.

Marine microbes have a major impact on both local and global environments. In addition to their primary metabolic activities, many species produce, or consume, growth-stimulating and growth-suppressing organic compounds (e.g., vitamins, organic toxins), while others emit "greenhouse" or ozone-destroying gases (e.g., methane and nitrous oxide) as normal by-products of cellular metabolism. Complex interactions and nutritional interdependencies of organisms occur in the marine environment. Consequently, it may be inappropriate to extrapolate data derived from pure cultures of laboratory-reared cells to microbial processes *in situ*.

Superimposed on these integrated metabolic processes are numerous physical and chemical interactions that define the complex and temporally variable marine habitat. Some of the higher frequency temporal variability is predictable (e.g., diurnal, tidal, seasonal) but other processes (e.g., storms, volcanic eruptions) are stochastic. On longer time scales (e.g., decades to centuries), coupled ocean-atmosphere interactions and other global processes can cause habitat variability and provide a mechanism for biodiversity or evolutionary change. Such is the complex nature of microbial life in the sea.

Of all the marine habitats investigated to date, those in the Southern Ocean are among the least well understood [*Fried-*

mann, 1993]. Although the antarctic marine environment (including all ocean, sea ice and island components south of the Antarctic Convergence zone) is one of the largest ecosystems on Earth (36 x 10^6 km^2) [*Petit et al.*, 1991], it is undersampled relative to other more accessible locations. Furthermore, the extreme variability in climate, solar radiation and sea-ice extent yields a physically and biologically variable habitat that is difficult to fully appreciate from a single field expedition. Repeated observations over several years and during all seasons, and comprehensive synoptic assessments of ocean circulation, chemistry and biology will be required to elucidate ecosystem structure and function.

The Palmer Long-Term Ecological Research (Palmer LTER) program was established in 1990 at Palmer Station, Antarctica as an interdisciplinary study to seek a general understanding of ecosystem processes and to model the interactions between key groups of organisms and the physical environment [*Smith et al.*, 1995]. For the past several years, one component of the Palmer LTER study ("Microbial Dynamics and Carbon Flux," D. Karl, P.I.) has focused on microbiological oceanography in the coastal and shelf waters west of the Antarctic Peninsula and within the seasonal ice pack. The central hypothesis of the Palmer LTER program is that the annual advance and retreat of sea ice is a major physical determinant of spatial and temporal changes in the structure of antarctic ecosystems. It is well known that sea ice can influence the timing and magnitude of primary production, krill recruitment and reproductive success of apex predators [*Fraser et al.*, 1992; *Smith et al.*, 1995]. Sea ice also provides one of the major habitats for microorganisms and certain food webs are entirely ice-associated [*Palmisano and Garrison*, 1993].

This chapter will provide information on Southern Ocean habitats and the microbial processes therein, including selected data summaries from recent field programs. A majority of the chapter discussion focuses on four topics in contemporary microbiological oceanography that are relevant to our long-term investigations of the western portion of the Antarctic Peninsula: (1) oxygen dynamics including photosynthesis, respiration and photorespiration, (2) bacterial growth and population regulation, (3) bioelement cycling as exemplified by dissolved nitrogen cycling rates and processes, and (4) export production and mesopelagic microbial processes. Although presented as separate subsections in this review, these four sets of processes are interdependent. This review will concentrate on marine habitats in the region west of the Antarctic Peninsula (Figure 1), however, some published data from other antarctic ecosystems are also presented. The information summarized here is intended to complement other chapters in this volume that also deal with various aspects of marine microbiology, in particular those prepared by *Garrison and Mathot* (Part III, Chapter 1), *Bidigare et al.* (Part III, Chapter 2) and *Smith et al.* (Part IV, Chapter 2). This work is also meant to build upon the recent reviews by *Vincent* [1988], *Karl* [1993] and *Knox* [1994].

2. CHRONOLOGY OF RECENT FIELD OBSERVATIONS

Pioneering microbiological studies conducted in a variety of antarctic marine habitats during the first half of the 20th century documented bacteria as an important component of the indigenous microbial assemblage [*McLean*, 1918; *Darling and Siple*, 1941; and references cited in *Sieburth*, 1965 and *Bunt*, 1971]. During the 1950's J. Bunt, H. McBee, J. Sieburth and A. E. Kriss initiated what we consider to be the beginning of antarctic marine microbial ecology as a scientific discipline. However, the methods that were at their disposal are, today, considered inappropriate and inaccurate. Furthermore, most of these investigations retained the traditional view of bacteria as isolated components of the ecosystem, and none of these studies was interdisciplinary in scope. Quantitative, *in situ* investigations of planktonic microbial communities south of the Antarctic Convergence during the past two decades are now forming a coherent picture of marine microbial processes in Southern Ocean habitats. Foremost among these interdisciplinary studies are the multi-year Second International Biomass Experiment (SIBEX), Antarctic Marine Ecosystem Research at the Ice-Edge Zone (AMERIEZ) [*Sullivan and Ainley*, 1987; *Smith and Garrison*, 1990], Research on Antarctic Coastal Ecosystem Rates (RACER) [*Huntley et al.*, 1991a], and the ongoing Palmer Long-Term Ecological Research (Palmer-LTER) [*Quetin and Ross*, 1992; *Smith et al.*, 1995] and the Southern Ocean Joint Global Ocean Flux Study (JGOFS) research programs. These modern studies have focused on precise and accurate physical and chemical descriptions of the microbial habitats, their associated populations and population interactions, including bacteria, viruses, unicellular algae, protozoans and small metazoans.

3. HABITAT CHARACTERISTICS

Although antarctic waters are perennially cold, and in some locations permanently ice-covered, there is nevertheless a large diversity of microbial habitats and, therefore, microbial assemblages. These microbial habitats range from hypersaline and supercooled sea-ice micro-environments to the open-ocean pelagic realm of the Antarctic Circumpolar Current (ACC). Superimposed on these spatially diverse marine habitats is an intense temporal variability, perhaps the most extreme seasonality observed anywhere in the world ocean. This is especially true for coastal ecosystems, which experience an annual cycle of sea-ice formation and ablation, as well as large variations in phytoplankton biomass and rates of primary production due to changes in mixed-layer depth and solar radiation. An excellent discussion of the physical setting of the region west of the Antarctic Peninsula, including geography, bathymetry, meteorology and hydrography, is presented elsewhere in this volume [*Hofmann et al.*, this volume].

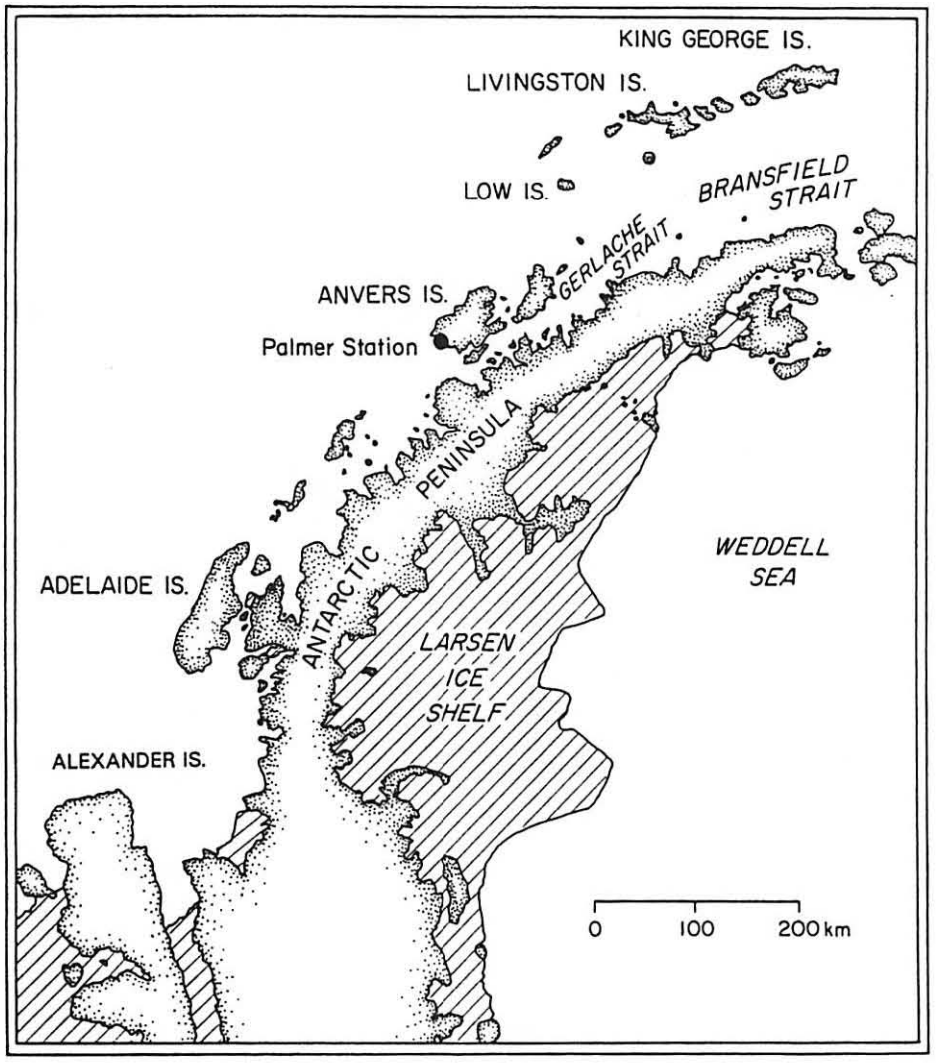

Fig. 1: Map of the Antarctic Peninsula showing the locations of Bransfield Strait, Gerlache Strait and the Weddell Sea. Permanent ice sheets are indicated by the diagonal line patterns. The Palmer LTER study region extends along the western side of the Antarctic Peninsula from Livingston Island to Alexander Island and seaward to approximately 200 km from the coast.

Ice is a dominant feature of the antarctic environment, and is known to play an important role in structuring antarctic ecosystems. For example, sea ice growth during austral fall and winter effectively divides the oceanic ecosystem into two dissimilar compartments: the water column and the pore spaces within the accreting pack [*Eicken*, 1992]. Furthermore, ice cover affects light quality and quantity as well as gas exchange rates. Complex ice structures and morphological processes, including frazil ice growth, snow layer flooding, pressure ridge genesis, thermally driven brine drainage and platelet ice formation all affect the sea ice community structure and function [*Ackley and Sullivan*, 1994].

Satellite remote sensing of the antarctic sea-ice zone between 1973 and 1975 showed a minimum coverage of 3 x 10^6 km^2 in February and a maximum of 20 x 10^6 km^2 in September-October [*Zwally et al.*, 1983]. The latter figure represents approximately 50% of the total area of the Southern Ocean and emphasizes the importance of the annual sea-ice cycle. The seaward boundary of the sea-ice zone is irregular in shape and variable in northern extent and in total coverage from year to year. This interannual variability has a direct influence on the biological productivity of the marginal ice-edge zone [*Smith et al.*, 1988].

The timing of the annual advance and retreat of sea ice in the Palmer LTER study is highly variable. Analysis of satel-

lite passive microwave data, available from the past 17 years, shows that the Palmer LTER study area has a mean annual ice cycle that typically involves a period of ice advance (~5 months), followed by a longer period of ice retreat (~7 months) [*Stammerjohn*, 1993; *Stammerjohn and Smith*, this volume]. In addition, these satellite data show evidence of a recurrent 6 to 8 year cycle, with high ice years (1979-82, 1986-87 and 1991-92) and low ice years (1983-85, 1988-90 and 1993-94). It is important to mention that the interdisciplinary RACER-1 (1986-87) experiment was during the most extensive ice year on record, and that RACER-2 (1989) was conducted during the lowest ice year on record [*Stammerjohn and Smith*, this volume]. Sea-ice extent and dynamics in the region west of the Antarctic Peninsula may be controlled by the upwelling of relatively warm Circumpolar Deep Water (CDW) onto the continental shelf. These upwelling events modify heat and salt fluxes, alter nutrient budgets and may provide a mechanism for control of plankton diversity.

Extreme seasonal variability in day length, low temperatures, generally high nutrient levels, and springtime water column stability mediated by sea ice melting and surface heating, are key factors controlling phytoplankton and bacterial population growth in waters of the Southern Ocean [*Smith et al.*, this volume]. In addition to providing increased light for the growth of photoautotrophic microorganisms, the seasonal changes in radiant energy result in local heating of the upper ocean, which stabilizes the surface waters, especially in coastal regions protected from deep, wind-driven mixing. The ablation of sea ice further stabilizes the water column through the addition of low-density meltwater. The net biological effect is a phytoplankton bloom [*Sverdrup*, 1953; *Smith and Nelson*, 1985; *Holm-Hansen et al.*, 1989; *Mitchell and Holm-Hansen*, 1991]. These potentially extensive blooms provide the bulk of carbon and energy required to sustain the entire antarctic food web and are important in the production and removal of particulate organic matter from the surface layer of the ocean and, perhaps, in the control of atmospheric carbon dioxide.

4. DIVERSITY AND DISTRIBUTIONS OF MICROBIAL POPULATIONS

Microorganisms are classified on the basis of size, phylogenetic relationships or nutritional requirements. The latter scheme includes both the energy source and the carbon source required for growth. Among bacteria in particular, there is a remarkable diversity of metabolic pathways [*Rittenberg*, 1969]. In addition to nutritional diversity, microbial assemblages in antarctic marine environments appear, initially, to be as phylogenetically diverse as temperate marine ecosystems. Among the most significant and unexpected results of the ribosomal RNA-based phylogenetic analysis of natural populations of antarctic micro-organisms was the discovery of a high abundance of archaebacteria in the marine

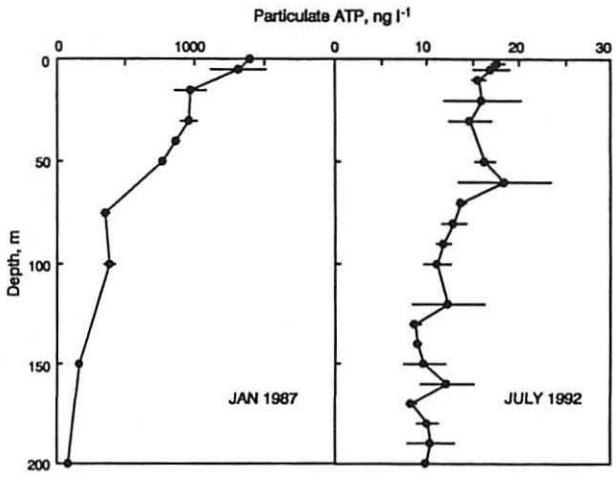

Fig. 2: Particulate ATP concentration profiles for a station located in Gerlache Strait sampled during the RACER program. [LEFT] Conditions during the spring-summer bloom in the 1986-87 austral summer showing surface ATP concentration of nearly 1500 ng l^{-1} (equivalent to a microbial biomass of approximately 375 mg C m^{-3}) and a steep concentration gradient with depth to a value of 15 mg C m^{-3} at 200 m. These summertime ATP concentrations are among the highest measured in non-polluted ocean waters. [RIGHT] Conditions in winter showing a rather uniform depth distribution and a much reduced microbial biomass of 2.5-4 mg C m^{-3} throughout the upper 200 m of the water column. These wintertime ATP concentrations are among the lowest ever reported for a surface ocean ecosystem [From: *Tien et al.*, 1992].

picoplankton [*DeLong et al.*, 1994]. Archaebacteria were previously thought to thrive only in hypersaline, hyperthermal or strictly anoxic habitats. The physiology and ecology of these antarctic archaebacteria is, at present, unknown.

The ocean waters west of the Antarctic Peninsula are characterized by a diverse and seasonally variable assemblage of microorganisms. During the spring-summer bloom of phytoplankton, the standing stock of living microorganisms (i.e., biomass) is equal to or greater than that found in any other non-polluted coastal waters. Total microbial biomass of ~375 mg C m^{-3} in the surface waters is not uncommon (Figure 2) [*Karl et al.*, 1991a]. During winter, these same surface waters are among the most oligotrophic on earth with microbial biomass of ~4 mg C m^{-3}. This nearly three orders of magnitude seasonal change in epipelagic biomass must have a major influence on the structure and function of the microbial food web and on the winter survival of metazoans dependent upon primary production as their ultimate food source. This feast-or-famine existence for microbial assemblages in the coastal waters of the region west of the Antarctic Peninsula emphasizes the importance of year round investigations of the marine ecosystem to understand bioelement cycling.

4.1. Phytoplankton and Bacterioplankton Uncoupling During the Spring Bloom

Field results from the RACER program revealed significant regional variability in the distribution and abundance of micro- (20-200 μm) and nano- (2-20 μm) phytoplankton, often with order of magnitude changes in surface ocean chlorophyll a (chl a) or particulate adenosine triphosphate (P-ATP) over horizontal scales of 100 km or less [*Bird and Karl*, 1991a; *Karl et al.*, 1991a; *Holm-Hansen and Mitchell*, 1991]. The geographic distribution of microbial assemblages in the coastal waters of the Antarctic Peninsula is the result of the complex hydrography and biological interactions [*Bird and Karl*, 1991a]. The distribution of biomass and primary productivity was strongly influenced by upper water column physical dynamics, specifically the depth of the surface mixed layer [*Mitchell and Holm-Hansen*, 1991]. During the spring bloom of photoautotrophic microorganisms, a substantial removal of total dissolved CO^2, [NO_3^-+NO_2^-], and PO_4^{3-} was observed, which corresponded to an upper water column (0-50 m) seasonal net production of 8410 mmol C m^{-2}, 827 mmol N m^{-2}, and 53 mmol P m^{-2} [*Karl et al.*, 1991b]. However, in spite of the strong spatial gradients in chl a and photoautotrophic production, bacterial biomass did not show strong spatial covariance with phytoplankton biomass either during or immediately after the bloom [*Karl et al.*, 1991a; *Karl*, 1993].

Results from the RACER program indicate that bacterial biomass, even during the spring bloom (i.e., at chl a concentrations >10 mg m^{-3}) are <1-2% of the contemporaneous phytoplankton standing stock (Table 1). In most other oceanic regions, bacterial biomass is ≥10% of the phytoplankton standing stock. Surface water bacterial cell abundances as low as 3-5 x 10^4 ml^{-1} are common in the coastal waters of the Antarctic Peninsula [*Karl*, 1993; *D. Bird and D. Karl, unpublished RACER and Palmer LTER data*]. Similar results have been reported for other Southern Ocean ecosystems [*Zdanowski and Donachie*, 1993].

As expected, bacterial productivities are also low (relative to phytoplankton productivities), especially during the spring bloom periods. Based on ^{3}H-leucine incorporation, *Tupas et al.* [1994a] reported bacterial production rates of 1-10 mg C $m^{-3}d^{-1}$ for a station in Gerlache Strait. Depth-integrated productivities (0-50 m) at the height of the bloom were <0.6 g C m^{-2} d^{-1} for bacteria compared to >5 g C m^{-2} d^{-1} for the phytoplankton community.

The apparent uncoupling of bacterioplankton and phytoplankton assemblages contrasts with analyses of temperate aquatic ecosystems [*Bird and Kalff*, 1984; *Cole et al.*, 1988]. By comparison to previous field studies, the RACER data suggest a deficit, of up to an order of magnitude, in bacterial cells at chl a concentrations of 2.5 g chl a l^{-1} or greater (Figure 3). A similar result was also evident in the AMERIEZ [*Cota et al.*, 1990] and Prydz Bay [*Lancelot et al.*, 1989] data sets collected outside the Antarctic Peninsula region, suggesting that eutrophic ecosystems of the Southern Ocean exhibit autotrophic-heterotrophic relationships that are fundamentally different from other marine habitats studied to date.

Possible mechanisms for the apparent uncoupling include differential temperature effects on microbial metabolism [*Pomeroy and Deibel*, 1986], enhanced substrate requirements at minimum growth temperatures [*Wiebe et al.*, 1993], direct competition for limiting organic substrates [*Karl and Bird*, 1993] and chemical antagonism [*Karl and Bird*, 1993]. None of these hypotheses can be rejected at the present time. However, it should be mentioned that both dissolved organic carbon (DOC) and nitrogen (DON) concentrations in coastal regions of the Antarctic Peninsula are sometimes lower than those reported for most surface ocean waters (Figure 4). Even at the height of the spring bloom when chl a is >20 μg l^{-1}, DOC and DON concentrations are much lower than the concentrations typically measured in the oligotrophic North Pacific subtropical gyre [*Karl et al.*, 1993b; *Tupas et al.*, 1994b]. Either dissolved organic matter (DOM) is not produced during phytoplankton blooms in antarctic coastal waters or DOM production is efficiently coupled to bacterial uptake. However without additional information on the chemical composition, rather than the DOC: DON elemental stoichiometry, it is difficult to predict the efficiency of DOM utilization (see also BACTERIAL GROWTH AND POPULATION REGULATION section).

These data on phytoplankton-bacterioplankton population dynamics raise interesting questions about the *in situ* growth states of antarctic bacteria and the possible existence of starved cells in the bacterial assemblages. *Grossman* [1994] has recently reported that only a small percentage (<15%) of the total bacteria in several diverse open water Southern Ocean habitats are responsive to ^{3}H-leucine, and even a smaller percentage are responsive to ^{3}H-thymidine. These microautora-diographic data are consistent with a starvation survival state for a majority of the bacterial cells [*Morita*, 1993]. On the other hand, data collected during independent investigations (see REGULATION OF BACTERIAL POPULATIONS section) suggest that bacteria may be growing at near maximal rates. This apparent discrepancy is almost certainly related to the spatial and temporal habitat variability that is a hallmark of the Southern Ocean ecosystem.

4.2. Microzooplankton

Microzooplankton are a diverse group of organisms that includes planktonic protozoans (e.g., ciliates, flagellates, radiolarians) and small metazoans (primarily larval and naupliar stages of macrozooplankton). As the name implies, these organisms are heterotrophic, "animal" plankton, feeding primarily on bacteria and small algal cells. However, certain choanoflagellate groups thought to feed on bacteria can also readily consume organic molecules over the molecular weight range 4 x 10^3 to 2 x 10^6 daltons [*Marchant and Scott*, 1993]. These observations suggest that they

TABLE 1. Comparison of Phytoplankton and Bacterioplankton Standing Stocks at a Station in Gerlache Strait during the Development and Demise of the Austral Spring Bloom [From: *Karl and Tien*, 1991]

Sampling Date (1989)	Depth	Phytoplankton Biomass[a] (μg C l^{-1})	Bacterial Biomass[b] (μg C l^{-1})	BACT-C/ PHYTO-C[c] (x 100%)
31 October	5	379	0.46	0.12
	10	389	0.60	0.15
	20	365	0.43	0.12
	30	100	0.83	0.83
	50	45	0.29	0.64
	75	21	0.21	1.0
	100	14	0.18	1.3
7 November	1	850	1.71	0.20
	5	805	1.36	0.17
	10	830	0.79	0.10
	20	191	1.39	0.73
	30	88	0.62	0.70
	75	14	0.08	0.57
	100	6	0.17	2.8
15 November	1	710	1.27	0.18
	5	763	1.15	0.15
	10	711	0.53	0.08
	20	453	0.51	0.11
	30	328	0.41	0.13
	50	38	0.29	0.76
	100	9	0.05	0.56
19 November	1	334	3.02	0.90
	5	369	3.95	1.0
	10	378	5.34	1.4
	20	382	1.11	0.29
	30	55	0.94	1.7
	50	24	0.39	1.6
	75	12	0.36	3.0
	100	9	0.17	1.9

[a]Phytoplankton biomass carbon is estimated from measured chlorophyll *a* concentrations, assuming a C:chlorophyll a ratio of 50 [*Vernet et al.*, 1991].
[b]Bacterial biomass carbon is estimated from measured P-LPS concentrations, assuming a C:P-LPS ratio of 6.35 [*Watson and Hobbie*, 1979].
[c]Phytoplankton biomass/bacterial biomass expressed as a percentage.

may utilize colloids and DOM in addition to bacteria as food sources. *Marchant* [1985] reported that choanoflagellates readily assimilate the excreted mucilage of *Phaeocystis* spp.

Alder and Boltovskoy [1991] have investigated the distributional patterns of microzooplankton in the region west of the Antarctic Peninsula. Silicoflagellates were the numerically dominant group of organisms, followed by dinoflagellates and tintinnids. The total microzooplankton biomasses ranged from <0.01 mg C m^{-3} in Bransfield Strait to >10 mg C m^{-3} in Marguerite Bay [*Alder and Boltovskoy*, 1991]. An authoritative review of antarctic protozooplankton has recently appeared [*Garrison and Gowing*, 1993].

4.3. Viruses

In the past decade, viruses have been identified as a dynamic component of microbial food webs [*Bratbak et al.*, 1994; *Smith et al.*, 1992; *Bird et al.*, 1993]. For samples

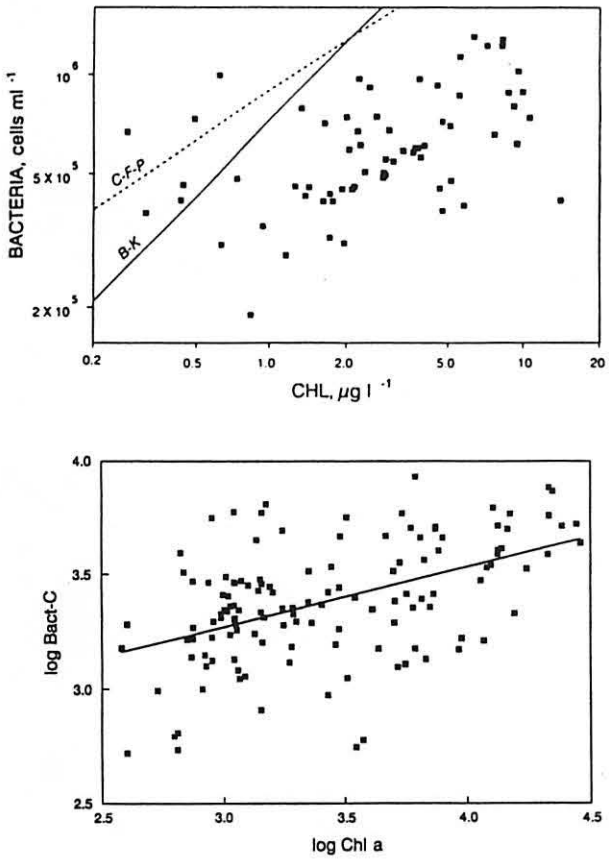

Fig. 3: Phytoplankton-bacterioplankton relationships for the RACER program study area. [TOP] Bacterial cell numbers versus chl a concentrations during the 1986-87 RACER experiment [From *Karl et al.*, 1991a]. The two lines represent the predictions based on previously published empirical relationships from a variety of aquatic environments: solid line, *Bird and Kalff* [1984]; dashed line, *Cole et al.* [1988]. [BOTTOM] Regression plot of the logarithm of bacterial biomass (log Bact-C) in units of ng C l^{-1} as determined by particulate lipopolysaccharide (P-LPS) [bacterial-C = P-LPS x 6.35; *Watson and Hobbie*, 1979] analyses versus the logarithm of chlorophyll a (log Chl a) in units of ng chl a l^{-1} for 132 surface water samples collected in the northern Gerlache Strait during the RACER program (October and November 1989) [From: *Karl and Tien*, 1991].

collected on two separate Drake Passage crossings, virus particle abundances ranged from 0.07 to 5.4 x 10^6 ml^{-1} with order of magnitude higher numbers in austral summer (Jan) compared to austral winter (Aug). The virus-to-bacterium ratios (VBR) were also substantially higher in Jan (VBR [Jan] = 16.8 ± 10.0, n = 9; VBR[Aug] = 5.6 ± 3.9, n = 8) [*Smith et al.*, 1992]. There was no systematic variation of virus particles with depth in the upper 200-300 m of the water column which may be a reflection of the deep surface mixed-layers that are characteristic of Drake Passage. In Paradise Harbor near the entrance to Gerlache Strait in austral spring, *Bird et al.* [1993] reported relatively low numbers of virus particles (<1 x 10^6 ml^{-1}) and low VBR ratios (i.e., <5). These authors noted distinct near surface virus particle depletions that could reflect either ultraviolet radiation damage or removal of viruses by adsorption onto sinking particles [*Bird et al.*, 1993]. The downward flux (i.e., loss rate) of virus particles at 60 m was 1-3 x 10^{12} m^{-2} d^{-1}, approximately 4% of the standing stock [*Bird et al.*, 1993]. On a subsequent Palmer-LTER program cruise, the surface water distributions of virus particles were evaluated over a broad habitat range from near shore coastal regions to the open ocean. In general, there was an onshore-to-offshore gradient in virus particles in surface waters with abundances of 3.2 x 10^5 to 1.7 x 10^6 ml^{-1} [*Maranger et al.*, 1994]. Again virus particle abundance was consistently lower in the surface waters (0-10 m), with a peak in abundance between 20-60 m [*Maranger et al.*, 1994]. An interesting aspect of this work revealed that subregions within the study area had substantially different virus assemblages as shown by a quantitative analysis of capsid dimensions. At selected stations, virus particles of all capsid diameter classes (e.g., <30 nM, 30-60 nM, 60-80 nM and >80 nM) were present while at other sites only small virus particles (<60 nM) were

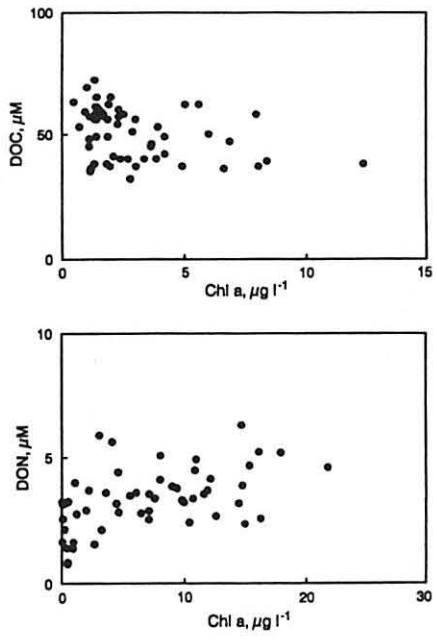

Fig. 4: Dissolved organic carbon [DOC, TOP] and dissolved organic nitrogen [DON, BOTTOM] concentrations versus phytoplankton abundance (expressed as chl a concentration) for samples collected in the RACER study area. DOC was measured using high temperature catalytic oxidation [*Tupas et al.*, 1994] and DON was measured using UV oxidation [*Karl et al.*, 1993b]. By comparison, the surface waters of the oligotrophic North Pacific subtropical gyre have the following values: DOC = 100- 125 µM, DON = 6-8 µM, chl a = 0.05-0.15 µg l^{-1}.

observed [*Maranger et al.*, 1994]. Because of host species specificity of viral infections, these data suggest that different microbial assemblages give rise to distinct viral assemblages.

While it is generally assumed that free virus particles are bacteriophages, there is little direct evidence to support that view at the present time. In a recent assessment of viral abundances in aquatic ecosystems it was concluded that "chl a explained more of the variance in viral abundance in aquatic ecosystems than did bacterial abundance" [*R. Maranger and D. Bird*, personal communication]. In antarctic waters where bacterial abundances are low, both in absolute numbers and in relationship to algal biomass, it seems unlikely that virus infection is an efficient mechanism of population control.

5. SOUTHERN OCEAN FOOD WEBS

Prior to 1980, energy flow in Southern Ocean habitats was thought to be dominated by relatively short and, therefore, efficient transfers from large (>20 μm) phytoplankton cells to krill and, subsequently, to apex predators. More recently, our concept of the antarctic marine food web was expanded to reflect the potential roles of heterotrophic microorganisms, including bacteria and protozoa [*Hewes et al.*, 1985]. These detritus-driven microbial loops [*Azam et al.*, 1983] are fueled by non-respiratory community carbon losses, i.e., dissolved and particulate organic matter released by excretion, predation and mortality (Figure 5). Because microbial food webs are composed of small organisms, they require an increased number of trophic levels to transfer carbon and energy from primary producers to apex predators. Most detritus-based food webs, therefore, constitute major energy sinks.

The structure and efficiency of the Southern Ocean food web is temporally variable [*Karl*, 1993]. Carbon and energy processing during the spring-summer phytoplankton bloom bears little resemblance to the mid-winter starvation condition It is reasonable to expect several independent and, perhaps, overlapping (in time, space or both) food webs, especially in coastal and shelf waters. The situation created during the shift of the phytoplankton community from large diatoms in early spring to smaller (<20 μm) flagellates 1-2 months later [*Holm-Hansen and Mitchell*, 1991] is one example of overlapping food webs.

6. OXYGEN DYNAMICS: PHOTOSYNTHESIS, RESPIRATION AND PHOTORESPIRATION

Plankton community production and respiration are the fundamental processes that drive carbon and energy flow in antarctic coastal ecosystems. In most marine ecosystems, there is a spatial and temporal separation between O_2 production (with concommitant CO_2 consumption) which is restricted to the near surface waters and O_2 consumption

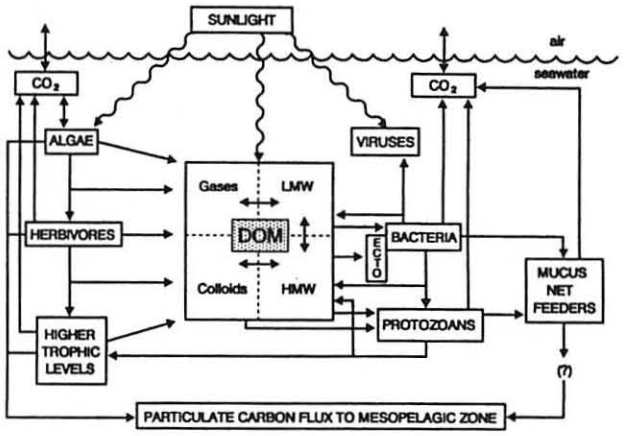

Fig. 5: Schematic representation of the flow of carbon and energy among the various components of the food web. At the center of the cartoon is the large and generally uncharacterized pool of dissolved organic matter (DOM) that consists of gases, low and high molecular weight (LMW and HMW) compounds and colloids. DOM quality and quantity control the existence and intensity of the microbial food web shown on the right-hand side of this schematic. The "Ecto" compartment shown attached to the bacteria represents the combined ectoenzymatic activity of this group. Ectoenzymes are largely responsible for the utilization of the large HMW pool of DOM that is now thought to control carbon (and nitrogen) flow to bacteria. [Adapted from: *Karl*, 1994].

(with concommitant CO_2 production) which occurs at all ocean depths. For ecosystems that support large phytoplankton populations or experience rapid bloom phenomena, there is also a transient and sometimes large accumulation of dissolved oxygen in the surface ocean. The ecological condition of dissolved O_2 in excess of the equilibrium air saturation value is termed hyperoxia [*Raven et al.*, 1994 a,b].

During phytoplankton blooms in antarctic coastal waters, hyperoxia results from the combined effects of extremely high rates of net photosynthesis, extremely low rates of chemoheterotrophic respiration and low rates of physical dissipation of the accumulated dissolved O_2, and may have an effect on community metabolism and carbon flow. Hyperoxia may be an even greater ecological consideration in ice algal communities where the diffusive fluxes of O_2 and CO_2 may be restricted. Biochemical effects of hyperoxia include inhibition of carbon fixation by ribulose-1,5-bisphosphate carboxylase/oxygenase (i.e., Rubisco), inhibition of nitrogenase and increased production of potentially toxic oxygen species including hydrogen peroxide (H_2O_2), superoxide radical anion, hydroxyl radical and singlet oxygen.

Photosynthesis and respiration largely control the ambient pools and turnover rates of dissolved inorganic carbon (DIC), DOC, oxygen (O_2) and inorganic nutrients. Under ideal growth conditions, carbon, nitrogen, phosphorus and oxygen vary in predictable stoichiometry [*Redfield et al.*, 19-

TABLE 2. Dissolved Oxygen Concentration Changes for the Water Collected at RACER Station A in Gerlache Strait for the Period 0130 hr, 15 Nov to 0040 hr, 16 Nov 1989 (Local Time) during the Declining Phase of the Spring Bloom (Data from D. Karl and D. Hebel, Unpublished).

Depth (m)	11/15 0130 hr[a]	ΔO_2[b]	11/15 0600 hr	ΔO_2	11/15 1200 hr	ΔO_2	11/15 1800 hr	ΔO_2	11/16 0040 hr
1.5	395.4	-4.0	377.6	+4.5	404.6	+3.1	423.0	-10.1	355.4
5	391.3	-2.0	382.1	+3.0	399.9	+3.4	420.3	-12.7	335.3
10	376.5	-3.4	361.3	+1.9	372.4	+2.5	387.6	-9.2	326.4
50	259.8	-1.8	251.6	+0.5	254.8	+0.1	255.2	+1.0	261.9
75	235.8	0.0	235.9	-0.4	233.3	+0.3	235.2	+0.7	239.8
150	247.3	-0.9	243.4	+0.9	248.8	-0.7	244.4	+0.6	248.7

[a]All concentrations, in units of μmol l^{-1}.
[b]ΔO_2 = signed change in O_2 concentration between consecutive casts, in units of μmol l^{-1} hr^{-1}.

63]. For nitrate-based photosynthesis and nitrate-regenerating respiration, the quantitative expectations are:

$$106\ CO_2 + 122\ H_2O + 16\ HNO_3 + H_3PO_4$$

$$\text{Photosynthesis} \rightarrow$$

$$\leftarrow \text{Respiration}$$

$$(CH_2O)_{106}(NH_3)_{16}(H_3PO_4) + 138\ O_2.$$

Rates of photosynthesis and respiration can be assessed directly by changes in O_2 or CO_2 concentrations during timed incubations or by using isotopic tracers (e.g., $^{14}CO_2$, $^{13}CO_2$, ^3H_2O, $^{18}O^{16}O$, $H_2{}^{18}O$). Analytical techniques such as CO_2 coulometry and computer-assisted micro-Winkler titration now achieve measurement precisions of ~0.05% and, in the case of O_2, can detect respiration rates ≤10 nmol O_2 l^{-1} hr^{-1} following a 1 day incubation. Indirect estimates based on the measurements of diagnostic enzyme activities (e.g., Rubisco, electron transport system) are also possible. Other techniques include estimation of O_2/CO_2 production or consumption rates from concentration changes in a given water mass. While this latter approach requires several assumptions concerning the importance of horizontal and vertical water advection and air-sea gas exchange, the major advantage is that measurements of seasonal (or longer) changes in metabolic reactants or products are less likely to be influenced by sampling bias [*Karl et al.*, 1991b].

Despite its technical simplicity and recognized importance, few measurements exist for total plankton respiration in marine ecosystems [*Williams*, 1984; *Jahnke and Craven*, 1995]. For antarctic microbial assemblages, these measurements are almost non-existent. During RACER-2, (Oct.-Nov. 1989), we conducted several experiments to measure changes in the O_2 concentrations in the water column of Gerlache Strait (Table 2 and Figure 6). The most remarkable feature of these field data was the relative constancy of O_2 over time for all water depths below approximately 20 m, whereas large temporal changes were observed in the upper portion of the water column (Figure 6). These diel fluctuations suggest that the majority of O_2 production and O_2 consumption occur in the upper euphotic zone (typically 0-10 m). Light-dependent increases in O_2 concentration ranged from 1.9-4.5 μmol O_2 l^{-1} hr^{-1} which was equivalent to a net carbon fixation rate of 23-54 mg C m^{-3} hr^{-1} (Table 2). Nighttime respiration rates in the upper water column were highest between 1800-0040 hr and averaged ~10 μmol O_2 l^{-1} h^{-1} (Table 2). Daily respiration exceeded photosynthesis in

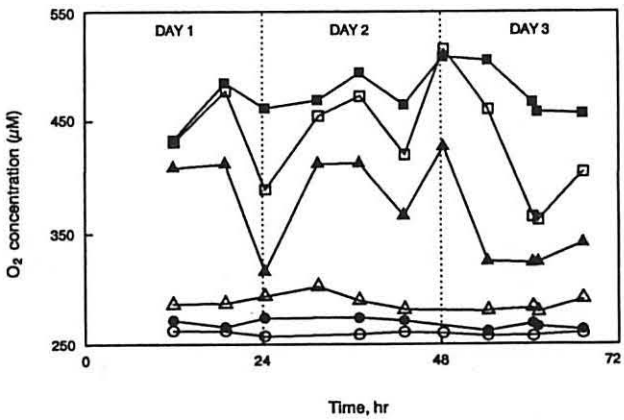

Fig. 6: Changes in dissolved oxygen concentrations measured from consecutive hydrocasts at a station in the northern portion of Gerlache Strait (64°11.7'S, 61°19.5'W) from 19-21 November 1989. The symbols are: solid square–2 m, open square–5 m, solid triangle–10 m, open triangle–20 m, solid circle–30 m and open circle–50 m.

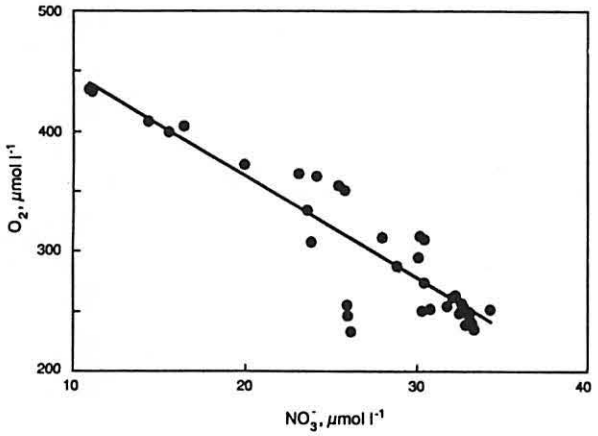

Fig. 7: Plot of dissolved oxygen (O_2) concentrations versus dissolved nitrate (NO_3^-) concentrations for water samples collected over the 0-200 meter depth range at a station in the northern portion of Gerlache Strait (64°11.7'S, 61°19.5'W) during the RACER field experiment (31 October 1989 to 19 November 1989). The regression analysis is: O_2 (µmol l^{-1}) = -8.507 NO_3^- (µmol l^{-1}) + 533; n = 40; r^2= 0.813 [From *Karl and Hebel*, 1990].

the upper 10 m of the water column. These net heterotrophic conditions are characteristic of the post-bloom period [*Karl*, 1993].

Spring bloom conditions in antarctic coastal waters do not exhibit a balance between photosynthesis and community respiration. This results in significant accumulations of O_2 (Figure 7), and deficits in DIC (and hence CO_2 partial pressure) and nutrients coupled with an accumulation of phytoplankton biomass [*Karl et al.*, 1991b]. If grazing pressure on the phytoplankton population is low and turbulent mixing is minimal, complete removal of inorganic nutrients would predict an ambient O_2 concentration of >600 µM (i.e., ~200% air saturation) which may have significant biological effects. Surface water O_2 concentrations in Gerlache Strait during the spring bloom of phytoplankton may exceed 500 µM, which is consistent with the above mass balance predictions (Figure 8). Similar hyperoxic conditions have been reported for Arthur Harbor in Dec. 1970 where dissolved O_2 and CO_2 partial pressures (pO_2 and pCO_2) were 120% and 15% of their respective air saturated values [*Shabica et al.*, 1977]. If inorganic nutrients are exhausted, the relatively large bloom-forming diatoms aggregate and

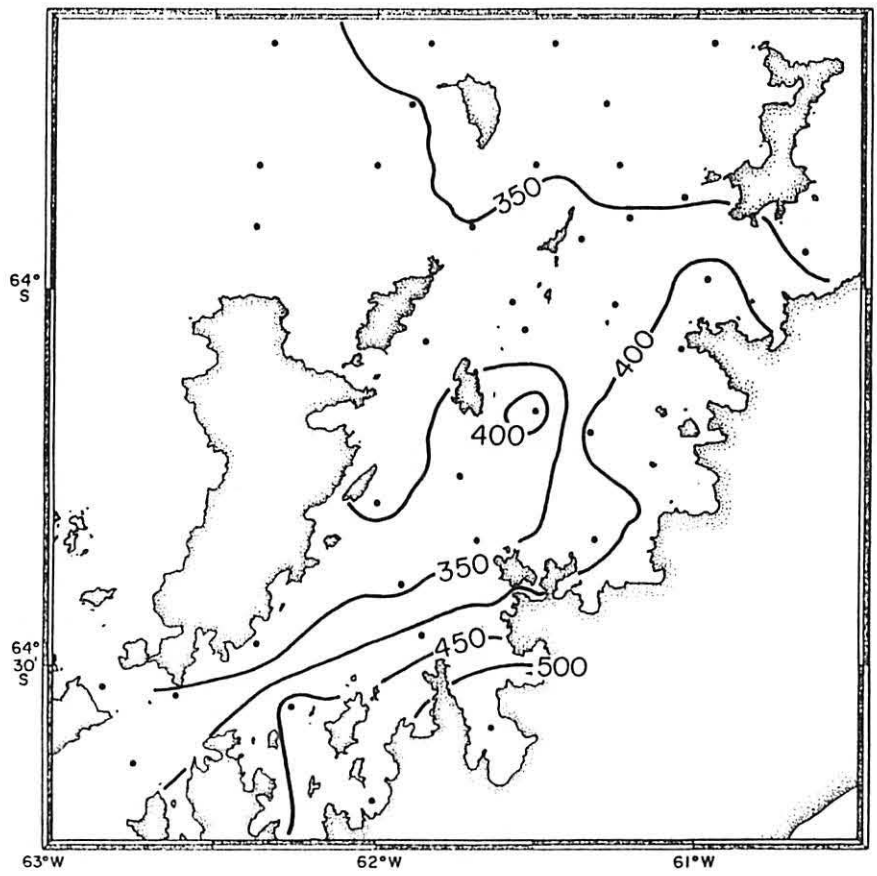

Fig. 8: Regional distribution of surface water (5 meters) dissolved oxygen content (in µmol l^{-1}) over the RACER study area for the sampling period (16-19 November 1989). Seawaters in equilibrium with atmospheric O_2 would have an O_2 concentration of ~350 µM [From *Karl and Hebel*, 1990].

sink from the euphotic zone resulting in a net removal of reduced carbon and other bioelements from the O_2 enriched surface waters. A further separation of dissolved O_2 from dissolved CO_2 and nutrients may result from the importance of ocean-feeding, air-breathing predators (e.g., seabirds and marine mammals) in coastal ecosystems of Antarctica [*Huntley et al.*, 1991b]. Their metabolic activities exacerbate the already large ocean-to-atmosphere gradients in pCO_2 and pO_2 by removing marine biomass (reduced carbon) for combustion by atmospheric O_2.

There are at least two major implications of hyperoxia in antarctic coastal waters: (1) phytoplankton photorespiration and reduction in net photosynthesis, and (2) accelerated photolytic degradation of dissolved organic matter. Photorespiration is the light-dependent uptake of O_2 and release of CO_2 by photosynthetic organisms [*Beardall*, 1989]. Plant photorespiration has been described as an inevitable consequence of the existence of atmospheric oxygen [*Lorimer and Andrews*, 1973] and is reported to occur in marine algae [*Burris et al.*, 1976; *Burris*, 1981]. Photorespiration should not be confused with light-dependent uptake of O_2 in the Mehler reaction [*Geider*, 1992]; the latter does not release CO_2 or result in the oxidation of carbon intermediates. During photorespiration, ribulose-1,5-bisphosphate (RuBP) is oxidized to glycolate, glycine and CO_2. The same active site in Rubisco is responsible for the carboxylase and oxygenase reactions (photosynthetic CO_2 fixation and O_2 consumption by photorespiration, respectively). Under normal atmospheric conditions the rate of the carboxylase reaction is four times faster than that of oxygenase. However, cellular increases in O_2 concentration relative to CO_2 lead to the competitive inhibition of the carboxylase reaction. The high O_2 concentration during antarctic blooms combined with the low CO_2 concentrations results in an O_2:CO_2 ratio that is far removed from the air saturated equilibrium state. Consequently, the environmental conditions existing during coastal plankton blooms in Antarctica would theoretically favor phytoplankton photorespiration over photosynthesis.

In contrast to "normal" heterotrophic respiration, photorespiration is not an energy-conserving mechanism. Because photorespiration involves net consumption of Calvin-Benson cycle intermediates, it can have a significant negative effect on the efficiency of gross photosynthesis [*Geider*, 1992]. *Burris* [1981] estimates that the photosynthetic quotient (PQ; i.e., rate of O_2 production divided by rate of CO_2 consumption) for marine phytoplankton decreases at high oxygen concentrations, most likely as a result of photorespiration. While a "normal" molar PQ is assumed to be near unity, the PQ may drop to 0.1 at O_2 concentrations of approximately 200% saturation (~600-650 μM for antarctic waters) [*Burris*, 1990]. Consequently, it is very likely that photorespiration may be an important but previously ignored aspect of phytoplankton metabolism in antarctic coastal ecosystems. It is possible that photorespiration may contribute to the "premature" demise of the spring bloom (i.e., termination of net photosynthesis in presence of sufficient light and inorganic nutrients). Because of the large demand for O_2 and the non-Redfield stoichiometry of the photorespiratory pathway (i.e., at least 3 moles O_2 consumed for each mole of CO_2 released [*Tolbert*, 1974]), this pathway would also cause an uncoupling of C and O cycles, at least in coastal waters.

Shipboard experiments conducted using phytoplankton cells collected from the LTER study area have documented a response to the addition of dissolved O_2 that is consistent with photorespiration. Relative to control samples incubated at ambient O_2 concentrations (372 μM), the ^{14}C-HCO_3^- incorporation for samples incubated at 593 μM, 790 μM, 1133 μM and 1405 μM O_2 was 74%, 18%, 15% and 11%, respectively, documenting a dramatic decrease in short-term rates of photosynthesis [*D. Karl*, unpublished results]. The addition of HCO_3^- partially restored the rates of photosynthesis, a result that is also consistent with the photorespiratory response to high O_2 concentrations.

Glycolate is a diagnostic by-product of photorespiration and a substrate for heterotrophic bacterial metabolism [*Wright and Shah*, 1975; *Fogg*, 1983]. Consequently, photorespiration might be expected to stimulate a secondary chemoheterotrophic community metabolism which will consume additional O_2 and produce respiratory CO_2. If tightly coupled from a community metabolism perspective, the entire algal photorespiration/bacterial respiration pathway which is triggered by high O_2 and low CO_2 could effectively lower ambient O_2 and replenish CO_2 resulting in a recovery of efficient net photosynthesis. However, to our knowledge these important metabolic processes have not been systematically investigated in Southern Ocean waters.

A second major effect of hyperoxic conditions is the increased potential for production of photoreactive O_2 derivatives and increased rate of photooxidation of dissolved and particulate organic matter. *Laane et al.* [1985] have emphasized the importance of considering photooxidation reactions in O_2 budget calculations of natural waters. The formation of superoxide radicals and H_2O_2 can occur biologically as a result of O_2 photoreduction in algae or abiotically through interactions between detrital organic matter and light. Consequently, an increased rate of free radical production during hyperoxia is very likely [*Raven*, 1991]. These reactions could lead to photolytic alteration of otherwise refractory organic matter, thereby providing substrates for chemoheterotrophic metabolism and growth. *Mopper and Zhou* [1990] have reported that deep-water DOM, possibly typical of the upwelled waters of the Antarctic Peninsula region (Figure 4), is nearly an order of magnitude more reactive to light than DOM collected from temperate surface waters. Studies of H_2O_2 distributions and fluxes in antarctic coastal waters are beginning to reveal the extent and importance of these processes [*Karl et al.*, 1993a; *Tien and Karl*, 1993; *Karl and Resing*, 1993]. Finally, photooxidative death resulting from the combined effects of hyperoxia, low CO_2 concentrations and high light levels has been hypothesized

to be the mechanism responsible for the sudden demise of hypereutrophic algal blooms in closed ecosystems [*Abeliovich and Shilo*, 1972] thus providing a precedent in nature. In fact, the effects may be exacerbated in cold climates where metabolic rates (and, hence, cellular repair rates) are slower.

7. BACTERIAL GROWTH AND POPULATION REGULATION

The microbial loop plays an important role in marine and freshwater plankton ecosystems in all climatic zones [*Hobbie*, 1994]. However, general models of microbial ecosystem dynamics continue to elude scientific understanding. Abundance (biomass) and growth rate (production) are among the most widely measured parameters in aquatic microbial ecology and the collective data set on these measurements has provided the necessary guidance for the design of the next generation of field experiments. A major obstacle, however, is our inability to characterize much of the DOM pool in the ocean, and to determine the rates at which its various components are utilized by bacteria.

Although a comprehensive model of microbial food web dynamics in the Scotia-Weddell Sea region has been published [*Lancelot et al.*, 1991], the general applicability of this model to Southern Ocean ecosystems is questionable. Growth of heterotrophic bacterioplankton is far more difficult to parameterize in ecological models than that of phytoplankton or microzooplankton. A functional response based on the *Monod* [1942] equation (a hyperbolic function analogous to the Henri-Michaelis-Menten equation) has been widely used to simulate nutrient limitation in plankton populations. What nutrients regulate bacterioplankton growth? Can bacterial growth be modelled as a functional response to bulk dissolved organic carbon or dissolved organic nitrogen?

Several plankton ecosystem models [*Fasham et al.*, 1990; *Moloney and Field*, 1991] have used mass-balance models based on *Goldman et al.* [1987] to predict ammonium uptake or remineralization depending on the C:N ratio of the organic substrate, but have neglected non-nitrogenous organic substrates such as carbohydrates [*Ducklow*, 1994]. While similar models modified to correct this oversight may simulate ammonium uptake and remineralization correctly, it is not clear that they can accurately represent the effects of nutrient limitation on bacterial growth rate. These simulations also utilize extremely simple parameterizations of the processes by which nonliving organic matter is produced, because realistic estimates of the rates of these processes, let alone models of the governing processes, are not possible with current knowledge. Specific respiration rates, or growth efficiencies, are also poorly constrained [*Bjørnsen*, 1986; *Kirchman et al.*, 1991; *Jahnke and Craven*, 1995]. Simulations of the global carbon cycle incorporating DOM with a constant turnover time, or "half-life," have shown better agreement with observed distributions of oxygen and phosphorus than those that exclude it [*Bacastow and Maier-Reimer*, 1991; *Najjar et al.*, 1992]. However, the rate of DOM utilization is unlikely to be constant, and turnover rates of significant components may differ by orders of magnitude between different oceanographic provinces [*Christian and Karl*, 1995].

Microbial food web interactions are complex, and many significant pathways of transfer of carbon or energy within the food web are difficult to quantify. This applies in particular to production of nonliving dissolved and particulate organic matter. While the excretion of low-molecular-weight organic compounds (LMW-DOM; ≤10,000 daltons) by phytoplankton is well documented [*Fogg*, 1983; *Bjørnsen*, 1988], much of the organic matter available to bacteria is believed to be polymeric compounds (P-DOM) [*Billen*, 1990] and the pathways by which phytoplankton biomass enters this pool are poorly understood. Grazing by both macro- [*Jumars et al.*, 1989] and microzooplankton [*Caron et al.*, 1985; *Nagata and Kirchman*, 1992] plays a role as may viral [*Bratbak et al.*, 1994] and bacterial [*Imai et al.*, 1993] infection. But the relative importance of these, and possibly other, mechanisms is not known with any accuracy for any marine environment, and is likely to vary greatly among oceanograpic regions, and, at high latitude, with the seasons.

Dissolved organic matter concentrations in the Antarctic Peninsula region include some of the lowest as well as the highest concentrations ever measured (Table 3). *Bölter and Dawson* [1982] observed extraordinarily high levels (>1000 μM) of DOC as well as dissolved amino acids, in the northern Bransfield Strait. *Prego* [1991] observed >200 μM DOC in the same area and using a similar technique. On the other hand, DON values of less than 3 μM have also been observed in surface waters of Bransfield Strait (Table 3 and Figure 4). These latter values are among the lowest ever measured in the surface ocean.

Tupas et al. [1994a] observed dissolved free amino acid (DFAA) concentrations of 200-700 nM in Gerlache Strait during RACER which is much higher than typically observed in temperate oceanic environments, despite the very low "total" DOC and DON concentrations discussed above. *Bölter and Dawson* [1982] give similar concentrations, but also reported extraordinarily high (up to 30 μM glycine equivalent) concentrations of dissolved combined amino acids (DCAA). *Manahan et al.* [1990] report concentrations similar to those of *Tupas et al.* [1994a] for selected amino acids in McMurdo Sound, but do not give the total DFAA concentration. The extremely high values observed by *Bölter and Dawson* [1982] occurred in conditions dominated by *Phaeocystis pouchettii* blooms. The RACER program did not encounter such blooms; during RACER the bloom phytoplankton community was diatom-dominated, except for a bloom of the prasinophyte *Pyramimonas* sp. [*Bird and Karl*, 1991b]. As these conditions both occur in the LTER area at the same season of different years, there may

TABLE 3. Measurements of Dissolved Organic Compounds in the Region West of the Antarctic Peninsula

Compound or Compound Class[1]	Sample Location	Season	Concentration Range	Reference
TOC	Elephant Island	Dec-Jan	27-200 μM	*Prego* [1991]
DOC	Bransfield Strait	Nov-Dec	180-1000 μM	*Bölter and Dawson* [1982]
DOC	Admiralty Bay	Mar	100-480 μM	*Dawson et al.* 1985]
DOC	Bransfield Strait	Dec-Jan	5.8-252 μM	*Zdanowski* [1985]
DOC	Gerlache Strait	Nov-Dec	36-72 μM	*Karl and Tien* [unpubl.]
DOC	Gerlache Strait	Dec	103-119 μM	*Pakulski and Benner* [1994]
DON	Gerlache Strait	Nov-Dec	1-6 μM	*Karl* [unpubl.]
DFAA	Bransfield Strait	Nov-Dec	0.7-2.0 μM	*Bölter and Dawson* [1982]
DFAA	Bransfield Strait	Dec-Jan	0-0.76 μM	*Zdanowski* [1985]
DFAA	Gerlache Strait	Feb	0.8-4.6 μM	*Haberstroh et al.* [1987]
	Drake Passage	Feb	0.3-6.0 μM	
DFAA	Gerlache Strait	Nov-Dec	0.2-0.7 μM	*Tupas et al.* [1994]
DCAA	Bransfield Strait	Dec-Jan	0-1.16 μM	*Zdanowski* [1985]
DCAA	Bransfield Strait	Nov-Dec	1-30 μM	*Bölter and Dawson* [1982]
D-MCHO	Bransfield Strait	Nov-Dec	0.3-1.4 μM	*Bölter and Dawson* [1982]
D-MCHO	Admiralty Bay	Mar	1.2-2.2 μM	*Dawson et al.* [1985]
D-PCHO	Bransfield Strait	Nov-Dec	0.5-5 μM	*Bölter and Dawson* [1982]
D-PCHO	Gerlache Strait	Dec	9-18 μM	*Pakulski and Benner* [1994]
D-TCHO	Gerlache Strait	Dec	14-21 μM	*Pakulski and Benner* [1994]
glutamic acid	Gerlache Strait	Feb	20-200 nM	*Haberstroh et al.* [1987]
	Drake Passage		3-300 nM	
glucose	Drake Passage	Jan	0-0.04 μM	*Hanson et al.* [1983a]
D-ATP	Drake Passage	Jan	0.13 nM	*Nawrocki and Karl* [1989]
	Gerlache Strait	Jan	1.2 nM	
	Gerlache Strait	Mar	<0.01 nM	
	Bransfield Strait	Jan	0.3-1.3 nM	
	Bransfield Strait	Mar	0.06 nM	
DMS	Drake Passage	Mar-Apr	0.7-3.2 nM	*Berresheim* [1986]
	Bransfield Strait	Mar-Apr	0.8-2.8 nM	
	Gerlache Strait	Mar-Apr	0.6-8.6 nM	
D-DNA	Gerlache Strait	Dec	2-3 μg l^{-1}	*Bailiff and Karl* [1991]
		Jan-Feb	0.1 μg l^{-1}	
		Mar	<0.01 μg l^{-1}	
methane	Drake Passage	Dec-Mar	1.5-3 nM	*Tilbrook and Karl* [1994]
	Bransfield Strait	Dec-Mar	4-9 nM	
	Gerlache Strait	Dec-Mar	4-5 nM	
D-LPS	Gerlache Strait	Oct-Nov	70-990 ng l^{-1}	*Karl and Tien* [1991]
urea	Admiralty Bay	Mar	0.5-1.6 μM	*Dawson et al.* [1985]

[1]Abbreviations: TOC = total organic carbon, DOC = dissolved organic carbon, DON = dissolved organic nitrogen, DFAA = dissolved free amino acids in glycine equivalents, DCAA = dissolved combined amino acids, D-MCHO = dissolved monosaccharides in glucose equivalents, D-PCHO = dissolved polysaccharides in glucose equivalents, D-TCHO = dissolved total carbohydrates, D-ATP = dissolved adenosine triphosphate, DMS = dimethylsulfide, D-DNA = dissolved deoxyribonucleic acid, D-LPS = dissolved lipopoly-saccharide.

be inter-annual variations in climatic or hydrographic forcing that result in dominance by different groups of autotrophs, affecting in turn the quantity and quality of DOM available to the bacteria.

7.1. Regulation of Bacterial Populations

When considering limitation of bacterial populations, the difference between limitation of standing crop (numbers or biomass) and limitation of growth rate is significant. Nutrient limitation in the sense implied by Liebig's Law is limitation of standing crop, and implies exhaustion of some essential nutrient. Even if the rate of growth is limited by some nutrient or combination of nutrients, the standing crop may be controlled by grazing or some other factor. It is also important to keep in mind that discussing what "limits" the rate of growth carries the ecological connotation that rapid growth maximizes fitness.

Bacterial numbers in the Antarctic Peninsula region are consistently lower than in most other aquatic environments, relative to chl a [*Karl et al.*, 1991a]. Bacterial growth rates, however, are comparable to other systems [*Bird and Karl*, 1990; *Tupas et al.*, 1994a], and ATP turnover experiments with ^{3}H-adenine indicate that the <1 μm fraction of the microbial community is as active as the larger cells [*Karl and Winn*, 1986].

In a recent experimental mesocosm evaluation of bottom-up versus top-down controls of the Southern Ocean microbial food web, bacterioplankton populations were found to be controlled (both in numbers and in growth rate) by heterotrophic nanoflagellate grazers [*Kuparinen and Bjørnsen*, 1992]. Bacterial growth rates in the absence and in the presence of grazers was 0.75 and ~0.25 d^{-1}, respectively.

The role of DOM as a proximate control on bacterial growth rate is uncertain. *Rivkin et al.* [1991] found no stimulation of bacterial growth in McMurdo Sound by glucose, glycine or glutamic acid, and concluded that the bacteria "had sufficient organic nutrients to sustain maximal or near-maximal growth." A greater variety of substrates should be tested before this conclusion is accepted, however. Extensive respiration of amino acid carbon, including glycine [*Tupas et al.*, 1994a] suggests that synthesis of the basic amino acid "skeleton" is not rate-limiting for growth of antarctic bacterioplankton. Synthesis of the R groups of some of the rarer amino acids may be the rate-limiting step, and experimental addition of a greater variety of amino acids should be attempted before a conclusion of substrate sufficient growth is warranted. Catabolism of thymidine [*Karl et al.*, 1991a] also suggests that antarctic seawater is far from being a medium rich enough to permit maximal growth on the organic substances present.

7.2. Ecosytem-level Processes

Bacteria evolve quickly. We can generalize that bacteria adapt to their "metazoan environment" rather than the other way around. In the 1 billion years that eukaryotes have existed, they have provided the bacteria with a variety of specialized niches. These environments change and the bacteria adapt. For this reason it may be useful to consider what is unusual about the antarctic marine environment as it relates to chemoheterotrophic bacterioplankton.

Antarctica is the only "eutrophic" environment where terrestrially derived organic matter is almost completely absent, although it is likely to play a small role in selected ice-free coastal environments. Eutrophic environments can be either "autoeutrophic" or "heteroeutrophic" (i.e., primary eutrophication can be inorganic or organic). There may be environments where the primary eutrophication is with inorganic nutrients, that become enriched in organic nutrients through phytoplankton production, but it is difficult to think of an example, except perhaps for blooms of *Phaeocystis pouchettii* [*Bölter and Dawson*, 1982; *Davidson and Marchant*, 1992]. A highly seasonal environment dominated by large cells gives a relatively small input of detrital organic matter. Phytoplankton excretion of LMW-DOM compounds is related to surface-to-volume ratio of phytoplankton [*Bjørnsen*, 1988], and possibly to nutrient depletion [*Joiris et al.*, 1982]. In either case this excretion is minimal during a diatom bloom, except possibly in the late stages when nutrients are exhausted. This could very well explain why dense phytoplankton blooms that occur in the coastal regions of the Antarctic Peninsula are not enriched in DOM (Figure 4). It could explain, as well, the uncoupling between chl a concentrations and bacterial cell numbers when compared to previous results from other, mostly, temperate aquatic ecosystems [*Bird and Kalff*, 1984]. Furthermore, many coastal, estuarine and lacustrine systems are enriched in inorganic nutrients derived in part from remineralization of allochthonous organic matter, i.e., the primary eutrophication is organic. These ecosystems comprise the majority of the data used by *Bird and Kalff* [1984].

Picophytoplankton are now recognized to be nearly ubiquitous in the world's oceans; Antarctic environments, however, may be an exception. Abundance of cyanobacteria in the Drake Passage decreases to insignificant levels south of the Antarctic Convergence [*Letelier and Karl*, 1989]. Picophytoplankton-dominated systems north of the Antarctic Convergence support a large microheterotroph biomass [*Christian and Karl*, 1994] relative to coastal antarctic habitats [*Karl and Tien*, 1991]. Reasons for this may be: (1) that small phytoplankton cells excrete a greater fraction of primary production due to high surface:volume ratios, (2) that microzooplankton grazing on picophytoplankton relaxes grazing pressure on heterotrophic bacteria or (3) that recycling of nitrogen by grazing microzooplankton stimulates bacterial production.

Furthermore, antarctic surface waters in winter are possibly the most oligotrophic on earth, with less biomass of microorganisms than the subtropical gyre of the North Pacific [*Tien et al.*, 1992]. Organisms having evolved in such a habitat have evolved mechanisms for surviving through the winter. The need to survive 3-6 months of prey scarcity may explain why antarctic micrograzers have

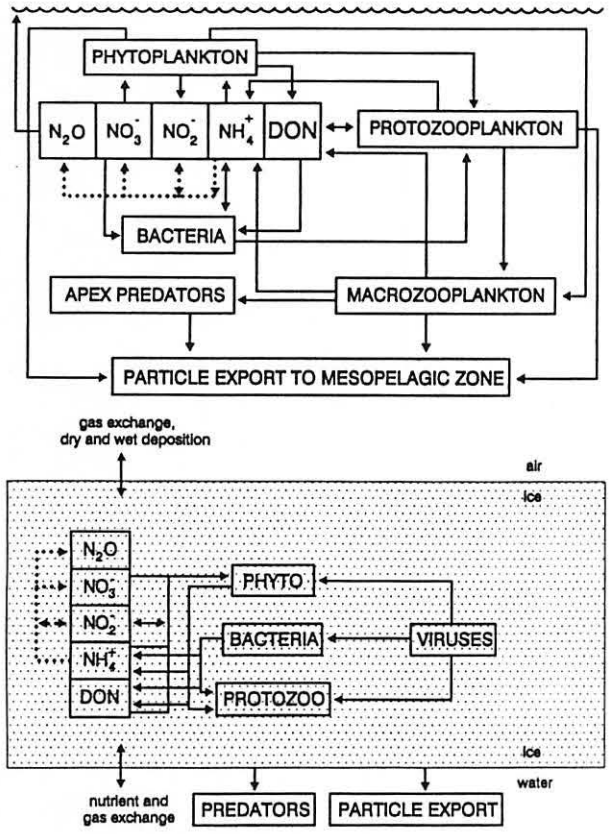

Fig. 9: Schematic representation of the "open water" and "ice-associated" N cycles in the region west of the Antarctic Peninsula. The dissolved N pools include: N_2O = nitrous oxide, NO_3^- = nitrate, NO_2^- = nitrite, NH_4^+ = ammonium and DON = dissolved organic nitrogen. The dotted lines and arrows represent the process of bacterial nitrification. Not shown in this schematic are atmospheric deposition of organic and inorganic compounds or the flux of dissolved nitrogen gas (N_2) into the marine plankton via the process of N_2 fixation. Neither of these processes is considered to be a major flux of N in marine ecosytems in the Antarctic Peninsula region.

adapted to grazing optimally at low prey concentrations and provide a mechanistic interpretation of the permanent low abundance of bacterioplankton based on simple models of predator-prey dynamics.

8. DISSOLVED NITROGEN DYNAMICS

Nitrogen is an essential element for the growth of all organisms. While the supply of fixed nitrogen (as nitrate) in antarctic waters is high and rarely growth-limiting except under extreme bloom conditions [*Holm-Hansen et al.*, 1989; *Karl et al.*, 1991b], a thorough study of N-dynamics yields useful information on the structure and functioning of the entire ecosystem (Figure 9). In this section, we focus on the productive coastal areas of the western Antarctic Peninsula and its seasonal ice pack. The following topics are considered: (1) the roles of phytoplankton, bacteria, protozoa and macrozooplankton in N cycling, (2) atmospheric N fluxes, both biotic and abiotic in origin, (3) nitrite distributions and dynamics, (4) nitrification and nitrous oxide production and (5) sea-ice nitrogen cycling.

8.1. Phytoplankton Assimilation of Nitrogen

Despite the abundance of nitrate in the Southern Ocean, ammonium appears to be the preferred and, perhaps, primary source of nitrogen supporting the growth of phytoplankton during spring and summer [*Olson*, 1980; *Glibert et al.*, 1982; *Rönner et al.*, 1983, *Probyn and Painting*, 1985; *Koike et al.*, 1986]. This is true even under bloom conditions, indicating that as the large nitrate pool (20 μM, or more) is being depleted, the small ammonium pool (<2 μM) is rapidly recycled. Uptake of ammonium can range from about half of total N uptake in the Scotia Sea during early spring [*Olson*, 1980], to >90% of the total in late summer [*Koike et al.*, 1986]. Nevertheless, under certain conditions nitrate is reduced to undetectable levels by phytoplankton growth [*Holm-Hansen et al.*, 1989; *Dore et al.*, 1992]. This implies that regeneration processes, in particular ammonification, are absent, repressed or separated in space. This probably results from the absence of grazers during the initial phase of the bloom which also accounts for the accumulation of phytoplankton biomass. Reduced grazing and ammonification may also account for the large relative uptake of nitrate (87%) vs. ammonium and urea (13%) during winter [*Cochlan et al.*, 1993b].

The observed shift in the nitrogen source from nitrate to ammonium generally parallels a shift in the size spectrum of the microbial community from larger to smaller organisms as described for the Bransfield Strait area by *Karl et al.* [1991a]. This is also consistent with the size fractionation experiments of *Koike et al.* [1986], showing that ammonium is taken up almost exclusively by the <20 μm fraction. These results indicate that despite the observed depletion of nitrate during the spring bloom, most of the primary production in antarctic waters is recycled and hence not available for export from the euphotic zone. These findings also imply an important role for the bacteria and grazers that remineralize nitrogen in maintaining the intensity of the bloom.

Dissolved organic nitrogen, while largely uncharacterized, may play an important role in the nutrition of antarctic phytoplankton. While DON is generally assumed to be excreted by phytoplankton [*Bronk et al.*, 1994] and utilized by heterotrophic bacteria, there is also the possibility of facultative algal heterotrophy. Antarctic diatoms (benthic, planktonic and ice-associated species) can rapidly assimilate amino acids at ambient concentrations [*Rivkin and Putt*, 1987]. This may be an important adaptation to an environment where light intensity is low for a significant portion of the year.

8.2. The Role of Bacteria in Antarctic Marine Nitrogen Cycling

Marine bacteria are both a source of regenerated ammonium and a sink for ammonium. Recent studies by *Tupas and Koike* [1991] and *Tupas et al.* [1994a] demonstrated that mixed bacterial assemblages simultaneously assimilate and regenerate ammonium; however, it is not clear whether individual cells do both. In the former study, ammonium supplied up to 80% of the new bacterial nitrogen, yet at the same time more than half of the DON taken up by these bacteria was remineralized to free ammonium. The authors suggested that amino acids are largely used in anabolic salvage pathways or respired while the subsequent assimilation of released ammonium provides nitrogen for growth via separate biosynthetic pathways. While not necessarily energy-efficient, this strategy allows greater versatility in the synthesis of amino acids. In contrast to previous studies, this indicates that the availability or lack of important amino acids rather than overall C:N ratio of the substrate pool may dictate whether bacteria act as net sinks for or net remineralizers of nitrogen in their natural environments.

In Gerlache Strait during the 1989 spring bloom, *Tupas et al.* [1994a] found that bacteria accounted for 8-25% of total ammonium assimilation, while at the same time, bacteria regenerated ammonium at 2-4 times the rate at which they assimilated it. Ammonium supplied 35-60% of the bacterial nitrogen demand; the rest must have been supplied by DON or nitrate. These data imply that bacteria both compete with phytoplankton for available ammonium and help to replenish that ammonium and also rely on phytoplankton and zooplankton for DON, making their role in the nitrogen cycle and the food web difficult to model. Overall, however, bacteria were net remineralizers during this study, suggesting that the rapid recycling of nitrogen by bacteria is crucial in maintaining the high rates of primary production seen in the coastal embayments of the Antarctic Peninsula.

8.3. The Roles of Nano-, Micro- and Macrozooplankton in Antarctic Marine Nitrogen Cycling

Macrograzers, particularly krill, are conspicuously abundant components of the antarctic marine environment. Krill are the primary food source for most apex predators and they represent a crucial link in the flow of energy. Krill and other large zooplankton play a role in the recycling of nitrogen as well. It is well known that krill and other netplankton excrete ammonium [*Bidigare*, 1981; *Ikeda and Mitchell*, 1982; *Biggs*, 1982; *Biggs et al.*, 1985], even during the austral winter when food is scarce [*Huntley and Nordhausen*, 1995]. However, both *Biggs* [1982] and *Huntley and Nordhausen* [1995] concluded that the macrozooplankton contribution to phytoplankton ammonium demand is negligible. *Biggs* [1982] suggested that either aggregations of zooplankton are undersampled, or that seabird nutrient recycling and ammonium from ice melt or microheterotrophic remineralization are also important in the ammonium budget of polar waters.

In our opinion, a systematic undersampling of macrozooplankton of the magnitude alluded to by *Biggs* [1982] seems unlikely. Seabird contributions to marine nitrogen recycling may be significant as they deposit a majority of their feces into the sea [*Staley and Herwig*, 1993]. However, their biomass and feeding rates are not well constrained [*Banse*, 1994]. Ammonium from ice melt is probably not very important, as will be discussed later. A likely explanation is that most nitrogen recycling is done by small organisms: protozoa and bacteria [*Holm-Hansen*, 1985]. However, dense swarms of krill may be locally important sources of ammonium [*Johnson et al.*, 1984].

A number of recent studies have provided evidence on the role of nano- and micrograzers [*Silver et al.*, 1980; *von Bröckel*, 1981; *Biggs et al.*, 1985; *Hewes et al.*, 1985; *Miller et al.*, 1985; *Koike et al.*, 1986]. As the phytoplankton community composition shifts from large diatoms to small flagellates through the summer, these become the link between the bacteria and small algae, and larger zooplankton such as krill. The relatively low growth efficiencies of microzooplankton result in substantial losses of nitrogenous compounds to the dissolved phase. *Tupas et al.* [1994a] estimated that bacteria can regenerate 27-55% of the total recycled ammonium during the spring bloom, and as *Biggs* [1982] estimates that netplankton can only regenerate 2% of the phytoplankton demand for ammonium, we conclude that at least one-half of the recycling of ammonium is carried out by nano- and microzooplankton. The most abundant of these small zooplankters are the choanoflagellates [*Buck and Garrison*, 1983; *Bird and Karl*, 1990].

8.4. Atmospheric Inputs of Fixed Nitrogen and Their Sources

Upwelled nitrate and microbially regenerated ammonium are usually considered to be the only significant sources of fixed nitrogen for primary production in the antarctic marine environment. However, *Parker et al.* [1978] reported high levels of ammonium and nitrate in antarctic ice and snow. *Parker et al.* [1978] suggested an auroral source of fixed nitrogen, and supporting evidence relating nitrate concentration to sunspot activity exists [*Parker and Zeller*, 1980]. In reporting high levels of fixed nitrogen, the authors asserted that the melting of nitrogen-rich continental ice may represent a significant input of new nitrogen to the coastal marine ecosystem. *Biggs* [1978] challenged their calculations, stating that the oceanic fixed N reservoir is underestimated, and that ammonium excretion by zooplankton is a larger source of nitrogen.

Ice derived from continental sources can represent new nitrogen to the marine ecosystem. However, estimation of nitrogen input from terrestrial ice melt is not straightfor-

ward. *Greenfield* [1992] points out that the impact of precipitation nitrogen to the marine environment is highly variable in both space and time. For example, the first few centimeters of each precipitation event deposits the highest levels of N. Further complicating the issue is the recent discovery that levels of nitrate in (at least) continental precipitation have shown an increase in recent years [*Mayewski and Legrand*, 1990]. Given such heterogeneity, accurate estimation of N input to antarctic ecosystems by precipitation requires broader coverage of measurements in both time and space.

The sources of the N (nitrate and ammonium) may well differ between continental and maritime precipitation. *Greenfield* [1992] found that precipitation falling in areas near penguin rookeries had greater ammonium content than precipitation in remote areas, indicating local atmospheric cycling of guano-derived N. *Myrcha et al.* [1985] measured the rates of guano transport during summer at King George Island and found that about 50% of the fresh guano was lost over a three-week period. Loss rates were correlated to ground temperature, hence insolation. High levels of ammonium in antarctic ice have also been noted by *Oradovskiy* [1974] and *Dore et al.* [1993]; the former attributed ammonium-rich layers in pack ice to a physical concentration mechanism, while the latter authors suggested the activity of ice-bound microheterotrophs, as the abundance of ammonium was correlated with active dark carbon assimilation. Again, sources of nitrogen derived from metabolic activity are recycled, while auroral or other abiotic sources which have been implicated in continental precipitation are considered new.

8.5. Nitrite Distributions and Dynamics in the Marine Antarctic Environment

Most studies of nitrogen in Antarctica have focused on nitrate and ammonium, with few considering the redox intermediate nitrite. Accumulations of nitrite in the water column indicate zones of active nitrogen cycling; the distribution of nitrite can be used to elucidate the nutritional state and regenerative capacity of the resident microbial communities. *Dore and Karl* [1992] used nitrite profiles to track the progression of the spring bloom in the Gerlache Strait. From 12-30 December 1991, depth-integrated nitrite increased systematically while depth profiles exhibited surface maxima and decreasing concentrations with depth. The authors postulated that these profiles followed the progression of nitrate assimilation during the early stages of the bloom, as nitrite is released during light-dependent assimilation [*Kiefer et al.*, 1976].

Blooms of phytoplankton are often associated with the edges of the receding antarctic seasonal ice packs, and may play a major role in the biogeochemical cycles of the Southern Ocean [*Smith and Nelson*, 1986]. The initiation of the ice edge bloom is thought to be dependent upon stabilization of the water column, either because of a low-density meltwater lens or because of reduced wind stress near the region of ice cover, or both. Receding ice edges display a gradation of nitrogen cycle processes, with evidence of rapid nitrate assimilation near the ice and evidence of increased heterotrophy and nutrient regeneration in the wake of the receding ice [*Nelson and Smith*, 1986; *Smith and Nelson*, 1990; *Karl et al.*, 1992; *Dore et al.*, 1992].

Dore et al. [1992] examined a series of nitrite profiles from a transect perpendicular to a receding ice edge in Marguerite Bay; the near-ice stations showed profiles similar to those collected during the same cruise in Gerlache Strait, indicating early bloom conditions. By contrast, the open waters of the bay showed nitrite accumulations at depth, indicating regeneration of nitrate through nitrification and a well-developed heterotrophic community. Nitrite production in surface waters by phytoplankton nitrate reduction and in deeper waters by nitrification have also been examined in the Scotia Sea in spring 1978 and the Ross Sea in summer 1978-79 by *Olson* [1981].

8.6. Nitrification in the Antarctic Marine Environment

Nitrification is the bacterially-mediated chemoautotrophic oxidation of ammonium to nitrite to nitrate, and is the fundamental process responsible for the long-term regeneration of oxidized nitrogen compounds (Figure 9). Few nitrification rate measurements exist for the Southern Ocean. *Olson* [1981] used ^{15}N tracer techniques to estimate nitrification rates in the Scotia Sea in spring 1978 and the Ross Sea in summer 1978-79. He found low rates, comparable to those measured in the oligotrophic North Pacific Ocean. *Priscu et al.* [1990], using a selective inhibitor ^{14}C uptake assay, also found low rates in the seawater of McMurdo Sound and along the Ross Ice Shelf, often too low to detect. *Dore et al.* [1993] and *J. Dore* [unpublished data] have used the same inhibitor-sensitive ^{14}C assay in the waters along the Antarctic Peninsula, with similar results. It appears that while nitrification is occurring in antarctic waters, it occurs at rates of less than a few nM per day. At these rates it is probably not a major source of oxidized nitrogen nor a significant mechanism of carbon fixation in the Southern Ocean, except perhaps in areas that lack photosynthetic activity, such as under the Ross Ice Shelf [*Horrigan*, 1981]. Within-ice nitrification, however, may be of much greater consequence, and will be discussed in a subsequent section of this review.

Nitrous oxide (N_2O), an important greenhouse gas implicated in ozone destruction, has also been undersampled in the antarctic marine environment. N_2O is a by-product of nitrification and is also produced during dissimilatory nitrate reduction. Attempts to measure N_2O production rates in Antarctica have been unsuccessful [*Priscu et al.*, 1990]. However, N_2O levels within the snowcover overlying ice in McMurdo Sound have shown a slight enrichment compared

to atmospheric values [*Gosink*, 1980], indicating a possible flux from the ice or underlying seawater to the atmosphere. Evidence from the North Atlantic [*Hahn*, 1975] has indicated that N_2O can be supersaturated in surface waters during phytoplankton blooms although the production mechanism in this case is unknown. Surface N_2O saturations of 94-106% have been reported for the McMurdo Sound region [*Priscu et al.*, 1990], 104-120% for the eastern Weddell Sea [*Weiss et al.*, 1992] and 103-113% for the Antarctic Peninsula region near Elephant Island [*Weiss et al.*, 1992]. In some cases, supersaturations may result from upwelling of N_2O-enriched deep waters along fronts and ice shelves. However, seasonal measurements of N_2O at a station in Gerlache Strait [*J. Dore and D. Karl*, unpublished] provide evidence for a biogenic source of N_2O in the surface waters of the Antarctic Peninsula region. N_2O concentrations in surface waters were on average slightly below air saturation in winter to approximately 110-115% saturation during the spring-summer period. These data suggest that coastal waters of the Antarctic Peninsula may be a seasonally variable source of N_2O to the atmosphere.

8.7. Nitrogen Cycling within Antarctic Sea Ice

Nutrient concentrations within antarctic sea ice have been measured by *Dieckmann et al.* [1991], who found seawater values of nitrate and silicate in young ice (<2 months old), depletions of silicate in older ice, and both depletions and enrichments of nitrate in older ice. They also found ammonium enrichments within older ice that they attributed to *in situ* nutrient regeneration by organisms living within the brine channels of the ice. High ammonium levels in ice have also been described by *Oradovskiy* [1974] and *Dore et al.* [1993]. They also found that this ammonium was not restricted to the lower portion of the ice, suggesting that heterotrophs were active throughout the ice or that ammonium was transported by brine flow or other mechanisms. Ammonium concentration was higher in thicker ice, suggesting that active microbial loops within ice take time to develop. Both *Dore et al.* [1993] and *Priscu et al.* [1990] measured substantial nitrification rates within antarctic sea ice, the latter investigators finding within-ice rates as much as 3 orders of magnitude higher than rates in the underlying water. While measured nitrification rates do not indicate a significant chemoautotrophic contribution to the total primary production of antarctic waters, they may indicate *in situ* nitrate production sufficient to support up to 70% of the nitrate demand of fast-ice algae. The time lag between formation of new sea ice and the establishment of an active microbial food web is evident in the data of *Dieckmann et al.* [1991], and their data further confirm that nitrification may be a significant source of nitrate. However, physical exchange of brine with underlying seawater driven by tidal processes [*Gosselin et al.*,1985; *Demers et al.*, 1985], or during refreezing of multi-year ice [*Fritsen et al.* 1994] is another potential source of fixed nitrogen for ice-associated microbial communities.

9. EXPORT PRODUCTION AND MESOPELAGIC MICROBIAL PROCESSES

The role of the ocean as a reservoir in the global carbon cycle is dependent largely upon the export flux of planktonic primary production from the euphotic zone [*Eppley and Peterson*, 1979; *Williams and von Bodungen*, 1989]. This supply of reduced carbon and energy to intermediate ocean depths occurs by downward advection and diffusion of dissolved organic matter [*Toggweiler*, 1989], gravitational settling of particulate matter [*McCave*, 1975] and by the vertical migrations of pelagic animals [*Longhurst and Harrison*, 1989] and phytoplankton [*Villareal et al.*, 1993]. Each of these individual processes, collectively termed the "biological pump" [*Volk and Hoffert*, 1985] is controlled by a distinct set of environmental factors and, therefore, the relative contribution of each process may be expected to vary with changes in habitat or with water depth for a given habitat.

Results from broad-scale, cross-ecosystem analyses suggest that the export of living and non-living materials from the euphotic zone is a positive, non-linear function of total integrated primary production [*Suess*, 1980; *Pace et al.*, 1987; *Martin et al.*, 1987; *Wassman*, 1990], with values ranging from less than 10% in oligoorophic waters to greater than 50% in productive coastal regions. It should be emphasized, however, that the field data from which the existing export production models were derived are limited and that open ocean and antarctic habitats are both underrepresented. A majority of the Southern Ocean is characterized by high surface nutrient concentrations but low rates of primary production and export production [*Holm-Hansen et al.*, 1977; *Honjo*, 1990]. *Broecker* [1982] suggested that if all the surface nutrients in the Southern Ocean were efficiently used by the phytoplankton, the biological pump activity could transfer a significant amount of atmospheric CO_2 to the ocean's interior. However, at the present time the biological pump appears to be functioning at less than full capacity in polar environments [*Knox and McElroy*, 1984]. A resolution of this Southern Ocean biological pump enigma is a topic of great importance in the study of oceanic carbon cycles.

9.1. Epipelagic Zone Processes: Particle Formation and Removal

The concept of new production, introduced by *Dugdale and Goering* [1967] and later expanded by *Eppley and Peterson* [1979] provides a conceptual framework for studies linking organic matter production in near surface waters with export to the mesopelagic zone. If compared over appropriate time and space scales, new production in a given ecosystem is equivalent to the amount of primary production

that is available for export, a value that is quantitatively balanced by the resupply of production rate-limiting nutrients [*Eppley*, 1989].

The intensive austral spring/summer phytoplankton bloom in the Antarctic Peninsula region can result in phytoplankton standing stocks in excess of 20 mg chl a m^{-3} and sustained production rates of 2-5 g C m^{-2} d^{-1} [*Holm-Hansen and Mitchell*, 1991]. Though the phytoplankton bloom productivity is well-documented, we know less about the fate of this seasonally-accumulated organic matter. In order to model carbon and energy flows in the antarctic coastal ecosystem, we require additional information on the residence time of particulate organic matter in the euphotic zone and on the processes responsible for controlling the rates of export.

In theory, phytoplankton production can be passed through the food web by the feeding activities of grazer populations, removed by gravitational settling of whole cells, converted to soluble organic matter or respired to carbon dioxide. During the past decade, numerous field experiments using particle interceptor traps (i.e., sediment traps) were conducted to determine the amount and nature of the particulate matter exported from representative marine and freshwater ecosystems [*Honjo*, 1990]. Various technical considerations and potential limitations of sediment traps in field studies are presented elsewhere [*Knauer and Asper*, 1989; *Wassman*, 1991]. A fairly extensive particle flux data base exists for the Antarctic Peninsula region (Table 4).

A major problem with direct field measurements of export production in Southern Ocean habitats is the spatial and seasonal variability in plankton rate processes. Phytoplankton blooms are transitory events. The herbivores adapted to feeding on blooms must be able to respond quickly either by coupled and equally rapid growth or through the use of active chemosensory mechanisms and motility [*Smetacek et al.*, 1990]. Protistan grazers (e.g., ciliates, choanoflagellates) belong to the former category and krill (*Euphausia superba*) to the latter. In fact, krill appear to use area-intensive searching and rapid feeding behaviors to exploit locally high food concentrations [*Hamner et al.*, 1983]. Dense krill swarms are common in the Antarctic Peninsula region [*Knox*, 1994].

Sediment-trap derived particle flux estimates in the Antarctic Peninsula region (Table 4) are among both the highest (>1 g C m^{-2} d^{-1} during and immediately following the spring bloom) and the lowest (< 0.05 mg C m^{-2} d^{-1} during austral winter) values reported for the world ocean. Furthermore, during the initial stages of the spring-summer phytoplankton bloom, particle export may be decoupled from contemporaneous new production for periods of several weeks or more [*Karl*, 1993]. Direct measurements of the downward particulate carbon (PC) and nitrogen (PN) fluxes at selected stations in Drake Passage (Sta. #20), Bransfield Strait (Sta. #39) and Gerlache Strait (Sta. #43) during the 1986-87 RACER experiment revealed different relationships between primary production and flux at each of these sites (Figure 10). In Drake Passage where biomass (chl a and ATP) and primary production were low and decreased gradually during the 3-month observation period, PC and PN flux also decreased in phase with total production. At Sta. #39, we observed a moderate bloom in Dec. 1986 with an abrupt decrease in production and biomass thereafter (Figure 10). The trend for PC and PN flux, however, was the opposite of that for production with a gradual increase during the 4-month period. The rates of particle formation and export appear to be decoupled at this site. At Sta. #43 in Gerlache Strait we encountered a large phytoplankton bloom with the highest biomasses and production rates measured in the RACER experiment. The patterns observed for production and particle flux were coherent but approximately 1 month out of phase (i.e., particle flux lagged particle production; Figure 10). Both the highest and the lowest PC and PN fluxes measured during the 1986-87 4-month RACER program were at Sta. #43 [*Karl et al.*, 1991b]. Although post-bloom production processes continued at moderate levels, particle export exhibited a much greater decrease. These results suggest that other removal or *in situ* consumption processes (i.e., epipelagic recycling and respiration) dominate.

Silica is a required macronutrient for diatoms and several other groups of antarctic microorganisms. Because of differences in the temperature effects on microbial decomposition of particulate organic carbon compared to the dissolution of biogenic Si (opal), the cold waters of Southern Ocean habitats preferentially preserve particulate Si relative to other bioelements. For example, *DeMaster et al.* [1991] estimate that sediments near the Polar Front are enriched 50-600 fold in biogenic Si relative to organic carbon. Furthermore, based on Si mass balance estimates for the Ross Sea, *Nelson et al.* [1991] suggest that virtually all of the biogenic Si exported from the euphotic zone must reach the sea floor indicating little dissolution during sinking. This contrasts sharply with the depth-dependent decrease in particulate organic carbon fluxes regardless of habitat.

Spatial and temporal (both seasonal and interannual) variability in antarctic habitats is dramatically reflected in the results of recent time-series sediment trap experiments (Figure 11). One of the most impressive antarctic sediment trap experiments conducted was the 30-month continuous record of total particle flux measured in the King George Island Basin of Bransfield Strait (Figure 11, top) [*Wefer*, 1989]. For each of the 3 consecutive spring bloom periods that were recorded, the timing, the peak flux, the total integrated flux and the temporal flux patterns were different. For example, the 1983-84 austral bloom was characterized by a relatively large and sustained (~60 d) export pulse which amounted to a seasonally-integrated value of >100 g m^{-2} before ending abruptly in early Feb. 1984. In the following austral summer, the entire export pulse amounted to only 12 g m^{-2}, nearly an order of magnitude less, and was restricted to a 2-week period in early Dec. (Figure 11, top). The export pulse during the third year was intermediate in total mass (~38 g

TABLE 4. Selected Particulate Carbon Flux Results from Sediment Trap Experiments Performed in the Region West of the Antarctic Peninsula

Station Location and Coordinates	Period of Collection	Sediment Trap Depth Range (m)	Type of Sediment Trap Array	Carbon Flux (mg m^{-2} d^{-1})	Reference
Bransfield Strait (62°30'S, 57°W)	Nov-Dec 1980	100	Drifting	97-546	*von Bodungen et al.* [1986]
Bransfield Strait (62°45'S, 55°W)	Nov-Dec 1980	100	Drifting	450-1,400	*von Bodungen et al.* [1986]
Bransfield Strait (62°30'S, 58°W)	Dec 1980	100	Drifting	28-39	*Liebezeit* [1985]
Bransfield Strait (62°45'S, 55°15'W)	Dec 1980	100	Drifting	120-160	*Liebezeit* [1985]
Bransfield Strait (62°45'S, 57°57'W)	Feb 1982	150	Moored	115	*Dunbar* [1984]
Bransfield Strait (62°43'S, 56°21'W)	Nov 1985	120	Moored	103	*von Bodungen et al.* [1987]
Bransfield Strait (63°25.5'S, 62°24.5'W; RACER Sta. #13)	Dec 1986-Mar 1987	100	Drifting	187-251	*Karl et al.* [1991b]
Bransfield Strait (63°12.8'S, 61°2.8'W; RACER Sta. #48)	Dec 1986-Mar 1987	100-200	Drifting	<36-251	*Karl et al.* [1991b]
Bransfield Strait (63°34.5'S, 61°27'W; RACER Sta. #39)	Dec 1986-Mar 1987	100	Drifting	87-149	*Karl et al.* [1991b]
Drake Passage (60°55'S, 57°06'W)	Dec 1980-Jan 1981	965-2,540	Moored	13.1-14.8	*Wefer et al.* [1982]
Drake Passage (61°56.3'S, 62°18'W; RACER Sta. #20)	Dec 1986-Mar 1987	100-200	Drifting	41-97	*Karl et al.* [1991b]
Bellingshausen Sea (two stations near 66°11'S, 68°12'W)	Feb 1982	50-100	Drifting	29-70	*Schnack* [1985]
King George Isl. Basin (62°16'S, 57°23'W)	Nov-Dec 1983	323-1,835	Moored	81-132	*Liebezeit and von Bodungen* [1987]
King George Isl. Basin (62°23'S, 57°52'W)	Dec 1983	100	Drifting	30	*von Bodungen* [1986]

TABLE 4. (continued)

Station Location and Coordinates	Period of Collection	Sediment Trap Depth Range (m)	Type of Sediment Trap Array	Carbon Flux (mg $m^{-2} d^{-1}$)	Reference
King George Isl. Basin (62°15.4'S, 51°31.7'W)	Dec 1983-Nov 1984	494-1,588	Moored	<0.05-93 (annual avg. = 8.20)	*Wefer et al.* [1988]
King George Isl. Basin (62°21'S, 57°44'W)	Nov-Dec 1984	100-680	Moored	46-79	*von Bodungen et al.* [1987]
King George Isl. Basin (62°22'S, 57°56'W)	Nov 1985	170-1,480	Moored	49-57	*von Bodungen et al.* [1987]
Gerlache Strait (64°14'S, 61°17'W; RACER Sta. #43)	Dec 1986-Mar 1987	100-200	Drifting	<36-373	*Karl et al.* [1991b]

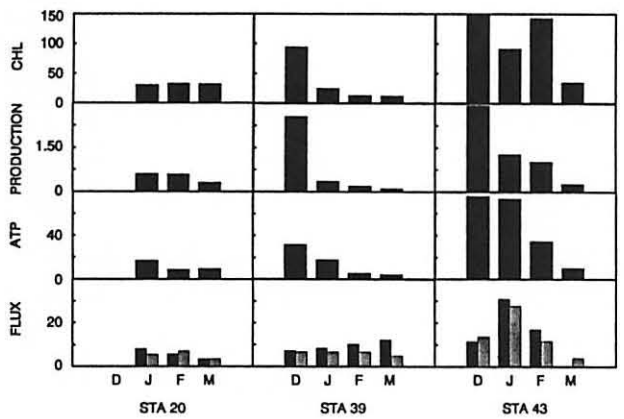

Fig. 10: Relationship between depth-integrated euphotic zone chl a (mg m^{-2}), primary production (mg C $m^{-2} d^{-1}$), ATP (mg m^{-2}) and particle flux (solid bar= carbon, in mmol $m^{-2} d^{-1}$, shaded bar= nitrogen x 6.6, in mmol $m^{-2} d^{-1}$) for three representative stations in the RACER-1 study area. The station coordinates were: #20 (61°56.25'S, 62°18.0'W), #39 (62°34.5'S, 61°27.0'W) and #43 (64°14.0'S, 61°17.0'W) [From: *Holm-Hansen and Mitchell,* 1991 and *Karl et al.,* 1991b].

m^{-2}), but the onset was earlier than in either of the previous two years. The fall export (Mar.-May) that was evident in 1984 and 1986 was absent in 1985. Particle flux during the 1-2 week periods immediately prior to the largest export values observed were indistinguishable from zero (<0.1% of the peak). Clearly both the onset and termination of the spring bloom are rapid phenomena in this coastal antarctic habitat.

The abrupt termination of the spring bloom export may be controlled, at least in part, by storm events which have the net effect of dissipating the phytoplankton crop and reducing net photosynthesis and growth. If the water column is allowed to restratify, a second spring bloom is possible (Figure 11, center). The total time-integrated mass flux observed during this approximately 2-month interrupted spring bloom in Gerlache Strait was >100 g m^{-2}, a value similar to the largest of the three austral spring events recorded at the King George Island Basin site.

A novel experiment conducted in the north-central Weddell Sea examined the changes in particle export associated with the formation and ablation of the annual pack ice. A time-series sediment trap mooring was deployed in open water near the retreating ice edge in Jan. 1985 and was recovered approximately 18 months later having recorded the particle export from two consecutive ice edge blooms (Figure 11, bottom). Several important features were evident. First, both the overall pattern of particle export and the absolute magnitude were quite different from the spring bloom features observed in King George Island Basin and Gerlache Strait. In 1985, the Weddell Sea particle export lagged, by approximately one month, the retreat of the ice edge over the trap mooring. Furthermore, there was a gradual increase in particulate flux which lasted for approximately 2 months. The peak export pulse occurred in mid-March followed by a gradually decreasing flux towards the winter minimum. This flux pattern contrasts sharply with the nearly instanta-

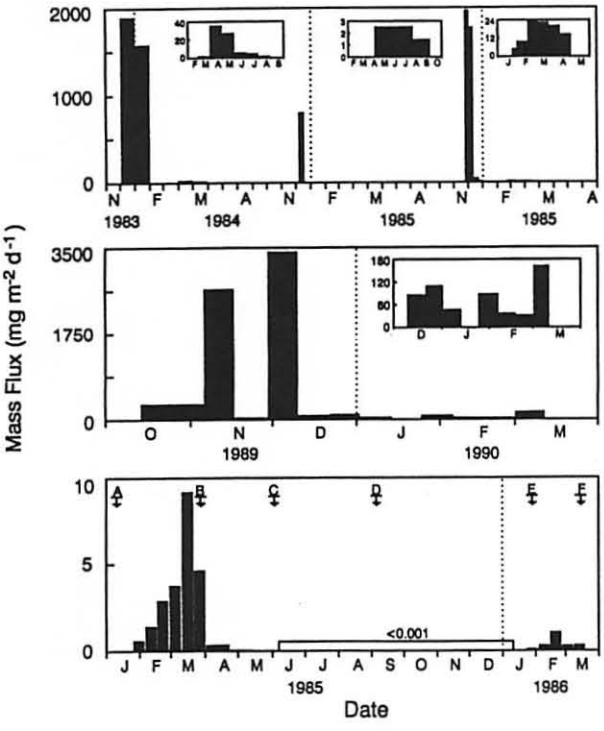

Fig. 11: Seasonal variability in the downward flux of particulate matter at three antarctic time-series sediment trap stations. [TOP] 30-month record of particle flux (total dry weight) from the Bransfield Strait ecosystem showing the intense annual and interannual variability observed in this region [From: *Wefer*, 1989]. [CENTER] Particle mass flux (total dry weight) versus time for a continuous 5-month period during the 1989-1990 austral summer. Inset presents an expanded view of the flux data collected from 9 December 1989 to 11 March 1990 [From: *Karl and Asper*, 1990]. [BOTTOM] Total flux for each period at the north-central Weddell Sea station during 1985 and 1986. Superimposed is the closest distance from the approximate ice edge to the sediment trap site 3 weeks before, during, and after the experiment, based on weekly Antarctic Ice Charts (NPOC) compiled from the NOAA polar orbiter, NASA Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR), GEOSAT altimeter, and visual data using NOPC ice coverage scales. (a) Ice-edge passage over the trap site during the 1985 regression. (b) The maximum opening of ice lasted about 60 days. The ice edge rapidly moved northward after early April 1985. (c) Ice edge passage over the trap site during the 1985 transgression. (d) 1985 maximum ice extension. The ice edge was 550 km north of the trap site. (e) Ice edge passage over the trap site during the 1986 regression. (f) Maximum ice opening during 1986. (g) Ice edge passage over the trap site during the 1986 transgression [From: *Fischer et al.*, 1988 and *Honjo*, 1990].

neous and isolated peaks observed in the coastal regions (Figure 11). A similar flux pattern was also observed in the Weddell Sea in 1986; however, the seasonally-integrated export of total mass varied considerably between consecutive years for the central Weddell Sea ice-edge ecosystem. The 1985 export pulse was ~0.25 g m^{-2}, and for 1986 it was ~0.025 g m^{-2}, one order of magnitude lower. In general, these open ocean particle fluxes are lower, by 2-3 orders of magnitude, than the fluxes measured in King George Island Basin and Gerlache Strait (Figure 11). The coastal ecosystem winter fluxes were below detection limits (<0.05 mg m^{-2} d^{-1}).

The low to undetectable fluxes of total mass and biogenic matter consistently observed during austral winter periods are enigmatic. Although the antarctic winter is known for harsh environmental conditions of deep-mixed layers and low solar radiation, most oceanic regions in the Antarctic Peninsula region support measurable net primary production year round. *Cochlan et al.* [1993a] measured chl a concentrations of 4 mg m^{-2} (0-75 m) and photosynthetic rates of 35-50 mg C m^{-2} d^{-1} at the RACER Station A (64°11.3'S, 61°19.5'W) in Gerlache Strait during July 1992. Furthermore, it was reported that the f-ratio of the wintertime phytoplankton assemblage (e.g., [NO_3^-] uptake rate divided by the sum of [NO_3^- + NH_4^+ + urea] uptake rates) was 0.87, suggesting that the majority of primary production was supported by "new" nitrogen [*Cochlan et al.*, 1993b]. In spite of these substantial production and new production rates, the measured wintertime export fluxes in antarctic coastal waters are <0.5 mg C m^{-2} d^{-1}.

Similar experiments conducted in the Weddell Sea in late winter revealed ice edge zone (60°S, 2°E) chl a values of 12 mg m^{-2} and primary production rates of 300-400 mg C m^{-2} [*Marra and Boardman*, 1984]. More recent results obtained during the first antarctic drifting ice station in the western Weddell Sea during Feb.-June 1992 documented the fall-to-winter development of a diverse microbial assemblage within porous layers of the multi-year ice. The ice camp was established at 71.4°S and the drift was northward to 65.8°S, along 53°W. During the period of observation, 1760 mg C m^{-2} and 200 mg N m^{-2} of algal biomass had accumulated in the porous ice, with daily production rates of 22-176 mg C m^{-2} [*Fritsen et al.*, 1994]. However, wintertime Weddell Sea export fluxes were undetectable (<0.001 mg C m^{-2} d^{-1}) [*Fischer et al.*, 1988].

There are several possible C-flux pathways for the wintertime primary production. It can either accumulate in place as phytoplankton biomass or be consumed by grazers, converted to DOM or respired (recycled) close to the source of production. Of these, the most feasible pathway appears to be respiration as both micro- and macrozooplankton grazing and biomass accumulation would sustain a finite particulate matter export. During the extended dark periods at these latitudes (~18 hr d^{-1}) the community consumes a larger fraction of contemporaneous primary production than during summer periods. Clearly, a resolution of these field measurements of moderate wintertime new production in the absence of measurable particulate export must be viewed as one of the major challenges to our understanding of the antarctic carbon cycle.

9.2. The Nature of the Export Flux

The nature (i.e., bulk chemical composition, particle identities and physical state) of the materials collected in free-drifting and bottom-moored sediment traps is variable in time and space. For example, *Dunbar* [1984], *Nöthig and von Bodungen* [1989] and *Wefer and Fischer* [1991] reported that feces are the dominant, recognizable organic component in sediment traps, suggesting that macrozooplankton grazing controlled the export of organic matter from those habitats. In contrast, *von Bodungen et al.* [1986] and *Karl et al.* [1991b] report a dominance of aggregated phytoplankton cells. *Bienfang and Ziemann* [1992] conclude that the size structure of the phytoplankton community is the most important parameter influencing sedimentation. Furthermore, *Riebesell et al.* [1991] have reported that aggregated phytoplankton derived from melting sea ice sink at rates that are three orders of magnitude greater than dispersed cells, implying a rapid sedimentation. At certain times of the year, "marine snow" may also comprise a majority of the collected particulate matter. Using a non-contact photographic profiling system, *Asper et al.* [1993] provided the first direct measurements of the concentrations and distributions of marine snow in Antarctica. Their results revealed very high marine snow concentrations, especially below 150 m, and support the hypothesis that suspended aggregates are scavenged from the water column thereby contributing to the downward vertical flux.

The variable nature of sinking particulate matter has important implications for modeling export processes and for gaining a general understanding of antarctic food webs. For example, if the primary producers themselves are exported by cell aggregation and gravitational settling, one might expect a much higher total sinking particle flux (when expressed as a percentage of primary production) when compared to ecosystems where 2nd or 3rd trophic level grazing activities dominate particle production and export. When grazers are abundant, most of the carbon (and other bioelements) initially produced during photosynthesis would be recycled and export flux ratio (i.e., export:total production) would be substantially reduced. Consequently, the largest export pulses might be expected to occur when phytoplankton populations begin to aggregate (e.g., when ice algae are melted from the seasonal pack or when open ocean blooms terminate) rather than during episodes of intense macrozooplankton grazing [*Matsuda et al.*, 1987].

9.3. Life Beneath the Euphotic Zone

In marine ecosystems, net photosynthesis is restricted to the upper 100-200 m of the water column depending upon water clarity. However, in antarctic coastal ecosystems during spring bloom events, the depth of the euphotic zone becomes progressively shallower as the phytoplankton community develops, and may be 20 m or less at the height of the bloom [*Holm-Hansen and Mitchell*, 1991]. Under these conditions, living phytoplankton cells are usually found in the permanently aphotic zone as a result of gravitational settling. Although these cells may still be photosynthetically competent, their ecological role at depth is not well known. Furthermore, ecosystems that exhibit relatively thin epipelagic zones (~20 m) are unstable, despite the seawater density stratification that creates them. Periodic storms are important for mixing cells downward and nutrients upward and thereby rapidly change the dimensions of both the epipelagic and mesopelagic zones.

A systematic study of the habitat beneath the euphotic zone in Antarctica has not been conducted. The microbiological focus has been on algal-bacterial-protozoan coupling in surface waters. A pioneering study of meso-pelagic zone microbial processes in Drake Passage was conducted by Hanson and colleagues [*Hanson and Lowery*, 1983; *Hanson et al.*, 1983 a,b]. The mesopelagic zone total microbial community biomass was 0.5-2.5 μg C l^{-1}, consistent with other oligotrophic ocean habitats [*Karl*, 1980]. All activity and growth measurements (e.g., glucose, thymidine and adenine assimilation) indicated that microbial activity beneath the euphotic zone decreased by 1-3 orders of magnitude compared to surface values [*Hanson and Lowery*, 1983; *Hanson et al.*, 1983a].

An interesting observation made during the Drake Passage expedition was a shift in the size spectrum of heterotrophic activity with increasing water depth. Below 100 m, heterotrophic activity was largely particle-associated (>3 μm). The authors suggested that particle export, fragmentation and colonization processes may be important in the mesopelagic zone of Drake Passage. Observations from our field experiments conducted in Gerlache Strait support their model. During the seasonal spring bloom, the downward flux of particulate biogenic matter changes rapidly from >200 mg C m^{-2} d^{-1} at 40 m to <75 mg C m^{-2} d^{-1} at 140 m (Figure 12). The change in particle flux with depth implies an efficient recycling or rapid conversion of the particulate matter to dissolved and suspended particulate matter. The C:N ratio of the collected particulate matter is consistent with bacterial growth on C rich (polysaccharide) particulate matter with a coupled conversion to bacterial biomass which has a characteristically low C:N ratio. This pattern of decreasing C:N ratio for sinking particulate matter with increasing depth is opposite to the trend observed in most open ocean habitats, and may be unique to the export of materials during these hypereutrophic coastal blooms. The previously-discussed uniformity of bacterial biomass and productivity in water samples collected from the upper mesopelagic zone regardless of season may simply indicate the low activity background onto which the metabolically-active, seasonally-phased vertical flux processes are superimposed. Without a proper, quantitative assessment of these particle-associated processes, carbon and energy flow within the antarctic mesopelagic zone may be underestimated.

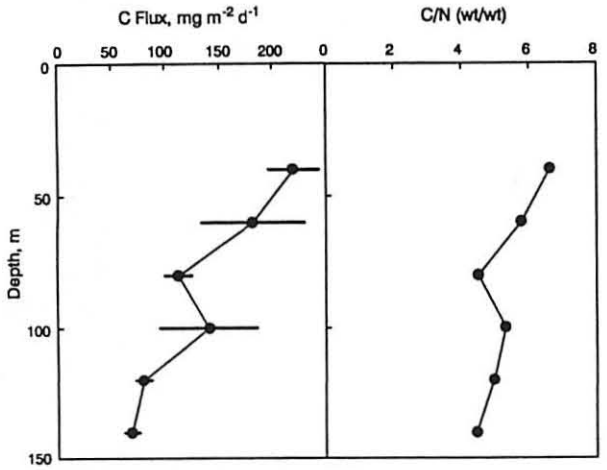

Fig. 12: [LEFT] Downward vertical flux of particulate carbon at various subeuphotic zone reference depths measured using a drifting sediment trap array. Samples were collected in Gerlache Strait (64°11.7'S, 61°19.5'W) during the RACER-2 expedition (Nov. 1989). [RIGHT] Particulate carbon to particulate nitrogen (C:N), expressed on a mass:mass basis, for materials collected in the RACER-2 sediment trap experiment.

10. SUMMARY AND PROSPECTUS

This review has tried to integrate several independent but interrelated topics in microbiological oceanography. Although a more "traditional" review on antarctic microbiology might have focused exclusively on bacteria, such a view, in our opinions, is inappropriate. It is difficult to discuss isolated groups of microorganisms if the stated intent is to understand ecosystem level processes. On the other hand, an integrated discussion is sometimes unsatisfactory because it lacks sufficient detail about individual organisms or their metabolic processes. We hope that our attempts to integrate selected information on antarctic microbial ecology will stimulate thought and encourage additional research in biogeochemical dynamics in the region west of the Antarctic Peninsula.

Although it is difficult to predict future developments in any field of science, it is likely that observational oceanography in the Southern Ocean will expand during the next decade as global environmental change threatens all of the earth's ecosystems. Antarctica may be particularly sensitive to greenhouse gas-induced global warming and to destruction of the stratospheric ozone layer, so these and other investigations are likely to be conducted there. Also, because the Southern Ocean presently contains a large reservoir of unused inorganic nutrients in the surface waters, it is a potential sink for atmospheric carbon dioxide. A thorough understanding of what limits primary production, especially in the high nutrient low chlorophyll offshore regions, and how both systematic and stochastic changes in primary production are coupled to higher trophic levels will also be required. Other ecological observations such as the apparent decoupling between heterotrophic bacteria and phytoplankton and the uncoupling of carbon and silica cycles need to be resolved before accurate ecological models can be constructed. Future oceanographic investigations must focus on these and other urgent global environmental issues. Finally, the hostile and remote conditions that characterize of much of Antarctica demands greater reliance on innovative measurement technologies such as instrumented ice-ocean environmental buoys [*Honjo et al.*, 1995] and autonomous under water/under ice vehicles for multidisciplinary ocean measurements. These and other engineering and intellectual developments will help bring these contemporary challenges into scientific focus.

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