

## Distribution Patterns of Benthic Microalgal Standing Stock at McMurdo Sound, Antarctica

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**Summary.** During the austral summer of 1975–76 and winter of 1977 benthic and water column chlorophyll *a* and phaeopigments were measured at several sites along the east and west sides of McMurdo Sound, Antarctica. Estimates of in situ primary productivity were made at some McMurdo Sound locations. Additionally, water column samples were collected at 5 stations in the Ross Sea during January, 1976. Standing stock data are analyzed to identify seasonal and spatial patterns. Variability in algal standing stock was related to ambient light levels and appeared to be mediated by ice and snow cover whereby the highest algal standing stock was present under high light conditions (low ice and snow cover, shallow water, summer). Differences in published benthic invertebrate densities appear to be closely allied to differences in benthic primary production, and less so to in situ planktonic ice microalgal production.

### Introduction

The benthic communities of McMurdo Sound have remarkably different invertebrate assemblages. The most profound differences are between the east and west sides of the Sound, but there also are north-south gradients and depth differences. The infaunal assemblage of the East Sound has higher densities than almost any other area in the world whereas some of those in the West Sound have very low densities similar to some deep-sea habitats. There is a decreasing north-south infaunal density gradient along the West Sound (Dayton and Oliver 1977). One obvious hypothesis to explain such patterns is that there are differences in the amount of primary production available to the benthic communities. One important factor controlling primary productivity is light, and patterns of ambient light differ widely across the Sound. For example, the ice rarely breaks out of the West Sound during the summer whereas the East Sound study areas usually have several months with open water. The northern part of the Sound has more light because the ice

cover trends to be thinner, has less snow and breaks out sooner. The deeper zones are inherently lighter than the shallow zones, especially during the summer bloom of planktonic algae which is concentrated in the upper 25 m. During this period the deeper areas are very dark.

Polar marine systems have three sources of primary production: phytoplankton, ice algae and benthic microalgae (see review by Horner and Schrader 1982). There are reasonably complete data for phytoplankton productivity in the McMurdo Sound region (Bunt 1964; Bunt and Lee 1970; Hodson et al. 1981) and some picture of ice algae productivity is emerging (Palmisano and Sullivan 1983; Palmisano et al. submitted). Often lacking in such community studies are data on the annual in situ benthic primary production. Here we present estimates of chlorophyll *a* and phaeopigments from the benthos and the water column at several sites along the east and west sides of McMurdo Sound in the austral summer of 1975/76 and winter 1977. Additionally, we offer preliminary primary productivity data.

### Materials and Methods

Study areas are depicted in Fig. 1. Sampling was done by scuba working through natural tide cracks or ice holes. Water samples were taken with Van Dorn bottles.

The benthic chlorophyll *a* and phaeophytin samples were taken with corers made from plastic tubes. After collection the samples were kept cold and dark. MgCO<sub>3</sub> was added, and the filter was frozen at –40 °C for a maximum of two months. They were then placed in a 50 ml centrifuge tube with 35 ml of 90% acetone. The tubes were shaken 1 h in the dark at 5 °C. They were then centrifuged at 3000 rpm for 10 min, and the supernatant was decanted and brought to 50 ml with acetone. Absorbance was measured at 750, 665, 663, 645 and 630 nm on a Beckman DB-G spectrophotometer with a 1 cm cell. The extracts were then acidified with one drop of 5% HCl and absorbance measured after 3 min at 750 and 665 nm. The chlorophyll *a* and phaeophytin pigments were calculated from Lorenzen's (1967) equation modified to a m<sup>2</sup> basis.

Phytoplankton samples were collected in a Van Dorn bottle from a 15 m depth except on the *Burton Island* cruise in the Ross Sea where water was sampled at 0, 50, 100 and 200 m. Cruise dates were January

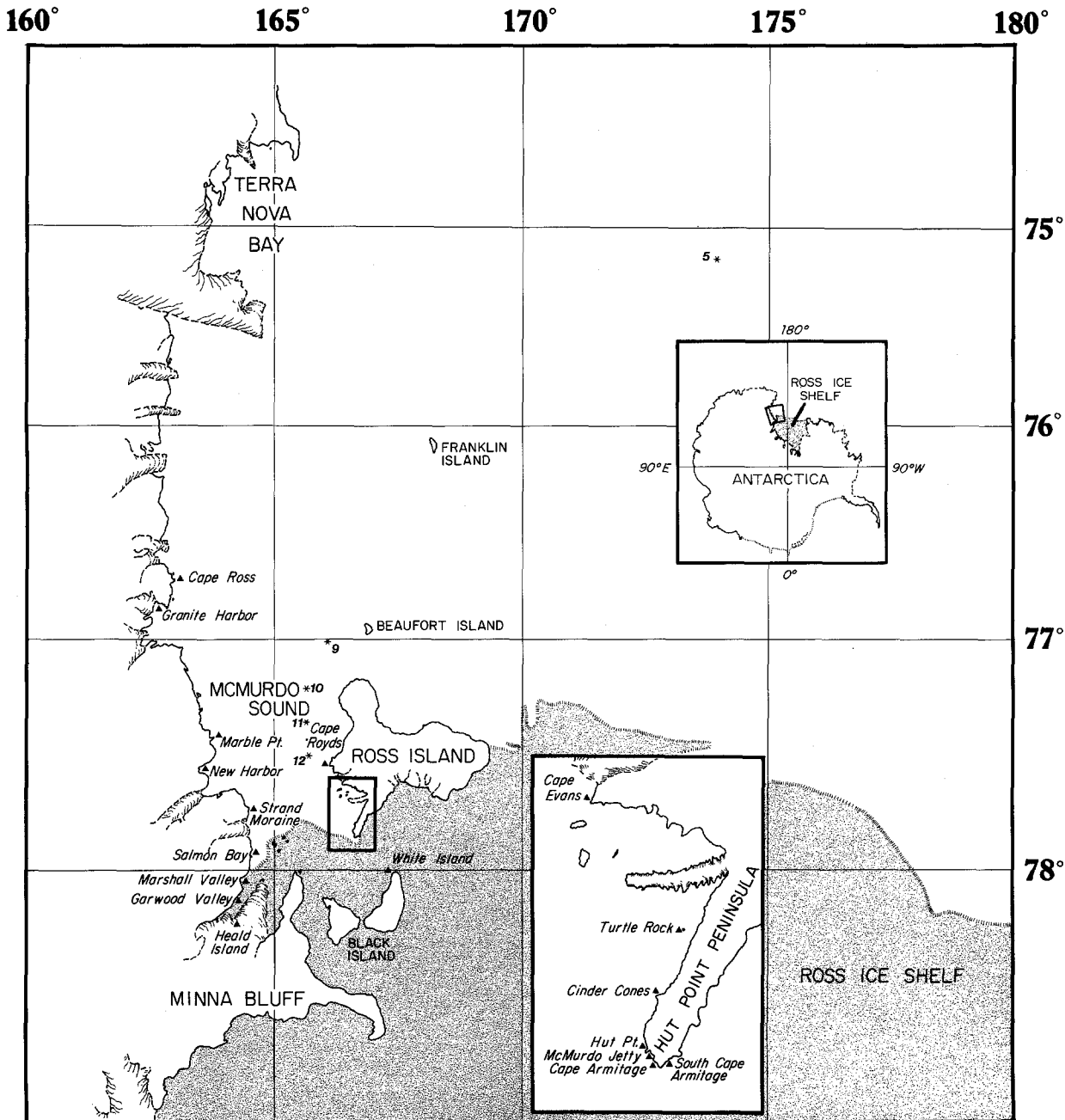


Fig. 1. Ross Island Vicinity. Triangles indicate SCUBA sampling sites. Asterisks indicate numbered January, 1976 Burton Island sampling stations

6 to 14, 1976. The productivity rates were measured in situ at 15 m with  $12 \mu\text{Ci NaH}^{14}\text{CO}_3$  incubated for 5 h (1000–1500). The sample was filtered onto Millipore HA membrane filters (0.45  $\mu$ ; 25 mm disc), placed in 15 ml Aquasol, and counted by the channels ratio method. The chlorophyll *a* and phaeophytin data were collected as for the benthic samples.

A modification of the in situ technique developed by Matheke and Horner (1974) was used for measuring benthic microalgal productivity. Briefly, four approximately 50 ml plastic tubes (one painted black) were used to collect small cores of the benthic sediment; the tubes were stoppered and injected with  $5 \mu\text{Ci NaH}^{14}\text{CO}_3$ . They were gently shaken and incubated in situ for 5 h from 1000–1500. Upon retrieval, samples were kept cold and dark and injected with 2 drops of  $\text{H}_3\text{PO}_4$  in order to remove inorganic  $\text{CO}_2$  and dissolve small fragments of shells not previously removed. The samples were then filtered on a GF/C filter within two hours of incubation; the filters were rinsed with 35 ml of filtered

seawater. The sediment and filter were frozen in vials. Wet oxidation was done in a trap with ethanalamine cocktail; extraction time was 6 h. The samples were counted on a Unilux II-A scintillation counter by channels ratio.

## Results

### Irradiance

Table 1 shows the relative irradiance at various localities and depths. With the exception of Cape Evans, very little light penetrated the ice and snow.

**Table 1.** Percent downwelling irradiance, ice and snow conditions at each site. N.D. means none detected. For each side of the Sound, sites are arrayed north to south

Location	Date	Annual ice thickness (m)	Snow cover (m)	Depth (m)	% surface downwelling irradiance
<b>East Sound</b>					
Cape Evans	22/11/75	0.1–0.2	0	9	2.78
Hut Point	10/11/75	2.6	0.02	25	0.31
Cape Armitage	24/10/75	2.2	0.75	25	0.24
Cape Armitage	29/10/75	2.0	0.3	43	N.D.
Cape Armitage	24/11/75	2.5	0.3	43	0.01
Cape Armitage	26/11/75	2.5	0.2	25	0.01
Cape Armitage	27/11/75			19	0.05
Cape Armitage	29/11/75	2.5	0.2	43	0.04
Cape Armitage	29/11/75	2.2	0.05	19	0.01
Cape Armitage	16/12/75	2.5	0.2	40	N.D.
Cape Armitage	21/12/75	2.2	0.2	25	N.D.
Cape Armitage	22/12/75	2.2	0.2	19	0.02
<b>West Sound</b>					
New Harbor	19/11/75	2.0	0	19	0.10
New Harbor	12/12/75	2.0	0 <sup>a</sup>	25	N.D.

<sup>a</sup> No snow, however, ice was covered with a thin layer of wind-blown soil

### Benthic Pigments

Standing stock of chlorophyll *a* and phaeopigments along the East Sound areas are shown in Tables 2 and 3. The dramatic effect of snow cover on benthic microalgal productivity can be seen for the November 6, 1975 data in Table 3 where the snow cover was removed from the ice above the sponge spicule mat. In a little over two weeks the chlorophyll *a* concentration increased from 756 to 960 mg Chl*a*/m<sup>2</sup> and the chlorophyll *a*/phaeopigment ratio doubled from 7.4 to 15.9. The brown patch under the cleared area was clearly visible to divers.

The effects of season on chlorophyll *a* and phaeopigments can be evaluated from data collected at the same sites in the winter of 1977. The chlorophyll *a* concentration in the 6 m site fell from 457 to 96 mg chl*a*/m<sup>2</sup> between December and June. The mg chl*a*/m<sup>2</sup> in the 18 m site fell from 310 to 95 between November 22 and March

25, the beginning of the austral winter. By August 18 the chlorophyll *a* was as low as 47 mg/m<sup>2</sup>. Similarly, the mg chl*a*/m<sup>2</sup> at the 24 m depth sponge spicule habitat (the control for the snow cleared area) fell from 842 on December 21 to 468 on March 3 to 374 on April 4 to 227 on July 11 and may have started recovering in the very dim light of the austral spring on August 18 when there was 259 mg chl*a*/m<sup>2</sup>. The chlorophyll *a* concentration at the 42 m site fell from a December 16 value of 518 mg chl*a*/m<sup>2</sup> to 168 mg chl*a*/m<sup>2</sup> on March 3. There are two caveats to these observations. First, the comparisons are of seasonal value only because summer data were collected in 1975 and the winter data in 1977. The two years were, in fact, somewhat different as the ice did not break out in 1976. The second discrepancy can be seen in the winter data from Hut Point (T. 2) which exhibited no seasonality. Here the sponge spicule mat had a

**Table 2.** Mean ( $\pm 95\%$  confidence interval) chlorophyll *a* and phaeopigments for benthic microalgae measured along the eastern side of McMurdo Sound during the austral summer 1975–1976 and winter 1977. Areas listed in north to south order (see Fig. 1)

Location	Date	Depth (m)	Substrate	Chl <i>a</i> mg/m <sup>2</sup>	Phaeopigments mg/m <sup>2</sup>	Chl <i>a</i> /phaeo	<i>N</i>
Cape Royds	26/10/75	25	mud and gravel	273 $\pm$ 109	253 $\pm$ 38.0	1.06 $\pm$ 0.33	4
Cape Evans	22/11/75	6	sand	293 $\pm$ 93.2	110 $\pm$ 71.1	2.86 $\pm$ 1.13	4
Cape Evans	22/11/75	19	mud and sand	913 $\pm$ 185	499 $\pm$ 119	1.87 $\pm$ 0.64	4
Turtle Rock	7/11/75	25	mud and gravel	139 $\pm$ 24.2	127 $\pm$ 30.1	1.11 $\pm$ 0.22	4
Turtle Rock	7/11/75	40	mud and gravel	60.8 $\pm$ 28.1	146 $\pm$ 42.0	0.43	
Cinder Cones	16/11/75	19	mud and gravel	241 $\pm$ 157	308 $\pm$ 131	0.81 $\pm$ 0.46	
Cinder Cones	16/11/75	25	mud and gravel	325 $\pm$ 73.3	283 $\pm$ 147	1.21 $\pm$ 0.38	4
Cinder Cones	16/11/75	40	sponge spicule	360 $\pm$ 146	86.4 $\pm$ 51.7	4.33 $\pm$ 1.19	4
Hut Point	12/11/75	25	mud and gravel	156 $\pm$ 106	310 $\pm$ 98.3	0.50 $\pm$ 0.26	4
Hut Point	12/11/75	40	sponge spicule	515 $\pm$ 399	99.7 $\pm$ 43.8	5.38 $\pm$ 4.30	4
Hut Point	5/4/77	40	sponge spicule	610 $\pm$ 255	192 $\pm$ 43.4	3.43 $\pm$ 2.28	5
Hut Point	9/4/75	31	sponge spicule	611 $\pm$ 230	175 $\pm$ 52.2	3.56 $\pm$ 1.18	5
Hut Point	9/4/75	43	sponge spicule	561 $\pm$ 46.8	99.4 $\pm$ 9.8	5.66 $\pm$ 0.69	4

**Table 3.** Mean ( $\pm 95\%$  confidence interval) chlorophyll *a* and phaeopigments for benthic microalgae at four stations at Cape Armitage (East Sound) for austral summer 1975 and winter 1977

Date	Depth (m)	Substrate	Chla mg/m <sup>2</sup>	Phaeopigments mg/m <sup>2</sup>	Ratio chla/phaeo	N
4/10/75	6	mud and gravel	351 $\pm$ 71.8	50.5 $\pm$ 14.3	7.12 $\pm$ 0.92	6
17/10/75	6	mud and gravel	269 $\pm$ 84	137 $\pm$ 65	2.06 $\pm$ 0.53	5
8/11/75	6	mud and gravel	294 $\pm$ 88.2	349 $\pm$ 262	1.08 $\pm$ 0.67	5
25/12/75	6	mud and gravel	457 $\pm$ 128	322 $\pm$ 111	1.45 $\pm$ 0.43	4
9/6/77	6	mud and gravel	96.0 $\pm$ 55.0	110 $\pm$ 89.6	0.89 $\pm$ 0.19	3
20/9/75	18	mud	533 $\pm$ 206	78.2 $\pm$ 36.5	6.90 $\pm$ 0.64	4
17/10/75	18	mud	383 $\pm$ 178	226 $\pm$ 71.0	1.73 $\pm$ 0.65	5
6/11/75	18	mud	265 $\pm$ 80.2	231 $\pm$ 37.1	1.15 $\pm$ 0.40	4
22/11/75	18	mud	310 $\pm$ 113	316 $\pm$ 30.5	0.97 $\pm$ 0.30	5
25/3/77	18	mud	95.2 $\pm$ 24.1	193 $\pm$ 44.0	0.50 $\pm$ 0.09	6
11/4/77	18	mud	76.2 $\pm$ 24.7	179 $\pm$ 36.8	0.43 $\pm$ 0.14	5
9/6/77	18	mud	51.8 $\pm$ 24.1	97.2 $\pm$ 41.9	0.54 $\pm$ 0.14	5
18/8/77	18	mud	47.3 $\pm$ 14.4	90.1 $\pm$ 27.8	0.53 $\pm$ 0.08	4
29/9/75	24	sponge spicule	863 $\pm$ 109	126 $\pm$ 21.8	6.90 $\pm$ 1.59	4
19/10/75	24	sponge spicule	756 $\pm$ 253	109 $\pm$ 57	7.41 $\pm$ 2.67	5
6/11/75 <sup>a</sup>	24	sponge spicule	960 $\pm$ 220	94.5 $\pm$ 63.2	15.9 $\pm$ 19.3	5
21/12/75	24	sponge spicule	842 $\pm$ 259	186 $\pm$ 225	5.88 $\pm$ 4.39	4
2/3/77	24	sponge spicule	468 $\pm$ 215	113 $\pm$ 39.5	4.12 $\pm$ 0.91	4
11/4/77	24	sponge spicule	374 $\pm$ 177	118 $\pm$ 62.8	3.37 $\pm$ 1.18	5
9/6/77	24	sponge spicule	227 $\pm$ 76	62.2 $\pm$ 15.1	3.63 $\pm$ 0.69	5
18/8/77	24	sponge spicule	259 $\pm$ 126	81.5 $\pm$ 35.2	3.18 $\pm$ 0.67	4
25/ 9/75	42	sponge spicule	317 $\pm$ 91.0	30.8 $\pm$ 11.2	10.5 $\pm$ 2.99	5
16/10/75	42	sponge spicule	360 $\pm$ 109	54.2 $\pm$ 30.9	6.81 $\pm$ 3.77	4
6/11/75	42	sponge spicule	344 $\pm$ 137	49.1 $\pm$ 15.3	6.97 $\pm$ 1.70	5
16/12/75	42	sponge spicule	518 $\pm$ 261	128 $\pm$ 44.0	4.14 $\pm$ 1.41	6
28/ 3/77	42	sponge spicule	168 $\pm$ 64.6	128 $\pm$ 90.1	1.53 $\pm$ 0.81	5

<sup>a</sup> Samples taken near area (10 m by 15 m) where 0.7 m deep snow was cleared from the ice above

mg chla/m<sup>2</sup> content of 515 on December 11, 1975 but in three similar areas in April, 1977 it varied from 561–610 mg chla/m<sup>2</sup>! Hut Point differs from the Cape Armitage areas in that there was much less snow cover due to ablation in late November. As such there is much greater light penetration from December through February than at Cape Armitage which is relatively dark during those months. In addition, the divers at Hut Point in April 1977 observed thick strands of *Phaeocystis* sp., a planktonic haptophycean alga that forms gelatinous colonies. This material had apparently settled to the bottom during the late December–February plankton bloom. The high concentration of *Phaeocystis* was not observed on the bottom at Cape Armitage. It is conceivable that the southerly currents (Dayton and Oliver 1977; Barry and Dayton, submitted) advect more material to Hut Pt. which may partially shelter Cape Armitage. Irrespective of these caveats, the issue of the fate of the benthic microalgae is unclear and deserves attention.

Standing stock estimates for the West Sound New Harbor site were much lower than in East Sound sites (Table 4). Note that with the exception of the 31 m site, these data represent collections from three sites about 1 month apart. The 19 m site stands out as being the most productive and having relatively high chlorophyll *a*/phaeopigment ratios. This site is shallower and very much lighter than the others. The high light levels result from

a large tide crack with open water and thin ice immediately above the site. Perhaps because there was a very high density of invertebrates (such as *Adamussium colbecki*, an abundant filter feeding bivalve, echinoids, various polychaetes, etc.) at this site, the concentration of chlorophyll *a* fell from 145 to 98 mg chla/m<sup>2</sup>. These concentrations might increase later in the season as the tide crack widens; in addition, a small melt water stream empties into the sea nearby. The fresh water collects in the tide cracks and apparently remains behind an ice barrier (T. DeLaca, personal communication), but microalgae material from this large tide crack system eventually may be advected toward the 19 m site.

Comparisons within similar depths between the West and East Sound sites are difficult because the mud and sponge spicule mat habitats are so different. An appropriate comparison of concentrations of chlorophyll *a* between sites of similar depths, substrata and dates can be made between Cinder Cones (Table 2) and New Harbor (Table 4); chlorophyll concentrations of 241 and 326 mg chla/m<sup>2</sup> at Cinder Cones compared with 145 and 48 mg chla/m<sup>2</sup> at New Harbor at 19 and 25 m, respectively. A more dramatic 18–19 m depth comparison can be made between the 913 mg chla/m<sup>2</sup> at Cape Evans (Table 2) and the relatively very high for New Harbor estimate of 145 mg chla/m<sup>2</sup>. Finally on November 22 there was an estimate of 310 mg chla/m<sup>2</sup> from Cape Armitage

**Table 4.** Mean ( $\pm 95\%$  confidence interval) chlorophyll *a* and phaeopigments for benthic microalgae at four sites at New Harbor West Sound) during austral summer 1975

Date	Depth (m)	Substrate	Chl <i>a</i> mg/m <sup>2</sup>	Phaeopigments mg/m <sup>2</sup>	Chl <i>a</i> /phaeo	<i>N</i>
15/11/75	19	sand and mud	145 $\pm$ 40.4	38.4 $\pm$ 18.3	4.14 $\pm$ 2.98	4
15/12/75	19	sand and mud	97.7 $\pm$ 22.9	46.1 $\pm$ 12.0	2.18 $\pm$ 0.66	5
15/11/75	25	sand and mud	48.2 $\pm$ 33.9	47.1 $\pm$ 31.5	1.15 $\pm$ 0.97	4
12/12/75	25	sand and mud	57.7 $\pm$ 31.9	57.1 $\pm$ 22.6	1.00 $\pm$ 0.24	4
10/11/75	31	sand and mud	18.3 $\pm$ 28.6	38.9 $\pm$ 34.5	0.44 $\pm$ 0.48	4
13/11/75	40	sand and mud	21.0 $\pm$ 8.80	35.2 $\pm$ 50.4	0.87 $\pm$ 0.72	4
8/12/75	40	sand and mud	38.1 $\pm$ 32.0	69.9 $\pm$ 35.3	0.55 $\pm$ 0.51	4

despite the fact that the site was under thick snow and ice. The values of 18–60 mg chl*a*/m<sup>2</sup> are probably more typical of the offshore New Harbor benthos: for similar substrata, depths and seasons these compare with values of 300–900 mg chl*a*/m<sup>2</sup> in the East Sound.

#### Phytoplankton Pigments

Unlike benthic pigment concentrations, phytoplankton pigment concentration do not show consistent East-West Sound differences (Table 5). The within site and site-to-site differences reflect advection and local differences in snow and ice. Advection of phytoplankton is especially important in the East Sound. The temporal differences at Cape Armitage represent the seasonal advection of

planktonic algae from the north (Dayton and Oliver 1977; Palmisano et al., in press). The White Island site is 30 km south of the edge of the permanent 10–100 m thick Ross Ice Shelf; certainly there is no in situ primary production there and all the chlorophyll pigments are advected from the north (Dayton and Oliver 1977). In contrast, the southern three sites on the West Sound (Garwood Valley, Marshall Valley and Heald Island) were also areas with at least semi-permanent ice cover. Here there is no evidence of consistent southerly current such as on the East Sound and there is little evidence of much advection (see also Hodson et al. 1981). The primary production which does occur at these West Sound southern sites may result from high productivity at the surface of the seawater in the many cracks and rifts (Barry, in prep.).

**Table 5.** Mean ( $\pm 95\%$  confidence interval) phytoplankton chlorophyll *a* and phaeopigments at 25 m. Sites are listed north to south, Cape Evans to White Island on the East Sound and Granite Harbor to Heald Island on the West Sound

Location	Date	Chl <i>a</i> mg/m <sup>3</sup>	Phaeopigments mg/m <sup>3</sup>	Chl <i>a</i> /phaeo	<i>N</i>
East Sound					
Cape Evans	27/ 1/77	0.50 $\pm$ 0.11	0.05 $\pm$ 0.07	10.4	4
McMurdo Jetty	2/ 2/76	3.14 $\pm$ 0.27	0.53 $\pm$ 0.20	6.22 $\pm$ 3.06	4
McMurdo Jetty	19/ 2/77	0.77 $\pm$ 0.18	0.20 $\pm$ 0.15	3.9	6
Cape Armitage	14/10/75	0.09 $\pm$ 0.28	0.15 $\pm$ 0.28	0.6	4
Cape Armitage	23/10/75	0	0.38 $\pm$ 0.78	–	4
Cape Armitage	2/11/75	0.04 $\pm$ 0.13	0.13 $\pm$ 0.40	0.3	4
Cape Armitage	28/11/75	0.04 $\pm$ 0.12	0.11 $\pm$ 0.22	0.4	4
Cape Armitage	9/12/75	0.30 $\pm$ 0.15	0.06 $\pm$ 0.11	10.0 $\pm$ 18.4	4
Cape Armitage	14/12/75	1.28 $\pm$ 0.23	0.03 $\pm$ 0.10	2 $\pm$ 6.63	4
Cape Armitage	20/12/75	0.85 $\pm$ 0.17	0.17 $\pm$ 0.17	6.8 $\pm$ 5.86	4
Cape Armitage	30/12/75	1.32 $\pm$ 0.31	0.21 $\pm$ 0.42	46.6 $\pm$ 62.3	5
Cape Armitage	25/ 3/77	0.05 $\pm$ 0.16	0.03 $\pm$ 0.25	1.7	4
White Island	3/ 1/76	0.62 $\pm$ 0.15	0.16 $\pm$ 0.01	4.97 $\pm$ 5.41	4
West Sound					
Granite Harbor	24/ 1/77	0.22 $\pm$ 0.06	0	–	5
Cape Ross	25/ 1/77	0.18 $\pm$ 0.06	0.10 $\pm$ 0.09	1.8	5
Mable Pt.	29/12/75	0.06 $\pm$ 0.11	0.03 $\pm$ 0.10	2.0	4
New Harbor	1/12/75	0.16 $\pm$ 0.17	0.08 $\pm$ 0.09	1.25 $\pm$ 2.29	4
New Harbor	19/12/75	0.12 $\pm$ 0.14	0	–	4
New Harbor	2/ 1/76	0.03 $\pm$ 0.004	0.19 $\pm$ 0.46	0.2	4
Strand Moraine	3/ 1/76	0.37 $\pm$ 0.31	0.07 $\pm$ 0.11	5.85 $\pm$ 15.1	4
Salmon Bay	27/12/75	0.31 $\pm$ 0.31	0.17 $\pm$ 0.21	0.95 $\pm$ 1.91	4
Garwood Valley	3/ 1/76	0	0.05 $\pm$ 0.11	–	4
Marshall Valley	12/ 2/77	0	0.03 $\pm$ 0.14	–	3
Heald Island	14/ 1/77	0.02 $\pm$ 0.06	0.02 $\pm$ 0.06	1.0	5

**Table 6.** Mean ( $\pm 95\%$  confidence interval) chlorophyll *a* and phaeopigments from Ross Sea, January 6 to 14, 1976

Station	Depth (m)	Chl <i>a</i> mg/m <sup>3</sup>	Phaeopigments mg/m <sup>3</sup>	Chl <i>a</i> /Phaeo	N
5 17°00'E, 75°10'S	0	0.24 $\pm$ 0.41	0.013 $\pm$ 0.06	0.83 $\pm$ 3.59	3
	50	0.37 $\pm$ 0.76	0	—	2
	100	0.13 $\pm$ 0.37	0	—	3
	200	0	0	—	2
9 166°12'E, 77°00'S	0	0.37 $\pm$ 0.85	0.17 $\pm$ 0.07	2.00 $\pm$ 8.61	3
	50	0.41 $\pm$ 0.07	0.03 $\pm$ 0.03	13.80 $\pm$ 13.50	3
	100	0.03 $\pm$ 0.38	0.03 $\pm$ 0.32	1.0	2
10 165°40'E, 77°13'S	0	1.40 $\pm$ 0.27	0.29 $\pm$ 0.38	6.55 $\pm$ 13.0	3
	50	0.67 $\pm$ 0.14	0.51 $\pm$ 0.70	1.40 $\pm$ 0.86	4
	100	0.15 $\pm$ 0.06	0	—	2
	200	0.25 $\pm$ 0.32	0.02 $\pm$ 0.25	12.5	2
11 165°42'E, 77°21'S	0	1.53 $\pm$ 0.39	0.11 $\pm$ 0.15	5.17 $\pm$ 6.80	5
	50	1.21 $\pm$ 0.23	0.26 $\pm$ 0.37	3.24 $\pm$ 4.65	4
	100	0.65 $\pm$ 0.32	0.43 $\pm$ 0.60	2.43 $\pm$ 6.08	3
	200	0.26 $\pm$ 3.62	0.15 $\pm$ 1.91	1.7	2
12 165°45'E, 77°30'S	0	1.57 $\pm$ 0.10	0.09 $\pm$ 0.15	27.00 $\pm$ 33.00	5
	50	1.37 $\pm$ 0.26	0.12 $\pm$ 0.23	2.21 $\pm$ 4.72	6
	100	1.05 $\pm$ 0.43	0.24 $\pm$ 1.02	5.01 $\pm$ 4.66	4
	200	0.21 $\pm$ 0.44	0.12 $\pm$ 0.83	2.68 $\pm$ 22.40	2

The *Burton Island* cruise allowed us to collect phytoplankton pigment concentration in the Ross Sea (Table 6). These concentrations are somewhat higher than from beneath the ice (Table 5). The phytoplankton system in the Ross Sea lacked the dense concentrations of *Phaeocystis* characteristic of the bloom conditions in McMurdo Sound.

#### *Benthic Productivity*

In situ benthic productivity measurements were attempted in each of the sites listed in Tables 2, 3 and 4, but most were too dark for our technique to measure any net productivity. However, at the 18 m site at Cape Evans we measured productivity rates of 51.3, 62.2 and 95.22 mg C/m<sup>2</sup>/h which yielded net estimates of 0.06, 0.07 and 0.10 mgC/mg chl*a*/h. The 18 m Cape Armitage site also produced some marginal rates in which the mg C/m<sup>2</sup>/h ranged from 0.8 to 2.6 with net rates of only 0.001 to 0.02 mgC/mg chl*a*/h. Similar marginal values recorded at the anomalously light 19 m site at New Harbor ranged from 0.1 to 2.6 mgC/m<sup>2</sup>/h with net rates ranging from 0.003 to 0.02 mgC/mg chl*a*/h.

#### **Discussion**

Perhaps the most interesting ecological characteristics of McMurdo Sound, Antarctica are the dramatic biological differences between invertebrate assemblages over relatively short distances of 15–30 km. The most striking example is the East-West comparison: the East Sound area includes dense assemblages of bryozoans, coelenterates and massive sponges on hard bottoms below 25 m

(Dayton 1979; Dayton et al. 1974) and some of the highest densities of soft bottom infauna in the world whereas the West Sound areas have the same hard bottom species but very much lower densities and a soft bottom infauna with very low densities (Dayton and Oliver 1977). A remarkably similar pattern has been described for the distribution and activity of bacterioplankton and the turnover of dissolved organic matter (Hodson et al. 1981). The most obvious explanation for such contrasting patterns is that the different sites are exposed to different amounts of food.

Of the tripartite microalgal assemblage, described by Horner and Schrader (1982), the differences across McMurdo Sound of ice algae (Palmisano and Sullivan 1983) and phytoplankton (Table 5) are not commensurate with the invertebrate differences. While relatively unimportant in Horner and Schrader's high Arctic study, the benthic microalgae here do exhibit striking differences with parallel the invertebrate patterns. Despite very low irradiance, high benthic algal standing crops were observed in the East Sound, but New Harbor in the West Sound was different. Here the ice usually does not break out during the daylight months and often does not go out at all as we commonly see two to three year's accumulation of annual sea ice at our New Harbor study area in Explorer's Cave. There is rarely any snow cover, but the strong winter katabatic winds usually carry soil onto the ice. In addition, probably because of the lack of snow, the microalgae growing on the bottom of the sea ice usually begin growth earlier. These algae may intercept much of the photosynthetically available radiation (PAR) that the benthic microalgae need. This interception is particularly acute when the ice does not go out because much of the previous year's ice microalgae are frozen into the ice and may remain photosynthetically active in the conspicuous

dark layer in the ice. Certainly at comparable depths the West Sound sites seem very much darker to divers.

Several points should be made about the standing stock data, some of which are extremely high. Most of these high readings occur in sponge spicule mats, and there are several reasons why this might be so. First, the spicule mat is an extraordinarily heterogeneous structure; sponge spicules form a complex lattice. Each spicule provides a substratum for diatom attachment and each is covered with diatoms. This structure provides a tremendous increase in area compared to almost any other habitat. In addition, this structure affords benthic microalgae protection from larger grazers yet exposes the microalgae to nutrients generated from the excretion of the many infauna in the mat. These hypotheses are supported by the very high chlorophyll *a*/phaeopigment ratios seen in the spicule mat habitat. Coincident with this hypothesis is the corollary that protection from grazing and the cold dark habitat allows accumulation of older benthic microalgae plus planktonic and ice microalgae settling from previous summer blooms. The rate of shift from chlorophyll *a* to phaeopigments can be seen in Tables 2 and 3. This gives a preliminary estimate of the degradation of the microalgae; it is not possible to differentiate simple senescence of the algae from grazing. Properly done, this would be a fascinating winter project as our winter data suggest that a reasonable population of microalgae survive the winter.

It is important to note that our standing stock data and efforts to measure in situ benthic productivity refer only to microalgae. We have no measure of the standing stock nor productivity of the populations of macroalgae, especially the red algae *Iridaea skottsbergii* and *Phyllophora antarctica* which are common along the East Sound. There are rocky habitats in deeper water (> 20 m) from Cape Evans northward; and in some of these areas the mats of microalgae are as much as 25 m thick, and large wracks of their fragments accumulate in depressions. We have never seen macroalgae south of Marble Point on the West Sound. They do occur north of Marble Point on isolated boulders and at Granite Harbor they appear heavily grazed by the echinoid, *Sterechnus neumayeri*. Certainly any complete East-West Sound comparison should include these macroalgae, and our unquantified observations suggest that almost all of the macroalgae occur along the East Sound.

Perhaps the most important issue not addressed in this paper is that of advection. The diverse high biomass benthic communities under the Ross Ice Shelf south of Ross Island (Dayton and Oliver 1977 and our unpublished deep-sea photographs) emphasize the importance of phytoplankton advected from the north along the east side of McMurdo Sound. The west side of the Sound,

however, lacks such a current and instead seems bathed by a slow northerly current (Dayton and Oliver 1977; Barry and Dayton, submitted). The very similar results of Dayton and Oliver and this paper for benthic patterns and those of Hodson et al. (1981) for bacterioplankton suggest that in situ light differences are important. However, many of the ecological patterns of McMurdo Sound must also be heavily influenced by oceanographic and sea ice patterns.

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