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NEARSHORE BENTHIC MARINE SEDIMENTS

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1. INTRODUCTION

1.1. Communities

Nearshore marine microbial communities receive nutrients from both the pelagic sea and terrestrial runoff. These periodic enrichments provide for an active and diverse microflora. Throughout Antarctic nearshore environments, a substantial nutrient-rich current enriches indigenous marine microbial communities (Littlepage, 1965; Seabrooke and Hufford, 1970; Barry, 1988). Extended

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photoperiods during the austral summer provide them with high photon flux when the sea ice and snow cover have gone. The nearshore currents and the austral summer photoperiod have recently been determined to exert substantial influence (at least on a seasonal scale) on sediment microorganisms and perhaps indirect influence on macrofaunal communities (Dayton and Oliver, 1977; White et al., 1985; Dayton et al., 1986; Smith et al., 1986a, 1989a). The viable biomass of microorganisms in sediments of Antarctic nearshore regions are of magnitude similar to that in more temperate and tropical environments (White, 1983; White et al., 1985; Smith et al., 1986a, 1989a; Table 5.1).

1.2. Distribution

The marine microeukaryotes that dominate the aerobic and euphotic nearshore Antarctic environments are microalgae (primarily diatoms), foraminiferans, dinoflagellates, some protozoa, and fungi. *Pseudomonas*, cyanobacteria, *Bacillus*, and *Vibrio* are the dominant prokaryotes in nearshore marine environments (Sieburth, 1975; White, 1983). Anaerobic, eubacterial, sulfate-reducing bacteria (Tanner and Herbert, 1981; Parkes, 1987) are present where suitable environmental conditions (e.g., sediment depth or anaerobicity in surficial microniches) exist. Foraminifera are prominent (Lipps et al., 1972; Finger, 1975; Krebs, 1983;

TABLE 5.1. Comparison of the Microbial Biomass in Two Antarctic Areas With Those of Deep-Sea Trenches and a Subtropical Estuary, Estimated Using Phospholipid Ester-Linked Fatty Acids (PLFA)

Site	Water Depth (m)	PLFA nmol gdw^{-1}[a]	Microbial Biomass Cells ($\times 10^8$) gdw^{-1}[b]
McMurdo Sound[c]	14–30	35	21
Arthur Harbor[d]	10–26	6	4
Venezuela Basin[e]	5,000	1	0.6
Puerto Rico Trench[f]	8,400	0.7	0.4
Florida estuary[g]	1	37	22

[a]Total cellular membrane phospholipid in nanomoles per gram dry weight of sediment.

[b]Number of microbial cells estimated by conversion of PLFA using a factor of 100 μmol PLFA g^{-1} bacteria (*E. coli*); 1 g bacteria is equivalent to 5.9×10^{12} cells (dry weight).

[c]Mean of four McMurdo Sound sites: 77°55'S, 166°08'W (n = 12).

[d]Mean of four Arthur Harbor sites: 64°46'S, 64°04'W (n = 12).

[e]Venezuela Basin site: 13°52'N, 67°48'W (n = 22).

[f]Puerto Rico Trench site: 19°48'N, 67°14'W (n = 4).

[g]Florida estuary site: 29°55'N, 84°31'W (n = 23).

DeLaca, 1985). Krebs (1983) showed that diatoms are predominant in the Arthur Harbor area.

In nearshore Antarctic environments, the oxygen-rich water keeps the top 1.5–2.0 cm of surficial sediments well oxygenated. Below this zone, the sediments become increasingly anaerobic because annual sea-ice accumulations around the continent suppress the high-energy wave action that would normally facilitate oxygenation of deeper sediments and because there are relatively few infaunal organisms to do so by their burrowing and feeding. Coastal storms with associated high winds do perturb this generally low-energy nearshore system, and during these storms significant resuspension of surficial sediments has been observed during an austral winter in McMurdo Sound (Berkman et al., 1986).

Antarctic microorganisms undergo two unique mechanisms of dispersion. One involves the formation of ice "feathers," protrusions above the sediment surface including accumulations of benthic microflora and other organisms. When sufficient ice accumulates, its buoyancy causes it to break free from the sediments and rise to the underside of the surface ice, often carrying associated microorganisms with it (Dayton et al., 1974; Walker and Marchant, 1989). When the ice is dispersed by storms, the organisms are transported with it. A second, described by Kauffman (1974) from investigations in Arthur Harbor, is gouging of sediment communities by passing icebergs. This disturbance releases organic and inorganic material from within the sediments and causes shifts in benthic community composition. Successional studies indicated that sediment topography returns to its original appearance within approximately one year, but the meiofaunal community remains varied in composition and quality for longer periods. Microflora and microfauna returned to the predisturbance condition more rapidly than the meiofauna.

The sediment composition of the McMurdo Sound region is dominated by wind-blown and glacially carried sand and small pebbles. In deeper areas free from ice scour, these materials are covered by fine silt, diatomaceous ooze, and at certain sites a dense sponge spicule mat. These are believed to be typical characteristics of all continental sediments. The physical and nutrient characteristics of Antarctic nearshore sediments have recently been reviewed by Vincent (1989).

1.3. Methods for Determination of *In Situ* Microbial Communities

Plate counts of seawater organisms consistently underestimate microbial communities compared to direct microscopic counts (Zobell, 1946, as cited by White, 1983; Jannasch and Jones, 1959) or estimations by extraction of adenosine triphosphate (ATP) (Holm-Hansen and Booth, 1966). Viable counts underestimate the number of bacteria present in soils compared to the biochemical determination of muramic acid, a cell-wall component (Miller and Casida,

1970). Some direct-counting methods require that microbes be quantitatively released from the sediment granules. Recent estimates for recovery of attached microorganisms by homogenization show that almost 60% of the microorganisms were released from the sediments (Moriarty, 1980; Newell and Fallon, 1982). The detection of polar lipids has been shown to be an excellent measure of the viable or potentially viable microbial biomass (White et al., 1979). On cell death, the intra- or intercellular phospholipases hydrolyze the polar lipids (which in nearly all microbes are phospholipids), forming neutral lipids. Membrane phospholipid ester-linked fatty acid (PLFA) analysis has been shown to be well correlated with measurements of enzyme activity, muramic acid content, respiratory activity, and total ATP in sediments (White et al., 1976; Balkwill et al., 1988). Use of PLFA analysis avoids any bias introduced by selective media or incomplete recovery from sediments for microscopic examination of sediment material. Although various microscopic and staining techniques may be relevant for filterable water-column organisms, they may not detect microorganisms attached to sediment particles. PLFA analysis not only provides an accurate measure of the viable or potentially viable microbial biomass but distinguishes among taxonomic groups (Ackman et al., 1968; Johns et al., 1977; Bobbie and White, 1980; Lechevalier, 1982; Sargent et al., 1988; Vestal and White, 1989), so it is a sensitive and quantitative tool for the determination of microbial biomass and community structure in sediments (Nichols, 1983; Nichols et al., 1987; Smith et al., 1985; Tunlid et al., 1985; Tunlid, 1986; White, 1986).

1.4. Chapter Objectives

Antarctic benthic sediments have only recently been investigated thoroughly. Studies prior to 1980 focused simply on detecting viable microorganisms. Recent descriptive endeavors have sought to establish the basic microbial ecology of these communities. These investigations provide good quantitative information, but typically only in areas adjacent to research stations. In this chapter, we discuss (1) sediment microbial biomass and distribution; (2) community structure, metabolic activities, and carbon assimilation and allocation within microbial lipids; (3) potential use of lipids in food-chain dynamics; (4) use of sediment microorganisms as indicators of anthropogenous contamination; and (5) bacterial enzymatic polymer degradation processes and rates within sub-Antarctic regions.

2. PAST AND PRESENT STUDIES

Benthic microbial communities could serve as important indicators of environmental perturbations if sufficient knowledge of their baseline status is

chronicled, and their role in remineralization and nutrient cycling is likely to be extremely important, but inaccessibility has limited investigations. Until recent improvements in protective dry suits for SCUBA divers, it was difficult to obtain sufficient undisturbed core samples of the nearshore sediments for accurate microbial analysis, and such recent advances as access dive holes through the sea ice have facilitated research in ice-covered areas. Future investigations of Antarctic marine microbial ecology will benefit from more advanced technologies and allow greater focus upon further physiological questions. The use of small submersibles will greatly extend the range and extent of benthic studies.

One of the first descriptions of a sedimentary bacterial community was accomplished by Walls (1967), who determined that bacteria from deep-sea sediments at the Antarctic convergence conformed to the general pattern of marine microorganisms of other regions. Antarctic marine bacteria are gram-negative motile rods, and the majority are facultative rather than obligate anaerobes. From a region under the Ross Ice Shelf (Fig. 5.1), a relatively low biomass of sediment microorganisms, ca. 10^7 cells gdw^{-1} (sediment), was measured and compared to deep-sea environments with similar constant physicochemical conditions (Holm-Hansen et al., 1978; Azam et al., 1979). Early investigations of marine sediment fungal associations were described by Fell (1968) as being composed primarily of basidiomycetes but as including also some *Cryptococcus, Sterigmatomyces,* and *Rhodosporidium.* Lipps et al. (1977) reported a considerable abundance of 11 species of diatoms and 10 species of Foraminifera from sediment samples collected at 68.5 m depth in George VI Sound. These investigators noted that diatom viability, which they based solely on pigments, may have led them to overestimate their predominance. Several sediment sites within Arthur Harbor and the vicinity were reported by Lipps et al. (1972) to display vertical zonation of foraminiferal biomass. These Foraminifera were associated with algae and invertebrates. An intertidal zone was described as containing diatoms and cyanobacterial films and a deeper zone as containing shelled protozoans such as *Cibicides, Rosalina, Haplophragmoides,* and *Trochammina* as dominants. Within the sloping mud bottom, species of agglutinated Foraminifera—*Psammosphaera, Trochammina,* and *Haplophragmoides*—were found. Below 38 m, the numbers of Foraminifera decreased considerably.

From descriptions of benthic Foraminifera within Port Foster and Deception Island on the Antarctic Peninsula, five dominant forms, *Fursenkoina fusiformis* Williamson, 1858; *Nonionella bradyii* (Chapman) Earland, 1934; *Miliammina arenacea* (Chapman 1916); *Trochammina malovensis* Heron-Allen and Earland, 1932; and *Globocrassidulina crassa* d'Orbigny, were reported (Finger, 1975). From the Bransfield Strait area, about 12 foraminiferan species dominated the community profile of 85 species identified. DeLaca (1985) reported large standing stocks of 10 species of rhizopods, which were capable of utilizing a variety of

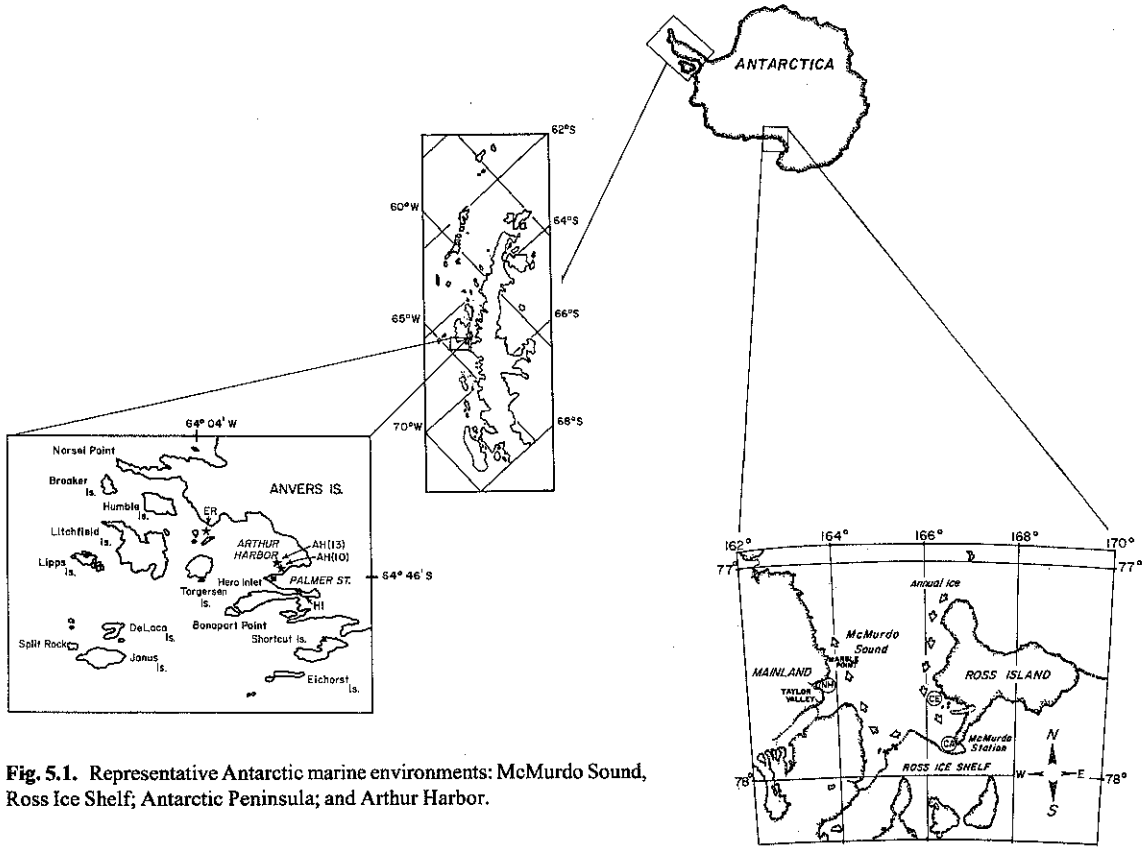

Fig. 5.1. Representative Antarctic marine environments: McMurdo Sound, Ross Ice Shelf; Antarctic Peninsula; and Arthur Harbor.

food sources, including dissolved organic matter (DOM, e.g., amino acids, carbohydrates, and lipids), protein hydrolysate, and bacteria. In an oligotrophic environment at New Harbor on the west side of McMurdo Sound, DeLaca (1982) identified a large (38 mm) agglutinated foraminiferan, *Notodendrodes antarctikos* DeLaca, Lipps, and Hessler, 1980. This species was shown to be capable of utilizing dissolved amino acids in concentrations of about 35 μM within the upper 1–2 cm of sediments. During feeding experiments this foraminiferan displayed carrier-mediated uptake of dissolved amino acids, as well as lipid-rich inclusions within the cytoplasm.

Few descriptive investigations of Antarctic benthic nearshore communities have been reported, but a substantial microbial community within sediments has been demonstrated. Microalgal (Dayton et al., 1986) and total microbial biomass (4–21 × 10^8 cells gdw^{-1} sediment, Smith et al., 1986a, 1989a, Table 5.1) are comparable to those of more temperate and tropical environments. A slightly lower bacterial biomass (4–16 × 10^7 cell gdw^{-1} sediment) has been estimated by ATP analysis for a Ross Ice Shelf site (Azam et al., 1979). This site has been compared to a deep-sea environment on the basis of its low temperature, seasonal low light, and relatively stable physiochemical conditions.

Psychrophilic and psychrotrophic bacterial isolates from benthic sediments within McMurdo Sound showed a higher incidence of plasmids (42%) than either seawater or sea-ice communities (Kobori et al., 1984). Of a total of 24 strains of bacteria isolated from sediments, 10 contained plasmids with a molecular weight of 1.5 Mdal or greater. Of all strains collected from seawater, sea ice, and sediments, 48 contained plasmids, and of these, only seven strains isolated from benthic sediments showed antibiotic resistance, an important baseline figure, as these ecosystems are presumably free from anthropogenous materials and selective pressures. The low light conditions to which benthic phototrophs are subjected in under-ice sedimentary environments (0–100 m depth) have not limited biomass to any obvious extent. Benthic algae have developed sensitive photoreceptive pigments (Palmisano et al., 1985; Rivkin and Putt, 1987a,b). A substantial benthic diatom community within McMurdo Sound has been determined to consist mainly of a large 100–400-μm diatom, *Trachyneis aspera* Peragallo, and smaller amounts of *Amphora antarctica* Hustedt. These algae are found attached to sponge spicules. Low abundances of marine diatoms were found within sediments under the Ross Ice Shelf. Kellogg and Kellogg (1984) suggested that the continuous low light conditions under this permanent ice shelf meant the diatoms were probably advected under the shelf by currents. The possible exception was an older diatom, *Trinacria excavata* Heiberg, 1863, believed to be a relict within these sediment deposits.

Few microbial investigations have been carried out of sub-Antarctic islands in the Antarctic Peninsula and Weddell Sea region. Those reported have dealt primarily with bacterial communities. The benthic microbiota, which was deter-

mined by direct counts, showed about a 2.3% d^{-1} increase in bacterial biomass associated with degradation of kelp on several sub-Antarctic islands (Delille and Cahet, 1983; Reichardt and Dieckmann, 1983; Bouvy et al., 1986; Reichardt, 1988). Bacterial growth rates at temperatures between 0 and 5°C were comparable to rates in more temperate environments (Reichardt and Dieckmann, 1983). Maximum bacterial growth was detected typically in austral spring and summer months, when kelp detritus is most abundant. However, no direct association between temperature and bacterial growth was established. The growth kinetics of bacteria associated with the macroalga *Himantothallus grandifolius* (A. & E. Gepp) Zinova, 1959, revealed an initial 1–3-day adaptation period before an exponential growth at 4–7 days. During growth periods, carbon and nitrogen levels were two and four times higher on colonized macroalgae than on fresh algae, indicating an active epiphytic bacterial association. Amphipod grazers were shown to prefer partially degraded thalli over fresh material as a food source (Reichardt and Dieckmann, 1983).

Stenothermic adaptation of Antarctic polymer-degrading bacteria from sediments has been reported for shelf sites of the South Shetland Islands. From these studies it was determined that increased enzyme synthesis at low temperature is a crucial component of detrital organic-matter degradation (Reichardt, 1988).

Several photosynthetic purple sulfur bacteria (Rhodospirillaceae, Chromatiaceae, and Chlorobiaceae) have been isolated from Signy Island sediments (Herbert, 1976; Herbert and Tanner, 1977), and one investigation of sulfate-reducing and denitrifying bacteria has been reported for Signy Island sediments (Tanner and Herbert, 1981). The microbial nitrification and denitrification processes within these Signy Island sediments were, on average, 0.5 ng N_2 fixed h^{-1} gdw^{-1} and 3.0 ng N_2 fixed h^{-1} gdw^{-1} sediment, respectively. These nitrogen-fixation rates under anaerobic conditions and *in situ* temperatures were determined to be significantly less than those reported for more temperate environments.

3. ANTARCTIC MICROBIAL COMMUNITY STRUCTURE OF MARINE SEDIMENTS

3.1. Heterotrophic Bacteria

Comparatively large bacterial communities of about 5.0×10^8 cells gdw^{-1} (McMurdo Sound; Smith et al., 1986a) and about 1.2×10^8 cells gdw^{-1} (Arthur Harbor; Smith et al., 1989a) have been detected in sediments by PLFA analysis. These biomasses are comparable to those in temperate and tropical nearshore regions, which typically range from 10^8 to 10^9 cells gdw^{-1} sediment. Azam et al. (1979) estimated bacterial biomass by epifluoresence microscopy at a site

beneath the Ross Ice Shelf to be 0.8–1.6 × 10^8 cells gdw^{-1}. This area, which is devoid of light and typically poor in water-column nutrients, has been compared to the deep sea. Even though biomass was lower at this site, autoradiographic analysis and respiration turnover times indicated a metabolic rate for sediment microorganisms two orders of magnitude higher than that for the water-column microorganisms. For less extreme regions under variable annual sea-ice conditions, 2–3% of this bacterial community is composed of anaerobic eubacteria, predominantly sulfate-reducing bacteria (Smith et al., 1986a), which are commonly found in marine sediments globally (Parkes, 1987; White, 1983). One report from Signy Island showed that substantial amounts (>10%) of the total microbial community was composed of the genus *Desulfovibrio* and other sulfate-reducing bacteria within intertidal sediments (Tanner and Herbert, 1981).

The bacterial composition for sites within both McMurdo Sound and Arthur Harbor show certain trends (Table 5.2). The influence of McMurdo Sound's nutrient-rich predominant current pattern is apparent in the greater microbial biomass values found in East Sound sediments during an austral summer season. Conversely, no effect of a dominant current regime on Arthur Harbor bacterial

TABLE 5.2. Biomass and Bacterial Metabolic Activity of Nearshore Microbial Communities From McMurdo Sound and Arthur Harbor, Antarctica

	Microbial Biomass[a]	^{3}H-Thymidine DPM[b]
McMurdo Sound[c]		
CA (1)	20	0.7
CA (2)	13	0.6
CE	45	1
NH	4	0.5
Mean (S.D.)	21 (18)	0.7 (0.2)
Arthur Harbor		
AH (10)	4.3	4.0
AH (13)	2.7	2.0
ER	3.6	4.5
HI	3.5	1.9
Mean (S.D.)	3.5 (0.7)	3.1 (1.3)

[a]Total cells (× 10^8) per gram dry weight of sediment. Calculated as 100 μmol PLFA g^{-1} bacteria (*E. coli*); 1 g bacteria is equivalent to 5.9 × 10^{12} cells (dry weight).

[b]Values for incorporations are DPMs (× 10^5) per hour per gram of sediment and represent the kill-control-subtracted mean of four samples. Numbers do not include any sulfate-reducing bacteria, which are incapable of thymidine incorporation.

[c]Sites for McMurdo Sound and Arthur Harbor as shown in Figure 5.1.

communities was apparent. A somewhat larger sulfate-reducing community was evident in Arthur Harbor sediments (2–5%) than in McMurdo Sound (2–3%). In a sub-Antarctic intertidal community at Signy Island, proteolytic and denitrifying bacteria were found to make up significant proportions of the total heterotrophic biomass (Tanner and Herbert, 1981). Delille and Cahet (1983) also reported a substantial proportion of sulfate-reducing bacteria in sediments of an Isles Kerguelen mussel bed, where peak abundance and numbers occurred during spring enrichments with allochthonous organic material.

3.2. Phototrophic Eukaryotes

Certain aspects of the abundance and distribution of eukaryotic phototrophic microorganisms in the sediment have recently been determined for McMurdo Sound (Dayton et al., 1986) and Arthur Harbor on the Antarctic peninsula (Krebs, 1973, 1983). Investigations for a peninsula site indicated marine planktonic and benthic microalgal communities consisted almost entirely of diatoms. The communities were quite heterogenous and showed increased growth during the austral summer season (Krebs, 1983). Similar seasonal blooms and dominance by diatoms have been reported by Kauffman (1974) for other peninsula sites.

Several investigations have also addressed physiological aspects of adaptive photosynthetic responses to irradiances (Palmisano et al., 1985; Rivkin and Putt, 1987a,b), and incorporation rates of radiolabeled organic and inorganic precursors (Rivkin and Putt, 1987a). Light saturation of a dominant benthic diatom, *Trachyneis aspera*, under annual sea ice in McMurdo Sound was determined to range between 6 and 11 $\mu E\ m^{-2}\ s^{-1}$ (Palmisano et al., 1985; Rivkin and Putt, 1987b). Photoinhibition measurements for *Trachyneis aspera* were reported by Rivkin and Putt (1987b) and Palmisano et al. (1985) to be 6–10 $\mu E\ m^{-2}\ s^{-1}$ and 300 $\mu E\ m^{-2}\ s^{-1}$, respectively. *Trachyneis aspera* showed active photosynthesis at extremely low light levels of $<0.6\ \mu E\ m^{-2}\ s^{-1}$ (Palmisano et al., 1985). Rivkin and Putt (1987b) also reported a low light saturation ($6\ \mu E\ m^{-2}\ s^{-1}$) for another benthic diatom, *Amphora antarctica*, from McMurdo Sound. The photoinhibition of *A. antarctica* was somewhat higher, ca. 30 $\mu E\ m^{-2}\ s^{-1}$, falling between the two determinations for *Trachyneis aspera*. Saturation and photoinhibition for both diatoms were below those of both sea-ice and planktonic species, indicating an adaptive response by benthic microalgae to low irradiances. Another study using radiolabeled substances showed that the sedimentary diatom *Trachyneis aspera* has the ability to incorporate organic acids heterotrophically. This ability could support metabolic demands during periods of low light or total darkness during austral winter (Rivkin and Putt, 1987a).

3.3. The Microbial Community

Investigations of sediment microbial communities from nearshore Antarctic marine sediments from two distinct regions revealed similar communities (Smith et al., 1986a, 1989a). Analysis by membrane phospholipid techniques showed that, in the top 2 cm of both McMurdo Sound and Arthur Harbor sediments, microalgae amounted to about 37% of the total microbial community and eubacteria to about 24%, including 3% obligate anaerobes (predominantly sulfate-reducing bacteria). The remainder (ca. 16%) of the microbiota was composed of other microeukaryotes (Table 5.3). This profile is assumed to be typical of continental Antarctic nearshore aphotic environments and reflects a stable and well-adapted benthic microbiota.

4. MICROBIAL METABOLIC RATES

4.1. Cellular Division Rates of Indigenous Bacteria

Rates of bacterial cell division in sediments are substantially less than those from more temperate and tropical systems, probably as a direct response to constant and extremely low temperatures. Rates of cell division as measured by ^{3}H-thymidine incorporation into DNA for McMurdo Sound revealed a rate four to five orders of magnitude lower than for a North Australian seagrass bed (Smith et al., 1986a). The rate at Arthur Harbor, an Antarctic Peninsula site, was two orders of magnitude lower than the same figure (Smith et al., 1989a). Production rates for Antarctic regions were about 0.02–0.4 mg C m^{-2} d^{-1}, considerably lower than those of temperate and tropical areas.

Within the Antarctic, regional differences in cellular division rates and productivity have been demonstrated (Table 5.4). McMurdo Sound's benthic bacterial communities are distinctly influenced by the dominant current pattern of the sound. The Arthur Harbor sites do not have a dominant directional current component but are under a tidal influence and show a similar pattern in benthic bacterial metabolic rates. In addition to nutrients supplied by currents, inputs by ice algae apparently stimulate the benthic bacterial community. White et al. (1984) noted an increase of ca. 70% in bacterial cellular division rates at a McMurdo Sound site upon sea-ice ablation and subsequent ice–algal sedimentation to the benthos. This potential source of carbon to benthic systems is quite large, as the carbon content of microalgae within the bottom 20 cm of sea ice can be as high as 4.1 gm C m^{-2} (Palmisano and Sullivan, 1983). Annual sea-ice ablation has been shown by satellite observations to amount to 11×10^{6}

TABLE 5.3. Microbial Community Structure of Nearshore Sediments From McMurdo Sound and Arthur Harbor, Antarctica

	Eubacteria[a]	Other Bacteria[b]	Diatoms and Algae[c]	Micro-eukaryotes[d]
McMurdo Sound[e]				
CA (1)	27[f]	2	42	17
CA (2)	27	3	33	14
CE	25	2	44	18
NH	16	2	38	19
Mean (S.D.)	24 (5)	2 (0.5)	39 (5)	17 (2)
Arthur Harbor				
AH (10)	21	5	36	11
AH (13)	20	2	36	12
ER	23	3	35	16
HI	25	4	33	15
Mean (S.D.)	22 (2)	4 (1)	35 (1)	14 (2)

[a]Marker PLFA for common eubacteria include i14:0, i15:0, a15:0, i16:1, i16:0, i17:0, a17:0, 17:0, and 18:1w7c.

[b]Marker PLFA for other bacteria (primarily sulfate-reducing bacteria) include i15:1w5, a15:1w5, i17:1, 10Me16:0, br17:0, 17:1w6, and cy17:0.

[c]Marker PLFA for diatoms and algae include 14:1w5c, 14:0, 16:4, 16:3, 16:2, 16:1w7c, 16:1w13t, 18:4w3, 18:3w3, 18:2w6, and 20:5w3.

[d]Marker PLFA for microeukaryotes include 18:1w9c, 20:4w6, 20:1w9c, 22:6w3, 22:4w6, and 22:5w3.

[e]McMurdo Sound and Arthur Harbor sites as shown in Figure 5.1.

[f]Values represent the sum of marker PLFA as a percentage of the total fatty-acid composition.

km^2 ice (net), with winter peaks of 17×10^6 km^2 and summer lows of 6.5×10^6 km^2.

4.2. Rates of Microbial Lipid Metabolism

Radiolabel incorporation into specific lipid classes has been used to study Antarctic sea-ice algal communities in the past (Palmisano et al., 1988) and Antarctic sediment microbial communities more recently (Smith et al., 1989c). Incorporation of several radiolabeled organic acids into total lipid of the benthic diatom *Trachyneis aspera* has been reported at ca. 5–15% of the total fixed carbon during 8-hour dark incubations (Rivkin and Putt, 1987b). When this diatom was incubated with ^{14}C-bicarbonate under the same conditions, and a 6 $\mu E\ m^{-2}\ s^{-1}$ photon flux, about 8–15% of the fixed carbon was located in the lipid fraction. This physiological response indicates that this benthic diatom can use organic acids under the low light and aphotic conditions common to high-

TABLE 5.4. Antarctic Bacterial Secondary Production Calculated From Incorporation of ^{3}H-Thymidine Into Bacterial DNA

	Specific Growth Rate (d^{-1})	Bacterial Productivity ($\mu g\ C\ m^{-2}\ d^{-1}$)[a]
McMurdo Sound		
Cape Armitage	0.003	5
Cape Evans	0.002	8
New Harbor	0.001	3
Mean (S.D.)	0.002 (0.001)	5 (2.5)
Arthur Harbor	0.10	35
Elephant Rocks	0.29	88
Hero Inlet	0.10	35
Mean (S.D.)	0.16 (0.15)	52 (31)

[a]Calculations of carbon production were made on the assumption of 25×10^{-15} C cell^{-1} (D. J. W. Moriarty, personal communication).

latitude environments during winter. The allocation patterns of cellularly fixed precursors into storage and structural lipids provides information on carbon allocation on a temporal scale. Allocation of fixed carbon into neutral, glyco-, and phospholipids by Arthur Harbor sediment phototrophs and heterotrophs during a 72-hour incubation period revealed different patterns in response to light and dark conditions (Fig. 5.2). Allocation of label was stable in the structural phospholipids but varied with time in the neutral and glycolipid fractions. The higher percentage of fixed carbon in dark incubations with ^{14}C-sodium acetate is believed to reflect a higher proportion of phospholipid-enriched heterotrophic bacteria. The overall lack of variation in allocation to phospholipid for both ^{14}C-bicarbonate and ^{14}C-acetate during the 72-hour incubation could indicate a "maintenance" condition (i.e., stable allocation into structural phospholipids). The importance of these measurements lies in their potential for interpretation of adaptive responses by benthic microorganisms to their ambient environmental conditions.

4.3. Environmental Effects

At least in the sediment, Antarcitc microorganisms show a lower rate of radiolabel incorporation at <0°C than do those of more temperate environments. Bacterial processes in nearshore sediments are important in mineralization and nutrient recycling, so the system has apparently acclimated to this lower rate of turnover (Tanner, 1983). Others investigating sediment communities within sub-Antarctic islands, along the Antarctic Peninsula and Weddell Sea, have noted less effect of temperature. These systems are most commonly investigated

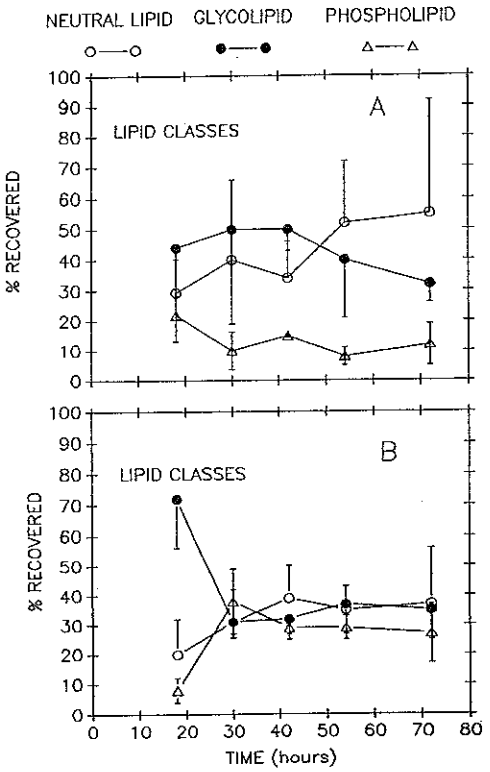

Fig. 5.2. Allocation of radiolabeled carbon by Arthur Harbor sediment microorganisms into neutral, glyco-, and phospholipids. Bicarbonate (**A**, light) and acetate (**B**, dark).

during the austral summer season, when temperatures are frequently above 0°C, and temperature does not seem to inhibit degradation of macroalgae by bacteria in sediments between 0°C and 9°C (Delille and Cahet, 1983; Reichardt and Dieckmann, 1983; Bouvy et al., 1986; Reichardt, 1988). Likewise, bacterial colonization rates of brown and red algal debris are comparable to those in more temperate climates. Increased rates of enzyme synthesis at 0°C on the Antarctic shelf near the South Shetland Islands have been proposed as a mechanism for degradation of biopolymer in low-temperature environments (Reichardt, 1988). The long photoperiods of the Antarctic spring and summer also influence benthic nearshore microbial communities. In ice-covered McMurdo Sound, <0.1% of the surface irradiance is detected in the water column below the average 1.5–2.0 m sea-ice and snow cover, but irradiances <0.6 $\mu E\ m^{-2}\ s^{-1}$ have been measured for McMurdo Sound sediments and shown to support a dense growth of the benthic diatom *Trachyneis aspera* (Palmisano et al., 1985). The *in*

situ primary production in this study was 0.01 mg C mg^{-1} Chl*a* d^{-1}, significantly lower than that for sea-ice algae, which is 8.4 mg C mg^{-1} Chl*a* d^{-1} (Palmisano et al., 1985). Phototrophs may survive under aphotic conditions by heterotrophy, as discussed above (Rivkin and Putt, 1987b). Last, the substantial ice-algal and open-water phytoplankton blooms in spring and summer seasons appear to be substantial sources of carbon for the benthic communities when they senesce and are advected to shore. Sedimentation rates of particulate material to sediments from open-water phytoplankton blooms and from fecal-pellet material at several peninsula and Weddell Sea sites range from 0.02 to 2.0 mg particulate organic carbon m^{-2} d^{-1} during spring blooms (von Bodungen, 1986; von Bodungen et al., 1986; Smith et al., 1989c).

5. ECOLOGICAL CONSIDERATIONS

5.1. Role of Microbes in Food-Chain Processes

Sediment microbial communities are important sources of food for associated meiofaunal and epibenthic invertebrates. Little attention has been afforded to this microscale process, and information on Antarctic benthic microbial–meiofaunal trophic structure is limited. Investigations by Kellogg et al. (1982) have demonstrated the use of benthic diatoms as food by the brittle star *Ophionotas victoriae* (T. J. Bell). At sites ranging in depth from 50 to 80 m at Argentine and Deception Islands and the Antarctic Peninsula, abundant diatom communities were found to contain 52 separate species. Of these, eight were found in the stomach contents of this brittle star. The diatoms most commonly found in the stomachs of Antarctic Peninsula specimens were, in order of abundance, *Nitzschia cylindrus* (Grunow) Hasle, *Navicula gelida* Grunow, 1984, *Biddulphia weissflogii* (Janisch) Grunow, 1881, *Chaetoceros dichaeta* Ehrenberg, *Eucampia antarctica* (Castracane) Mangin, 1915, *Ni. curta* (Van Heurck) Hasle, *Ni. hemii* (Mangin) Hasle, 1965, and *Ni. turgiduloides* Hasle, 1965. For Ross Sea specimens, three diatoms species, *Ni. curta, E. antarctica*, and smaller amounts of *Ni. cylindrus*, were found in the stomach contents of this same brittle star. Kellogg et al. (1982) concluded that these brittle stars produce little chemical dissolution or mechanical breakage of diatoms upon feeding, as little damage was apparent upon microscopic examination of stomach contents.

One of the most promising methods for determination *in situ* of which microorganisms are consumed by higher trophic levels involves following the accumulation of biomarker lipids in consumers (Culkin and Morris, 1970; Mayzaud, 1976; Johns et al., 1980; Nichols, 1983). This technique has been used to demonstrate the role of phytoplankton in the diet of zooplankton (Lee et al., 1971; Bottino, 1975; Sargent and Whittle, 1981; Falk-Peterson et al., 1987).

Johns et al. (1980) have shown that differences in the algal diets of limpets can be reflected by their fatty acid composition. When these gastropods do not have macroscopic algae in their diet (as indicated by a determination of fatty acid components), they show a preference for bacteria as a food source. Fatty acid biomarkers have been used in determining the diet of filter feeders (Culkin and Morris, 1970). Using lipid markers as well as other biochemical markers made possible determination of partitioning of microbial food sources by two grazing, sympatric amphipods (Smith et al., 1982b). Recently, application of these techniques to Antarctic systems has suggested that Antarctic sea-ice and planktonic microalgae are both components of the diet of benthic organisms. Major sterol components of the sea-ice diatom *Nitzschia cylindrus* (trans 22-dehydrocholesterol) and of the planktonic microalga *Phaeocystis pouchetii* (Hariot) Langerheim (brassicasterol) have been found in the stomach contents of benthic grazers during a spring bloom. Both the sea star *Odontaster validus* (P. Koehler) and the nematode *Deontostoma* sp. contained large proportions of these marker lipids, as well as significant proportions of the fatty acids 16:1w7c, 18:1w9c, and 18:1w7c (which are also major components of the microalgae) in their stomach content (Smith et al., 1986b).

5.2. Microbes as Indicators of Environmental Contamination

Several investigations into the utility and sensitivity of microorganisms as *in situ* indicators of environmental perturbations have focused on the use of microbial biochemical-component analysis (Smith et al., 1982a; White, 1982; Parker et al., 1984; Parkes and Taylor, 1985; Schropp et al., 1988). Schropp et al. (1988) have shown, using PLFA, that increasing metal concentrations cause sediment microorganisms to shift from a balance of microeukaryotic and prokaryotic organisms to a community in which prokaryotes predominate. This same shift occurs in response to exposures to oil- and gas well-drilling fluids in sediments (Smith et al., 1982a) and among microorganisms associated with corals (Parker et al., 1984). Certain gram-negative prokaryotes appear to proliferate under these conditions, which are unfavorable to microeukaryotes and gram-positive prokaryotes. This short-term opportunistic response by microbes can serve as a quantitative tool for use in toxicity assessment.

Bacterial assemblages also have the ability to degrade certain pollutants. Further research can indicate whether the anaerobic sedimentary microbes respond to contaminants in a similar fashion. The oil spill near Palmer Station would be an ideal place to test the use of PLFA analysis for quantitative measurement of these processes, as two seasons of pre-spill measurements are available.

Other biochemical components (e.g., sterols) can be used as indicators of eucaryotic organisms associated with human sewage contamination, and 5α-

TABLE 5.5. Composition of Major Sterols From McMurdo Sound Sediment Microorganisms and Microeukaryotes

Sterol[a]	Ca (1)[b]	CE	NH
cholesta-5,22E-en-3β-ol (trans-22-dehydrocholesterol)	12.2[c]	17.1	20.2
cholest-5-en-3β-ol (cholesterol)	25.9	34.8	26.7
24-methylcholesta-5,22E-dien-3β-ol (brassicasterol)	14.2	12.0	7.6
24-methylcholest-5-en-3β-ol (24-methylcholesterol)	4.3	6.4	5.6
24-ethylcholest-5-en-3β-ol (24-ethylcholesterol)	5.7	5.6	9.0
Total sterol[d]	370	610	240

[a]Sterols reported are the five major components of 24 sterols detected at the three sites representing approximately 70% of the total sterol composition.

[b]McMurdo Sound sites as shown in Figure 5.1.

[c]Values are the percent amount of the total sterols.

[d]Values are the total pmol gdw^{-1} of detected sterols.

cholestanol (coprostanol) has been used as an indicator of sewage contamination in temperate environments (Hatcher and McGillivary, 1979). To date, the presence of 5α-cholestanol in Antarctica has been confined to deep-water (400–800 m) marine sediments (Venkatesan et al., 1986; Venkatesan, 1988) and has been attributed to feces from marine animals rather than human sewage. Coprostanol was absent or below detection limits in sediments collected in shallow water (less than 30 m) for surface sediments at Cape Armitage and Cape Evans in McMurdo Sound (Smith et al., 1989b; Table 5.5). These data provide important information on the possible untreated sewage accumulation near McMurdo Station. It remains to be seen whether Antarctic benthic communities exposed to the combined environmental stresses of low temperature and seasonally low aphotic conditions are capable of recovering from anthropogenous impact.

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