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MICROBIAL PROCESSES IN THE SOUTHERN OCEANS

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1. INTRODUCTION

Heterotrophic bacteria and other microorganisms are ubiquitous in the marine environment, regardless of latitude, water depth, or distance from continental land masses. Antarctic waters are no exception. Pioneering microbiological research conducted there during the first half of the twentieth century documented the presence of bacteria as an important component of the indigenous microbial assemblage (McLean, 1918; Darling and Siple, 1941; references cited by Sieburth, 1965, and Bunt, 1971). Although these data and the methods by which they were collected (e.g., 37°C plate-count determinations) are now considered primitive and are of little value in contemporary models of microbial processes, their historical significance should not be overlooked.

During the 1950s, Bunt (1955), McBee (1960), Sieburth (1958, 1959, 1960), and Kriss (Kriss et al., 1960a,b) conducted more modern studies, but their methods would still be considered inaccurate by today's standards. For example, the report that most surface water samples collected south of the Antarctic

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Convergence contained fewer than 10 bacterial cells ml^{-1} (Sieburth, 1965) is known to be at least three orders of magnitude too low. Reviews by both Sieburth (1965) and Bunt (1971) lamented our superficial knowledge of polar ecosystems. The former called for the development of better methods for the study of autochthonous microflora and for the conduct of better-planned and executed interdisciplinary studies combining ocean physics, chemistry, and microbiology, and the latter stressed the need for more detailed studies of microheterotrophic processes and control mechanisms. These two research themes are again emphasized in this review.

More recent quantitative, *in situ* investigations of microbial communities south of the Antarctic Convergence are beginning to yield a coherent picture of microbial processes and rates. In this review I try to summarize the marine Antarctic microbiological research conducted since 1960, with an emphasis on studies since 1975. The focus is on microbial habitats, their associated populations, and population interactions; studies of pure cultures are discussed only where the information is relevant to our understanding of *in situ* microbial processes.

For the purposes of this review, I define *microorganism* as any small (≤ 200 μm) organism or cell, so bacteria, viruses, unicellular algae, protozoans, and small metazoans are considered, but I focus primarily on the chemoheterotrophic bacterioplankton populations. For additional discussions of specific microbial inhabitants of Antarctic waters or of microbial processes in specialized Antarctic marine habitats, the reader should consult the excellent monograph by Vincent (1988), and the recent review by Wynn-Williams (1990). (For further discussion in this volume see El-Sayed and Fryxell, Chapter 2; Garrison and Gowing, Chapter 3; Palmisano and Garrison, Chapter 4; and White et al., Chapter 5.)

2. ANTARCTIC MARINE HABITATS: DIVERSITY IN TIME AND SPACE

Although Antarctic waters are perennially cold and in some locations permanently ice-covered, there is a large diversity of microbial habitats and, therefore, microbial assemblages. These microbial habitats range from the hypersaline and supercooled sea-ice microenvironments to the open-ocean pelagic realm of the Antarctic Circumpolar Current and the geothermally heated waters of the Scotia Arc. Furthermore, most microorganisms live in microenvironments on length scales of millimeters or less, which are frequently associated with suspended particles, plant and animal surfaces, or physical discontinuities of the seawater or sea-ice column (Karl, 1982). Within these usually diffusion-controlled microenvironments, which have properties unlike those of the surrounding open waters, there is a potential for the enrichment of specialized groups of microorganisms.

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 fluctuations in mixed-layer depth and solar radiation. Clearly it is difficult, if not misleading, to make broad generalizations regarding microbial processes in Antarctic waters. Consequently, I present microbiological results in the context of individual case studies, with particular attention to the geographical location (open sea, continental shelf, coastal embayment, etc.) and, especially, to the season in which each investigation was performed. As could be expected, given the logistical difficulties involved in austral winter research, the extant data come from coastal habitats oversampled in the summer and grossly undersampled in the winter.

2.1. Regional Geography and Major Oceanic Provinces

The distribution, abundance, and productivity of microorganisms are all influenced by hydrographic processes, including large-scale ocean circulation and mixing. These in turn are controlled by atmospheric forcing, topography, bathymetry, and the physical characteristics of the water column. Temperature, the distribution of inorganic and organic nutrients, photosynthetically available radiation (PAR), and the presence of ice are also important in controlling the rates of microbial processes.

The southern oceans encompass three deep basins (>4 km); several prominent rises, ridges, and plateaus; and, in certain regions, numerous islands. This bathymetric mosaic influences both deep and near-surface ocean currents. Furthermore, as a result of isostatic adjustment of its massive ice cap, the continental shelves of Antarctica are fairly deep (400–500 m) in comparison to similar features at lower latitudes.

Although the ocean surrounding Antarctica comprises portions of the Atlantic, Pacific, and Indian Oceans, oceanographers have found it convenient to refer to this circumpolar body of water as a unit, sometimes called the Southern Ocean (Foster, 1984). Its zonation is based primarily on the distribution of physical properties (temperature and salinity) and major ocean current systems. A dominant feature is the existence of a quasi-stationary front, the Antarctic Convergence (AC; also known as the Polar Front), which defines the boundary between the cold Antarctic surface water and the warmer sub-Antarctic waters to the north (Fig. 1.1). For the purposes of this review, I define the southern oceans as the body of water that lies south of the AC. By that definition, its surface area is 36×10^6 km^2, approximately one-tenth that of the world oceans (Laws, 1985). On the basis of its characteristically steep temperature gradient, the AC is also

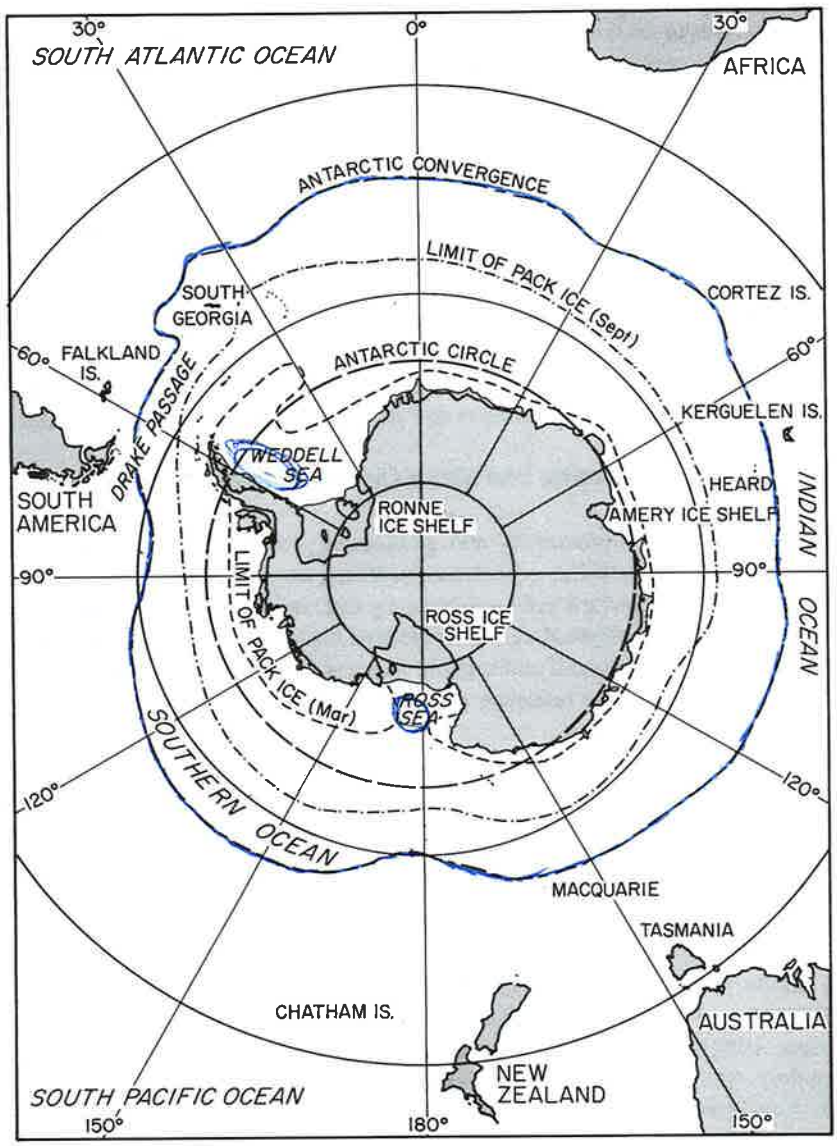


Fig. 1.1. Map of Antarctica showing the positions of the Antarctic Convergence, the summer and winter extents of pack ice, and the major continental ice shelves. Redrawn from Deacon (1982) and Crary (1962).

considered to be an important biogeographical boundary (Deacon, 1982), but it is clearly not a barrier to the exchange of nutrients or biomass (G. Hempel, 1985).

A major ocean current, the Antarctic Circumpolar Current (ACC; also known as the West Wind Drift) extends to the north of the AC and includes coastal waters of the South American, African, and Australian continents (Fig. 1.1). The ACC transports more water than any other current system in the world ocean (Foster, 1984). At its northern boundary, it intersects the major gyres of the South Atlantic, South Indian, and South Pacific oceans, where water exchange and mixing occur (especially in the abyssal regions). The sharp transition between the sub-Antarctic waters of the ACC and the warmer waters to the north is referred to as the subtropical convergence.

To the south of the AC is the Antarctic Divergence (AD), a major transition zone located at a latitude ranging from 62-63°S in the Indian Ocean sector to 70-71°S north of the Ross Sea (Deacon, 1982). The AD defines the boundary between predominant westerly winds to the north of the AD and predominant easterly winds to the south. The frictional stress of the wind on the water, combined with the effect of the rotation of the earth, causes an Ekman divergence, resulting in upwelling throughout this transition zone.

In addition to these broadly defined current systems and transition zones, numerous localized frontal zones, gyres, and eddies support enhanced biological activity (Lutjeharms et al., 1985). Although less thoroughly studied than the major current systems, these smaller-scale features may exert a greater influence on microbial diversity, abundance, and metabolic rates. Finally, superimposed on these mean conditions are localized high-frequency variations in weather and ocean currents due to the chain of atmospheric depressions moving from west to east along variable tracks (Deacon, 1982), as well as low-frequency temporal variability from the more predictable seasonal cycles.

2.2. Major Water Masses

The southern oceans contain, in addition to the regionally and temporally variable surface waters, three major distinct water masses: the Antarctic Intermediate Water, Antarctic Bottom Water, and Antarctic Circumpolar Water (Foster, 1984; Carmack, 1990). Antarctic Intermediate Water is formed by mixing across the fronts in the vicinity of the AC and moves northward at an equilibrium depth of approximately 1,000 m. Antarctic Bottom Water is formed at source regions in the western Weddell Sea and Ross Sea (Carmack, 1977). At -0.5°C and a salinity of 34.66 , it is the densest water in the world ocean. It flows northward into all three major ocean basins and can be traced to at least 50°N in the Pacific Ocean (Tchernia, 1980). The Antarctic Circumpolar Water (also referred to as "Warm Deep Water") is the largest of the three. It is formed by an admixture of North Atlantic Deep Water, which flows from the eastern South

Atlantic and Indian oceans, and colder low-salinity surface waters. By volume, the Antarctic Circumpolar Water mass is the largest marine microbial habitat in Antarctic waters.

2.3. Sea Ice, Ice Shelves, and Polynyas

Ice is a dominant feature of the Antarctic environment. Important habitats for marine microorganisms include the sea-ice habitat and the continental glaciers, which extend into the sea as ice shelves. The former includes both the "permanent" (or at least multi-year) sea ice, which is present year-round (e.g., in the western Weddell Sea and Bellingshausen Sea), and the seasonal sea ice, which forms around the entire continent during the Antarctic winter and melts during each austral summer (Fig. 1.1). The physical and structural characteristics of Antarctic sea ice have been thoroughly reviewed by Maykut (1985) and A. J. Gow and Tucker (1990).

Satellite remote sensing of the Antarctic sea-ice zone between 1973 and 1975 showed a minimum coverage of 3×10^6 km^2 in February and a maximum of 20×10^6 km^2 in September–October (Zwally et al., 1983). The latter figure represents approximately 50% of the total area of the southern oceans and emphasizes the importance of the annual cycle of sea-ice formation and ablation. The seaward boundary of the sea-ice zone is irregular in shape and variable in northern extent and hence in total coverage from year to year. This interannual variability has a direct influence on the biological productivity of the marginal ice-edge zone (W. O. Smith et al., 1988).

A complex microbial community has been described from the sea-ice habitat (called "SIMCO" for sea-ice microbial community; Sullivan, 1985; Palmisano and Garrison, Chapter 4, this volume), which is in continuous flux as a result of the annual cycle of ice dynamics. The sea ice, although extensive and ubiquitous, is not always contiguous. Leads (open cracks within an otherwise ice-covered region) and coastal polynyas (persistent ice-free regions within the sea-ice canopy) are also common. Although these ice-free regions have not been studied in detail, they are clearly unique physical and chemical environments and may also represent unique habitats for microorganisms. During spring and summer, the outer edge of the pack ice is of particular importance to microorganisms because of the effects of ice melting on water-column stratification and is discussed below.

Freshwater ice is also present in the Antarctic marine environment. For example, in the Ross and Weddell seas, ice sheets extend from the continent to form the Ross, Amery, and Ronne ice shelves (Foster, 1984; Fig. 1.1). These shelves may exceed 800 m in thickness, excluding solar radiation from the underlying seawater. The ice shelves move continually seaward (at about 1 m day^{-1}). They eventually crack at their leading edges and form icebergs up to 100

km long by 200–300 m thick (Foster, 1984). Radok et al. (1975) have estimated that the total mass of icebergs is equal to about one-third the mass of sea ice at its maximum seasonal extent.

2.4. Seasonal Cycles and the Spring/Summer "Bloom"

A characteristic property of high latitudes is the extreme annual variability in solar radiation, resulting largely from low solar altitude and extremes in day length (Holm-Hansen et al., 1977). During the austral summer, the daily light flux in Antarctic waters can exceed that in the tropics primarily as a result of the length of the solar day (e.g., 22 hr at 64°S); during austral winter the flux is significantly reduced (Fig. 1.2). Moreover, mean solar irradiance can vary by a

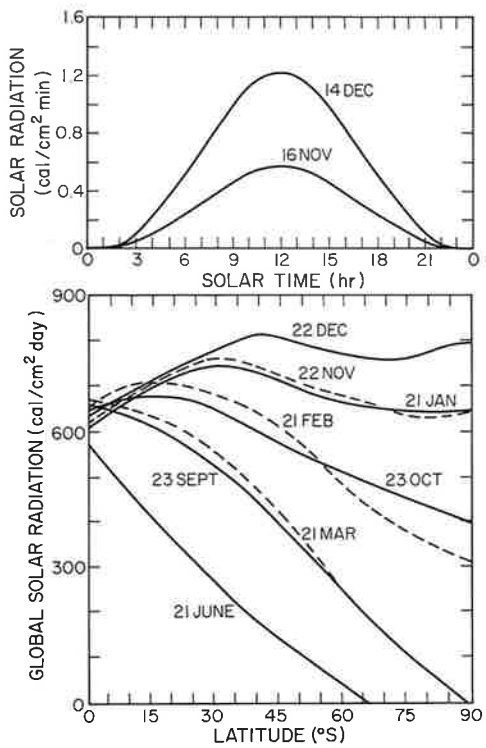


Fig. 1.2. Top: Diurnal variation in the incident solar radiation at 64°S for 16 November and 14 December; **bottom**: Latitudinal profiles of computed mean values of the daily clear sky insolation in the Southern Hemisphere for selected critical dates. An unpolluted atmosphere with mean amounts of precipitable water was assumed. Redrawn from Holm-Hansen et al. (1977).

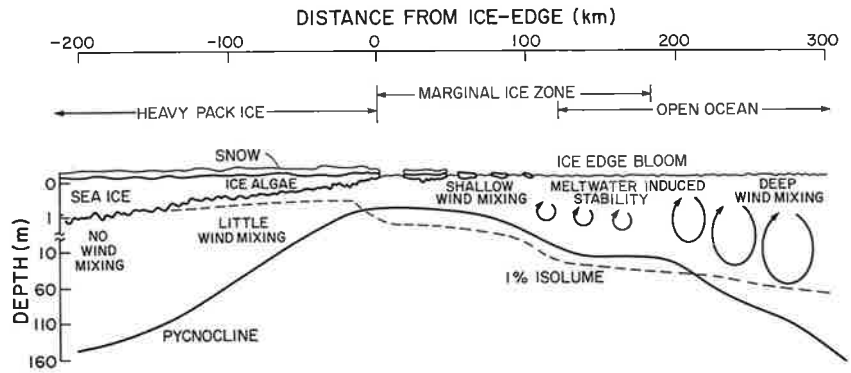


Fig. 1.3. Schematic model of the environmental conditions at the marginal ice edge that are necessary for a sustained phytoplankton bloom. Redrawn from Sullivan et al. (1988).

factor of two as a result of variations in cloud cover (Bishop and Rossow, in press).

In addition to providing PAR for the growth of phototrophic microorganisms, the seasonal increase in radiant energy results 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, also caused by radiant heating, further stabilizes the water column through the addition of low-density meltwater (Fig. 1.3). The net effect of these factors is the formation of a phytoplankton bloom (Sverdrup, 1953; W. O. 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 may also be important in the removal of particulate organic matter from the surface layer of the ocean (see next section). The role of these intensive spring blooms in the proliferation of heterotrophic microorganisms is discussed below.

2.5. The Southern Ocean "Biological Pump"

The oceans act as a regulator of atmospheric CO_2 content and are therefore central to the emerging debate over the effects of increasing levels of greenhouse gases. Current estimates suggest that the world ocean has already assimilated nearly one-half of the anthropogenously produced CO_2 (Broecker et al., 1979).

The rate of removal of atmospheric CO_2 is controlled by both physical and biological processes. First, the partial pressure of CO_2 in the surface oceans is in dynamic equilibrium with that in the atmosphere. This exchange can be rapid and is influenced by ocean circulation and oceanic biological activity (Sarmiento

and Toggweiler, 1984; Siegenthaler and Wenk, 1984; Karl et al., 1991b). Second, biological processes in the surface ocean produce particulate carbon, which sinks into the deep ocean, where it is either remineralized en route to the seabed or buried in deep-sea sediments (Brewer et al., 1986). The ocean's interior is therefore continuously enriched with elements like carbon, nitrogen, phosphorus, and silicon as a result of the combined processes of surface ocean production, particulate matter flux, and dissolution and remineralization. This series of processes has been termed the "biological pump" (Moore and Bolin, 1987).

The rate and efficiency of the biological pump vary among different oceanic habitats and are thought to be controlled by inorganic nutrient inputs from outside the euphotic zone. The export of particulate organic matter resulting from the biological pump (also referred to as "new production") can be measured by sediment traps positioned near the base of the euphotic zone (Eppley, 1989).

Recent box models of the ocean–atmosphere system have demonstrated the potential importance of the southern oceans in the regulation of atmospheric CO_2 (Ennever and McElroy, 1985; Toggweiler and Sarmiento, 1985; Wenk and Siegenthaler, 1985), but the factors controlling the biological pump appear to be different from those in other oceanic regions. For example, the majority of the Southern Ocean is characterized by high surface nutrient concentrations but generally low rates of primary production and export production (Holm-Hansen et al., 1977; Honjo, 1990). Broecker (1982) has pointed out that, if all the surface nutrients in the southern oceans were used by the phytoplankton, the resultant biological pump could transfer significant amounts of atmospheric CO_2 to the ocean's interior. It does not appear to be functioning at full capacity, however (Knox and McElroy, 1984), and the excess inorganic nutrients are ultimately removed during the formation of Antarctic Deep and Antarctic Intermediate water masses. Resolution of this enigma is of great importance in the study of oceanic carbon cycles.

3. METHODOLOGY: ACCURACY AND LIMITATIONS

Rapid advances in our understanding of microbial processes in the marine environment can usually be traced to innovative developments in methodology or instrumentation. We are presently methods-limited. As the ecological questions and hypotheses under investigation become more refined, new techniques will be required and will make the current methods obsolete (Karl, 1986). We should therefore anticipate and encourage the development and application of novel approaches.

A plethora of methods is currently available for the estimation of the abundance, biomass, metabolic activity, and growth of microorganisms (Brock, 1971;

van Es and Meyer-Reil, 1982; White, 1983; Karl, 1986). The limitations of each method must be identified so that we can interpret our field results with caution, self-criticism, and accuracy. Assay "assumptions" too readily become "facts" with the extensive and uncritical use of any method, technique, or instrument. The plate-count method is a prime example (Sieburth, 1959). Even today this traditional method, which must be considered an anachronism among our "current" methods (Schmidt, 1973), is used in Antarctic field studies (Zdanowski, 1982; Simidu et al., 1986). Nevertheless, although unreliable methods can only provide questionable data, if we lose sight of the ecological processes we endeavor to understand while we scrutinize and debate the validity of experimental approaches, microbial ecology will stagnate. The investigator must keep in mind that even questionable data may be better than none at all.

A review of studies since 1975 of microbial (and, in particular, bacterial) processes in the southern oceans reveals that most of the data were obtained by one or more of three basic methods: (1) biomass estimation by direct microscopy, (2) metabolic activity estimation by the uptake and assimilation of labeled organic substrates, and (3) productivity estimation by ^{3}H-thymidine (^{3}H-Tdr) assimilation.

3.1. Direct Microscopy

Enumeration as a quantitative assessment of the standing crop of microorganisms (i.e., biomass) is a fundamental objective of all studies of aquatic microbial ecology. One must know the total microbial biomass and, preferably, the partitioning of total biomass into major taxonomic groups (e.g., bacteria, algae, protozoans) to interpret other data on material or energy flux through the microbial assemblage. Direct microscopic methods using ultraviolet (UV) autofluorescence (for pigmented microorganisms); exogenously added UV-sensitive fluorochromes such as AO, DAPI, FITC, or Hoechst 33258 (for nonpigmented microorganisms); and fluorescent-labeled antibodies (for specific subpopulations) have become the methods of choice for identifying, counting, and sizing microorganisms in natural environments. Microscopy, although certainly the most direct method, is far from ideal. Major criticisms include (1) subjectivity (in differentiation of cells from nonliving particles and of living from nonliving cells and cell sizing), (2) labor intensity, (3) relative insensitivity (especially for detection of single cells and dwarf cells), and (4) lack of a convenient standard reference material for determination of accuracy and precision.

Even if direct microscopic methods were relatively free from error and bias, we would still be left with uncertainties involved in the extrapolation of the microscopically derived estimates of biovolume (expressed as μm^3) to units of total carbon (the desired unit of biomass for most comparative ecological

studies). To convert biovolume to biomass carbon, one must make a series of assumptions regarding the average bulk density of the cells, the average percentage dry weight, and the average dry-weight-to-C ratio. Substantial variation has been found in each of these parameters in laboratory-grown microorganisms (Romanenko and Dobrynin, 1978; Newell and Statzell-Tallman, 1982; Bakken and Olsen, 1983; Bratbak and Dundas, 1984; Simon and Azam, 1989), and unfortunately, none of these properties can be determined directly in field-collected samples. In most ecological studies, the investigators accept that enumeration and biovolume are based on estimates and apply, by citation, one of the published extrapolation factors. Unfortunately, even these biovolume-to-C conversion factors exhibit a considerable range: 1.21×10^{-13} g C μm^{-3} (Watson et al., 1977), 2.20×10^{-13} g C μm^{-3} (Bratbak and Dundas, 1984), and 5.6×10^{-13} g μm^{-3} (Bratbak, 1985). One must conclude that a biomass-C estimate derived from direct microscopic analysis of a field sample might be within only ±100% of the real value.

3.2. Heterotrophic Activity

The uptake and assimilation of ^{14}C-organic compounds has been used extensively to analyze the "heterotrophic potential" of natural microbial communities (Parsons and Strickland, 1962; Wright and Hobbie, 1965, 1966). Although this kinetic approach represented a conceptual breakthrough and one of the most fundamental methodological developments in modern aquatic microbiology (Karl, 1986), it is not without problems and limitations. When it is applied, a mixed population must be treated conceptually as a finite number of equivalent responsive metabolic sites that conform to a uniform set of kinetic variables, an assumption that unfortunately is not valid (P. J. leB. Williams, 1973; Wright and Burnison, 1979; Azam and Hodson, 1981; E. A. Laws, 1983; Li, 1983). Furthermore, it is impossible to know for sure whether a particular substrate (usually a monomeric constituent like glucose, glutamic acid, acetate, etc.) is representative of the largely uncharacterized dissolved organic matter (DOM) present in the marine environment. If microorganisms in nature prefer to use dissolved polymeric substrates (protein, nucleic acids, complex carbohydrates), for example, or if multiple dissolved constituents are utilized simultaneously, we may be underestimating the potential C flux through the microheterotrophic compartments. This problem is especially serious for estimation of "percentage respiration" by simple monitoring of the $^{14}C\text{-}CO_2$ evolved during a short-term incubation with a preselected radiolabeled substrate.

In 1973, Azam and Holm-Hansen formulated a significant refinement of the measurement of heterotrophic potential by suggesting the use of high-specific-activity ^{3}H-labeled organic substrates instead of the previously used ^{14}C-compounds. The advantage lies in the ability to make a direct estimate of the turnover

time of the substrate pool at ambient pool concentrations. Also, if the "free" dissolved natural substrate pool can be measured independently, one can combine these concentration data with the turnover time calculations to estimate the *in situ* mass flux (g C l^{-1} hr^{-1}) for the particular ecosystem under investigation.

3.3. Heterotrophic Growth and Production

The development of methods to estimate the rates of bacterial production (expressed in units of μg C l^{-1} d^{-1}) and specific growth rate (μ, expressed in units of d^{-1}) in nature has been largely unsuccessful. The existing methods are either nonspecific (e.g., SO_4 assimilation, adenine assimilation, adenine nucleotide pool turnover), unreliable (e.g., frequency of dividing cells, change in cell numbers during timed incubations), or inaccurate (e.g., thymidine assimilation). Unlike those under ideal laboratory conditions, bacteria in most Antarctic marine environments probably do not grow very rapidly (specific growth rate, $\mu < 0.1$–0.3 d^{-1}) and during the austral winter season may not grow at all. Unbalanced and discontinuous growth may be the norm, and if so, our general laboratory models of growth, biosynthesis, and cell division may not be applicable to field samples. The measurement of these important microbial processes is fundamental to our understanding of the role of heterotrophic bacteria in Antarctic marine ecology and will benefit from development and refinement of methods.

In recent years, ^{3}H-Tdr has been widely used to measure the rate of heterotrophic bacterial DNA synthesis, a process that is theoretically correlated with cell division and biomass production (Brock, 1971; Fuhrman and Azam, 1980; Moriarty, 1986). The assumptions inherent in the application of this method to natural microbial assemblages are numerous, generally untested, and sometimes untestable. In my opinion, the four most crucial assumptions are (1) that the uptake of Tdr is restricted to, and occurs uniformly in, all heterotrophic bacteria, (2) that the dilution of the exogenously added Tdr by ambient extracellular and intracellular pools and by *de novo* synthesis either is negligible or can be directly measured and corrected for, (3) that catabolism of Tdr does not occur, and (4) that there is a constant relationship between Tdr incorporation and biomass production.

The first three assumptions are apparently not valid for microbial assemblages in nature (E. A. Laws, 1983; Fallon and Newell, 1986; Rivkin, 1986; Douglas et al., 1987; Jeffrey and Paul, 1988; Davis, 1989; Brittain and Karl, 1990, and references contained therein). Applications of the ^{3}H-Tdr method to Antarctic microbial assemblages, in particular, have revealed that there is no simple correction for isotope dilution (Kogure et al., 1986) and that ^{3}H-Tdr appears to be extensively catabolized (Karl et al., 1991a). Finally, independently derived extrapolation factors used to convert ^{3}H-Tdr uptake to bacterial production have ranged more than 100-fold (Fuhrman and Azam, 1980; Kirchman et

al., 1982; Ducklow and Hill, 1985; Cho and Azam, 1988; Coveney and Wetzel, 1988), and it now appears almost certain that the "conversion factor" will have to be determined anew for each microbial assemblage.

Nevertheless, this method is still commonly used in field studies, as reliable alternatives do not currently exist. Assimilation of ^{3}H-leucine (Kirchman et al., 1985) may emerge as the method of the 1990s for measurement of bacterial productivity, but it, too, relies on numerous assumptions that are difficult to confirm in natural assemblages. If our methods are necessarily flawed, then we should at least exercise caution in the interpretation of the resultant data.

4. TROPHIC MODELS

Before 1980, energy flow in Antarctic marine habitats was believed to be adequately modeled by a relatively short and therefore highly efficient transfer from large phytoplankton cells (>35 μm) to krill to higher trophic levels (e.g., whales, seals, and birds). More recently, this classical, linear view of the Antarctic food chain (Hart, 1942; Tranter, 1982) has been expanded to reflect the roles of other herbivorous and carnivorous macrozooplankton, including copepods, ostracods, and gelatinous predators (Hopkins, 1985); benthic secondary productivity and plankton–benthos coupling (Clarke, 1985); and energy flow through microheterotroph (bacterial) and protozooplankton (flagellate and ciliate) assemblages (Hewes et al., 1985). In fact, we can expect our views on the structural complexity of the Antarctic food web to expand further as we incorporate additional processes, such as algal mixotrophy (Rivkin and Putt, 1987; Palenik and Morel, 1990), algal dasmotrophy (Estep and MacIntyre, 1989), antibiosis (Sieburth, 1959, 1960), potential growth limitation by trace elements (Martin, 1989) or vitamins (Carlucci and Cuhel, 1977), protozoan assimilation of dissolved organic matter (Sherr, 1988), bacterial chemolithoautotrophy (Horrigan, 1981; Priscu and Palmisano, 1986), the role of pelagic viruses (Bratbak et al., 1990; Proctor and Fuhrman, 1990), and photochemical cycling of organic matter (Kieber et al., 1989). Subeuphotic-zone microbial processes, benthic productivity, and the role of sinking particles in the coupling of carbon production and carbon consumption processes also need elaboration.

The concept of a highly efficient and simple Antarctic marine food chain is apparently no longer tenable, but comprehensive, quantitative studies of energy and carbon flow through the entire Antarctic food web still do not exist. At best, only order-of-magnitude estimates for a few selected study areas are available. Consequently we must view these food-web models as hypotheses that require and deserve a thorough, quantitative field evaluation.

As pointed out above, extreme seasonal ranges in environmental parameters are a hallmark of Antarctic ecosystems; annual productivity in many Antarctic marine habitats is dominated by the development of the spring bloom. Therefore,

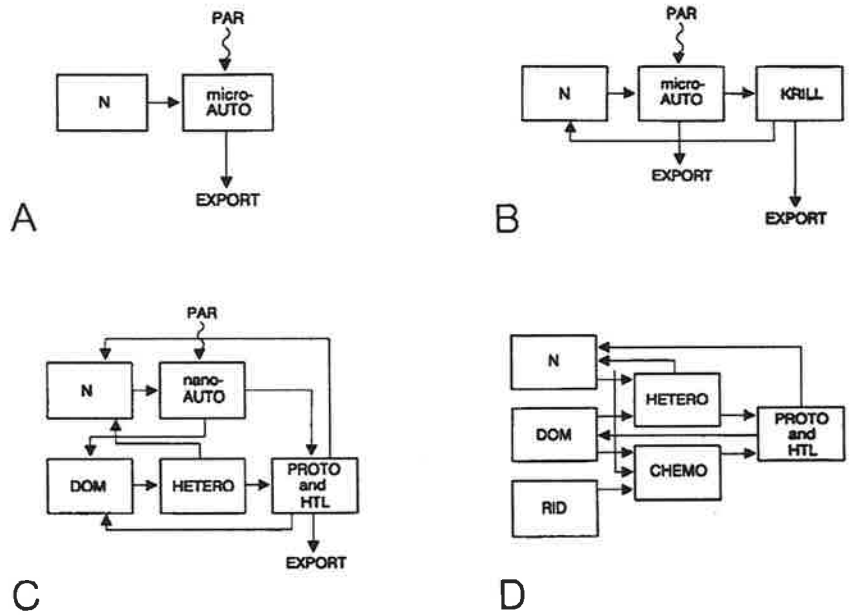


Fig. 1.4 Hypothetical Antarctic trophic models: **A**: Early spring (October–November) bloom of large (≥20 μm) autotrophic cells, primarily diatoms (micro-AUTO) following water column stratification. The energy source is photosynthetically available radiance (PAR). At the beginning of this period, there are high concentrations of dissolved inorganic nutrients (N) that are nearly stoichiometrically consumed as phytoplankton biomass accumulates. There is little grazing during this initial bloom period. New (i.e., NO_3-based) primary production is high (f-ratios ≥0.75), and export of particulate organic matter (POM) from the euphotic is dominated by the sinking of algae. **B**: Late spring–early summer period (December–January), during which krill (and other macrozooplankton) grazing processes are largely responsible for algal biomass consumption. Export of POM is at a seasonal maximum during this period and is dominated by krill fecal pellets. Production of algal biomass is balanced by rates of consumption/removal, and nutrient concentrations (N) are also relatively invariant with time. **C**: The late summer period (January–March) is dominated by microbial loop processes including the appearance of small (≤20 μm) algal cells, primarily autotrophic flagellates (nano-AUTO), and substantial populations of heterotrophic bacteria (HETERO), protozoans (PROTO), and other higher trophic levels (HTL). Regenerated (i.e., NH_4-based) primary production is high (f-ratios ≤0.4) and export of POM is reduced relative to that of the early summer period. Dissolved organic matter (DOM), which accumulates during the late spring/early summer period of intense grazing, death and autolysis of micro-AUTO populations is consumed by the HETERO populations. Nutrient (N) regeneration exceeds nutrient uptake, and algal consumption exceeds algal production during this period. As a consequence, the standing stock of algal biomass decreases, and the ambient pools of N increase. **D**: The winter food web is dominated by heterotrophic (HETERO) and chemolithoautotrophic (CHEMO) bacterial processes in the absence of a substantial PAR energy flux. The chemolithoautotrophs grow at the expense of reduced inorganic detritus (RID), which accumulates during the late summer–fall period. Total ecosystem production, plant biomass, and export of POM during this period are low to undetectable. This hypothetical succession of food webs for the southern oceans is most representative of coastal and ice-edge habitats where spring phytoplankton blooms are known to occur. In the open

the trophic structure and ecological efficiency of Antarctic food webs are highly dependent upon these seasonal cycles in primary production. Conceptually, at least four different trophodynamically defined phases of the "bloom-dominated" annual production cycle can be hypothesized (Fig. 1.4A–D). Phase A (early spring) corresponds to the initiation of the phytoplankton bloom. NO_3-based (i.e., "new") production dominates; dissolved inorganic nutrients (C, N, P, Si) are removed and nearly quantitatively converted to algal biomass, which accumulates in the euphotic zone; excretion is low; macrozooplankton grazing is minimal; the microbial loop is absent; particle export is low and dominated by sinking phytoplankton cells; and benthic processes are dormant. Phase B (early summer) corresponds to the period of maximum macrozooplankton grazing. NH_4-based (i.e., regenerated) production dominates; algal biomass shifts from cells larger than 20 μm (primarily diatoms) to cells smaller than 20 μm (primarily flagellates); production of DOM by excretion, grazing, death, and autolysis is high; bacterial and microzooplankton populations expand; particle export is high and is dominated by macrozooplankton (primarily krill) fecal pellets; and benthic metabolism is high. Phase C (late summer) corresponds to the postbloom period. Phytoplankton standing stocks and production are low, bacterial and protozoan production are high, virus particles and nonliving detritus accumulate, particle flux is low and dominated by microzooplankton fecal pellets and organic aggregates, and benthic metabolism continues. Finally, phase D corresponds to the austral winter period. Photoautotrophy is low and supplemented by chemolithoautotrophy (e.g., nitrification), bacterial cells exhibit a "starvation–survival" response, microzooplankton populations are low, standing stocks of particulate matter (both living and nonliving) are low, inorganic nutrients are high, and particle flux and benthic metabolism are at their annual minima.

In the remote "blue water" regions of the southern oceans, where phytoplankton standing stocks are low throughout the year and where the spring bloom does not develop (El-Sayed, 1988), microbial loop processes (Fig. 1.4C) may be more important. This extreme variability in the hypothesized trophic structure of Antarctic marine ecosystems underscores the importance of conducting field studies during each phase to understanding of the complete annual cycles of carbon and other biologically important elements.

As this review emphasizes planktonic microorganisms and in particular heterotrophic bacteria, it may be appropriate to take a closer look at the microbial food web, which I hypothesized is most active during the postbloom, late-summer period (see Figs. 1.4C, 1.5). Central components of this model, which

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ocean ("blue-water") regions, the ecosystem is likely to be dominated by microbial loop processes (C) and characterized by low standing stocks of algae, complex food webs, and low rates of production and particle export.

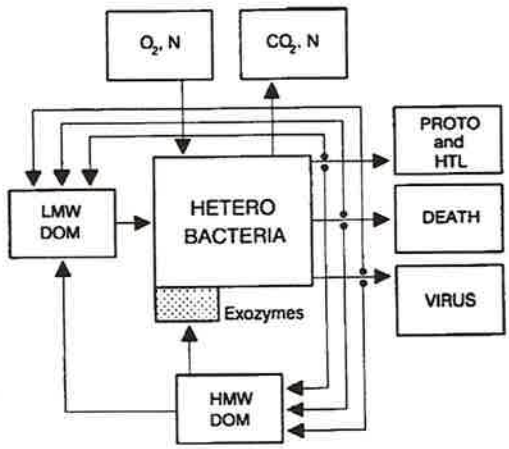


Fig. 1.5. Schematic representation of the role of heterotrophic bacteria (HETERO BACTERIA) in Antarctic marine microbial loop (also refer to Fig. 1.4C). In this ecosystem model, bacteria rely upon the availability of "utilizable" low- and high-molecular-weight dissolved organic matter (LMW DOM and HMW DOM) for their carbon and energy demands. The molecular composition of these available carbon pools determines the production rate, growth yield, and end-product formation. In the absence of available substrate, bacteria exhibit a characteristic starvation–survival response. HMW DOM, which cannot be used directly, is made available by the action of attached (periplasmic) or cell-free exoenzymatic activities or by chemical hydrolysis (e.g., polysaccharides + $H_2O \rightarrow$ monosaccharides). During metabolism, heterotrophic bacteria consume oxygen (O_2) and produce carbon dioxide (CO_2). The stoichiometry of O_2/CO_2 dynamics is again determined by the DOM pool composition. Dissolved nutrients (N), including N, P, S, and a variety of trace elements, are also required for balanced growth. Depending upon the molecular composition of the substrates utilized, N may also be regenerated. Bacterial biomass is removed by the combined effects of grazing by protozoans (PROTO) and higher trophic levels (HTL), death and autolysis (DEATH), and viral infection (VIRUS), all of which return some carbon and energy to both the LMW and HMW DOM pools.

Central components of the model (Fig 1.5)
should ideally be quantified so as to comprise an adequate quantitative test of the microbial loop hypothesis, include the biomass, cell-size spectrum, growth rates, and removal rates (both predatory and nonpredatory, including natural death) of (1) the phytoplankton assemblage and (2) the bacterial assemblage; (3) the concentrations and turnover rates of individual "model" compounds in both the low- (e.g., monomeric substrates) and high-molecular-weight (e.g., polymeric substrates) pools, as well as the efficiency of bacterial utilization of these compounds; and (4) biomass, grazing rates, food preference (by both particle size and taxonomic type), growth rates, and ecological efficiency of individual protozoan populations.

These parameters must be treated as the "master variables" and assessed during each regional study. As mentioned above, they are difficult to obtain and,

in general, lack the accuracy and precision required for a quantitative test of the microbial loop hypothesis. Even if one could demonstrate the existence of a robust microheterotrophic community, uncertainties surrounding some of the most fundamental processes in the microbial loop hypothesis (e.g., growth yields) prevent us from extrapolating the commonly measured ecosystem parameters to any reliable conclusions. The application of inverse formalisms may be useful in this regard (Vezina and Platt, 1988), but to my knowledge this approach has not been incorporated into studies of the Antarctic marine food web.

5. PHYSIOLOGICAL RESPONSES TO THE ANTARCTIC MARINE ENVIRONMENT

5.1. Organic Nutrient Supply and Mechanisms of Starvation Survival

As mentioned above, the primary energy input (i.e., PAR) to Antarctic waters is severely limited during the austral winter (Fig. 1.2), so one might anticipate a substantial decrease in photoautotrophic processes and in the near-surface heterotrophic processes that rely upon them. Even heterotrophic microbial assemblages living well below the euphotic zone might be affected by this seasonality, because we now know that there is a rapid and direct coupling between the surface primary production and the downward flux of utilizable particulate organic carbon (Suess, 1980; Deuser, 1986; Pace et al., 1987).

Important questions have been raised concerning (1) the process of algal-population overwintering, in particular, the roles of resting spore formation, algal heterotrophy, and the mechanisms of spring seeding of viable algal stocks; (2) the role of chemolithoautotrophic CO_2 fixation during dark winter periods; (3) the magnitude of wintertime heterotrophic bacterial processes in the water column and sea-ice habitats; and (4) the source(s) of dissolved organic matter required to sustain this net heterotrophic wintertime ecosystem.

Antarctic marine investigations during austral winter are relatively rare because of practical, logistical concerns (presence of sea ice, availability of suitable research vessels, personnel safety, and expense) and the previous lack of a strong scientific justification and desire for such investigations. Within the past few years, however, several expeditions have been mounted primarily in the area of the Antarctic Peninsula, and results are beginning to emerge (Hanson et al., 1983b; Marra and Boardman, 1984; Kottmeier and Sullivan, 1987).

On the other hand, a fairly extensive literature exists on the effects of nutrient starvation on the survival of bacteria of high-dissolved-carbon environments. The laboratory studies of ANT-300, a psychrophilic *Vibrio* sp. initially isolated

from a depth of 300 m in the Antarctic Convergence by R. Morita during the 1972 cruise 46 of the RV *Eltanin*, are particularly relevant. This bacterial strain exhibits a unique response to organic-nutrient starvation conditions that might be analogous to those imposed on natural assemblages of heterotrophic bacteria during Antarctic winter. Although we have no assurance that the results observed for ANT-300 will apply to Antarctic bacterioplankton in general, they can form the basis of testable ecological hypotheses.

The starvation–survival response actually consists of two independent processes, (1) the need to maintain cellular integrity and to cope with low nutrient flux without losing the ability to respond quickly and competitively when nutrients become available and (2) the need to maintain the species against all forms of loss (death, autolysis, predation, parasitism, etc.) in the absence of growth. Only the former has been studied in any detail.

When heterotrophically growing cultures of ANT-300 are harvested, washed, and resuspended in an organic-carbon-free medium, the cells undergo characteristic morphological and physiological changes in preparation for starvation survival. During the first two days of starvation and continuing for at least three weeks, mean cell diameter decreases significantly (from >1.5 μm to <0.4 μm), culture optical density decreases, and, simultaneously, morphology shifts from rod-shaped to coccoid (Novitsky and Morita, 1976). The resulting "dwarf" cells resemble cells commonly found in many oceanic habitats and support the hypothesis that many bacteria in the marine environment are starved (Stevenson, 1978).

The net effect of these changes in cell size, volume, and morphology is an increase in the surface-to-volume ratio. These changes may confer a greater chance of survival for at least two reasons. First, they may increase the cells' ability to scavenge energy-yielding substrates from nutrient-limited environments (Morita, 1982). Second, size reduction may also serve as a mechanism of predator avoidance, as protozoa preferentially consume larger bacteria (Andersson et al., 1986; Gonzalez et al., 1990).

A more detailed and comprehensive analysis of the effects of starvation on the viability and stability of ANT-300 used growth rate as a dependent variable (Moyer and Morita, 1989a). Three separate stages of starvation survival were observed (Fig. 1.6): an initial two-week period during which the various populations exhibited fluctuations in viability; a second, approximately eight-week period during which an overall decrease in viability depended on the prestarvation growth rate; and a final period during which viability stabilized at about 0.3% of the initial population, regardless of prestarvation growth rate. This stabilization of viability may be a manifestation of a condition referred to as metabolic arrest, which has been hypothesized to occur during long-term starvation (Morita, 1988).

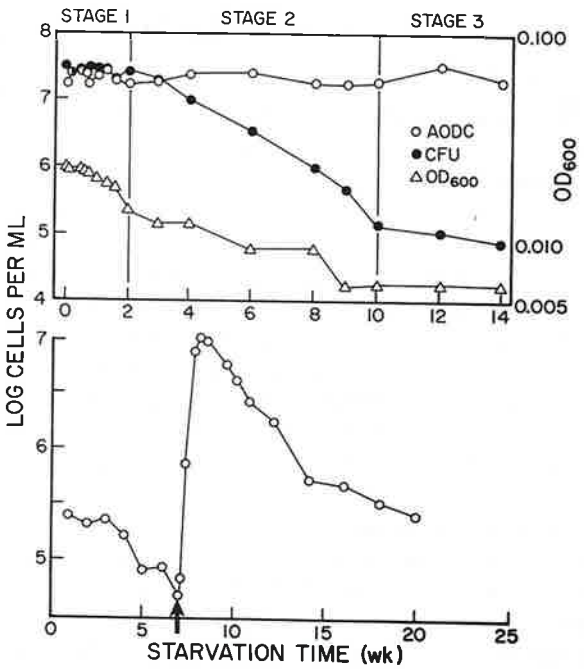


Fig. 1.6. Top: Effects of starvation on cell number, cell viability, and optical density (OD) of the culture medium for the marine bacterium ANT-300. Prior to starvation, the cells were grown in continuous culture at $\mu = 0.057\ hr^{-1}$. The three stages in the starvation response are characterized by (stage 1) periods of large fluctuations with moderate overall decrease in viability and OD, (stage 2) a period of rapid loss in viability with time with a greater than 99% overall decrease, and (stage 3) a period of stabilization. Redrawn from Moyer and Morita (1989a). **Bottom**: Recovery of the marine bacterium ANT-300 from starvation following the addition of low-level nutrients to a previously starved population. Arrow indicates the time of addition of a 1% glucose solution. Redrawn from Novitsky and Morita (1978).

One interesting result was that total acridine orange (AO) microscopic cell counts remained more or less constant for periods of at least 25 weeks, in spite of a decrease in viability (Amy et al., 1983; Moyer and Morita, 1989a). This result implies that cell lysis was minimal and that the long-term survival of the population was probably not the result of "cryptic growth" (the growth of a portion of the population at the expense of cellular materials released from dead cells). The precise condition of the nonviable, AO-stained cells is not known.

In addition to the dramatic morphological changes, starved ANT-300 sometimes reduces its endogenous respiration by >99% (Novitsky and Morita, 1977), mostly within the first two days. This reduction is probably a major factor in the

long-term survival of individual cells, as it would allow the cells to conserve carbon and energy. In spite of this starvation-induced dormancy, ANT-300 cells retain high-affinity active-transport systems (Faquin and Oliver, 1984) that enable them to respond quickly and efficiently to the addition of utilizable organic nutrients. When nutrients were added to a seven-week-old starved culture, cell numbers and total cell mass immediately increased 100-fold (i.e., with no lag period), then returned to the starved condition after the glucose was depleted (Novitsky and Morita, 1978; Fig. 1.6).

These results, if found to be characteristic of starved cells in general, would imply that starved bacteria in Antarctic waters should be able to capitalize on sudden or unpredictable nutrient inputs, as well as those that might be related to regular seasonal cycles such as the spring bloom. Furthermore, DOM production (by whatever means) and DOM utilization by heterotrophic bacterioplankton should be tightly coupled in time and space under both summer and winter conditions. The validity of this prediction is discussed below, in the case study section.

The effect of starvation on the intracellular concentrations and turnover rates of individual classes of major macromolecular constituents (protein, RNA, and DNA) has also been studied with ANT-300 cultures and other isolates from marine environments. Starved cells exhibited a rapid decrease in total cellular protein with the onset of starvation (Amy et al., 1983), which appeared to stabilize after several weeks depending upon the prestarvation growth rate of the cultures (Moyer and Morita, 1989b). Total concentrations of DNA and RNA also decreased significantly during the first two weeks of starvation (Novitsky and Morita, 1977; Amy et al., 1983). On a per-cell basis (total cells) only 5.2% of the original DNA and 85% of the original RNA remained after 12–13 weeks of starvation of batch cultures of ANT-300 (Moyer and Morita, 1989b). Some differences were observed for cells that entered starvation conditions from chemostat cultures of known growth rates, but in all cases the DNA decreased by at least 90% during the starvation period (Moyer and Morita, 1989b). In experiments comparing starved populations that were initially derived from batch- and chemostat-grown ANT-300 cultures, the slowest-growing chemostat culture tested (dilution rate = 0.015 hr^{-1}) maintained the highest ratio of nucleoid volume to cell volume. It was hypothesized that these slow-growing cells were better adapted for starvation survival than their faster-growing counterparts (Moyer and Morita, 1989b).

Clearly, there are several potential limitations to the extrapolation of laboratory data on ANT-300 to the *in situ* conditions of Antarctica. First, ANT-300 represents only one strain of psychrophilic bacteria and may or may not be a reliable "model" system for the study of starvation–survival mechanisms in Antarctic marine systems. Furthermore, ANT-300, although capable of long-term survival under oligotrophic conditions simulated in the laboratory, grows

only in the presence of relatively high concentrations of organic nutrients. In contrast, the "low-nutrient" bacteria that have been isolated from a variety of marine environments may be truly adapted for oligotrophic conditions, may respond differently to the presumed low-nutrient Antarctic winter conditions, and may be more representative of bacterial populations there. Finally, the laboratory starvation–survival experiments do not adequately assess the effects of removal of cells by natural processes of sedimentation, protozoan grazing, and other forms of direct predation. In nature, these processes may remove starving or starved cells otherwise not able to reproduce under ambient environmental conditions.

5.2. Effects of Temperature on Microbial Rate Processes

The active microbial components of most Antarctic marine environments (with the possible exception of those influenced by geothermal heating) are, by definition, either psychrophilic (uniquely adapted for optimal growth at low temperatures) or psychrotrophic (cold-tolerant but requiring temperatures of 15–20°C for optimal growth) (*sensu* Morita, 1975). Psychrophilic bacteria were first isolated from Antarctic ocean waters by Ekelof during the Swedish Antarctic Expedition of 1901–1903 (cited by Morita, 1975), and successful enrichments have been carried out by many investigators since the initial discovery (e.g., Straka and Stokes, 1960; Morita, 1966; Wiebe and Hendricks, 1971; Irgens et al., 1989; McGuire et al., 1987). Despite the apparent ubiquity of psychrophilic bacteria in these waters, it is difficult to ascertain whether the various heterotrophic bacterial assemblages are dominated by psychrophiles or by psychrotrophs.

Results from laboratory-based competition studies indicate that, at low temperatures (<4°C), psychrophiles will outgrow psychrotrophs in continuous culture at both high and low organic-substrate concentrations (Harder and Veldkamp, 1971). Consequently, one might argue that psychrophilic bacteria would be selected for under the near-freezing temperatures of most Antarctic habitats. Nevertheless, available evidence suggests that psychrotrophic microorganisms are present and therefore are presumably competitively successful. Unfortunately, attempts to measure the relative abundances of psychrophiles and psychrotrophs by temperature-enrichment techniques (Morita and Burton, 1970; Wiebe and Hendricks, 1971; J. A. Gow and Mills, 1984) are difficult to interpret because the selectivity associated with these methods is unknown.

Several independent Antarctic field studies have evaluated the heterotrophic response of natural microbial assemblages to variations in incubation temperature. Hodson et al. (1981) reported that bacterial assemblages collected from McMurdo Sound have temperature optima for the assimilation of a variety of organic substrates at or near the ambient seawater temperatures (0–2°C). Incubation at temperatures above 5°C generally resulted in inhibition of the assimila-

tive capacity of the microbial assemblages. They concluded that bacteria are well adapted for growth at low temperatures (i.e., showed a psychrophilic response). In contrast, Morita et al. (1977) and Hanson and Pope (1981) concluded that increasing incubation temperature from 0 to 15°C increased metabolism and growth of microbial assemblages collected from the near-surface Antarctic marine waters. Hanson and Pope (1981) concluded that the low ambient temperatures of the polar habitat might suppress bacterial productivity (i.e., that the bacteria showed a psychrotrophic response). These differences may reflect regional variability in the temperature response of indigenous microheterotrophic assemblages. In any case, the relative importance of psychrophiles and psychrotrophs in Antarctic ocean waters remains an open question.

5.3. The Sorokin Hypothesis

The production of organic matter by phytoplankton and its utilization by heterotrophic bacterioplankton in the world ocean are often uncoupled in time and space. On the basis of a series of field experiments conducted in the tropical Pacific and Indian oceans, Sorokin (1971a–c; Sorokin et al., 1985) has suggested that bacterioplankton productivity is dependent on water depth; the 100-fold (or greater) decrease in total metabolism and biosynthesis between surface (≤500 m) and deep (≥1,000 m) waters, he argues, is due to temperature rather than substrate availability. His data on "potential" production (growth at 30°C, as opposed to growth at 2°C) were presented as evidence for the existence of oxidizable DOM at depths corresponding to Antarctic Intermediate and Antarctic Deep Water (Sorokin, 1972; Sorokin et al., 1977). He further suggested that secondary production in the tropical ocean exceeds the contemporaneous rates of primary production (which he also concludes have been underestimated by the standard ^{14}C method) and that the "excess" carbon and energy required to sustain this imbalance are derived in dissolved form from the sub-Antarctic regions during the formation of deep and intermediate water masses. In **Sorokin's** opinion, models must take into account horizontal transport rather than treating the ocean as a series of isolated vertical sections if the ecosystem energy budget is to be balanced (Sorokin, 1971a).

According to Sorokin's DOM transport model, the high latitudes support a comparatively high primary production, but *in situ* heterotrophic utilization is suppressed by low ambient temperatures and low standing stocks of microorganisms. If Sorokin's hypothesis is shown to be valid for large portions of the tropical and subtropical global ocean, then we would be required to alter our views on oceanic productivity and trophodynamics.

Sorokin's conclusions were disputed by several investigators. Skopintsev (1972) argued that the DOM in the "deep ocean water" is oxidized during its meridional transport from Antarctic waters, that this remineralization is re-

flected in the chemical composition (e.g., O_2, PO_4, NO_3, and total CO_2 content) of the deep and intermediate water masses, and that DOM that remains in the water mass when it reaches the tropical ocean is probably refractory, humic-acid-like material, which would not be expected to support bacterial growth at either low or high temperatures. He did not explicitly comment on Sorokin's shipboard experimental data on the growth of mesopelagic-zone bacteria at elevated temperatures, which indicated otherwise.

Steeman-Nielsen (1972) also criticized Sorokin but primarily on the basis of the methodology used in his field experiments (dark fixation of ^{14}C-HCO_3 as a measure of heterotrophic carbon assimilation; Romanenko, 1964) and the design of his field experiments (shipboard incubation of seawater samples). Whereas Sorokin suggested that rates of primary production measured using Steeman-Nielsen's method were in error, Steeman-Nielsen concludes that Sorokin's rates of bacterial production are overestimates. Furthermore, Steeman-Nielsen (1972) argued that the measured rates of primary production are entirely sufficient to support the zooplankton of that region but made no mention of the requirements of heterotrophic bacteria.

Relying heavily on published values of DOM to emphasize the fact that marked horizontal gradients of DOM do not exist in the Pacific Ocean, Banse (1974) also concluded that Sorokin's ecosystem model cannot be reconciled with the geographic distributions of DOM but stopped short of dismissing his hypothesis altogether, concluding that "it is left undecided whether the bulk of the DOM entering the Pacific deep sea is oxidized in the warm-water sphere (as suggested by Sorokin), or in the deep sea itself." Resolution of this fundamental ecological question should be a high-priority objective.

After this initial flurry of criticism, Sorokin's hypothesis was largely ignored, but recent work has tempered several of the initial criticisms. In particular, historical measurements of DOM have recently been called into question (P. M. Williams and Druffel, 1988), and it has been suggested that DOM concentrations in the world ocean have been systematically underestimated by a factor of 4 to 10 (Sugimura and Suzuki, 1988). These new results also indicate the existence of vertical (and possible horizontal) structure that had not been observed previously. For example, these new DOM concentrations are shown to be inversely correlated with apparent oxygen utilization (AOU), consistent with *a priori* expectations of the Sorokin hypothesis. These AOU–DOM correlations were not evident from the historical data base. P. M. Williams and Druffel (1988) conclude that, if these new data are confirmed by independent investigations, "there is a lot of explaining to do concerning the source(s) of this DOM, its relative stability to chemical and microbial oxidation and its molecular composition."

Of course, mere detection of microheterotrophic activity in Antarctic ocean waters does not establish that the carbon budget is locally balanced. A rigorous

test of the Sorokin hypothesis will ultimately require careful, quantitative studies of DOM production, including the potentially important process of the hydrolysis/dissolution of sinking particulate organic matter; an assessment of the microheterotrophic carbon demands; and knowledge of the rate of formation of Antarctic Intermediate and Antarctic Bottom water masses.

5.4. The Pomeroy-Deibel Hypothesis

In an attempt to reconcile the high rates of metazoan secondary productivity often observed during the spring bloom in cold-water habitats, Pomeroy and Deibel (1986) suggested that temperature might play a fundamental role in food-web function and ecosystem efficiency. Although their studies addressed productivity at high northern latitudes, they may also be directly applicable to the marine microbial assemblages of Antarctica.

In their ecosystem model, Pomeroy and Deibel (1986) hypothesized that low-temperature suppression of bacterial activity, relative to photosynthesis, might significantly restrict energy flow through the microbial loop and therefore allow transfer of more carbon and energy to higher (metazoan) trophic levels (Fig. 1.7). Implicit in this model is that within the microbial loop bacteria function as a "sink" rather than a trophic "link" for carbon and energy (Pomeroy, 1974; Pomeroy and Wiebe, 1988).

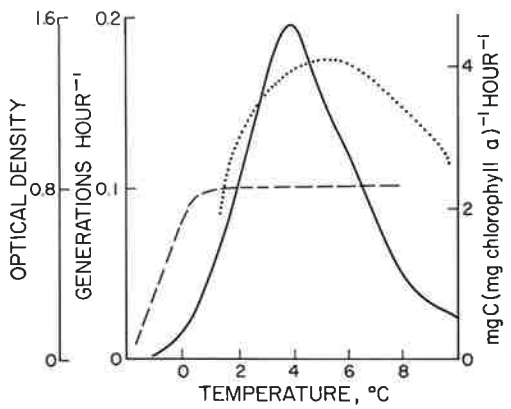


Fig. 1.7. Differential growth of phytoplankton, expressed as mg C (mg chlorophyll *a*)$^{-1}$ hr^{-1} (dashed line), and bacteria, expressed either as generations hr^{-1} (dotted line) or optical density of the culture (solid line), as a function of temperature. These results suggest a suppression of bacterial growth, relative to phytoplankton, at very low temperatures (≤1°C). Redrawn from Pomeroy and Deibel (1986).

Field observations conducted off the east coast of Newfoundland indicated that, within a critical temperature range between -1.8 and 1°C, primary production was suppressed significantly less than bacterial growth or respiration and tend to support their temperature-regulation model. On the other hand, Li and Dickie (1987) found that even at a water temperature of -0.3°C, both microheterotrophic and autotrophic populations in Bedford Basin, Nova Scotia, were active and suffered no apparent differential temperature suppression. Kottmeier and Sullivan (1988) also tested the Pomeroy-Deibel hypothesis directly in an experiment using mixed microbial assemblages derived from sea ice. They found algae ($^{14}CO_2$ uptake) and bacteria (^{3}H-Tdr uptake) to respond similarly to low temperature; the maxima for the growth of autotrophs and heterotrophs overlap from 4 to 7°C. Field results on the effects of temperature on photosynthesis in Antarctic marine phytoplankton assemblages also suggest that rates are highest at temperatures between 2 and 11°C and fall off sharply at lower and higher temperatures (Neori and Holm-Hansen, 1982; Tilzer and Dubinsky, 1987; Lancelot et al., 1989). These data indicate that naturally occurring autotrophic populations exhibit a low-temperature (<2°C) suppression of metabolic activity.

A major limitation to the interpretation of these temperature-dependent growth studies is the uncertainty of equating these short-term incubations of mixed microbial assemblages with the actual responses (including species succession) likely to occur among these diverse populations. Another is the relationship, if any, between psychrophilic and psychrotrophic bacteria. A microbial assemblage dominated by psychrophilic bacteria would not be expected to show a low-temperature inhibition of heterotrophic processes, whereas one dominated by psychrotrophs might well do so. The availability of nutrients and therefore the growth or starvation "state" of the organisms might also affect the results.

The Arrhenius equation, or derivations thereof, which is often used to evaluate the relationships between temperature and the metabolic responses of complex microbial communities (Takahashi and Ichimura, 1971; Pomeroy and Deibel, 1986; Li and Dickie, 1987; Kottmeier and Sullivan, 1988), can rigorously be applied only to single chemical reactions or to multiple reactions in which the first step is rate-limiting. There is no theoretical basis for an extrapolation to mixed populations of microorganisms (Karl, 1985). Furthermore, both genotypic and phenotypic adaptations may have occurred among Antarctic marine bacteria as a result of long-term exposure to low temperature (Jones and Morita, 1985; Russell, 1990). Because of the greater seasonal variation in seawater temperature, the selection pressures on North Atlantic microorganisms might not be the same as those expected to occur in Antarctic habitats, but the

Pomeroy-Deibel hypothesis does provide a framework for the design and conduct of field experiments on the effects of temperature on autotrophic and microheterotrophic processes.

6. MICROBIAL RATE PROCESSES: SELECTED CASE STUDIES

Measurements of the biomass, substrate uptake rates, productivity, and specific growth rates of microbial assemblages from a variety of Antarctic marine habitats indicate substantial regional and temporal variability (Tables 1.1, 1.2). Turnover times for selected organic substrates range from ≤1 day for dissolved ATP in McMurdo Sound to >50 years for dissolved glucose and uridine beneath the Ross Ice Shelf (Table 1.1). Pomeroy et al. (1990) also reported extremely long turnover times (≥500 yr!) for leucine assimilation by microbial assemblages in the Arctic Ocean. These long residence times may have direct bearing on the Sorokin hypothesis discussed above.

For the majority of the Antarctic marine habitats investigated to date, the turnover times of selected organic substrates appear to be on the order of one to several weeks (Table 1.1). These relatively long turnover times argue for slow uptake rates, large ambient pools, or both. In the absence of direct estimates of the ambient pools, it is impossible to know whether the addition of the ^{14}C or ^{3}H tracer (the sum of the radioisotopically labeled molecules and the nonlabeled carrier) affected the ambient concentration of substrate or not. If it did, the ambient-pool turnover times are overestimated by these radiotracer techniques.

Several investigators have made direct measurements of either the total dissolved organic carbon (DOC) concentration or specific constituents thereof. Surface water DOC values range from 1–2 mg C l^{-1} in the Weddell Sea (El-Sayed and Taguchi, 1981), 1–6 mg C l^{-1} in Admiralty Bay, King George Island (Dawson et al., 1985), and 0.5–1.4 mg C l^{-1} in the southern Drake Passage (Zdanowski, 1985) to 6–12 mg C l^{-1} in the Bransfield Strait (Bolter and Dawson, 1982). These values must be considered conservative, however, because none of these data are from the use of "high-temperature" combustion methods (Sugimura and Suzuki, 1988). Dissolved free amino acids (DFAA), dissolved combined amino acids (DCAA), urea, dissolved DNA, dissolved ATP, and dissolved polysaccharides have all been detected in Antarctic marine habitats (Hodson et al., 1981; Bolter and Dawson, 1982; Mezykowski, 1982; Dawson et al., 1985; Zdanowski, 1985; Haberstroh et al., 1987; Bailiff and Karl, 1991). However, no direct correlation is apparent between DOM pools and microheterotrophic activity (Morita et al., 1977; Bolter and Dawson, 1982; Bird and Karl, 1991), perhaps as a result, in part, of our inability to distinguish between the total and "microbiologically available" pools (King and Klug, 1982; Karl, 1986) or, in

part, of a temporal uncoupling of organic matter production by phototrophs and consumption by heterotrophs.

The variability observed in bacterial cell numbers, productivity, and specific growth rates for Antarctic marine habitats (Table 1.2) covers the full range of these parameters measured in temperate and tropical marine ecosystems, indicating that there is nothing inherently unique about Antarctic bacterial assemblages. Nevertheless, the extremely wide range that is observed, sometimes even over relatively small horizontal space scales within the same season (Kottmeier et al., 1987; Cota et al., 1990; Sullivan et al., 1990; Bird and Karl, 1991), suggests strong local environmental control of bacterial rate processes.

An exhaustive summary of all microbiological studies conducted in the southern oceans, or even those conducted after 1975, is beyond the scope of the present review. Instead I have elected to discuss several "case studies" intended to present a representative account of current field data, hypotheses, and critical thinking about Antarctic marine microbial ecology.

6.1. Weddell-Scotia Sea Marginal Ice Zone

Studies of Antarctic and Arctic environments have characterized a unique and variable (in both time and space) transition region to the polar environment (summarized by W. O. Smith, 1987). Studies of the Ross Sea marginal sea-ice front in austral spring have documented an intense bloom of phytoplankton at the receding ice edge, which the authors attributed to increased vertical stability of the water column caused by the melting of ice (W. O. Smith and Nelson, 1985; Fig. 1.3). Studies of the sea-ice column have revealed the presence of a unique microbial community composed largely of algae and bacteria (Palmisano and Sullivan, 1983; Grossi et al., 1984; Garrison et al., 1986; Kottmeier et al., 1987; Palmisano and Garrison, Chapter 4, this volume). During the period of sea-ice ablation, these organisms might constitute a readily available food supply for higher trophic levels, as well as a potential seed stock for the ice-edge spring bloom.

In spite of these previous studies, a number of important ecological questions remain unanswered, in particular, the immediate fate of the ice-melt-induced productivity pulse, including such processes as sedimentation and macrozooplankton grazing, and the response, if any, of the microbial loop.

The Antarctic Marine Ecosystem Research at the Ice-Edge Zone (AMERIEZ) program was a multidisciplinary investigation of pelagic ecosystem structure and processes designed to build upon previous research at the marginal sea-ice zone (Sullivan and Ainley, 1987; W. O. Smith and Garrison, 1990). Its two unifying hypotheses were (1) that the pack-ice edge is a major oceanographic feature characterized by increased biomass and biological productivity and (2)

TABLE 1.1. Selected Results of Microheterotrophic Substrate Uptake, Turnover Rates, and Mass Fluxes for a Variety of Antarctic Ocean Habitats

Location	Date	Substrate	Kinetic Parameters		Mass Flux[b]	Reference
			T_t[a] (d)	V_{max} (ng l^{-1} hr^{-1})	(ng l^{-1} hr^{-1})	
Kerguelen Island	Dec. 1970	Glucose	24	9.2	—[c]	Gillespie et al. (1976)
(sta. 16)		Glutamate	16	19	—	
North of AC[d] (sta. 5)	Jan. 1972	Glutamate	37	35	—	Morita et al. (1977)
South of AC (sta. 9)	Jan. 1972	Glutamate	33	56	—	Morita et al. (1977)
Ross Ice Shelf (sta. 16)	Jan. 1972	Glutamate	13	63	—	Morita et al. (1977)
Beneath the Ross	Dec. 1977	Glucose	20,800	—	—	Azam et al. (1979)
Ice Shelf (sta. J-9)		Uridine	25,000	—	—	
		Thymidine	6,250	—	—	
		ATP	5,000	—	—	
Scotia Sea	Feb.–Mar.	Leucine	1	—	—	Azam et al. (1981)
	1981	Glucose	4	—	—	
McMurdo Sound						
East Sector	Jan. 1978	Leucine	5	—	—	Hodson et al. (1981)
(0–200 m)		Glucose	4.8	—	—	
		ATP	0.2–0.5	—	37–133	
West Sector	Jan. 1978	Leucine	128	—	—	
(0–200 m)		Glucose	833	—	—	
		ATP	1–3	—	1.1–9.63	

Bransfield Strait	Nov.–Dec. 1980	Amino acids	2–83	—	50–600	Bolter and Dawson (1982)
		Glucose	4	—	200–1,000	
Drake Passage (0–100 m)		Glucose	4–20	—	—	Hanson et al. (1983a)
Arthur Harbor	Feb. 1986	Amino acids	8–58	—	—	Herwig et al. (1986)
		Glutamate	8–27	—	—	
Southern Drake Passage (0–200 m)	Feb. 1987	Glutamate	3.5–11	—	13–225	Haberstroh et al. (1987)
Gerlache Strait (0–200 m)	Feb. 1987	Glutamate	3–8	—	8–400	Haberstroh et al. (1987)
Weddell-Scotia Sea						
Ice-covered waters	Nov.–Dec. 1983	Amino acids	83	—	—	Sullivan et al. (1990)
Open waters	Nov.–Dec. 1983	Amino acids	13	—	—	

[a] T_t, turnover time.

[b] Calculated from T_t estimate and direct measurement of ambient substrate concentration.

[c] — indicates no data available.

[d] AC, Antarctic Convergence.

TABLE 1.2. Selected Results on the Abundance, Productivity, and Growth Rates for Bacterioplankton Assemblages in a Variety of Antarctic Ocean Habitats

Location	Date	Cell Numbers[a] (ml^{-1})	Biomass (mg C m^{-3})	Production[b] (mg C m^{-3} d^{-1})	μ[c] (d^{-1})	Reference
Sodruzhestvo Sea	Dec. 1982–Jan. 1983	2–8 × 10^5	6–40	0.05–3[d]	—	Samyshev (1986)
Pacific-Indian Ocean sector	Dec. 1983–Feb. 1984	~ 2 × 10^5	—	0.07–0.8	~0.1	Kogure et al. (1986)
Scotia Sea	Feb.–Mar. 1981	2–5 × 10^5	—	—	0.17–0.35	Azam et al. (1981)
McMurdo Sound	Dec. 1978	2–10 × 10^5	—	0.01–1.7	—	Fuhrman and Azam (1980)
Prydz Bay	Mar.–Apr. 1984	2.1–3.3 × 10^5	3.9–5.6	0.1–0.6	0.03	Painting et al. (1985)
Atlantic sector	Jan.–Feb. 1981	0.6–6 × 10^5	1.9–19	0.5–2.6[d]	0.02–0.16	Samyshev et al. (1987)
Ross Sea	Nov.–Dec. 1982	0.02–0.3 × 10^6	0.6–4.7	0.005–0.1	0.002–0.05	Kottmeier et al. (1987)
Drake Passage	Sept.–Oct. 1980	0.1–0.5 × 10^6	0.8–4.2	2.6–17.1	0.9–2.1	Hanson et al. (1983b)

Bransfield Strait to Marguerite Bay	Aug.–Sept. 1985	—	—	0.1–0.6	—	Kottmeier and Sullivan (1987)
Weddell Sea	Nov.–Dec. 1983					
	Open water	0.06–0.3 × 10^6	0.2–17.3	0.001–9	0.002–1.2	Sullivan et al. (1990)
	Ice edge	0.01–0.2 × 10^6	0.2–5.1	0.002–2.4	0.004–0.9	
	Mar. 1986					
	Open water	0.01–0.6 × 10^6	0.3–15.2	0.05–6.7	0.04–1.8	Cota et al. (1990)
	Ice edge	0.03–0.4 × 10^6	0.5–8.6	0.002–1.0	0.007–1.1	

[a]Cell numbers measured by epifluorescence microscopy.

[b]Production measured by ^{3}H-Tdr incorporation, unless otherwise noted.

[c]μ = specific growth rate.

[d]Measured by dark ^{14}C-CO_2 uptake (Romanenko, 1964).

that the seasonal advance and retreat of the ice margin, which represents an ecological interface between two communities, strongly affects the natural history of most organisms in the vicinity (Sullivan and Ainley, 1987). To date, these general hypotheses, and ecological predictions thereof, have been systematically evaluated during three comprehensive research expeditions to the marginal ice-edge zone of the Weddell Sea (Fig. 1.8) during austral spring (10 November–2 December 1983), austral autumn (7–27 March 1986), and austral winter (9 June–13 August 1988). Hallmarks of the AMERIEZ program have been its truly interdisciplinary approach and its strong component on microplankton rate processes. Another unique aspect has been the incorporation of satellite remote-sensing imagery to define the mesoscale variability and dynamics of the ice-edge zone in the area of interest (Comiso and Sullivan, 1986;

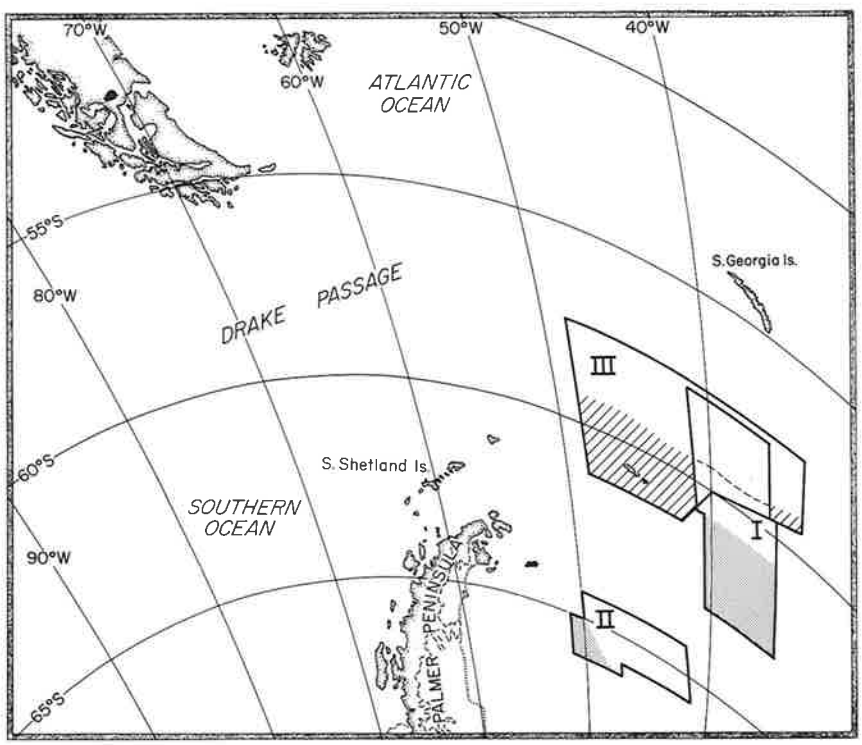


Fig. 1.8. Locations of the AMERIEZ study regions for the three separate field experiments: I, austral spring (10 November–2 December 1983); II, austral autumn (7–27 March 1986); and III, austral winter (9 June–13 August 1988). Location of ice shown by shaded region within each grid. Redrawn from Smith and Garrison (1990).

Sullivan et al., 1988). The experimental design consisted of a sampling grid of discrete stations running more or less perpendicular to the ice-edge margin and extending 100–250 km south into the pack ice and more than 200 km north into the open regions of the Weddell-Scotia Sea (Nelson et al., 1987). During both AMERIEZ I (1983) and II (1986), two ships were employed to obtain quasi-synoptic hydrographic and biogeochemical data on these transects. In this way, the investigators could sample and compare microbial assemblages seaward of the ice-edge influence, within the ice-melt region and beneath the pack ice.

The AMERIEZ results already available on microbial rates and processes are substantial. Hydrographic observations generally support the previous model of meltwater-induced stratification of the water column as an important factor responsible for the accumulation of phytoplankton biomass near the ice edge, especially during austral spring (Nelson et al., 1987). As expected, the frontal zone of increased biological productivity exhibited seasonal variability (Nelson et al., 1989). During the austral winter 1988 cruise, deep vertical mixing (to about 125 m) and low productivity were observed at the region of maximum ice extent (Husby et al., 1989). The measured rates of primary production for spring, autumn, and winter were 521 ± 226, 126 ± 81, and about 30 mg C m^{-2} d^{-1}, respectively (Cota et al., 1990; Sullivan et al., 1990; W. O. Smith and Nelson, 1990).

Higher levels of biomass and production at the ice-edge margin, especially in spring, were also evident both at the higher trophic levels (Ainley et al., 1986; Fraser and Ainley, 1986) and within various components of the detritus-based microbial loop and are described in more detail below.

During the austral spring 1983 cruise, the ice-edge margin was retreating at a mean rate of approximately 5 km d^{-1} (Comiso and Sullivan, 1986), which resulted in a mosaic of areas of stratified low-density meltwater surrounded by regions with deep (60–100 m) mixed layers, which in turn produced a heterogeneity in the distribution of biota (Nelson et al., 1987). The region of maximum phytoplankton biomass (measured as Chl*a*) was at least 100–300 km from the ice edge (Sullivan et al., 1990). Large-scale spatial heterogeneity was also observed in the distributions of bacterioplankton biomass. Although Sullivan et al. (1990) state that "bacterioplankton exhibited distribution patterns similar to those of phytoplankton," their data do not always support this claim (Fig. 1.9). For the eastern transect, bacterial biomass displayed a well-defined maximum (about 9 mg C m^{-3}) immediately (<10 km) seaward of the ice edge, whereas phytoplankton stocks remained relatively depleted for a distance of at least 200–300 km into open water (Sullivan et al., 1990; Fig. 1.9). For the western transect, the distribution of bacterioplankton biomass was nearly homogeneous (3–7 mg C m^{-3}) over a large spatial scale (about 500 km), even though Chl*a* distributions revealed a well-defined core of elevated concentration with an order-of-magnitude gradient over about a 100-km spatial scale (Fig. 1.9). The mean (± standard

deviation) depth-integrated (0–100 m) estimates for bacterial biomass in the ice-covered and open waters near the ice edge were 154 ± 119 and 258 ± 89 mg C m^{-2}, respectively (Table 1.3). On the basis of a C:Chl*a* ratio of 32 (Nelson et al., 1987), the extrapolated ratios of phytoplankton to bacterial carbon were 4.8 for ice-covered and 17.6 for open waters (Sullivan et al., 1990). The ratios of POC to bacterial carbon were approximately 33, regardless of sampling location. Bacteria must therefore comprise a relatively small percentage of the available standing stock of particulate matter during the initial period of the spring bloom at the ice-edge margin.

Similar mesoscale spatial heterogeneities were also observed for estimates of microheterotrophic activity (amino acid assimilation) and production (thymidine assimilation). Statistical analyses of bacterial and algal population rate measurements revealed several weak but significant ($P < 0.05$) positive correlations, which suggest time- and space-coupled autotrophic and heterotrophic processes. Depth-integrated (0–100 m) rates of bacterioplankton production were 20 ± 18 and 70 ± 65 mg C m^{-2} d^{-1} for ice-covered and open waters, respectively (Table 1.3), and averaged approximately 11% of the contemporaneous rate of primary production.

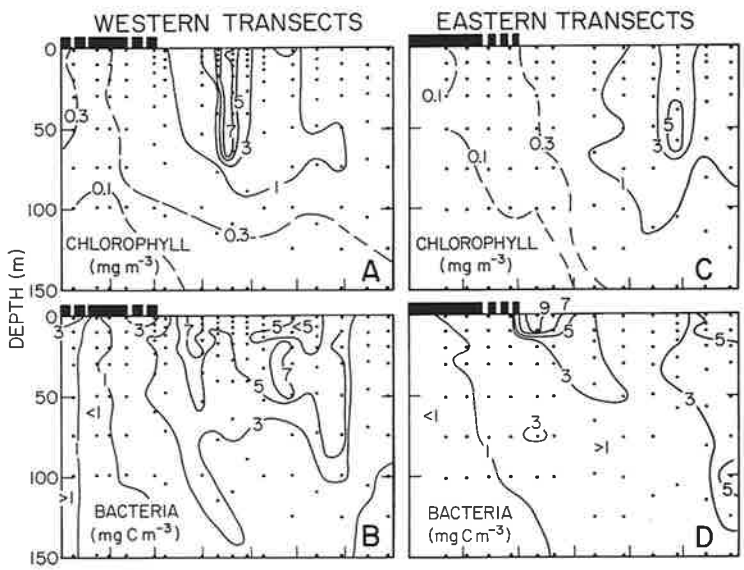


Fig. 1.9. Vertical sections of chlorophyll *a* (mg m^{-3}) and bacteria (mg C m^{-3}) for the western and eastern transects of the austral spring 1983 AMERIEZ expedition to the marginal ice zone of the Weddell-Scotia Sea. Black bars in the upper left-hand corner of each graph indicate the ice cover. Redrawn from Sullivan et al. (1990).

During the autumn 1986 expedition, the ice edge was close to its seasonal extreme and nearly stationary (Comiso et al., 1990). The local hydrographic regime was characterized by a shallow (approximately 35 m) mixed layer overlying a strong pycnocline (Cota et al., 1990). Heterotrophic microbial assemblages displayed biomass and activity maxima that were generally congruent with those measured for the photoautotrophic assemblage, with higher values in the open water regions of the ice-edge margin and extending 100 km seaward (Cota et al., 1990). Bacterial biomass and production in these open-water regions averaged 3.1 ± 2.0 mg C m^{-3} and 1.3 ± 1.0 mg C m^{-3} d^{-1}, respectively (Table 1.3). In the open-water areas, maximum growth rates of the bacterioplankton assemblage were approximately one order of magnitude greater than those of phytoplankton (0.06 vs. 0.59 d^{-1}; Cota et al., 1990). Minimal values for biomass, productivity, and growth rate were consistently recorded under the pack ice or at depth in the water column. Euphotic-zone depth-integrated values for bacterial production in the open waters near the ice edge averaged 96 ± 69 mg C m^{-2} d^{-1}, which often exceeded the contemporaneous rate of primary production. These data clearly reveal a microheterotrophic succession following the spring–sum-

TABLE 1.3. Regional Means and Standard Deviations for Microbial Community Parameters Observed in Ice-Covered and Open Waters of the Marginal Ice-Edge Zone During the AMERIEZ Research Project[a]

	November–December 1983		March 1986	
Property	Ice-Covered Waters	Open Waters Near Ice Edge	Ice-Covered Waters	Open Waters Near Ice Edge
Chlorophyll				
(mg m^{-3})	0.25 ± 0.16	2.9 ± 2.6	0.08 ± 0.03	0.28 ± 0.24
(mg m^{-2})	21 ± 10	142 ± 81	9 ± 2	29 ± 18
Bacterial biomass				
(mg C m^{-3})	1.8 ± 2.1	3.7 ± 1.9	2.9 ± 1.7	3.1 ± 2.0
(mg C m^{-2})	154 ± 119	258 ± 89	229 ± 59	382 ± 172
Primary production				
(mg C m^{-3} d^{-1})	3.8 ± 3.0	14.8 ± 15.8	2.1 ± 1.8	2.8 ± 3.4
(mg C m^{-2} d^{-1})	269 ± 87	521 ± 226	137 ± 58	126 ± 81
Bacterial production				
(mg C m^{-3} d^{-1})	0.3 ± 0.4	1.2 ± 1.5	0.2 ± 0.2	1.3 ± 1.0
(mg C m^{-2} d^{-1})	20 ± 18	70 ± 65	19 ± 10	96 ± 69
Algal growth rate				
(d^{-1})	0.08 ± 0.06	0.11 ± 0.08	0.07 ± 0.06	0.06 ± 0.06
Bacterial growth rate				
(d^{-1})	0.34 ± 0.31	0.42 ± 0.29	0.15 ± 0.15	0.59 ± 0.32

[a]Areal estimates are for euphotic-zone depths only. From Cota et al. (1990).

mer bloom (see Fig. 1.4C), but the data currently available from the AMERIEZ program do not permit a quantitative evaluation of the source(s) of carbon and energy required to sustain this net heterotrophic ecosystem metabolism.

Although the AMERIEZ program participants compiled the most comprehensive ice-edge database available to date, the experimental design is still open to criticism on the basis of their use of multiyear data to infer a seasonal cycle, which ignores the importance of well-documented interannual variability and uncertainties in the interpretation of synoptic primary and secondary production rate measurements without complementary information on antecedent or subsequent ecosystem processes (e.g., successional events). Unfortunately, without a more complete time series including observations of particle flux, quantitative assessment of seasonal carbon and energy flow is still beyond the scope of even this most comprehensive study.

6.2. Drake Passage

The Drake Passage, between South America and Antarctica, is a vital "choke point" in the circulation of Antarctic marine water masses, so data on water transport there are essential for estimating geochemical mass fluxes. Because it is also the main transit corridor for resupply ships for the numerous scientific bases on King George Island and throughout the Antarctic Peninsula, one might expect an extensive scientific literature on its microbial ecology, but high-quality data on microbial biomass and rate processes are rare in this well-traveled sector and are restricted primarily to a set of publications by Hanson and co-workers (Hanson and Lowery, 1983; Hanson et al., 1983a,b). These papers also contain the only available data on microbial biomass and production rates for intermediate and abyssal Antarctic waters.

Hanson and his colleagues sought to determine the metabolic status of Antarctic marine microplankton, especially whether growth was balanced or unbalanced, steady-state or discontinuous. Unbalanced growth occurs when populations are shifting between two steady-state conditions, which might be caused by environmental perturbations. Because of the well-established spatial and temporal heterogeneity of phytoplankton populations and the low but relatively uniform organic nutrient concentrations in the deep sea, they hypothesized that microheterotrophic populations fluctuate between balanced and unbalanced growth. This hypothesis was tested in the oceanic waters of the Drake Passage during a research expedition in January 1980 (Fig. 1.10).

Samples were collected from the sub-Antarctic zone, the Polar Front, and the northern edge of the Antarctic zone. Water-column profiles sampled both the Antarctic Intermediate Water and Antarctic Circumpolar Deep Water. Water samples were analyzed for microbial biomass, rates of ^{14}C- and ^{3}H-labeled glucose uptake, and (for ^{14}C) respiration, ^{3}H-Tdr incorporation, and ^{3}H-adenine

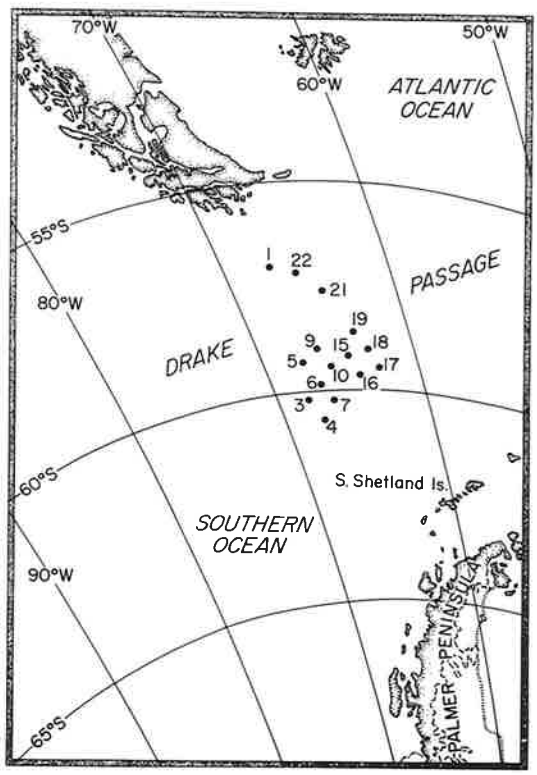


Fig. 1.10. Map of the Drake Passage showing the station locations of the R. Hanson field study. Redrawn from Hanson and Lowery (1983).

assimilation. The last method reveals the RNA:DNA production rate ratio (Karl, 1981) and was used to evaluate the balanced-growth hypothesis.

The biomass of bacterioplankton at various stations in the Drake Passage during January 1980 was low but variable; total bacterial numbers ranged from 0.1 to 2 × 10^8 cells l^{-1} (Hanson et al., 1983a). Total ATP concentrations ranged from 30–150 ng l^{-1} in surface waters to 2–10 ng l^{-1} below 500 m (Hanson et al., 1983a) and were characteristic of previously studied oligotrophic ocean habitats (Karl, 1980). In surface waters, bacterial C (from direct microscopy) as a percentage of total microbial C (from ATP) ranged from 0.36 to 2.6% (mean, 1.5%) again indicating that bacteria comprise a negligible portion of the microbial assemblage.

All activity or growth indices (glucose, thymidine, and adenine assimilation) indicated that surface microbes were most active and that below the euphotic

zone metabolic activity decreased by 1–3 orders of magnitude (Hanson and Lowery, 1983; Hanson et al., 1983a). At selected stations in the Drake Passage, the turnover time for glucose in subeuphotic waters exceeded one year (Hanson et al., 1983a).

An interesting observation made during this expedition was a shift in the size distribution of microheterotrophic activity with water depth toward particle-associated (>3 μm) microbes at depths ≥100 m. The authors suggested that these results may be caused by large-particle export, fragmentation, and subsequent colonization by bacterial populations in the mesopelagic zone. This process of microbe–particle interaction may have important implications for organic matter decomposition and nutrient regeneration in Antarctic marine habitats.

Minimum estimates of the productivity of microheterotrophic populations in the upper 200 m of the water column were 0.12–1.2 mg C m^{-2} d^{-1} on the basis of glucose uptake and thymidine incorporation data, but an independent report of bacterioplankton productivity in the Drake Passage during September–October 1980, which used the frequency of dividing cells (FDC) to estimate instantaneous growth rate constants, reported bacterial productivity estimates 1–2 orders of magnitude higher, especially near the pack ice and Polar Front (Hanson et al., 1983b). Whether these differences reflect regional or temporal variations in microheterotrophic rate processes or simply reflect differences and uncertainties of the analytical methods used cannot be established.

Results of simultaneous determinations of RNA and DNA production indicated a mean RNA:DNA rate ratio of 6:1 for Drake Passage microplankton assemblages and showed no significant trend with sample depth (Fig. 1.11). This value is within the range observed for tropical and temperate marine plankton communities (Karl, 1981) and is consistent with the theoretical predictions and laboratory data derived from pure cultures during balanced growth (Rosset et al., 1966; Dennis and Bremer, 1974; Brunschede et al., 1977). On the basis of these results, the authors tentatively concluded that the Drake Passage microbial assemblages were in a transient state of balanced growth but that subcomponents of the total population existed in a variety of growth states and thereby accounted for the scatter observed in the measured RNA:DNA production ratios (Hanson and Lowery, 1983).

6.3. Prydz Bay

A comprehensive investigation of plankton in the Prydz Bay region (Fig. 1.12) was conducted during February–April 1987 aboard the MV *Nella Dan* (voyage 7 of the Australian Antarctic Division). By the end of the cruise in late March, pack ice was beginning to form adjacent to the continental ice shelves (Fig. 1.12). The expedition established a station grid that included the open sea, the divergence frontal region, and the marginal ice zone.

The field experiments were designed around the "ecophysiological" model of phytoplankton and bacterioplankton growth (Lancelot et al., 1989) developed by

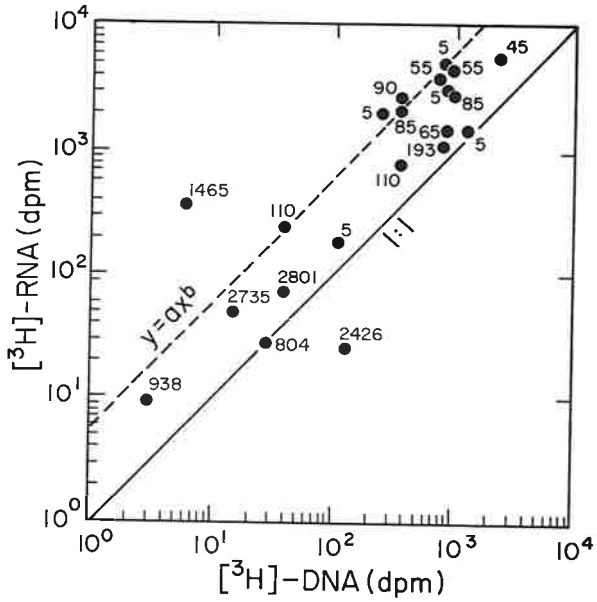


Fig. 1.11. Comparison of ^{3}H-adenine incorporation (dpm) into RNA and DNA pools of microplankton in the water column of the Drake Passage. Numbers next to symbols indicate sample depth. A statistical analysis of these data revealed that 92% of the samples had a RNA:DNA rate ratio <100:1, and 76% were <10:1 but >1:1. The best-fit regression is $y = ax^b$ ($a = 6$, $b = 1$, $r = 1$, $F = 47$, $P < 0.001$), indicating a mean RNA:DNA rate ratio of 6:1. Redrawn from Hanson and Lowery (1983).

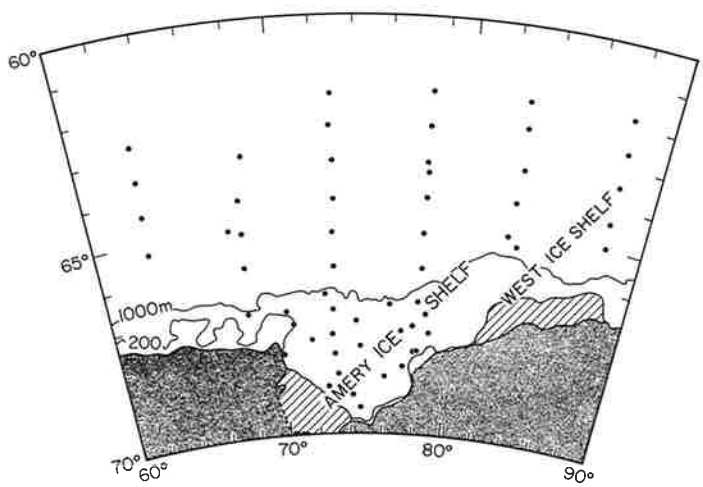


Fig. 1.12. Map of Prydz Bay showing the location of the MV *Nella Dan* stations relative to the continent and ice shelves. Redrawn from Lancelot et al. (1989).

C. Lancelot, G. Billen, S. Mathot, and colleagues on the basis of their work in Belgian coastal waters and the North Sea. The model incorporated both fundamental principles of biochemistry related to cell growth and division and environmental determinants such as light and nutrient history for phototrophic populations and the important distinction between high- and low-molecular-weight organic substrates for microheterotrophic populations (the "HSB" model of Billen and Fontigny, 1987; see also Fig. 1.5). Although idealized, it served to identify potentially important microbial rate processes and control mechanisms. Only those results relevant to bacterioplankton dynamics are summarized here.

In addition to the "standard" estimates of bacterial biomass by epifluorescence microscopy and production/growth rate by ^{3}H-Tdr incorporation, measurements were also made of exoproteolytic activity to evaluate the potential rates of high-molecular-weight DOM utilization and of bacterial mortality by microzooplankton (2–20 μm) grazing and other mechanisms.

The results did not reveal the expected positive correlations between phytoplankton and bacterioplankton standing crops (Bird and Kalff, 1984; Cole et al., 1988). Billen and Becquevort (1991) hypothesized that the "anomalous" Prydz Bay results are explained by a lag in the growth response of bacterioplankton following the spring phytoplankton bloom. Billen and Becquevort (1991) suggested that, rather than being caused by a differential temperature inhibition, as suggested in the Pomeroy-Deibel hypothesis, the delay is due to the inherent composition of the DOM pools. During the initiation of the bloom, predominantly high-molecular-weight DOM is produced by the phytoplankton, and these constituents require hydrolysis by exozymes (extracellular enzymes) before the carbon and energy they contain becomes available for bacterial growth, which would, they suggest, cause approximately one month's delay in the bacterial biomass and activity peak.

In support of this hypothesis, Lancelot et al. (1989) and Billen and Becquevort (1991) presented a simulation model of bacterioplankton dynamics that was based upon the production, accumulation, and utilization of high- and low-molecular-weight substrates. Unfortunately, no direct measurements were made of the "hypothetical" biopolymers, and the few data given on "total" DOC pools (as measured by UV-assisted persulfate oxidation and CO_2 detection) indicate a nearly constant pool throughout the period of observation (Lancelot et al., 1989). Furthermore, given the fairly complex horizontal circulation patterns in Prydz Bay (N. R. Smith et al., 1984), the model might not be reliable unless mesoscale physical dynamics are included.

Two possible alternative hypotheses are (1) that production of extracellular carbon by the phytoplankton rather than its utilization by microheterotrophs is delayed and (2) that growth of micro- and macrozooplankton populations is delayed relative to the initiation of the spring bloom (see Fig. 1.4) and is followed

by a period of intense feeding and a rapid response of microheterotrophs to the organic substrates generated during the grazing processes.

In any case, Billen and colleagues have clearly focused attention on the importance of several parameters of carbon and energy flow through plankton assemblages, namely direct and indirect production of dissolved organic matter by phytoplankton, the molecular composition of the total DOC pool, and particularly, temporal lags and successional stages.

6.4. Ross Ice Shelf

A permanent floating shelf of glacial ice more than 400 m thick completely covers the southern portion of the Ross Sea, preventing photosynthesis over a large area of the Antarctic coastal ocean (Figs. 1.1, 1.13). Before direct field observations, hypotheses about the community there included (1) a specialized assemblage uniquely adapted for life in this extreme habitat, (2) a "normal" but sparse deep-sea fauna capable of living in a hyperoligotrophic environment, and (3) total absence of life. Samples taken through pressure cracks or recently opened leads near the edge of the ice shelf contained organisms (Littlepage and

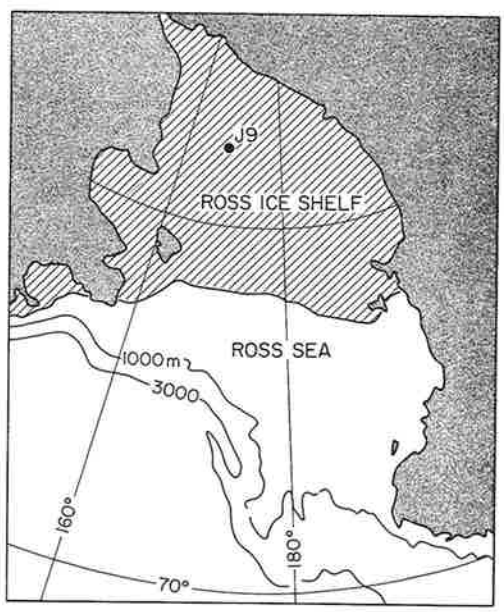


Fig. 1.13. Map of the Ross Ice Shelf showing the location of station J9, where the RISP experiment was conducted. Redrawn from Jacobs et al. (1979).

Pearse, 1962; Lipps et al., 1977; Hodson et al., 1981), but no evidence was available for the existence of life far removed from potential carbon and energy exchange with the open sea.

A primary objective of the Ross Ice Shelf Project (RISP) was to drill a hole through a remote portion of the Ross Ice Shelf and to sample the seawater and sediments below. In December 1977, a hole was successfully opened through 420 m of glacial ice (Clough and Hansen, 1979). The RISP site (82°22.5'S, 168°37.5'W) was located 450 km from the open sea and was isolated from any known sources of contemporaneous photoautotrophic organic carbon production (Fig. 1.13). Samples were collected by means of Van Dorn bottles, submersible pumps, baited traps, nets, and bottom samplers.

The water beneath the shelf was 237 m deep. Bacterial abundance, estimated by epifluorescence microscopy, was low and ranged between 0.9 and 1.2×10^7 cells l^{-1} (Holm-Hansen et al., 1978; Azam et al., 1979), and was similar to that reported from deep-sea habitats worldwide. At 10^{-14} g per cell (Watson et al., 1977), bacterial C beneath the Ross Ice Shelf was approximately 100 ng l^{-1}.

Particulate ATP concentrations were also low, ranging from 0.04 to 0.6 ng l^{-1} (Azam et al., 1979), two to three orders of magnitude lower than those measured at the seaward edge of the shelf (Hodson et al., 1981) and once again typical of abyssal ocean values (Karl, 1980). Assuming a ratio of biomass carbon to ATP of 250:1, the measured ATP values corresponded to 10–150 ng C l^{-1}, similar to those derived for bacterial C on the basis of direct microscopic estimates. The correspondence between these estimates suggests that bacteria comprise a majority of the total microbial assemblage.

Rates of microheterotrophic activity, based on the assimilation and respiration of radioisotopically labeled glucose, yielded turnover times in excess of 5×10^5 hr (Azam et al., 1979; Table 1.1). These values are among the lowest metabolic rates measured in marine habitats. Nevertheless, these sparse, metabolically arrested bacterial populations did show net incorporation of ^{3}H-Tdr, ^{3}H-uridine, and ^{3}H-ATP, suggesting a net biosynthesis of macromolecules and, presumably, net growth (Azam et al., 1979).

The presence of a variety of large (>35 μm), intact pennate diatoms, dinoflagellates, silicoflagellates, and metazoan species led Azam et al. (1979) to hypothesize that a functional planktonic food web exists beneath the Ross Ice Shelf, but these authors failed to define the precise pathway of carbon and energy flow there. In the absence of *in situ* production, these communities must rely solely on the advection of reduced carbon from the productive, open portions of the Ross Sea, so the rate of water exchange would ultimately limit microbial biomass and productivity.

Measurements of natural isotope concentrations in seawater samples collected beneath the shelf at the RISP site provided valuable information on the rates of water exchange. The ^{3}H data obtained during the 1977–78 RISP field

season indicated that the waters beneath the Ross Ice Shelf have exchanged with the open Ross Sea since the advent of atmospheric bomb testing in the early 1960s (Michel et al., 1979). These unexpected results were confirmed by the ^{14}C activities, which indicated that waters collected 22 m below the ice must have been in the open Ross Sea within the previous six years (Michel et al., 1979). This unambiguous evidence for rapid mixing might explain the presence of a functional microplankton food web beneath the ice shelf.

An alternate hypothesis was presented by Horrigan (1981), who suggested, on the basis of experiments conducted during the 1978–79 RISP field season, that "primary production," defined broadly as fixation of inorganic carbon, occurs under the Ross Ice Shelf in the absence of sunlight through the oxidation of ammonium by nitrifying bacteria. According to her calculations, the 1.5 g C m^{-2} yr^{-1} potentially fixed by this process could sustain the macrofauna reported to occur at the RISP site. Actually, this proposed chemolithotrophy must be viewed as secondary production, from a thermodynamic perspective, as the required dissolved ammonium is presumably derived from the mineralization of organic matter initially produced by photosynthesis. Consequently, the upper limit on the amount of energy potentially available through it is still constrained by phototrophic production (Wetzel et al., 1972; Karl and Knauer, 1984), but given the extremely low standing stocks of organisms and their low metabolic requirements, these alternative detrital pathways may prove more important under the ice than in regions of high solar energy flux (see also Priscu and Palmisano, 1986; Priscu et al., 1990). Clearly, more data are needed before an accurate quantitative assessment of nitrification (and other chemolithotrophic reactions) can be made.

6.5. Southern Bransfield Strait

In 1981, the Committee to Evaluate Antarctic Marine Ecosystem Research (Steele, 1981) identified the coastal zone of the Antarctic Peninsula as one of several Antarctic marine ecosystems needing comprehensive, interdisciplinary study. The coastal shelf region is thought to be especially important because it supports an extensive spring bloom of phytoplankton, has a high annual rate of primary production, and is a principal breeding, feeding, and spawning ground for Antarctic krill (I. Hempel et al., 1979; Ross and Quetin, 1982; Brinton et al., 1986). However, the processes responsible for the biological richness of this ecosystem are not well understood, and comprehensive data on microbial rates and element cycling (especially the role of microheterotrophs) in this region are relatively few.

During 1986–87, an interdisciplinary group of scientists conducted a comprehensive four-month field study of 69 stations within a sampling grid of high spatial resolution (Fig. 1.14). The 25,000-km^2 Research on Antarctic Coastal

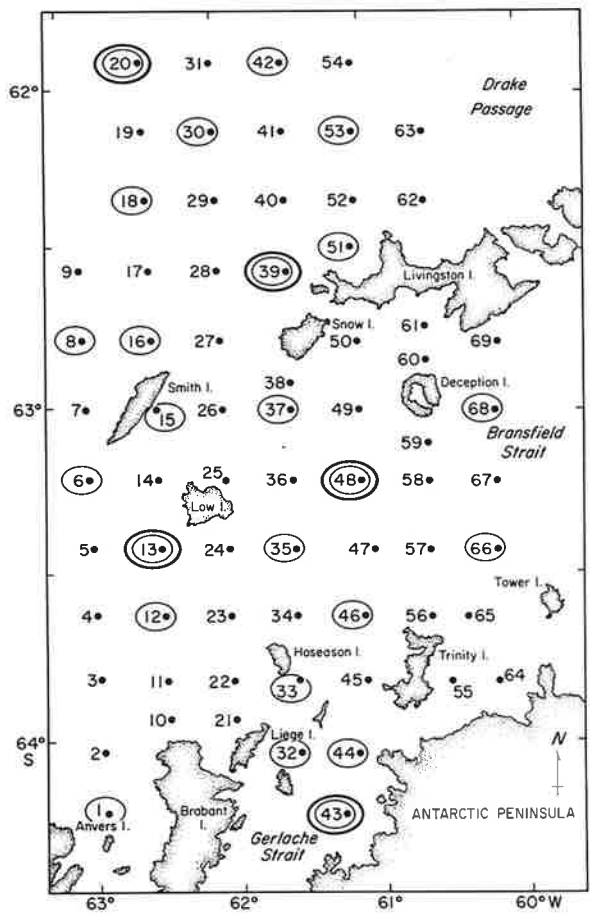


Fig. 1.14. Map of 1986–87 RACER study area showing the locations of the 69 stations occupied in this field program. All 69 stations were visited once during the monthly "fast-grid" sampling program; the 25 circled stations (single and double circle) indicate where more comprehensive vertical profiles were obtained; the 5 double-circled stations indicate where sediment trap deployments were made. Redrawn from Huntley et al. (1991).

Ecosystem Rates (RACER) study area was small in comparison to the entire Antarctic Peninsula coastal region, but contained several representative habitats, including (1) two shelf environments (Antarctic Peninsula and South Shetland Islands) considered to be key habitats for adult and larval krill; (2) two distinct deep-water zones (the western basin of the Bransfield Strait and the shelf-break

region of the Southern Drake Passage); (3) the frontal zone, or meander, between the Bellingshausen Sea and the Bransfield Strait water masses; and (4) the eutrophic coastal regions of the northern Gerlache Strait (Fig. 1.14).

The two central hypotheses of the RACER program were the "stability–productivity hypothesis," which states that upper-ocean physical dynamics control productivity at all levels of the food web and that productivity is significantly greater in nearshore stratified waters than in offshore regions, and the "island effect–residence time hypothesis," which states that islands and irregular bottom topography interrupt the flow of waters onto the coastal shelf, increasing mean residence time and allowing for greater productivity there than in offshore regions (Huntley et al., 1987, 1991). To address these general hypotheses and their ecological predictions, the RACER program combined studies of upper-ocean physics, photobiology and biooptics, microbiology, particle flux, and the distribution and physiological rates of krill, zooplankton, and nekton. Only selected results on microbial rates and processes are summarized here.

During the four-month period of field observation, RACER program scientists documented a substantial bloom of phytoplankton with highest concentrations (expressed as Chl*a*) in the northern Gerlache Strait region in January 1987 (Holm-Hansen and Mitchell, 1991; Fig. 1.15A). This distribution of biomass and primary productivity was highly correlated with upper-water-column physical dynamics and especially with the depth of the surface mixed layer (Mitchell and Holm-Hansen, 1991). During the spring bloom of phototrophic 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 8,410 mmol C m^{-2}, 827 mmol N m^{-2}, and 53 mmol P m^{-2} (Karl et al., 1991b). Order-of-magnitude onshore-to-offshore gradients were evident; primary production rates were highest in the coastal zone and lowest in the Drake Passage (Holm-Hansen and Mitchell, 1991; Karl et al., 1991b). In spite of these strong spatial gradients in Chl*a*, the putative microheterotrophic populations, i.e., bacteria, displayed no congruence with photoautotrophic biomass either during (Fig. 1.15B) or immediately after (Karl et al., 1991a) the bloom.

These results, which suggest an uncoupling of bacterioplankton and phytoplankton population dynamics, contrast with extensive cross-ecosystem 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 (Fig. 1.16; Karl et al., 1991a). A similar result is evident in the AMERIEZ (Cota et al., 1990) and Prydz Bay (Lancelot et al., 1989) data sets, suggesting that eutrophic regions of the southern oceans may exhibit an autotrophic–heterotrophic relationship fundamentally different from that in other habitats studied to date. In this regard, ecosystem processes in the coastal shelf region

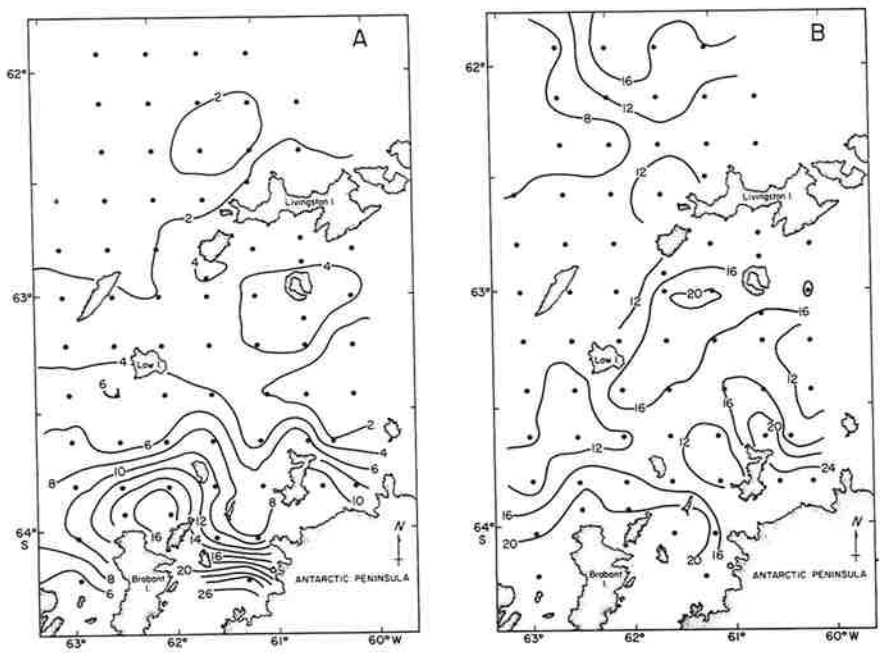


Fig. 1.15. Regional distributions of (**A**) chlorophyll *a* concentrations (mg Chl*a* m^{-3}) and (**B**) bacterial carbon concentrations (mg C m^{-3}) for the surface waters of the RACER study area in January 1987.

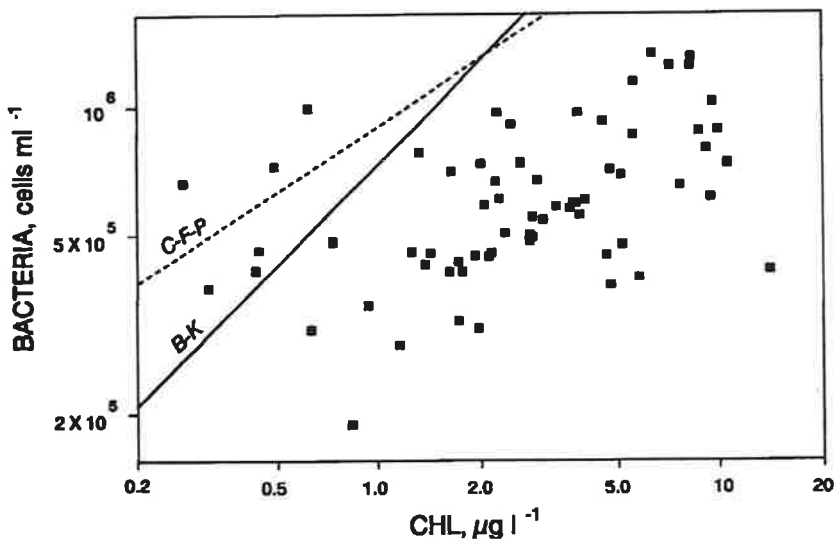


Fig. 1.16. Relationship between bacterial cell numbers and Chl*a* concentrations for samples collected during the 1986–87 RACER field study. The two lines represent the predictions based on empirical relationships for a variety of aquatic environments: solid line (B–K), Bird and Kalff (1984); dotted line (C–F–P), Cole et al. (1988). Redrawn from Karl et al. (1991a).

of the Bransfield Strait from December 1986 to January 1987 appear to be adequately described by the food web models presented in Fig. 4A, B.

During the RACER field experiment, measurements were also made of the heterotrophic assimilation of ^{3}H-glutamate (^{3}H-Glu) and ^{3}H-Tdr. During the four-month period of observation, the rate of ^{3}H-Tdr incorporation into macromolecules varied by two orders of magnitude; ^{3}H-Glu incorporation varied 170-fold (Bird and Karl, 1991; Fig. 1.17A). The highest mean values and greatest spatial variation in microheterotrophic activity occurred in January (Fig. 1.17A) at the height of the spring bloom. Because ^{3}H-Tdr was extensively catabolized by the microheterotrophic assemblages in the RACER study region (Karl et al., 1991a), no attempt was made to extrapolate ^{3}H-Tdr incorporation data to rates of bacterial productivity or growth.

An examination of the relationships among hydrographical and biological parameters was carried out through a study of spatial autocorrelation structure and regression modeling (Bird and Karl, 1991). Low-order positive and high-order negative autocorrelations were associated with the gradient in biological activity from maxima in the northern Gerlache Strait to minima in the Drake Passage (Bird and Karl, 1991). Primary factors correlated with microheterotrophic activity were total phytoplankton pigment concentration (Chl*a* plus phaeopigments), total microbial biomass (ATP concentration), and bacterial abundance. This onshore-to-offshore spatial polarization in microheterotrophic activity, however, was evident only in January.

Positive, recurrent relationships between various biological and physical parameters suggested that prediction and modeling of microheterotrophic rate processes within this Antarctic marine ecosystem may be feasible. Multivariate regression analysis revealed that ^{3}H-Glu incorporation could best be modeled with knowledge of the concentrations of pigments, particulate DNA, and bacterial cells (Bird and Karl, 1991; Fig. 1.17B).

A second RACER field study was conducted in October and November 1989 in a smaller 4,000-km^2 region of the northern Gerlache Strait and southwestern Bransfield Strait (Fig. 1.18; Huntley et al., 1990) that examined more closely the degree of coupling between autotrophic and heterotrophic microbial assemblages before and during the intensive spring bloom. Although most of the data are still under analysis, several general features were evident. First, the net accumulation of algal biomass was very rapid and extensive; maximum Chl*a* concentrations ranged from less than 0.5 g l^{-1} on 9 October to more than 16 g l^{-1} approximately one month later (Holm-Hansen and Vernet, 1990). Bacterial abundance was nevertheless low throughout the period of observation (mean cell numbers were 2.5×10^5 ml^{-1} before and 3.5×10^5 ml^{-1} during the bloom; Bird and Karl, 1990). Consistent with the results obtained during the 1986–87 expedition, bacterial cell abundance was not correlated with either Chl*a* (Holm-Hansen and Vernet, 1990) or total microbial biomass (Tien et al., 1990) distributions. During the initial stages of the bloom, there was little evidence for either bacterial production or bacterial biomass removal by protozoan grazing (Bird and Karl, 1990).

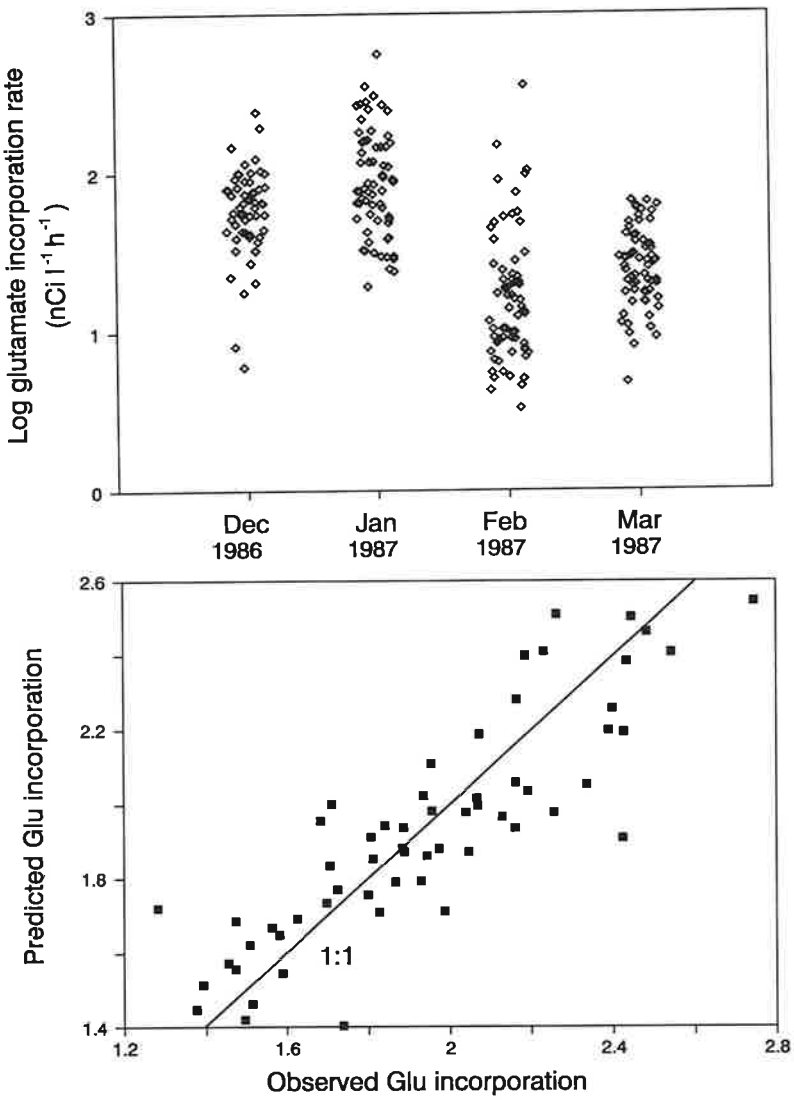


Fig. 1.17. Top: Seasonal rates of ^{3}H-glutamate labeling of macromolecules across the 1986–87 RACER study area. All data have been transformed to logarithms. Redrawn from Bird and Karl (1991). **Bottom**: Scatter plot showing observed ^{3}H-glutamate (Glu) incorporation rates in January 1987 in the RACER study area versus rates predicted from a model based on pigment concentation, particulate DNA, and bacterial abundance: Log Glu incorporation (nCi l^{-1} h^{-1}) = -1.01 + 0.37 log pigment concentration (g l^{-1}) + 0.44 log particulate DNA (g l^{-1}) + 0.40 log bacterial abundance (cell ml^{-1}). The solid line is the 1-to-1 line of correspondence. Redrawn from Bird and Karl (1991).

These results support the previously described ecosystem model for the southern oceans (Fig. 1.4A,B), and suggest that the microbial loop is repressed during the initial phase of the spring bloom, but a more thorough analysis of the potential mechanism(s) responsible for this apparent suppression of microheterotrophic production will require the complete RACER-II data set, which at present is not available.

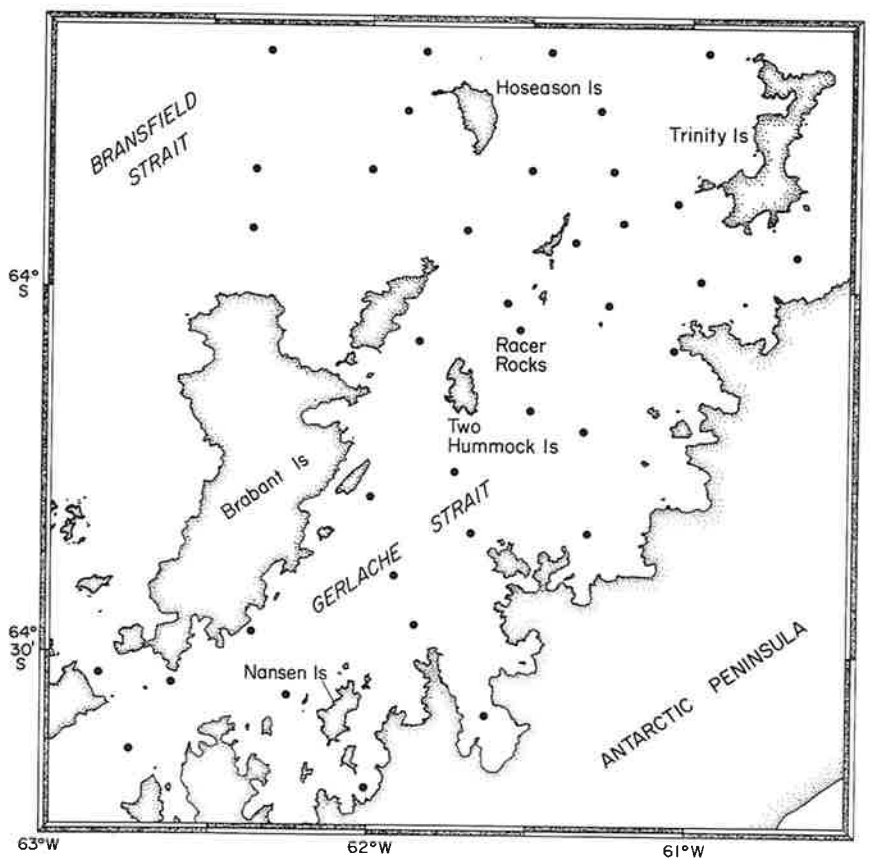


Fig. 1.18. Map showing the locations of the stations occupied in the 1989 RACER-II field study. Redrawn from Huntley et al. (1990).

7. SUMMARY AND PROSPECTUS

During the past decade, rapid advances have been made in our understanding of microbial processes in the southern oceans. A general conceptual framework for the role of microheterotrophs is now beginning to emerge, but the quantitative details of the rates and mechanisms still require more precise and accurate methods and the conduct of more comprehensive field studies. In particular, the spatial and temporal variability we now know exists in Antarctic marine microbial assemblages must be carefully documented and fully understood before any conclusions can be drawn about the role of bacterioplankton in the food web.

The dimensions of the region under discussion are large, by any standard, and our integrated ecosystem models are currently limited by the lack of an adequate, representative sampling effort. Many important ecological studies are under investigation, but few if any processes are satisfactorily resolved. In our field studies of Antarctic microbial communities to date, we have concentrated on phototrophs and devoted a less intensive research effort to the study of microheterotrophic populations. Mesopelagic, deep-sea, and benthic microbial processes have been virtually ignored. These are all fertile areas for future research.

Despite our present limitations, prospects for the future are bright. Recent advances in molecular biology (DeLong et al., 1989; Giovannoni et al., 1990) now provide a novel set of techniques for more comprehensive hypothesis testing in oceanic ecosystems. The increased use of remote sensing techniques, including satellite and aircraft imagery (Shuchman and Onstott, 1990), autonomous buoys equipped with chemical and optical sensors (Fukuchi et al., 1988), and the deployment of bottom-moored sediment traps (Fischer et al., 1988; Karl and Asper, 1990) and acoustical arrays will eventually provide a much-needed time-series database on Antarctic marine seasonal cycles. Continued methods development and the transfer of novel technologies and instrumentation to studies of Southern Ocean microbial ecology should be anticipated and fully encouraged.

Several currently underrepresented areas of investigation appear to be poised for expansion. These include studies designed to gain a better understanding of microbial loop processes and especially sources and molecular characterization of ambient DOM pools, quantitative measurements of the efficiency of bacterial utilization of DOM, rates of microzooplankton grazing, and the role of pelagic viruses in the Antarctic marine ecosystem. Furthermore, we need to establish the basic growth status of the microheterotrophic assemblages (i.e., whether they are substrate-starved or nutrient-replete, show balanced or unbalanced growth) and to ascertain with greater precision the master variables (e.g., cell number, biomass, productivity) of the microheterotrophic populations.

Although Antarctica is best known for its extremely low temperatures, future research may, in part, also focus on high-temperature habitats. The continent of

Antarctica and the surrounding oceans contain some of the world's largest but least studied volcanic provinces. The Bransfield Strait is known to be an active marginal basin where submarine volcanism and hydrothermal activity have recently been discovered (Whiticar et al., 1985; Suess et al., 1987; Schlosser et al., 1988). Hydrothermal vent bacteria and perhaps specialized macrofauna very probably occur in these submarine volcanic settings. These potential discoveries assume an even greater global significance given the tectonic history of the Drake/Antarctic spreading center and the relative isolation of this region from other known hydrothermal vent ecosystems (Karl, 1987).

Future research efforts are also likely to include a number of multidisciplinary studies designed to examine the interactions among biological, physical, and chemical processes. Foremost among these is the rapidly evolving Joint Global Ocean Flux Study (JGOFS), an international program broadly intended to increase our understanding of the oceanic carbon cycle and the role of biogeochemical cycles in climate change. It includes (U.S. GOFS Planning Report 11, May 1990) (1) process studies designed to capture key regular events and to generate a fundamental understanding of the system, (2) a global survey of biogeochemical oceanic properties designed to provide essential data for constraining models and for utilizing satellite observations, (3) time-series observations of long duration at strategic sites, and (4) a vigorous modeling effort to assimilate results, expand knowledge, and generate new testable hypotheses.

Many of the critical processes central to the JGOFS program objectives require detailed understanding of microorganisms and interactions among the various trophic levels of the marine food web. Because of the potentially strategic role of the Antarctic waters in global biogeochemical models, they have been selected as one of several habitats for the conduct of a major process-oriented JGOFS research effort in the 1990s. Furthermore, efforts continue in the United States to establish one or more Long-Term Ecological Research (LTER) sites in Antarctica (NSF, Division of Polar Programs Long Range Plan, April 1990) in order to gain a better understanding of interannual variability and to generate new hypotheses.

A final area of concern and increased awareness is the effect of human activities on Antarctic marine ecosystems (see also Nienow and Friedmann, Chapter 9, this volume). The potential environmental impact of point-source pollution from research vessels, scientific bases, and tourism must be carefully monitored and assessed. The grounding of the MV *Bahia Paraiso* near Palmer Station in January 1989 and the subsequent release of more than 150,000 gallons of petroleum to the surrounding bays (Kennicutt et al., 1990) point out the potential for serious, deleterious effects. Studies designed to evaluate the environmental impact of the release of toxic heavy metals, untreated sewage, and litter, especially near major research bases, will become increasingly important as the scope and magnitude of research activities accelerate in the near future.

Moreover, the Antarctic "ozone hole," which is believed to be the result of global atmospheric chlorofluorocarbon pollution (Rowland, 1989) and attendant increased solar UV flux, comprises a potential threat to microorganisms in near-surface waters. I hope that by the time the next review of "Microbial Processes in the Southern Ocean" is prepared, we will have made significant progress toward these goals.

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REFERENCES

Ainley, D. G., W. R. Fraser, C. W. Sullivan, J. J. Torres, T. L. Hopkins, and W. O. Smith, Jr. 1986. Antarctic mesopelagic micronekton: evidence from seabirds that pack ice affects community structure. Science 232:847–849.

Amy, P. S., C. Pauling, and R. Y. Morita. 1983. Starvation-survival processes of a marine vibrio. Applied and Environmental Microbiology 45:1041–1048.

Andersson, A., U. Larsson, and A. Hagstrom. 1986. Size-selective grazing by a microflagellate on pelagic bacteria. Marine Ecology Progress Series 33:51–57.

Azam, F., and R. E. Hodson. 1981. Multiphasic kinetics for D-glucose uptake by assemblages of natural marine bacteria. Marine Ecology Progress Series 6:213–222.

Azam, F., and O. Holm-Hansen. 1973. Use of tritiated substrates in the study of heterotrophy in seawater. Marine Biology 23:191–196.

Azam, F., J. R. Beers, L. Campbell, A. F. Carlucci, O. Holm-Hansen, F. M. H. Reid, and D. M. Karl. 1979. Occurrence and metabolic activity of organisms under the Ross Ice Shelf, Antarctica, at Station J9. Science 203:451–453.

Azam, F., J. W. Ammerman, and N. Cooper. 1981. Bacterioplankton distributional patterns and metabolic activities in the Scotia Sea. Antarctic Journal of the United States 16:164–165.

Bailiff, M. D., and D. M. Karl. 1991. Dissolved and particulate DNA dynamics during a spring bloom in the Antarctic Peninsula region, 1986–87. Deep-Sea Research 38:1077–1095.

Bakken, L. R., and R. A. Olsen. 1983. Buoyant densities and dry-matter contents of microorganisms: conversion of a measured biovolume into biomass. Applied and Environmental Microbiology 45:1188–1195.

Banse, K. 1974. On the role of bacterioplankton in the tropical ocean. Marine Biology 24:1–5.

Billen, G., and S. Becquevort. 1991. Phytoplankton–bacteria relationship in the Antarctic marine ecosystem. Pro Mare Symposium on Marine Arctic Ecology, Trondheim, Norway.

Billen, G., and A. Fontigny. 1987. Dynamics of a *Phaeocystis*-dominated spring bloom in Belgian coastal waters. II. Bacterioplankton dynamics. Marine Ecology Progress Series 37:249–257.

Bird, D. F., and J. Kalff. 1984. Empirical relationships between bacterial abundance and chlorophyll

concentration in fresh and marine waters. Canadian Journal of Fisheries and Aquatic Science 41:1015–1023.

Bird, D. F., and D. M. Karl. 1990. RACER: bacterial growth, abundance and loss due to protozoan grazing during the 1989 spring bloom. Antarctic Journal of the United States 25:156–157.

Bird, D. F., and D. M. Karl. 1991. Spatial patterns of glutamate and thymidine assimilation in Bransfield Strait, Antarctica during and following the austral spring bloom. Deep-Sea Research 38:1057–1075.

Bishop, J. K. B., and W. B. Rossow. In press. Investigations of global short wave surface irradiance fields using International Satellite Cloud Climatology Project (ISCCP) data. Proceedings of the Second Conference on Oceans from Space, Venice, Italy, IAPSO, San Diego, CA.

Bolter, M., and R. Dawson. 1982. Heterotrophic utilisation of biochemical compounds in Antarctic waters. Netherlands Journal of Sea Research 16:315–332.

Bratbak, G. 1985. Bacterial biovolume and biomass estimations. Applied and Environmental Microbiology 49:1488–1493.

Bratbak, G., and I. Dundas. 1984. Bacterial dry matter content and biomass estimations. Applied and Environmental Microbiology 48:755–757.

Bratbak, G., M. Heldal, S. Norland, and T. F. Thingstad. 1990. Viruses as partners in spring bloom microbial trophodynamics. Applied and Environmental Microbiology 56:1400–1405.

Brewer, P. G., K. W. Bruland, R. W. Eppley, and J. J. McCarthy. 1986. The Global Ocean Flux Study (GOFS): Status of the U.S. GOFS Program. EOS, Transactions of the American Geophysical Union 67:827–832.

Brinton, E., M. Huntley, and A. W. Townsend. 1986. Larvae of *Euphausia superba* in the Scotia Sea and Bransfield Strait in March 1984—development and abundance compared with 1981 larvae. Polar Biology 5:221–234.

Brittain, A. M., and D. M. Karl. 1990. Catabolism of tritiated thymidine by aquatic microbial communities and incorporation of tritium into RNA and protein. Applied and Environmental Microbiology 56:1245–1254.

Brock, T. D. 1971. Microbial growth rates in nature. Bacteriological Reviews 35:39–58.

Broecker, W. S. 1982. Glacial to interglacial changes in ocean chemistry. Progress in Oceanography 11:151–197.

Broecker, W. S., T. Takahashi, H. J. Simpson, and T. H. Peng. 1979. Fate of fossil fuel carbon dioxide and the global carbon budget. Science 206:409–418.

Brunschede, H., T. L. Dove, and H. Bremer. 1977. Establishment of exponential growth after a nutritional shift-up in *Escherichia coli* B/r: accumulation of deoxyribonucleic acid, ribonucleic acid and protein. Journal of Bacteriology 129:1020–1033.

Bunt, J. S. 1955. The importance of bacteria and other microorganisms in the sea-water at Macquarie Island. Australian Journal of Marine and Freshwater Research 6:60–65.

Bunt, J. S. 1971. Microbial productivity in polar regions. Society for General Microbiology Symposium 21:333–354.

Carlucci, A. F., and R. L. Cuhel. 1977. Vitamins in the South Polar seas: distribution and significance of dissolved and particulate vitamin B_{12}, thiamine, and biotin in the southern Indian Ocean. Pages 115–128 in G. A. Llano (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Gulf Publishing Company, Houston, TX.

Carmack, E. C. 1977. Water characteristics of the Southern Ocean south of the Polar Front. Pages 15–41 in M. Angel (ed.), A Voyage of Discovery. Pergamon Press, Oxford.

Carmack, E. C. 1990. Large-scale physical oceanography of polar oceans. Pages 171–222 in W. O. Smith, Jr. (ed.), Polar Oceanography, Part A: Physical Science. Academic Press, San Diego.

Cho, B. C., and F. Azam. 1988. Heterotrophic bacterioplankton production measurement by the tritiated thymidine incorporation method. Archiv für Hydrobiologie Beihefte Ergebnisse der Limnologie 31:153–162.

Clarke, A. 1985. Energy flow in the Southern Ocean food web. Pages 573–580 in W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.

Clough, J. W., and B. L. Hansen. 1979. The Ross Ice Shelf Project. Science 203:433–434.

Cole, J. J., S. Findlay, and M. L. Pace. 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Marine Ecology Progress Series 43:1–10.

Comiso, J. C., and C. W. Sullivan. 1986. Satellite microwave and in situ observations in the Weddell Sea ice cover and its marginal ice zone. Journal of Geophysical Research 91:9663–9681.

Comiso, J. C., N. G. Maynard, W. O. Smith, Jr., and C. W. Sullivan. 1990. Satellite ocean color studies of the Antarctic ice edge in summer/autumn. Journal of Geophysical Research 95:9481–9496.

Cota, G. F., S. T. Kottmeier, D. H. Robinson, W. O. Smith, Jr., and C. W. Sullivan. 1990. Bacterioplankton in the marginal ice zone of the Weddell Sea: biomass, production and metabolic activities during austral autumn. Deep-Sea Research 37:1145–1167.

Coveney, M. F., and R. G. Wetzel. 1988. Experimental evaluation of conversion factors for the tritiated thymidine incorporation assay of bacterial secondary productivity. Applied and Environmental Microbiology 54:2018–2026.

Crary, A. P. 1962. The Antarctic. Scientific American 207:1–16.

Darling, C. A., and P. A. Siple. 1941. Bacteria in Antarctica. Journal of Bacteriology 42:83–98.

Davis, C. L. 1989. Uptake and incorporation of thymidine by bacterial isolates from an upwelling environment. Applied and Environmental Microbiology 55:1267–1272.

Dawson, R., W. Schramm, and M. Bolter. 1985. Factors influencing the production, decomposition and distribution of organic and inorganic matter in Admiralty Bay, King George Island. Pages 109–114 in W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.

Deacon, G. E. R. 1982. Physical and biological zonation in the Southern Ocean. Deep-Sea Research 29:1–15.

DeLong, E. F., G. S. Wickham, and N. R. Pace. 1989. Phylogenetic stains: ribosomal RNA-based probes for the identification of single cells. Science 243:1360–1363.

Dennis, P. P., and H. Bremer. 1974. Macromolecular composition during steady-state growth of *Escherichia coli* B/r. Journal of Bacteriology 119:270–281.

Deuser, W. G. 1986. Seasonal and interannual variations in deep water particle fluxes in the Sargasso Sea and their relation to surface hydrography. Deep-Sea Research 33:225–246.

Douglas, D. J., J. A. Novitsky, and R. O. Fournier. 1987. Microautoradiography-based enumeration of bacteria with estimates of thymidine-specific growth and production rates. Marine Ecology Progress Series 36:91–99.

Ducklow, H. W., and S. M. Hill. 1985. Tritiated thymidine incorporation and the growth of heterotrophic bacteria in warm core rings. Limnology and Oceanography 30:260–272.

El-Sayed, S. Z. 1988. Productivity of the Southern Ocean: a closer look. Comparative Biochemistry and Physiology 90B:489–498.

El-Sayed, S. Z., and S. Taguchi. 1981. Primary production and standing crop of phytoplankton along the ice-edge in the Weddell Sea. Deep-Sea Research 28A:1017–1032.

Ennever, F. K., and M. B. McElroy. 1985. Changes in atmospheric CO_2: factors regulating the glacial to interglacial transition. Pages 154–162 in E. T. Sundquist and W. S. Broecker (eds.), The Carbon Cycle and Atmospheric CO_2: Natural Variations Archaen to Present. Geophysical Monograph 32, American Geophysical Union, Washington, D.C.

Eppley, R. W. 1989. New production: history, methods, problems. Pages 85–98 in W. H. Berger, V. S. Smetacek, and G. Wefer (eds.), Productivity of the Ocean: Present and Past. John Wiley, Chichester.

Estep, K. W., and F. MacIntyre. 1989. Taxonomy, life cycle, distribution and dasmotrophy of *Chrysochromulina*: a theory accounting for scales, haptonema, muciferous bodies and toxicity. Marine Ecology Progress Series 57:11–21.

Fallon, R. D., and S. Y. Newell. 1986. Thymidine incorporation by the microbial community of standing dead *Spartina alterniflora*. Applied and Environmental Microbiology 52:1206–1208.

Faquin, W. C., and J. D. Oliver. 1984. Arginine uptake by a psychrophilic marine *Vibrio* sp. during starvation-induced morphogenesis. Journal of General Microbiology 130:1331–1335.

Fischer, G., D. Futterer, R. Gersonde, S. Honjo, D. Ostermann, and G. Wefer. 1988. Seasonal variability of particle flux in the Weddell Sea and its relation to ice cover. Nature 335:426–428.

Foster, T. D. 1984. The marine environment. Pages 345–371 in R. M. Laws (ed.), Antarctic Ecology, vol. 2. Academic Press, London.

Fraser, W. R., and D. G. Ainley. 1986. Ice edges and seabird occurrence in Antarctica. BioScience 36:258–263.

Fuhrman, J. A., and F. Azam. 1980. Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica, and California. Applied and Environmental Microbiology 39:1085–1095.

Fukuchi, M., H. Hattori, H. Sasaki, and T. Hoshiai. 1988. A phytoplankton bloom and associated processes observed with a long-term moored system in Antarctic waters. Marine Ecology Progress Series 45:279–288.

Garrison, D. L., C. W. Sullivan, and S. F. Ackley. 1986. Sea ice microbial communities in Antarctica. BioScience 36:243–250.

Gillespie, P. A., R. Y. Morita, and L. P. Jones. 1976. The heterotrophic activity for amino acids, glucose and acetate in Antarctic waters. Journal of the Oceanographical Society of Japan 32:74–82.

Giovannoni, S. J., T. B. Britschgi, C. L. Moyer, and K. G. Field. 1990. Genetic diversity in Sargasso Sea bacterioplankton. Nature 345:60–63.

Gonzalez, J. M., E. B. Sherr, and B. F. Sherr. 1990. Size-selective grazing on bacteria by natural assemblages of estuarine flagellates and ciliates. Applied and Environmental Microbiology 56:583–589.

Gow, A. J., and W. B. Tucker III. 1990. Sea ice in the polar regions. Pages 47–122 in W. O. Smith, Jr. (ed.), Polar Oceanography, Part A: Physical Science. Academic Press, San Diego.

Gow, J. A., and F. H. J. Mills. 1984. Pragmatic criteria to distinguish psychrophiles and psychrotrophs in ecological systems. Applied and Environmental Microbiology 47:213–215.

Grossi, S. M., S. T. Kottmeier, and C. W. Sullivan. 1984. Sea ice microbial communities. III. Seasonal abundance of microalgae and associated bacteria, McMurdo Sound, Antarctica. Microbial Ecology 10:231–242.

Haberstroh, P. R., M. D. Bailiff, G. Tien, G. T. Taylor, D. Jones, B. Tilbrook, M. Nawrocki, and D. M. Karl. 1987. RACER: dissolved free amino acid concentrations, molecular composition, and microbial uptake rates in the Bransfield Strait. Antarctic Journal of the United States 22:153–156.

Hanson, R. B., and H. K. Lowery. 1983. Nucleic acid synthesis in oceanic microplankton from the Drake Passage, Antarctica: evaluation of steady-state growth. Marine Biology 73:79–89.

Hanson, R. B., and D. H. Pope. 1981. Bacterioplankton adaptation and growth in different zones of the southern ocean. Antarctic Journal of the United States 16:130–132.

Hanson, R. B., H. K. Lowery, D. Shafer, R. Sorocco, and D. H. Pope. 1983a. Microbes in Antarctic waters of the Drake Passage: vertical patterns of substrate uptake, productivity and biomass in January 1980. Polar Biology 2:179–188.

Hanson, R. B., D. Shafer, T. Ryan, D. H. Pope, and H. K. Lowery. 1983b. Bacterioplankton in Antarctic ocean waters during late austral winter: abundance, frequency of dividing cells, and estimates of production. Applied and Environmental Microbiology 45:1622–1632.

Harder, W., and H. Veldkamp. 1971. Competition of marine psychrophilic bacteria at low temperatures. Antonie van Leeuwenhoek 37:51–63.

Hart, T. J. 1942. Phytoplankton periodicity in Antarctic surface waters. Discovery Reports 21:261–365.

Hempel, G. 1985. Antarctic marine food webs. Pages 266–270 in W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.

Hempel, I., G. Hempel, and A. de C. Baker. 1979. Early life history stages of krill (*Euphausia superba*) in Bransfield Strait and Weddell Sea. Meeresforschungen 27:267–281.

Herwig, R. P., J. T. Staley, and J. S. Maki. 1986. Heterotrophic activities in the marine surface waters near penguin rookeries of the Antarctic Peninsula. Antarctic Journal of the United States 21:164–166.

Hewes, C. D., E. Sakshaug, and O. Holm-Hansen. 1985. Alternative pathways at lower trophic levels in the Antarctic food web. Pages 277–283 in W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.

Hodson, R. E., F. Azam, A. F. Carlucci, J. A. Fuhrman, D. M. Karl, and O. Holm-Hansen. 1981. Microbial uptake of dissolved organic matter in McMurdo Sound, Antarctica. Marine Biology 61:89–94.

Holm-Hansen, O., and B. G. Mitchell. 1991. Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. Deep-Sea Research 38:961–980.

Holm-Hansen, O., and M. Vernet. 1990. RACER: phytoplankton distribution and rates of primary production during the austral spring bloom. Antarctic Journal of the United States 25:141–144.

Holm-Hansen, O., S. Z. El-Sayed, G. A. Franceschini, and R. L. Cuhel. 1977. Primary production and the factors controlling phytoplankton growth in the Southern Ocean. Pages 11–50 in G. A. Llano (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Gulf Publishing Company, Houston, TX.

Holm-Hansen, O., F. Azam, L. Campbell, A. F. Carlucci, and D. M. Karl. 1978. Microbial life beneath the Ross Ice Shelf. Antarctic Journal of the United States 13:129–130.

Holm-Hansen, O., B. G. Mitchell, C. D. Hewes, and D. M. Karl. 1989. Phytoplankton blooms in the vicinity of Palmer Station, Antarctica. Polar Biology 10:49–57.

Honjo, S. 1990. Particle fluxes and modern sedimentation in the Polar Oceans. Pages 687–739 in W. O. Smith, Jr. (ed.), Polar Oceanography. Part B: Chemistry, Biology and Geology. Academic Press, San Diego.

Hopkins, T. L. 1985. Food web of an Antarctic midwater ecosystem. Marine Biology 89:197–212.

Horrigan, S. G. 1981. Primary production under the Ross Ice Shelf, Antarctica. Limnology and Oceanography 26:378–382.

Huntley, M. E., P. Niiler, O. Holm-Hansen, and D. M. Karl. 1987. Research on Antarctic ecosystem rates. Antarctic Journal of the United States 22:135–137.

Huntley, M. E., P. Niiler, O. Holm-Hansen, M. Vernet, A. Amos, E. Brinton, and D. M. Karl. 1990. RACER: an interdisciplinary study of spring bloom dynamics. Antarctic Journal of the United States 25:126–128.

Huntley, M. E., D. M. Karl, P. Niiler, and O. Holm-Hansen. 1991. Research on Antarctic Coastal Ecosystem Rates (RACER): an interdisciplinary field experiment. Deep-Sea Research 38:911–941.

Husby, D. G., R. D. Muench, and J. T. Gunn. 1989. Oceanic observations in the Scotia Sea marginal ice zone June-August 1988. NOAA Technical Memorandum NOAA-TM-NMFS-SWFC-127. 64 pp.

Irgens, R. L., I. Suzuki, and J. T. Staley. 1989. Gas vacuolate bacteria obtained from marine waters of Antarctica. Current Microbiology 18:261–265.

Jacobs, S. S., A. L. Gordon, and J. L. Ardai, Jr. 1979. Circulation and melting beneath the Ross Ice Shelf. Science 203:439–443.

Jeffrey, W. H., and J. H. Paul. 1988. Effect of 5-fluoro-2'-deoxyuridine on [^{3}H]thymidine incorporation by bacterioplankton in the waters of southwest Florida. Applied and Environmental Microbiology 54:331–336.

Jones, R. D., and R. Y. Morita. 1985. Low-temperature growth and whole-cell kinetics of a marine ammonium oxidizer. Marine Ecology Progress Series 21:239–243.

Karl, D. M. 1980. Cellular nucleotide measurements and application in microbial ecology. Microbiological Reviews 44:739–796.

Karl, D. M. 1981. Simultaneous rates of ribonucleic acid and deoxyribonucleic acid syntheses for

estimating growth and cell division of aquatic microbial communities. Applied and Environmental Microbiology 42:802–810.

Karl, D. M. 1982. Microbial transformations of organic matter at oceanic interfaces: a review and prospectus. EOS, Transactions of the American Geophysical Union 63:138–140.

Karl, D. M. 1985. Effects of temperature on the growth and viability of hydrothermal vent microbial communities. Biological Society of Washington Bulletin 6:345–353.

Karl, D. M. 1986. Determination of in situ microbial biomass, viability, metabolism, and growth. Pages 85–176 in J. S. Poindexter and E. R. Leadbetter (eds.), Bacteria in Nature, vol. 2. Plenum, New York.

Karl, D. M. 1987. Bacterial production at deep-sea hydrothermal vents and cold seeps: evidence for chemosynthetic primary production. Pages 319–360 in M. Fletcher, T. R. G. Gray, and J. G. Jones (eds.), Ecology of Microbial Communities. Cambridge University Press, Cambridge.

Karl, D. M., and V. L. Asper. 1990. RACER: particle flux measurements during the 1989–90 austral summer. Antarctic Journal of the United States 25:167–169.

Karl, D. M., and G. A. Knauer. 1984. Detritus-microbe interactions in the marine pelagic environment: selected results from the VERTEX experiment. Bulletin of Marine Science 35:550–565.

Karl, D. M., O. Holm-Hansen, G. T. Taylor, G. Tien, and D. F. Bird. 1991a. Microbial biomass and productivity in the western Bransfield Strait, Antarctica during the 1986–87 austral summer. Deep-Sea Research 38:1029–1055.

Karl, D. M., B. D. Tilbrook, and G. Tien. 1991b. Seasonal coupling of organic matter production and particle flux in the western Bransfield Strait, Antarctica. Deep-Sea Research 38:1097–1126.

Kennicutt, M. C., S. T. Sweet, W. Fraser, M. E. Culver, W. L. Stockton, K. Dunton, L. Martin, D. M. Karl, L. Quetin, D. Laur, C. D. Amsler, R. M. Ross, R. Rowley, M. Neushul, J. Hyland, J. Kennett, J. Campbell, M. Fry, B. Todd, A. Bennett, Z. A. Eppley, M. Rubega, T. Targett, P. Grecay, O. L. Palma, G. Ferrerya, and V. Alder. 1990. Oil spillage in Antarctica. Environmental Science and Technology 24:620–624.

Kieber, D. J., J. McDaniel, and K. Mopper. 1989. Photochemical source of biological substrates in sea water: implications for carbon cycling. Nature 341:637–639.

King, G. M., and M. J. Klug. 1982. Glucose metabolism in sediments of a eutrophic lake: tracer analysis of uptake and product formation. Applied and Environmental Microbiology 44:1308–1317.

Kirchman, D., H. Ducklow, and R. Mitchell. 1982. Estimates of bacterial growth from changes in uptake rates and biomass. Applied and Environmental Microbiology 44:1296–1307.

Kirchman, D., E. K'nees, and R. Hodson. 1985. Leucine incorporation and its potential as a measure of protein synthesis by bacteria in natural aquatic systems. Applied and Environmental Microbiology 49:599–607.

Knox, F., and M. B. McElroy. 1984. Changes in atmospheric CO_2: influence of the marine biota at high latitude. Journal of Geophysical Research 89:4629–4637.

Kogure, K., K. Fukami, U. Simidu, and N. Taga. 1986. Abundance and production of bacterioplankton in the Antarctic. Memoirs of the National Institute of Polar Research, Special Issue, 40:414–422.

Kottmeier, S. T., and C. W. Sullivan. 1987. Late winter primary production and bacterial production in sea ice and seawater west of the Antarctic Peninsula. Marine Ecology Progress Series 36:287–298.

Kottmeier, S. T., and C. W. Sullivan. 1988. Sea Ice Microbial Communities (SIMCO). 9. Effects of temperature and salinity on rates of metabolism and growth of autotrophs and heterotrophs. Polar Biology 8:293–304.

Kottmeier, S. T., S. M. Grossi, and C. W. Sullivan. 1987. Sea ice microbial communities. VIII. Bacterial production in annual sea ice of McMurdo Sound, Antarctica. Marine Ecology Progress Series 35:175–186.

Kriss, A. E., S. S. Abyzov, M. N. Lebedeva, I. E. Mishustina, and I. N. Mitskevich. 1960a. Geographic

regularities in microbe population (heterotroph) distribution in the world ocean. Journal of Bacteriology 80:731–736.

Kriss, A. E., M. N. Lebedeva, and I. N. Mitskevich. 1960b. Micro-organisms as indicators of hydrological phenomena in seas and oceans—II. Investigation of the deep circulation of the Indian Ocean using microbiological methods. Deep-Sea Research 6:173–183.

Lancelot, C., G. Billen, and S. Mathot. 1989. Ecophysiology of phyto- and bacterioplankton growth in the Southern Ocean. Belgian Scientific Research Programme on Antarctica Scientific Results of Phase One (October 1985–January 1989), vol. 1. Plankton Ecology. 97 pp.

Laws, E. A. 1983. Plots of turnover times versus added substrate concentrations provide only upper bounds to in situ substrate concentration. Journal of Theoretical Biology 101:147–150.

Laws, R. M. 1985. Introduction: Antarctic biology, 1974–1983. Pages 1–3 in W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.

Li, W. K. W. 1983. Consideration of errors in estimating kinetic parameters based on Michaelis-Menten formalism in microbial ecology. Limnology and Oceanography 28:185–190.

Li, W. K. W., and P. M. Dickie. 1987. Temperature characteristics of photosynthetic and heterotrophic activities: seasonal variations in temperate microbial plankton. Applied and Environmental Microbiology 53:2282–2295.

Lipps, J. H., W. N. Krebs, and N. K. Temnikow. 1977. Microbiota under Antarctic ice shelves. Nature 265:232–233.

Littlepage, J. L., and J. S. Pearse. 1962. Biological and oceanographic observations under an Antarctic ice shelf. Science 137:679–681.

Lutjeharms, J. R. E., N. M. Walters, and B. R. Allanson. 1985. Oceanic frontal systems and biological enhancement. Pages 11–21 in W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.

Marra, J., and D. C. Boardman. 1984. Late winter chlorophyll *a* distributions in the Weddell Sea. Marine Ecology Progress Series 19:197–205.

Martin, J. H. 1989. Glacial–Interglacial CO_2 change: the iron hypothesis. Paleoceanography 5:1–13.

Maykut, G. A. 1985. The ice environment. Pages 21–82 in R. A. Horner (ed.), Sea Ice Biota. CRC Press, Boca Raton, FL.

McBee, R. H. 1960. Intestinal flora of some Antarctic birds and mammals. Journal of Bacteriology 79:311–312.

McGuire, A. J., P. D. Franzmann, and T. A. McMeekin. 1987. *Flectobacillus glomeratus* sp. nov., a curved, nonmotile, pigmented bacterium isolated from Antarctic marine environments. Systematics and Applied Microbiology 9:265–272.

McLean, A. L. 1918. Bacteria of ice and snow in Antarctica. Nature 102:35–39.

Mezykowski, T. 1982. Distribution of dissolved amino acids, dissolved saccharides and urea in southern Drake Passage and Bransfield Strait during BIOMASS-FIBEX, 1981. Polish Polar Research 3:171–182.

Michel, R. L., T. W. Linick, and P. M. Williams. 1979. Tritium and carbon-14 distributions in seawater from under the Ross Ice Shelf Project ice hole. Science 203:445–446.

Mitchell, B. G., and O. Holm-Hansen. 1991. Observations and modeling of the Antarctic phytoplankton crop in relation to mixing depth. Deep-Sea Research 38:981–1007.

Moore, B., and B. Bolin. 1987. The oceans, carbon dioxide and global climate change. Oceanus 29:9–15.

Moriarty, D. J. W. 1986. Measurement of bacterial growth rates in aquatic systems from rates of nucleic acid synthesis. Advances in Microbial Ecology 9:245–292.

Morita, R. Y. 1966. Marine psychrophilic bacteria. Oceanography and Marine Biology Annual Review 4:105–121.

Morita, R. Y. 1975. Psychrophilic bacteria. Bacteriological Reviews 39:144–167.

Morita, R. Y. 1982. Starvation–survival of heterotrophs in the marine environment. Advances in Microbial Ecology 6:171–198.

Morita, R. Y. 1988. Bioavailability of energy and its relationship to growth and starvation survival in nature. Canadian Journal of Microbiology 34:436–441.

Morita, R. Y., and S. D. Burton. 1970. Occurrence, possible significance and metabolism of obligate psychrophiles in marine waters. Pages 275–285 in D. W. Hood (ed.), Symposium on Organic Matter in Natural Waters. University of Alaska, College, AK.

Morita, R. Y., R. P. Griffiths, and S. S. Hayasaka. 1977. Heterotrophic activity of microorganisms in Antarctic waters. Pages 99–113 in G. A. Llano (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Gulf Publishing Co., Houston, TX.

Moyer, C. L., and R. Y. Morita. 1989a. Effect of growth rate and starvation–survival on the viability and stability of a psychrophilic marine bacterium. Applied and Environmental Microbiology 55:1122–1127.

Moyer, C. L., and R. Y. Morita. 1989b. Effect of growth rate and starvation–survival on cellular DNA, RNA, and protein of a psychrophilic marine bacterium. Applied and Environmental Microbiology 55:2710–2716.

Nelson, D. M., W. O. Smith, Jr., L. I. Gordon, and B. A. Huber. 1987. Spring distributions of density, nutrients, and phytoplankton biomass in the ice edge zone of the Weddell-Scotia Sea. Journal of Geophysical Research 92:7181–7190.

Nelson, D. M., W. O. Smith, Jr., R. D. Muench, L. I. Gordon, C. W. Sullivan, and D. M. Husby. 1989. Particulate matter and nutrient distributions in the ice-edge zone of the Weddell Sea: relationship to hydrography during late summer. Deep-Sea Research 36:191–209.

Neori, A., and O. Holm-Hansen. 1982. Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. Polar Biology 1:33–38.

Newell, S. Y., and A. Statzell-Tallman. 1982. Factors for conversion of fungal biovolume values to biomass, carbon and nitrogen: variation with mycelial ages, growth conditions, and strains of fungi from a salt marsh. Oikos 39:261–268.

Novitsky, J. A., and R. Y. Morita. 1976. Morphological characterization of small cells resulting from nutrient starvation of a psychrophilic marine vibrio. Applied and Environmental Microbiology 32:617–622.

Novitsky, J. A., and R. Y. Morita. 1977. Survival of a psychrophilic marine vibrio under long-term nutrient starvation. Applied and Environmental Microbiology 33:635–641.

Novitsky, J. A., and R. Y. Morita. 1978. Possible strategy for the survival of marine bacteria under starvation conditions. Marine Biology 48:289–295.

Pace, M. L., G. A. Knauer, D. M. Karl, and J. H. Martin. 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. Nature 325:803–804.

Painting, S. J., M. I. Lucas, and J. M. E. Stenton-Dozey. 1985. The South African SIBEX I cruise to the Prydz Bay region, 1984: X. Biomass and production of bacterioplankton in Prydz Bay, Antarctica, and phytoplankton, detritus and bacterial relationships. South African Journal of Antarctic Research 15:42–52.

Palenik, B., and F. M. M. Morel. 1990. Amino acid utilization by marine phytoplankton: a novel mechanism. Limnology and Oceanography 35:260–269.

Palmisano, A. C., and C. W. Sullivan. 1983. Sea ice microbial communities (SIMCO). 1. Distribution, abundance, and primary production of ice microalgae in McMurdo Sound, Antarctica in 1980. Polar Biology 2:171–177.

Parsons, T. R., and J. D. H. Strickland. 1962. On the production of particulate organic carbon by heterotrophic processes in sea water. Deep-Sea Research 8:211–222.

Pomeroy, L. R. 1974. The ocean's food web, a changing paradigm. BioScience 24:499–504.

Pomeroy, L. R., and D. Deibel. 1986. Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. Science 233:359–361.

Pomeroy, L. R., and W. J. Wiebe. 1988. Energetics of microbial food webs. Hydrobiologia 159:7–18.

Pomeroy, L. R., S. A. Macko, P. H. Ostrom, and J. Dunphy. 1990. The microbial food web in Arctic seawater: concentration of dissolved free amino acids and bacterial abundance and activity in the Arctic Ocean and in Resolute Passage. Marine Ecology Progress Series 61:31–40.

Priscu, J. C., and A. C. Palmisano. 1986. Contribution of carbon fixed by nitrifying bacteria during ice cover in McMurdo Sound, Antarctica. Antarctic Journal of the United States 21:171–172.

Priscu, J. C., M. T. Downes, L. R. Priscu, A. C. Palmisano, and C. W. Sullivan. 1990. Dynamics of ammonium oxidizer activity and nitrous oxide (N_2O) within and beneath Antarctic sea ice. Marine Ecology Progress Series 62:37–46.

Proctor, L. M., and J. A. Fuhrman. 1990. Viral mortality of marine bacteria and cyanobacteria. Nature 343:60–62.

Radok, U., N. Streten, and G. E. Weller. 1975. Atmosphere and ice. Oceanus 18:16–27.

Rivkin, R. B. 1986. Incorporation of tritiated thymidine by eucaryotic microalgae. Journal of Phycology 22:193–198.

Rivkin, R. B., and M. Putt. 1987. Heterotrophy and photoheterotrophy by Antarctic microalgae: light-dependent incorporation of amino acids and glucose. Journal of Phycology 23:442–452.

Romanenko, V. I. 1964. Heterotrophic assimilation of CO_2 by bacterial flora of water. Microbiology 33:679–683.

Romanenko, V. I., and E. G. Dobrynin. 1978. Specific weight of the dry biomass of pure bacterial cultures. Microbiology 47:220–221.

Ross, R., and L. Quetin. 1982. *Euphausia superba*: fecundity and physiological ecology of its eggs and larvae. Antarctic Journal of the United States 17:166–167.

Rosset, R., J. Julien, and R. Monier. 1966. Ribonucleic acid composition of bacteria as a function of growth rate. Journal of Molecular Biology 18:308–320.

Rowland, F. S. 1989. Chlorofluorocarbons and the depletion of stratospheric ozone. American Scientist 77:36–45.

Russell, N. J. 1990. Cold adaptation of microorganisms. Philosophical Transactions of the Royal Society of London B 326:595–611.

Samyshev, E. Z. 1986. Bacterioplankton of Antarctic waters: concentration, production and bacterial destruction. Oceanology 26:508–512.

Samyshev, E. Z., A. I. Gaydamak, E. A. Chepurnova, and Y. A. Shulyakovskiy. 1987. Abundance and biomass of bacterioplankton in Antarctic waters. Hydrobiological Journal 23:46–53.

Sarmiento, J. L., and J. R. Toggweiler. 1984. A new model for the role of the oceans in determining atmospheric PCO_2. Nature 308:621–624.

Schlosser, P., E. Suess, R. Bayer, and M. Rhein. 1988. ^3He in the Bransfield Strait waters: indication for local injection from back-arc rifting. Deep-Sea Research 35:1919–1935.

Schmidt, E. L. 1973. The traditional plate count technique among modern methods: chairman's summary. Pages 453–454 in T. Rosswall (ed.), Modern Methods in the Study of Microbial Ecology. Ecological Research Committee of NFR, Stockholm, Sweden.

Sherr, E. B. 1988. Direct use of high molecular weight polysaccharide by heterotrophic flagellates. Nature 335:348–351.

Shuchman, R. A., and R. G. Onstott. 1990. Remote sensing of the polar oceans. Pages 123–169 in W. O. Smith, Jr. (ed.), Polar Oceanography, Part A: Physical Science. Academic Press, San Diego.

Sieburth, J. M. 1958. Antarctic microbiology. American Institute of Biological Sciences Bulletin 8:10–12.

Sieburth, J. M. 1959. Antibacterial activity of Antarctic marine phytoplankton. Limnology and Oceanography 4:419–424.

Sieburth, J. M. 1960. Acrylic acid, an "antibiotic" principle in *Phaeocystis* blooms in Antarctic waters. Science 132:676–677.

Sieburth, J. M. 1965. Microbiology of Antarctica. Pages 267–295 in J. van Mieghem and P. van Oye (eds.), Biogeography and Ecology in Antarctica. Junk, The Hague.

Siegenthaler, U., and T. Wenk. 1984. Rapid atmospheric CO_2 variations and ocean circulation. Nature 308:624–626.

Simidu, U., K. Kogure, K. Fukami, and C. Imada. 1986. Heterotrophic bacterial flora of the Antarctic Ocean. Memoirs of the National Institute of Polar Research, Special Issue, 40:405–412.

Simon, M., and F. Azam. 1989. Protein content and protein synthesis rates of planktonic marine bacteria. Marine Ecology Progress Series 51:201–213.

Skopintsev, B. A. 1972. A discussion of some views on the origin, distribution, and composition of organic matter in deep ocean waters. Oceanology 12:471–474.

Smith, N. R., D. Zhaoqian, K. R. Kerry, and S. Wright. 1984. Water masses and circulation in the region of Prydz Bay, Antarctica. Deep-Sea Research 31:1121–1147.

Smith, W. O., Jr. 1987. Phytoplankton dynamics in marginal ice zones. Oceanography and Marine Biology Annual Review 25:11–38.

Smith, W. O., Jr., and D. L. Garrison. 1990. Marine ecosystem research at the Weddell Sea ice edge: the AMERIEZ program. Oceanography Magazine 3:22–29.

Smith, W. O., Jr., and D. M. Nelson. 1985. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science 227:163–166.

Smith, W. O., Jr., and D. M. Nelson. 1990. Phytoplankton growth and new production in the Weddell Sea marginal ice zone during austral spring and autumn. Limnology and Oceanography 35:809–821.

Smith, W. O., Jr., N. K. Keene, and J. C. Comiso. 1988. Interannual variability in estimated primary productivity of the Antarctic marginal ice zone. Pages 131–139 in D. Sahrhage (ed.), Antarctic Ocean and Resources Variability. Springer-Verlag, Berlin.

Sorokin, Y. I. 1971a. On the role of bacteria in the productivity of tropical oceanic waters. Internationale Revue der Gesamten Hydrobiologie 56:1–48.

Sorokin, Y. I. 1971b. Abundance and production of bacteria in the open water of the central Pacific. Oceanology 11:85–94.

Sorokin, Y. I. 1971c. Bacterial populations as components of oceanic ecosystems. Marine Biology 11:101–105.

Sorokin, Y. I. 1972. Microbial activity as a biogeochemical factor in the ocean. Pages 189–204 in D. Dyrssen and D. Jagner (eds.), The Changing Chemistry of the Oceans. Wiley, New York.

Sorokin, Y. I., E. B. Pavelyeva, and M. I. Vasilyeva. 1977. Productivity and the trophic role of bacterioplankton in the region of equatorial divergence. Polskie Archiwum Hydrobiologii 24:241–259.

Sorokin, Y. I., A. I. Kopylov, and N. V. Mamaeva. 1985. Abundance and dynamics of microplankton in the central tropical Indian Ocean. Marine Ecology Progress Series 24:27–41.

Steele, J. H. 1981. An Evaluation of Antarctic Marine Ecosystem Research. National Academy Press, Washington, D.C. 99 pp.

Steeman-Nielsen, E. 1972. The rate of primary production and the size of the standing stock of zooplankton in the oceans. Internationale Revue der Gesamten Hydrobiologie 57:513–516.

Stevenson, L. H. 1978. A case for bacterial dormancy in aquatic systems. Microbial Ecology 4:127–133.

Straka, R. P., and J. L. Stokes. 1960. Psychrophilic bacteria from Antarctica. Journal of Bacteriology 80:622–625.

Suess, E. 1980. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. Nature 288:260–263.

Suess, E., M. Fisk, and D. Kadko. 1987. Thermal interaction between back-arc volcanism and basin sediments in the Bransfield Strait, Antarctica. Antarctic Journal of the United States 22:47–49.

Sugimura, Y., and Y. Suzuki. 1988. A high temperature catalytic oxidation method of non-volatile

dissolved organic carbon in seawater by direct injection of liquid sample. Marine Chemistry 24:105–131.

Sullivan, C. W. 1985. Sea ice bacteria: reciprocal interactions of the organisms and their environment. Pages 160–171 in R. Horner (ed.), Ice Biota. CRC Press, Boca Raton, FL.

Sullivan, C. W., and D. G. Ainley. 1987. Antarctic marine ecosystem research at the ice-edge zone, 1986. Antarctic Journal of the United States 22:167–169.

Sullivan, C. W., C. R. McClain, J. C. Comiso, and W. O. Smith, Jr. 1988. Phytoplankton standing crops within an Antarctic ice edge assessed by satellite remote sensing. Journal of Geophysical Research 93:12487–12498.

Sullivan, C. W., G. F. Cota, D. W. Krempin, and W. O. Smith, Jr. 1990. Distribution and activity of bacterioplankton in the marginal ice zone of the Weddell-Scotia Sea during austral spring. Marine Ecology Progress Series 63:239–252.

Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. Journal du Conseil International pour l'Exploration de la Mer 18:287–295.

Takahashi, M., and S. Ichimura. 1971. Glucose uptake in ocean profiles with special reference to temperature. Marine Biology 11:206–213.

Tchernia, P. 1980. Descriptive Regional Oceanography. Pergamon Marine Series, 3. Pergamon Press, New York. 253 pp.

Tien, G., L. Asato, V. L. Asper, D. F. Bird, A. M. Brittain, D. V. Hebel, R. Letelier, and D. M. Karl. 1990. RACER: microbial processes in the northern Gerlache Strait, 1989–1990. Antarctic Journal of the United States 25:152–154.

Tilzer, M. M., and Z. Dubinsky. 1987. Effects of temperature and day length on the mass balance of Antarctic phytoplankton. Polar Biology 7:35–42.

Toggweiler, J. R., and J. L. Sarmiento. 1985. Glacial to interglacial changes in atmospheric carbon dioxide: the critical role of ocean surface water in high latitudes. Pages 163–184 in E. T. Sundquist and W. S. Broecker (eds.), The Carbon Cycle and Atmospheric CO_2: Natural Variations Archaen to Present. Geophysical Monograph 32, American Geophysical Union, Washington, D.C.

Tranter, D. J. 1982. Interlinking of physical and biological processes in the Antarctic Ocean. Oceanography and Marine Biology Annual Review 20:11–35.

van Es, F. B., and L.-A. Meyer-Reil. 1982. Biomass and metabolic activity of heterotrophic marine bacteria. Pages 111–170 in K. C. Marshall (ed.), Advances in Microbial Ecology, vol. 6. Plenum Press, New York.

Vezina, A. F., and T. Platt. 1988. Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Marine Ecology Progress Series 42:269–287.

Vincent, W. F. 1988. Microbial Ecosystems of Antarctica. Cambridge University Press, Cambridge. 304 pp.

Watson, S. W., T. J. Novitsky, H. L. Quinby, and F. W. Valois. 1977. Determination of bacterial number and biomass in the marine environment. Applied and Environmental Microbiology 33:940–946.

Wenk, T., and U. Siegenthaler. 1985. The high-latitude ocean as a control of atmospheric CO_2. Pages 185–194 in E. T. Sundquist and W. S. Broecker (eds.), The Carbon Cycle and Atmospheric CO_2: Natural Variations Archaen to Present. Geophysical Monograph 32, American Geophysical Union, Washington, D.C.

Wetzel, R. G., P. H. Rich, M. C. Miller, and H. L. Allen. 1972. Metabolism of dissolved and particulate detrital carbon in a temperate hard-water lake. Memorie dell'Istituto Italiano di Idrobiologia Dottor Marco de Marchi 29:185–243.

White, D. C. 1983. Analysis of microorganisms in terms of quantity and activity in natural environments. Pages 37–66 in J. H. Slater, R. Whittenbury, and J. W. T. Wimpenny (eds.), Microbes in their Natural Environments. Symposium 34, Society for General Microbiology, Cambridge University Press, Cambridge.

Whiticar, M. J., E. Suess, and H. Wehner. 1985. Thermogenic hydrocarbons in surface sediments of the Bransfield Strait, Antarctic Peninsula. Nature 314:87–90.

Wiebe, W. J., and C. W. Hendricks. 1971. Simple, reliable cold tray for the recovery and examination of thermosensitive organisms. Applied Microbiology 22:734–735.

Williams, P. J. leB. 1973. On the question of growth yields of natural heterotrophic populations. Pages 400–401 in T. Rosswall (ed.), Modern Methods in the Study of Microbial Ecology. Ecological Research Committee of NFR, Stockholm, Sweden.

Williams, P. M., and E. R. M. Druffel. 1988. Dissolved organic matter in the ocean: comments on a controversy. Oceanography Magazine 1:14–17.

Wright, R. T., and B. K. Burnison. 1979. Heterotrophic activity measured with radiolabelled organic substrates. Pages 140–155 in J. W. Costerton and R. R. Colwell (eds.), Native Aquatic Bacteria: Enumeration, Activity and Ecology. American Society for Testing and Materials, Baltimore, MD.

Wright, R. T., and J. E. Hobbie. 1965. The uptake of organic solutes in lake water. Limnology and Oceanography 10:22–28.

Wright, R. T., and J. E. Hobbie. 1966. Use of glucose and acetate by bacteria and algae in aquatic ecosystems. Ecology 47:447–464.

Wynn-Williams, D. D. 1990. Ecological aspects of Antarctic microbiology. Pages 71–146 in K. C. Marshall (ed.), Advances in Microbial Ecology, vol. 11. Plenum Press, New York.

Zdanowski, M. K. 1982. Distribution of saprophytic bacteria in the southern Drake Passage and in the Bransfield Strait (February–March 1981, BIOMASS-FIBEX). Polish Polar Research 3:183–191.

Zdanowski, M. K. 1985. Distribution of bacteria, organic carbon and amino acids in the southern part of Drake Passage and in Bransfield Strait during the BIOMASS-SIBEX (December 1983–January 1984). Polish Polar Research 6:43–63.

Zwally, H. J., C. L. Parkinson, and J. C. Comiso. 1983. Variability of Antarctic sea ice and changes in carbon dioxide. Science 220:1005–1012.