ANTARCTIC LIMNOLOGY: A REVIEW

By RONALD B. HEYWOOD

ABSTRACT. Information on Antarctic inland waters is presented against a background of historical, geographical, topographical, geological and climatic detail because of prevailing widespread ignorance about Antarctica in general.

Present knowledge suggests that aridity is the most important climatic factor determining the variety of lake and pool environments in Antarctica. Comparison with Arctic inland waters indicates that the considerably poorer biota of Antarctica largely reflects the isolation and the youth of the ecosystem.

The review clearly reveals the need for basic, comprehensive research programmes in all areas of the continent.

Now that there is increasing international interest in Antarctic biology it is important that comprehensive reviews of present knowledge be made available to stimulate the interest of the general scientific public and thereby encourage greater participation in Antarctic research. A brief review of Antarctic limnology has already been published (Goldman, 1970). This immediate second review is justified on several grounds. The available information, although meagre, merits more detailed consideration and, in view of widespread ignorance about Antarctica in general, it is pertinent to present this information against a background of historical, geographical, topographical, geological and climatic detail. Also, present knowledge permits useful comparison with Arctic inland waters and discussion of those features of Antarctic lakes which are unique, characteristically polar or merely typical of oligotrophic conditions.

HISTORICAL BACKGROUND

Studies of a primarily limnological nature have rarely been carried out in Antarctica, and the meagre information available must be extracted from widely scattered general narratives and technical reports. That there is so little information is perhaps surprising for two reasons. First, the interest of biologists in Antarctica was stimulated as long ago as 1775 by the collections and drawings of naturalists who had accompanied James Cook on his pioneer voyage of exploration. Secondly, expeditions have been particularly numerous from the nineteenth century onwards and their total number is now over 150 (a chronological list of expeditions has been published by Roberts (1958*a*, *b*). But biology was always a minor by-product of these expeditions. Work was mainly confined to the collection of specimens, often poorly preserved and poorly documented, and the subsequent taxonomic evaluation sometimes took place many years later. Even so, various national expeditions at the turn of the century (Belgian, 1897–99; German, 1901–03; Swedish, 1901–03; British, 1901–04, 1907–09; Scottish, 1902–04; French, 1903–05; 1908–10) provided valuable information on the fresh-water flora and fauna. A particularly important contribution was made by members of the British Antarctic Expedition, 1907–09, which was based on Ross Island. They provided the first descriptions of the Antarctic lake environment as well as making extensive biological collections (Murray, 1910*a*, *b*, *c*, *d*; Penard, 1911; West and West, 1911; David and Priestley, 1914; Mawson, 1916). However, their reports did not stimulate more intensive limnological research. Although biology took precedence over all other disciplines in the Discovery Investigations, 1925–38, the work was almost entirely oceanographic and only a little fresh-water material was collected. This and a small collection made by members of the British Graham Land Expedition, 1934–37, was nevertheless valuable as it showed a considerable southward extension of the known range of several crustacean species in the Antarctic Peninsula region (Harding, 1941).

The establishment of permanent shore stations by several nations after World War II increased the potential for scientific research, but priority was still given to the physical and earth sciences, and biology was neglected (Ingham, 1964). Collections were still made, however, by station personnel in their spare time, and some ecological studies were carried out on birds and seals (Holdgate, 1965).

Biological research in the Antarctic only came of age after the International Geophysical

Year (I.G.Y.) (1 July 1957–31 December 1958) (Holdgate, 1969), the activities and success of which roused widespread interest. In 1958 the International Council of Scientific Unions established the Special (now Scientific) Committee on Antarctic Research (S.C.A.R.) to co-ordinate future research. At the third meeting of S.C.A.R. (March 1959) guide lines for marine and terrestrial biology were drafted, and a year later, a permanent working group on biology was constituted.

But even after encouragement given by S.C.A.R. the official interest of many nations is still understandably pre-occupied with the more fundamental disciplines of Antarctic exploration —survey, geology and glaciology—and with those disciplines requiring the minimum of logistic support in the field—meteorology and upper atmosphere physics.

Ecological studies are demanding of logistic support because sites must be visited throughout the year and the time and frequency of sampling are dictated by the objects of study and not by the weather or availability of transport. Antarctic limnologists are in an especially disadvantageous position. Station sites are chosen because of their ease of relief by sea or air, the accessibility of the hinterland and the demands of the main scientific disciplines to be pursued. Close proximity to pools and lakes is accidental. Consequently, the innumerable inland water bodies known to exist in Antarctica have received little attention, and this, until recently, had been almost entirely of a taxonomic and biogeographic nature. Even this type of study has been very sporadic. Knowledge of all groups is far from complete and insufficient to permit any useful general interpretation (Hirano, 1965).

PRESENT KNOWLEDGE

Temperature and aridity are factors which can have a considerable effect on any environment. Antarctica (Fig. 1) is a cold desert. Conditions are severest in the centre of east Antarctica (Vostok; lat. 78°27′S., long. 106°52′E., annual mean temperature −55° C, annual precipitation 5 cm. water equivalent) and ameliorate gradually with decreasing latitude (Signy Island; lat. 60°43′S., long. 45°38′W., annual mean temperature −4.0° C, annual precipitation 40 cm. water equivalent). Even in the warmer areas, lakes and pools freeze over for 8–12 months of the year. Under such extreme conditions, factors other than ambient temperature directly determine the depth to which a water body freezes and the duration of the ice cover. The degree of aridity governs several of these factors. It also determines directly and indirectly the chemical composition of the waters and the amount of light available in them. These are factors of major ecological significance. Aridity is therefore the most important climatic factor determining the variety of lake and pool environments in Antarctica.

In terms of aridity, Antarctica can be divided into four intergrading divisions which conveniently correspond to distinct geographical regions (Table I):

i. The continental ice sheet.
ii. Continental inland ice-free areas, known unofficially as "oases".
iii. Continental coastal areas and adjacent islands.
iv. The Antarctic Peninsula and adjacent islands.

These geographical regions form a suitable framework on which to base this review.

The breadth of the field under review precludes any one schema from being entirely adequate and that adopted here fails in dealing with the biota since similar aquatic environments can exist under dissimilar climatic conditions. Furthermore, the flora and fauna of a habitat are determined by factors such as isolation and problems of dispersal as well as the chemical and physical properties of the environment. For convenience the information on the biota is presented in a more general form.

To aid coherence I have been deliberately selective in my review of the literature, and have confined myself to areas south of lat. 60°S.

Lakes and pools of the continental ice sheet

Russian survey teams have found lakes in mountains protruding through the continental ice sheet in areas of Dronning Maud Land, far from the coast. The only information that I have been able to find on these lakes is that they do not freeze solid during the winter (Bardin, 1963). No further comment can therefore be made.

TABLE I. CLIMATIC DATA FOR SOME ANTARCTIC REGIONS

Locality	*Temperature* (°C)					*Annual mean wind speed* (m./sec.)	*Total annual precipitation* (cm. water)	*Relative humidity* (per cent)	*Annual mean cloud cover* (tenths)	*Sunshine duration* (percentage of total possible)
	Mean			*Min.*	*Max.*					
	Annual	*Summer*	*Winter*							
Continental ice sheet										
Vostok (lat. 78°27′S., long. 106°52′E.)	−55·0	—	—	−88·3	−23·0	4·6	5·0	—	3·0	—
Continental inland ice-free areas										
South Victoria Land (lat. 77°10′S., long. 161°00′E.)	−18·0	−3·1	—	−62·0	+12·3	5·0†	15·0	45	4·6†	—
Schirmacher Ponds (lat. 70°45′S., long. 11°20′E.)	−10·8	−2·0	−16·1	−35·5	+6·6	10·2	—	51	—	—
Bunger Hills (lat. 66°16′S., long. 100°45′E.)	−8·2	+0·4	−16·3	−43·0	+11·6	6·9†	—	—	4·6†	—
Continental coastal areas										
Ross Island (lat. 77°51′S., long. 166°37′E.)	−17·6	−5·6	−25·9	−50·6	+5·6	6·4	11·9	57	6·2	35·6
Ongul Islands (lat. 69°00′S., long. 39°35′E.)	−11·4	−2·6	−17·7	−42·7	+6·5	6·4	—	74	6·7	—
Vestfold Hills (lat. 68°35′S., long. 77°58′E.)	−10·0	−0·9	−16·9	−36·9	+6·6	5·1	—	62	6·5	—
Antarctic Peninsula and adjacent islands										
Marguerite Bay, west coast of peninsula (lat. 68°11′S., long. 67°01′W.)	−6·7	−0·5	−12·1	−40·0	+8·3	4·3	36·0	79	7·4	—
Hope Bay, east coast of peninsula (lat. 63°24′S., long. 56°59′W.)	−6·3	−1·3	−10·8	−32·2	+14·0	6·4	—	79	7·3	—
Signy Island, South Orkney Islands (lat. 60°43′S., long. 45°38′W.)	−4·2	+0·1	−9·6	−34·4	+10·6	7·6	40·6*	84	8·7	10·4

* From Laurie Island.

† Summer data only.

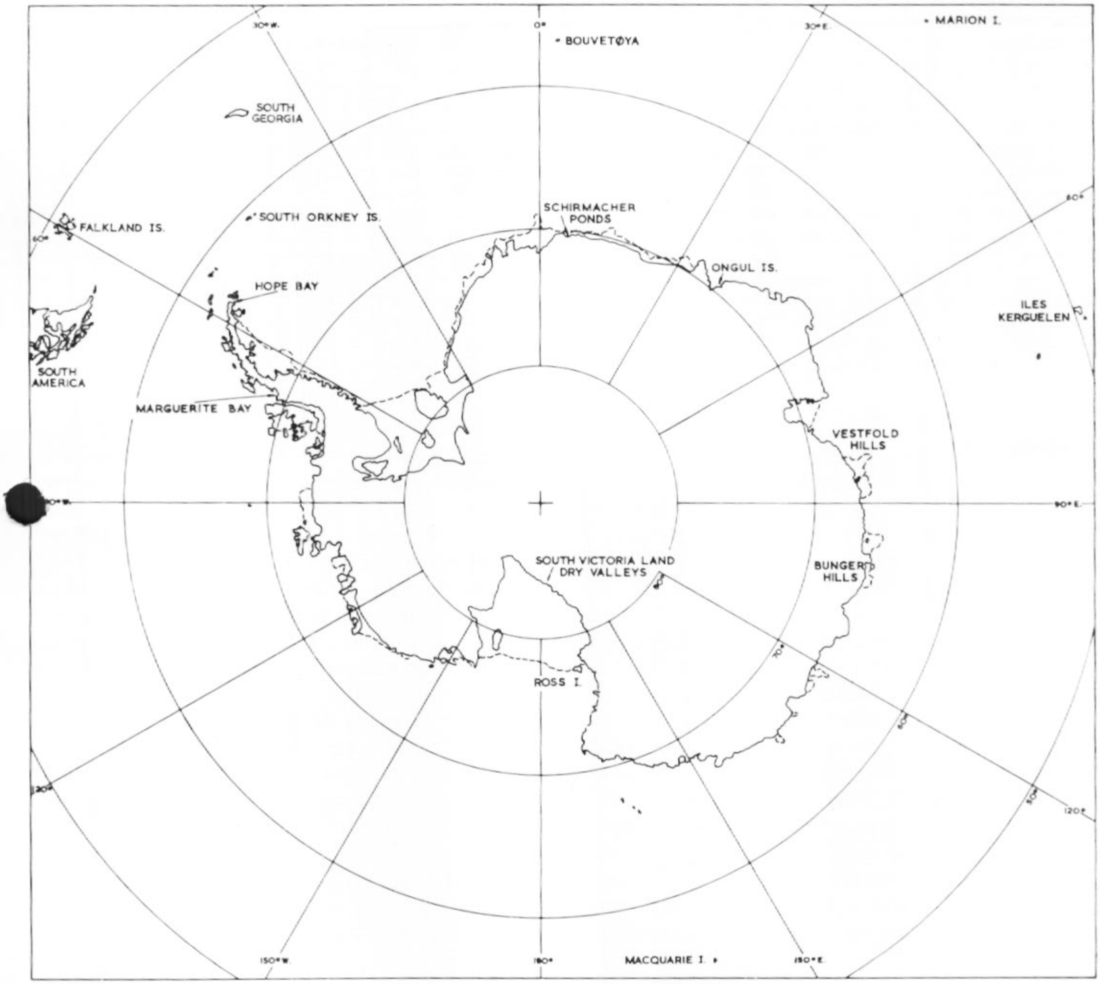

Fig. 1. Sketch map of Antarctica showing place-names referred to in the text.
- - - Edge of ice shelf.

Lakes and pools of the continental inland ice-free areas

These areas are unusual in that they never have even prolonged snow cover, although the surrounding terrain is perpetually ice-covered. Limnological research has been carried out in three of these areas—south Victoria Land dry valleys, the Bunger Hills and Schirmacher Ponds (Fig. 1).

Geography and geology

The south Victoria Land dry valleys (lat. 77°10′–77°45′S., long. 160°20′–163°00′E.) form two large areas on the west side of McMurdo Sound. One area, 2,500 km.², lies between Mackay and Ferrar Glaciers and the second area, 1,200 km.², lies 50 km. to the south-east, between Blue and Koettlitz Glaciers. The topographical relief consists of east-trending high ridges rising over 1,000 m. above wide, flat valley floors. The bedrock is formed of gneisses, marbles, schists and metagreywackes, intruded by granite and capped by thick, light-coloured shales and sandstones (Clark, 1965). The shales and sandstones have been injected by thick sills and sheets of dolerite. The bedrock of the valleys is covered by moraines and scoria. Numerous lakes and pools occupy depressions of glacial, tectonic and volcanic origin. Several are large; Lake Bonney has a total length of 7·4 km., maximum width of 0·84 km. and a maximum recorded depth of 32 m.

The Bunger Hills (lat. 65°54′–66°24′S., long. 100°24′–101°30′E.) are in Wilkes Land. They are moderately low, rounded hills, 425 km.² in area. Although on the coast, they are separated from the open sea by the Shackleton Ice Shelf (approximately 80 km. wide) and are therefore considered to be "inland" in this review. The bedrock is crystalline schists and gneisses with migmatites and charnockites and is overlain by moraines (Warren, 1965). Numerous water bodies occupy depressions of glacial and tectonic origin. The largest, Lake Figurnoye, is 18 km. long, 1 km. wide, with a maximum recorded depth of 137 m.

The Schirmacher Ponds area (lat. 70°45′S., long. 11°20′–11°55′E.) is a small (23 km.²) narrow strip of land on the Kronprinsesse Astrid Kyst of Dronning Maud Land which may also be considered "inland", since it is bordered to the north by an ice shelf approximately 90 km. wide. The terrain is simple: from precipitous 15–60 m. high cliffs overlooking the ice shelf, the land rises gradually in a series of low rocky ridges, orientated north-north-east and north-east, but does not exceed 200 m. above sea-level in altitude. The present-day relief was largely formed by ice scour along faults. Some of the larger valleys may be pre-glacial (Bardin, 1964). The bedrock is migmatized, Precambrian basic and acid gneisses, mainly garnet-, garnet-biotite-, biotite-amphibole- and biotite-amphibole-pyroxene-gneisses, often cut by pegmatitic veins (Konovalov, 1962). Moraine deposits are thin, varying from a 1 m. thick layer in depressions in the northern part of the area to isolated boulders on slopes. Over 50 lakes and pools occupy ice-deepened depressions in the valleys. There is a marked north–south gradation in size. 15 of the southern lakes are large and vary up to 32 m. in depth. The largest, also called Lake Figurnoye, is 1·3 km. long, 0·7 km. wide but has a maximum recorded depth of only 6 m.

Climate

Several factors combine to ameliorate the temperature within the oases. The prevailing winds blow from the polar ice sheet and are strong and dry (annual mean relative humidity approximately 50 per cent). The air is warmed adiabatically as the winds sweep down the valleys. Precipitation is therefore extremely low and snow cover is quickly removed as drift and by ablation. Rock has a low albedo and so the valleys absorb a considerable amount of radiation. In the Schirmacher Ponds, the albedo of the rock is 20 per cent in the summer, rising to 30–50 per cent when partly covered with snow during the winter, in contrast to the 82–90 per cent albedo of surrounding snow-covered ice surfaces (Artem'yev, 1966). When covered with a high, thin cloud layer, the Schirmacher Ponds receive a substantial increase in scattered radiation flux resulting from the secondary reflection of radiation reflected from the surrounding ice. Rusin (cited by Rubin, 1965) has shown that the Bunger Hills may have a radiation budget surplus of more than 37,000 cal. cm.$^{-2}$ yr.$^{-1}$, whereas the nearby ice shelf may have a deficit of 5,000 cal. cm.$^{-2}$ yr.$^{-1}$. Positive temperatures at ground level have been recorded as early as mid-October in the Schirmacher Ponds when the average daily air temperatures (at a height of 2 m.) are still −14° C. Rocky surfaces may attain temperatures as high as +40° C during January (Kruchinin and Simonov, 1967*a*). Nudel'man (1959) reported that surface soil temperatures may be +35° C in the Bunger Hills during the summer. The air in the "oases" is further warmed by long-wave radiation from the rock. As a result of these phenomena, annual mean air temperatures are 5 deg. higher than over adjacent ice-clad areas, and conditions are exceptionally arid.

The relatively warm conditions are an effect and not a cause of deglaciation. One current view of the origin of the south Victoria Land dry valleys is that a lowering of plateau ice level to the west of the area resulted in the shutting off of ice flow through the valleys by obstructions of hard, corrasion-resistant dolerite sills (McKelvey and Webb, 1961). Stagnant ice in the valleys was lost by sublimation. Wilson (1967) attributed the lowering of plateau ice to a change in the precipitation/evaporation balance of the general area more than 60,000 yr. ago.

There appear to be significant differences in aridity between the three "oases". The south Victoria Land dry valleys and the Schirmacher Ponds are the extremes, the latter being the least arid area. There are probably two main reasons for the differing aridity. First, the "oases" differ considerably in area. Air will be much more affected by long-wave radiation when moving over 3,700 km.² of bare rock (south Victoria Land dry valleys) than when moving over only 23 km.² (Schirmacher Ponds). Secondly, the Schirmacher Ponds "oasis" receives copious amounts of water from the surrounding ice each summer. Adiabatic warming of the air entering this oasis probably begins when the winds sweep down from Wohlthatmassivet, approximately 100 km. to the south. The ice sheet between the mountains and "oasis" thaws to an extraordinary degree. At the height of the melt period (December–January) the surface over a wide area is flooded with melt water flowing towards the "oasis". Some streams are 20–25 km. long (Konovalov, 1962). The amount of water entering the other "oases" appears to be relatively small and its influence is further reduced by the greater areas of bare rock.

TABLE II. PHYSICAL AND CHEMICAL PROPERTIES OF LAKES IN THE CONTINENTAL INLAND ICE-FREE AREAS

Location	*Date*	*Depth* (m.)	*Temp.* (°C)	*pH*	*Conductivity* (μmho)	Na$^+$ (p.p.m.)	K$^+$ (p.p.m.)	Mg^{++} (p.p.m.)	Ca^{++} (p.p.m.)	Cl$^-$ (p.p.m.)	SO$_4^=$ (p.p.m.)	PO$_4^{\equiv}$ (p.p.m.)	NO$_3^-$ (p.p.m.)	*Total solids* (p.p.m.)	*Reference*
South Victoria Land dry valleys															
Lake Vanda	1 Jan. 1962	6	3·5	7·4	555	30	9	[illegible]	44	134	4	—	—	—	Angino and others, 1965
		18	6·7	7·4	1,990	99	29	47	181	564	12	—	—	—	
		42	8·5	7·3	2,700	127	35	70	264	827	36	—	—	—	
		48	10·5	7·2	5,265	228	53	173	614	1,910	80	—	—	—	
		51	12·0	6·9	22,220	746	142	915	2,730	8,590	200	—	—	—	
		66	22·0	6·1	250,000*	6,761	766	7,684	24,254	75,870	770	—	—	—	
Lake Bonney	15 Dec. 1962	6	1·25	8·1	3,085	327	25	87	73	765	168	0	—	—	Angino and others, 1964
		15	7·00	6·8	140,845	16,900	1,260	13,000	1,110	70,300	2,230	0·34	—	—	
		30	0·75†	7·3	212,765	41,300	2,730	25,900	1,540	140,000	2,850	0	—	—	
Lake Fryxell	Summer	4·5	1·0	7·9	1,600	172	23	108	42	640	40	0·4	—	—	Angino and others, 1962
		6	1·25	7·2	4,854	1,350	108	129	77	1,640	144	1·3	—	—	
		12	2·25	7·0	22,727	2,050	187	229	33	2,740	460	2·1	—	—	
Lake Porkchop	Summer	—	—	—	—	5	2·7	2·6	7·7	5·6	12·7	—	—	—	Yamagata and others, 1967*a*
Lake Penny	Summer	—	—	—	—	12	6·7	2·7	20·2	25·6	19·8	—	—	—	Yamagata and others, 1967*a*
Lake Ward	Summer	—	—	—	—	5	2·3	1·4	10·4	11·9	11·9	—	—	—	Yamagata and others, 1967*a*
Lake Marshall	Summer	—	—	—	—	24	4·2	1·6	13·2	14·4	39·5	—	—	—	Yamagata and others, 1967*a*
Don Juan Pond	Summer	—	—	—	—	11,500	160	1,200	114,000	212,000	11	—	12·7	—	Meyer and others, 1962
Schirmacher Ponds															
Lake near glacier	12 Feb. 1961	—	—	5·2	—	4·14‡		1·32	2·20	3·85	9·12	—	—	26·73	Bardin and Leflat, 1965
Lake Figurnoye (=Zub)	16 Feb. 1961	—	—	5·6	—	4·83		0·24	2·00	3·50	5·76	—	—	23·16	Bardin and Leflat, 1965
Lake Dlinnoye	13 Feb. 1961	—	—	6·5	—	7·13		2·16	3·60	7·35	8·16	—	—	46·06	Bardin and Leflat, 1965
Unnamed lake	10 Feb. 1961	—	—	6·4	—	31·74		4·80	6·40	25·90	25·44	—	—	144·91	Bardin and Leflat, 1965
Lake Krugloye	12 Feb. 1961	—	—	5·1	—	83·26		14·40	18·80	95·90	80·16	—	—	374·87	Bardin and Leflat, 1965
Unnamed lake	14 Feb. 1961	—	—	6·8	—	22·31		7·68	17·20	20·30	41·76	—	—	170·71	Bardin and Leflat, 1965
"Sea inlet"	13 Feb. 1961	—	—	6·3	—	20·70		1·92	2·80	26·95	14·88	—	—	74·57	Bardin and Leflat, 1965
Antarctic sea-water	—	—	—	—	—	10,556	380	1,272	400	18,980	2,649	—	—	—	Meyer and others, 1962

* From Armitage and House (1962).

† Bottom temperatures as low as −2·5° C recorded.

‡ Combined Na$^+$K$^+$ concentration.

The Schirmacher Ponds "oasis" appears to have been deglaciated relatively recently (Bardin, 1964). Both this "oasis" and the Bunger Hills may be representative of earlier stages in the history of the south Victoria Land dry valleys. Although the unique climate may be an effect and not a cause of the original deglaciation, the conditions, once established, do promote thawing of surrounding ice and are therefore the cause of further deglaciation. The Schirmacher Ponds "oasis" may eventually extend as far south as Wohlthatmassivet where further progress may be halted by the increase in altitude, as may have happened in the south Victoria Land dry valleys (Wilson, 1967).

The varying proximity of different areas to external sources of water promote aridity gradients within each "oasis". The effects of variation in aridity at inter- and intra-oasis level can clearly be seen in weathering processes, vegetation and the considerable diversity of lake and pond types.

Weathering

Extensive weathering by wind erosion and exfoliation occurs in most areas of the south Victoria Land dry valleys and Bunger Hills. In the few areas where water is released from snowdrifts and in areas where water flows in from nearby glaciers and icefields, weathering is also by frost action and nivation. Salt weathering has been observed throughout the south Victoria Land dry valleys (Wellman and Wilson, 1965; Neall and Smith, 1967). Salt solutions, predominantly nitrates, chlorides and calcite, carried inland from the sea, penetrate minute cracks, and on crystallizing rend the rocks apart. Because of the aridity, rocks and soils in these oases contain large amounts of soluble salts. These salts appear to be leached out and made available to the lakes and ponds in only a few areas. Wilson (1967) has pointed out that the low air temperatures are a further restriction and permafrost restricts the percolation of ground water through sediments. In temperate regions this can contribute large quantities of soluble salts to lakes and ponds. Consequently, primary production in certain lakes is apparently restricted by shortage of nutrient salts (p. 49), although soluble nitrates at least are known to be abundant in surrounding rocks.

There has been little weathering in the Schirmacher Ponds area, which appears to have been only recently deglaciated. It is most apparent, in the form of nivation in *névé* basins and frost-wedging where snowdrifts lie on the leeward sides of hills near the continental ice sheet. Considerable water erosion occurs in localized areas where the main streams of melt water enter the "oasis". No information appears to be available on the cycling of salts in this "oasis". Biological observations (p. 50) suggest that the supply of nutrient salts is not limiting. This is probably an indirect consequence of the influx of melt water from surrounding icefields.

Vegetation

The vegetation in the "oases" is extremely sparse and often consists only of crustose lichens and moss cushions. Even lichens are absent from most areas of the south Victoria Land dry valley floors. Mosses tend to be restricted to water channels and seepage areas (Nudel'man, 1959). Small amounts of algae also grow in seepage pathways; Holm-Hansen (1964) reported extensive mats of *Prasiola crispa* in Taylor Dry Valley, south Victoria Land dry valleys. The availability of liquid water certainly appears to be the main limiting factor, for Bardin (1964) discovered dense colonies of fructose lichens and mosses covering an area of several square metres in one wet narrow fissure in the Schirmacher Ponds oasis. Another important factor must be the lack of shelter by snow cover from the severe low temperatures and high winds during winter. Few lakes, pools and streams in the "oases" can therefore gain humic compounds produced by external biological agents.

Lakes and pools

Chemical properties. The mineral content of the water bodies in each "oasis" varies considerably (Table II). Some contain almost pure water but most are brackish or extremely saline. The mineral content in most cases appears to be mainly related to the amount of inflowing melt water and the evaporation rate. Hence the lakes and pools of the Schirmacher Ponds contain generally fresher waters than those of the south Victoria Land dry valleys. However, in both areas most lakes and pools are drying up and are surrounded by beach lines marking earlier levels of their waters. There are also many dry beds. Unfortunately the water bodies of the Bunger Hills cannot be brought into the present discussion, the only information available being that some of them are saline to the taste.

Salinities 14 times greater than sea-water have been recorded in the south Victoria Land dry valleys (Meyer and others, 1962). The larger lakes of this "oasis" have strange chemical profiles. The upper layers of water are essentially fresh (total ionic concentration less than 1,000 p.p.m.), although the chloride concentration is high (Table II). The lower layers, however, are extremely saline (Lake Vanda, 3 × sea-water; Lake Bonney, 11·7 × sea-water).

Goldman and others (1967) stated that the chemical content of Lake Vanda varies very little throughout the year but no values were given. No other work on seasonal variation appears to have been carried out.

The origin of the salts in the south Victoria Land dry valleys lakes is not known and evidence gained from chemical assay is inconclusive (Angino and others, 1962, 1964, 1965). The salts may have resulted from volcanic activity, wind-blown sea spray and relict sea-water. Some research workers have suggested that salts are slowly leached from surrounding rock in spite of the arid conditions (Meyer and others, 1962; Tedrow and others, 1963; Jones and Faure, 1967). The low deuterium content of the water (Ragotzkie and Friedman, 1965) and the geomorphology of the area (Nichols, 1962*a*) suggest that Lake Vanda in Wright Valley does not contain fossil sea-water. The concentration of salts in the bottom waters is thought to have arisen from the evaporation of a larger, less saline lake during a period to which Nichols (1962*b*, 1963) referred as Loop–Trilogy interglacial time. Following a climate change in late Trilogy time (7,000 yr. ago) melt water from retreating glaciers entered the lake basin to form the upper fresh layer. Little mixing occurred for several reasons: there was a considerable density difference; the amount of inflowing melt water was originally small and therefore its velocity was negligible; a permanent ice cover prevented wind-generated turbulence; the melt water may have flowed out over an ice cover initially; the fresh-water layer, as it grew deeper, inhibited mixing. Wilson (1964) suggested that the climatic change occurred only 1,200 yr. ago. A series of well-preserved terraces, rising 50 m. above the present lake level, indicate that the volume of water in the lake is again decreasing. Data obtained for Lakes Bonney and Fryxell in Taylor Valley suggest, but do not prove, a sea-water origin for these waters or extensive sea-water contamination (Angino and others, 1964; Boswell and others, 1967). Analysis of ionic ratios also suggests warm springs and leaching as sources of ions. More recent work is no more conclusive (Yamagata and others, 1967*a*).

Holm-Hansen (1963*a*) has demonstrated, by ^{15}N assimilation, that the alga *Nostoc commune* is able to fix atmospheric nitrogen. Although the alga is found in the south Victoria Land dry valleys, its distribution is extremely localized and few water bodies can benefit from soluble nitrogen released from these plants.

No work has been carried out on the fresh-water lakes and pools known to exist in this "oasis" (Table II).

In the Schirmacher Ponds the variation in the mineral content of the water bodies shows a south to north trend, the southern lakes receiving the most melt water and generally having the lowest mineral contents. Many of these southern lakes are interconnected and all have outflow streams. Their levels fluctuate sharply from day to day with the amounts of melt water. The water level of Lake Glubokoye (maximum recorded depth 32 m.) may rise by over 3 m. in summer (Simonov and Fedotov, 1964). In contrast, the conditions in the central and northern parts of the "oasis" approach the general conditions of the south Victoria Land dry valleys. The water bodies are generally small shallow ponds, about 100 m. in diameter and 1 m. in depth. They receive very little melt water and are drying up. Dry lake depressions are frequent in the northern part of the Schirmacher Ponds. In addition, numerous pools appear all over the Schirmacher Ponds during the melt period but their waters quickly evaporate in the dry air of the strong prevailing winds. No chemical details of the more saline water bodies are available.

Bardin and Leflat (1965) divided the lake and pond waters of the Schirmacher Ponds "oasis" into three types:

Sulphate-sodium type	Ionic concentration is low and ionic composition is similar to that of snow. Found in lakes receiving large amounts of melt water.

Carbonate-sodium type	Total ions vary from 46 to 171 mg./l. Water produced by metamorphosis [*sic*] of sulphate-sodium snow water, presumably by concentration through evaporation.
Chloride-sodium type	A further stage in the metamorphosis [*sic*] of sulphate-sodium snow water.

The sodium : chloride ratio was greater than 1 in all the lakes Bardin and Leflat examined and they considered this strong evidence for the waters having a common continental origin (ice and snow melt and precipitation) and there having been no contamination by sea-water.

Physical properties. The extent to which lakes and pools freeze, and the duration of the ice cover, are determined by many factors. Perhaps the most important single factor in the "oases" is salinity. The salts in many lakes and ponds have probably depressed the freezing point of the waters below the ambient mean winter temperature, which may be below −40° C. From October to December 1961, Meyer and others (1962) recorded temperatures ranging from −24° to −3° C in Don Juan Pond, south Victoria Land dry valleys. The freezing point of the water was −48° C. In other lakes and pools, concentration by removal of water molecules during the actual process of freezing may eventually depress the freezing point below ambient temperature.

Important factors for less saline waters are mean depth and volume, duration of polar night, persistence of insulating snow cover, exposure to solar radiation, nature of surrounding substrata and elevation of site. Pools and shallow lakes freeze solid during winter but thaw completely at sometime during summer. Deeper lakes may freeze to depths of over 6 m. and retain a thick ice cover over all but shallow peripheral areas during summer. The ice layer is insulating and can therefore limit the final ice thickness achieved under a given ambient mean winter temperature. The main source of heat for most lakes is solar radiation. Persistent snow cover with its high albedo can prolong the period of ice cover but this is unlikely to be a problem to most lakes and pools in these arid areas.

The effect of the duration of polar night is clearly shown by Lake Figurnoye, Schirmacher Ponds. Although shallow (4–6 m.) and having a total salt content of only 23 p.p.m., the lake has an ice cover only 2·0 m. thick during winter (Simonov and Fedotov, 1964) when the mean ambient temperature is −16° C. The lake must receive all its heat from solar radiation as there are no geothermal sources. As the ice is usually snow-free, a considerable amount of solar radiation must reach the underlying water. The heat budget must be balanced or negative for a period of time only slightly longer than the short (under 2 months) polar night. A temperature of 4·3° C for the whole water layer has been recorded in mid-November but this temperature may have been reached much earlier. Were the polar night as long as in the south Victoria Land dry valleys (4 months), the lake would probably be frozen solid for the greater part of the winter.

Examples illustrating the effect of different surrounding substrates may also be drawn from the Schirmacher Ponds "oasis". Lakes closely associated with the continental ice sheet freeze over first, followed by the central then northern lakes (Bardin, 1964). Conversely, the northern and central lakes, which are surrounded entirely by rock outcrops, become ice-free before the southern lakes, which may not open until late January, if at all. The effect cannot, however, be due entirely to the relative albedos of rock and ice/snow. Inflowing water can also raise or lower the temperature. The close proximity of ice and snow fields implies copious supplies of water which have gained little, if any, heat from contact with solar-heated rock.

Variation in elevation usually means variation in thermal environment. All other things being equal, elevation will have minimal effect in these areas where solar radiation is the all-important heating factor. However, Calkin and Bull (1967) quoted elevation as being partly responsible for the fact that Lake Vida, Victoria Valley, south Victoria Land dry valleys, is permanently frozen solid whilst lakes in environments similar except for elevation are only frozen to depths of 4–6 m.

The factors affecting depth and duration of ice cover, with the exception of polar night, are independent of latitude.

Summer temperatures of most lakes and pools are dependent upon insolation and therefore vary considerably. The range is generally from 1° to 8° C, but temperatures as high as 15° to

17° C have been recorded in shallow water bodies (Kruchinin and Simonov, 1967*a*) which lose completely any ice cover they may have acquired. Although during calm periods with intense sunlight, temperatures are usually highest at the bottom of these shallow lakes and pools, where most of the solar energy is absorbed, such waters are normally isothermal during the summer because of complete and continual stirring by strong winds. In deep lakes which remain ice-covered but for narrow leads formed over the shallow peripheral regions an inverse thermal gradient is maintained in their waters throughout the year.

Unusual temperature profiles have been recorded for several saline lakes in the south Victoria Land dry valleys (Fig. 2). The temperature at the bottom of Lake Vanda is around +25° C throughout the year. The maximum temperature in Lake Bonney is +7·5° C but this occurs in water at a depth of 13 m. Temperatures as low as −2·5° C have been recorded near the lake bottom. Lake Fryxell has a temperature profile similar to Lake Bonney, the maximum temperature of +2·3° C occurring at 9 m. depth. All three lakes have a permanent ice cover and occur in an area where the ambient mean annual temperature is −18° C. The decrease in density expected from the increase in temperature is more than compensated in each lake by an increase in salt content. The temperature profiles are stable and vary very little throughout the year. Conflicting evidence and interpretation have produced two theories for the heat source in these lakes (Wilson and Wellman, 1962; Angino and others, 1964, 1965; Hoare and others, 1964, 1965; Ragotzkie and Likens, 1964; Shirtcliffe, 1964; Shirtcliffe and Benseman, 1964; Hoare, 1966, 1968; Goldman and others, 1967). It seems likely that Lake Vanda gains heat

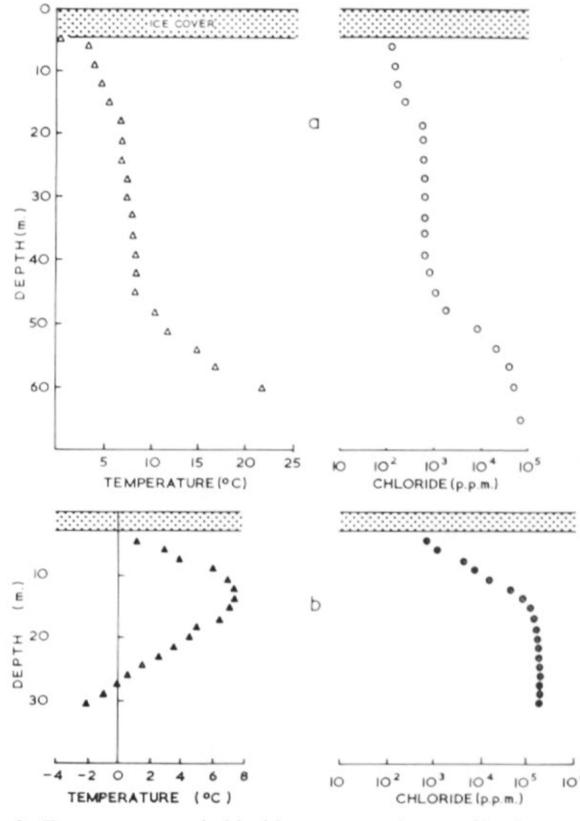

Fig. 2. Temperature and chloride-concentration profiles for:
a. Lake Vanda (data from Angino and others (1965)).
b. Lake Bonney (data from Shirtcliffe and Benseman (1964)).

from both solar radiation and geothermal sources, whereas Lakes Bonney and Fryxell receive heat from solar radiation only. Controversy and investigation continue.

Solar heating at depth implies extremely clear ice. The albedo of the ice cover over Lakes Vanda and Bonney varies from 20 to 60 per cent during the summer as the surface is altered by insolation and ablation (Goldman and others, 1967). Apart from the surface layers, the ice is extremely clear. Measurements of light penetration through the 3–4 m. of ice cover and waters of these two lakes showed that over 21 per cent of incident visible light penetrated the ice of Bonney and 13–20 per cent entered the waters of Lake Vanda (Mason and others, 1963). Long vertical crystals of 5 cm. average width, extending from top to bottom of the ice sheet, probably act as light pipes and facilitate the transmission of solar energy into the water. Vertical extinction coefficients for the upper waters were 0·141 (Lake Bonney) and 0·049 (Lake Vanda) for unfiltered light. Lake Vanda is probably one of the clearest lakes in the world with extinction coefficients of 0·038 in blue light and 0·055 in green light (5 January 1963). The waters of many lakes and pools in the "oases" are very clear since they receive little allochthonous material.

"*Sea inlets*" *of the Schirmacher Ponds*

An interconnected chain of unique lakes lies between the rock of the Schirmacher Ponds and the ice shelf to the north (Kruchinin and Simonov, 1967*b*). The lake basins are drowned cirques and range in depth from 25 m. (eastern lake) to 150 m. (western lake). All have a permanent ice cover, 3·0–3·5 m. thick in winter and 2·0–2·5 m. in summer. Narrow leads form along the landward edge of the lakes during the summer. Water levels rise and fall over irregular semi-diurnal periods. The average amplitude of the fluctuations varies from 1·5 m. (springs) to 0·3 m. (neaps) and the absolute maximum recorded is 2·5 m. These figures are similar to those recorded for the open sea, 100 km. to the north. There is obviously some channel under the ice shelf connecting lake to sea and the lakes were originally described as sea inlets. However, chemical analyses have subsequently shown that the lakes contain only fresh water (Table II). The temperature regime also differs from that typical of sea inlets. The temperature of Antarctic sea surface waters usually fluctuates between −1·7° and −1·9° C but water temperatures recorded in these lakes only vary between +0·1° and +0·3° C.

A recent survey of the subglacial relief of this area found that, north of the Schirmacher Ponds, the bedrock falls steeply to depths of over 800 m. and afterwards rises in the direction of the seaward edge of the ice shelf. The bedrock is very dissected and, although the ice shelf is 500 m. thick, sea-water must penetrate quite close to the Schirmacher Ponds. The lakes are thought to be connected to the sea by one or several steep, relatively narrow fissures in the bedrock leading from the western lake. The fresh water probably descends a considerable distance down these fissures, if not over their whole length. Because of the supercooling of fresh water in contact with sea-water, under-water ice may form a porous plug in the fissures. During incoming tides, fresh water from the fissures enters the lake system under the pressure of sea-water, returning to the fissures as the pressure subsides. No mixing occurs because of the considerable differences in density. Melt water flowing into the lakes is discharged into the sea through these sub-lacustrine fissures. When the excess melt water passes from the narrow fissures into the wider channel(s) filled with sea-water, it may freeze at the bottom of the floating ice shelf.

Lakes and pools of the continental coastal areas and adjacent islands

Limnological research has been carried out in three main areas—Ross Island, Ongul Islands and the Vestfold Hills (Fig. 1). The small amount of work that has been carried out in other coastal areas (Thomas, 1965; Fukushima, 1966; Meyer and others, 1967) indicates that the water bodies found in the main research areas are probably representative of all coastal types.

Geography and geology

Ross Island (lat. 77°33′S., long. 168°00′E.) lies east of McMurdo Sound at the outer edge of the Ross Ice Shelf. The island is 2,300 km.^{2} in area and is formed by four large, and several small, volcanic cones. Mount

Erebus rises 3,721 m. above sea-level. The ground falls steeply from the mountains in a series of ridges and parasitic volcanic cones. The island is ice-clad but for a few coastal areas, the largest of which are Capes Barne, Crozier and Royds, and Hut Point Peninsula. The exposed rock is trachyte and basalt covered with kenyte, an alkali olivine-basalt lava. Erratics of igneous, sedimentary and metamorphic rocks, and moraines are common (Ferrar, 1907; David and Priestley, 1914; Debenham, 1923; Treves, 1962). Numerous lakes and pools lie in valleys between the high dykes (65–100 m.) and ridges of the ice-free areas. The majority of the water bodies are small and very shallow (mean depth less than 1 m.). Blue Lake (Cape Royds) is one of the largest, having a length of 800 m. and a maximum recorded depth of 7 m. The origins of the basins may be complex. David and Priestley (1914) ascribed their origin to corrasion by an extension of the Ross Ice Shelf. However, Debenham (1923) pointed out that this description was incomplete. The present basins are depressions left after several flows of lava had solidified over land probably made irregular by glacial corrasion. Debenham also suggested that two of them, Deep Lake and Sunk Lake, are the result of heavy lava flows consolidating over ice; the basins were formed by settlement and faulting of the lava after it had solidified and while the ice disappeared from underneath.

The Ongul Islands (lat. 69°00′S., long. 39°35′E.) lie in the north-east corner of Lützow-Holmbukta. The group consists of two main islands separated by a strait only 30 m. wide, and many scattered small islands. The terrain is rugged although the highest point is only 48 m. a.s.l. There is no permanent ice cover and during the summer more than 80 per cent of the land is clear of snow. The hills, mainly *roches moutonnées*, have a relief of 15–20 m. and the rock is largely microperthite-granodiorite-gneiss, showing various combinations of biotite, hornblende, hypersthene, augite and garnet (Tatsumi and others, 1957). The valleys are mostly covered with sands and gravels scattered with erratics of exotic rock such as basalt, bearing glacial striae. The islands were obviously once covered with an extension of the continental ice sheet. Numerous pools occupy depressions, presumably ice-scoured, in the valleys. The pools are small, averaging 20–30 m. in diameter, and 30 cm. in depth (Fukushima, 1961). There are also streams. Some of the shallow basins have probably been filled with wind-blown sand and gravel forming the wet areas which Fukushima referred to as "marshy" areas.

The Vestfold Hills (lat. 68°25′–68°40′S., long. 77°50′–78°35′E.) lie on the coast of Princess Elizabeth Land where they form, with numerous offlying islands, an ice-free area, approximately 500 km.². The mainland portion is deeply dissected by extensive fjords. Hills and islands rise to a maximum altitude of about 160 m. but they are mostly between 30 and 100 m. in height. The rock is of a variety of gneiss, predominantly pyroxene-quartz-feldspar, intruded by numerous dolerite dykes (McLeod, 1964*b*). Numerous lakes and pools lie in depressions produced by glacial corrasion. The largest lakes are several kilometres in length and are up to 100 m. deep.

Climate

The climate in continental coastal areas of Antarctica is largely determined by the interaction of dry katabatic winds flowing from the continental plateau and moist oceanic winds moving in from the north-east. Conditions are generally less arid than those prevailing in the "oases". Relative humidities and total annual precipitation vary widely from area to area as the balance between the differing air masses is affected by local topography. Katabatic winds rapidly decrease in strength on reaching sea-level (Dralkin; cited by Rubin, 1965) and any drift snow carried by them is deposited in a zone between 10 and 30 km. offshore. This phenomenon may account for a large proportion of the snow deposited on the Ongul Islands, which are normally separated from the open sea by up to 100 km. of sea ice. Absorption and re-radiation of solar radiation by bare rock ameliorates the summer temperatures on the Ongul Islands and in the Vestfold Hills. The effect is counterbalanced on Ross Island by the high thermal capacity of the ice cap covering most of the island.

Weathering

Wind erosion, frost and salt wedging, and nivation occur in the continental coastal areas. Wind erosion is the predominant process in the Ongul Islands (Tatsumi and others, 1957) and in the Vestfold Hills (Law, 1959) but frost wedging is the most extensive form of weathering in the McMurdo Sound area and probably in most other continental coastal areas (Nichols, 1966; Ugolini, 1970). Solifluction is affecting the surface layers of soil in some areas but the phenomenon is not widespread (Nichols, 1966; MacNamara, 1969). Soluble salts released by weathering are more readily available to lakes and pools in these areas than in the "oases" because of the higher precipitation amounts. However, the major source of ions is sea-water.

Vegetation

Climatic differences between the three coastal areas under discussion and the "oases" are insufficient to cause any significant difference in the terrestrial flora. The areas are therefore remarkably sterile; a few lichens and mosses grow on and between the rocks, and small

Table III. Physical and chemical properties of lakes in the continental coastal areas

Location	*Date*	*Depth* (m.)	*Temp.* (°C)	*pH*	*Conductivity* (µmho)	Na^+ (p.p.m.)	K^+ (p.p.m.)	Mg^{++} (p.p.m.)	Ca^{++} (p.p.m.)	Cl^- (p.p.m.)	$SO_4^=$ (p.p.m.)	$PO_4^{\equiv}$ (p.p.m.)	NO_3^- (p.p.m.)	*Total solids* (p.p.m.)	*Reference*
Ross Island															
Cape Evans															
Unnamed pool	9 Jan. 1964	—	5·4	—	—	1,600	10·1	106·4	38·5	1,549	313	—	—	—	Yamagata and others, 1967*b*
Unnamed pool	9 Jan. 1964	—	4·5	—	—	2,550	12·5	129·7	55·4	2,406	644	—	—	—	Yamagata and others, 1967*b*
Unnamed pool	9 Jan. 1964	—	2·2	—	—	480	17·7	37·3	18·6	540	465	—	—	—	Yamagata and others, 1967*b*
Unnamed pool	9 Jan. 1964	—	3·7	—	—	1,800	72·0	183·8	80·0	2,782	867	—	—	—	Yamagata and others, 1967*b*
Unnamed pool	9 Jan. 1964	—	3·3	—	—	3,710	203·0	395·0	156·0	6,042	1,140	—	—	—	Yamagata and others, 1967*b*
Skua Lake	9 Jan. 1964	—	5·8	—	—	108	9·6	15·4	7·1	221	41	—	—	—	Yamagata and others, 1967*b*
Skua Lake	Summer	—	8·0	8·52	1,400	—	—	—	—	510	60	—	—	—	Armitage and House, 1962
Unnamed pool	Summer	—	6·5	9·25	6,000	—	—	—	—	2,270	380	—	—	—	Armitage and House, 1962
Unnamed pool	Summer	—	6·5	8·98	3,000	—	—	—	—	1,445	—	—	—	—	Armitage and House, 1962
Cape Royds															
Unnamed lake	Summer	—	6·0	8·62	610	—	—	—	—	190	—	—	—	—	Armitage and House, 1962
Clear Lake	Summer	—	1·2	9·5	690	—	—	—	—	220	44	—	—	—	Armitage and House, 1962
Green Lake	Summer	—	4·8	9·52	6,400	—	—	—	—	2,715	480	—	—	—	Armitage and House, 1962
Coast Lake	Summer	—	4·5–6·5	8·32	750	—	—	—	—	275	40	—	—	—	Armitage and House, 1962
Home Lake	Summer	—	3·2	9·0	8,200	—	—	—	—	1,675	1,220	—	—	—	Armitage and House, 1962
Home Lake	14 Jan. 1964	—	3·4	—	—	905	64·0	59·6	28·4	1,061	708	—	—	—	Yamagata and others, 1967*b*
Blue Lake	14 Jan. 1964	—	0·05	—	—	15·5	3·2	0·9	1·1	30·5	0	—	—	—	Yamagata and others, 1967*b*
Unnamed pool	14 Jan. 1964	—	4·8	—	—	2,460	264·0	228·0	55·2	3,891	674	—	—	—	Yamagata and others, 1967*b*
Crater pool	25 Dec. 1963	—	1·00	—	—	—	—	1·4	4·0	18·9	2·0	—	—	—	Yamagata and others, 1967*b*
Stranded moraines pool	10 Jan. 1964	—	0·25	—	—	10·5	1·9	1·0	7·9	26·7	1·0	—	—	—	Yamagata and others, 1967*b*
Ongul Islands															
Lake O-ike	21 Jan. 1962	—	7·0	7·0	5,500	51·1	2·5	7·2	5·4	100	13·1	—	—	—	Yamagata and others, 1967*b*
South Pond	21 Jan. 1962	—	6·0	7·3	5,800	47·5	2·4	5·8	3·7	95·6	18·8	—	—	—	Yamagata and others, 1967*b*
Unnamed pool	22 Jan. 1962	—	4·0	7·0	1,100	260	12·0	30·4	17·8	464	72·2	—	—	—	Yamagata and others, 1967*b*
Lake Kamome	23 Jan. 1962	—	10·0	7·0	2,200	92·6	4·2	14·1	9·6	185	14·7	—	—	—	Yamagata and others, 1967*b*
Lake Miname	23 Jan. 1962	—	11·0	7·0	460	499·0	26·1	66·3	47·6	1,005	119	—	—	—	Yamagata and others, 1967*b*
Unnamed pool	23 Jan. 1962	—	15·0	7·0	4,500	47·5	2·5	4·4	3·8	85·1	12·4	—	—	—	Yamagata and others, 1967*b*
Vestfold Hills															
Lake Dingle	27 Aug. 1962	0	−17·3	—	—	66,600	2,610	9,410	2,220	137,000	2,860	—	—	221,000	McLeod, 1964*a*
		6·7	−17·1	—	—	69,300	2,700	9,840	2,240	139,000	2,910	—	—	227,100	
		13·7	−16·8	—	—	70,600	2,700	9,870	2,240	140,000	2,910	—	—	229,100	
	21 Jan. 1962	0	−3·9	—	—	67,000	2,610	8,560	1,990	125,000	2,980	—	—	209,000	McLeod, 1964*a*
		5·2	+1·6	—	—	71,000	2,700	9,860	2,260	143,000	2,930	—	—	232,000	
		10·3	+5·0	—	—	71,500	2,700	9,850	2,270	145,000	2,940	—	—	235,700	
Lake Stinear	27 Aug. 1962	0	−19·4	—	—	78,600	2,610	10,100	2,[illegible]	148,000	2,620	—	—	245,000	McLeod, 1964*a*
		2	−17·9	—	—	78,600	2,610	10,600	2,[illegible]	151,000	2,640	—	—	249,000	
		5	−18·0	—	—	78,600	2,620	10,500	2,140	152,000	2,700	—	—	248,700	
	21 Jan. 1963	0	−6·7	—	—	78,600	2,620	10,050	2,060	148,000	2,780	—	—	245,100	McLeod, 1964*a*
		6·7	−2·8	—	—	78,600	2,620	10,450	2,140	151,000	2,610	—	—	248,600	
		13·6	+4·7	—	—	78,600	2,620	10,500	2,180	153,000	2,670	—	—	251,000	
Lake Deep	21 Jan. 1963	0	−7·7	—	—	78,800	4,710	14,850	2,280	169,000	2,470	—	—	273,000	McLeod, 1964*a*
		7·7	+4·7	—	—	78,800	4,710	14,980	2,280	169,000	2,470	—	—	273,300	
		15·2	+4·7	—	—	78,800	4,710	14,950	2,280	169,000	2,550	—	—	273,400	
Lake Chubb	21 Aug. 1962	0	—	—	—	78,700	4,710	14,880	2,120	170,000	2,280	—	—	274,100	McLeod, 1964*a*

amounts of algae grow in seepage pathways. Few water bodies can receive allochthonous organic material. However, conditions in other continental coastal areas are known to be more favourable for plant life. Rudolph (1963) described the vegetation of Cape Hallett, north Victoria Land (lat. 72°19′S., long. 170°18′E.) as luxuriant compared with the McMurdo Sound area.

Lakes and pools

Chemical properties. The mineral content of lakes and pools in the continental coastal areas varies considerably (Table III). But here high salinities are primarily correlated with sea-water contamination. David and Priestley (1914) concluded that all the waters they examined on Ross Island were contaminated by sea spray. They described the ice of Green Lake as being sticky with sea spray after heavy blizzards which occurred before the sea froze. They also pointed out that even when the sea is frozen, extruded salts are picked up by the overlying snow which is eventually blown inland. Watanuki (1963) has measured the large amounts of salt carried over the Ongul Islands in the strong prevailing winds. Most workers have concluded that the pools here contain water originating as snow, now heavily contaminated by wind-blown sea spray (Sugawara and Torii, 1959; Fukushima, 1961; Sugawara, 1961; Meguro, 1962; Ambe, 1966). Sugawara attributed the variation between ratios of certain ions in pool and sea water to synfractionation (the successive fractionation and separation of various ions through evaporation while the spray droplet is suspended in air; certain salts are lost before the droplet itself falls). Other workers have been more cautious and concluded that there are, as yet, insufficient data to explain the origin of the water and the subsequent enrichment of certain ions (Yamagata and others, 1967*a*).

Law (1959) was of the opinion that the salinity of all waters in the Vestfold Hills was primarily due to windborne sea spray. More recent work by McLeod (1964*a*), however, has clearly shown that at least one valley was originally a narrow arm of the sea and was eventually isolated by isostatic uplift of the land or eustatic fall of the sea. The ground is impregnated with salt and four lakes at least contain relict sea-water which has been concentrated by evaporation and the addition of salts leached from the surrounding ground. McLeod attributed the change in ratios of certain ions (from the ratios in the original sea-water) to the deposition of certain salts in the lake sediments, the principal one being sodium sulphate (similar ideas have been invoked for explaining ionic ratio changes in Lakes Bonney, Fryxell and Vanda of the south Victoria Land dry valleys (Angino and others, 1962, 1964, 1965)).

Although not the prime factor, as in the "oases", evaporation may still contribute significantly to the high salinities recorded in most areas. The effect is most pronounced in the Vestfold Hills where most of the lowland lakes are undrained and brackish or saline (Law, 1959). On Ross Island, water loss by ablation of the ice surface may amount to 15–40 cm./yr. (David and Priestley, 1914).

Some of these coastal lakes may have access to a further and very important source of ions—the organic wastes of birds and seals. Goldman and others (1963) have recorded the effect on productivity in lakes on Ross Island (p. 50).

There has been practically no work on seasonal variation in chemical composition and ionic concentration. McLeod (1964*a*) reported a spring/summer decrease in salinity occurring in the surface waters of the very saline Lakes Dingle, Stinear, Deep and Chub in the Vestfold Hills. This was caused by inflowing melt water forming a layer on the denser lake water before being gradually mixed by wind action.

Physical properties. The salinity of the waters affects the freezing-over of relatively few lakes in the continental coastal areas. Brine with a freezing point of −45° C was found under 1·75 m. of ice covering Green Lake, a 2 m. deep lake at Cape Royds, Ross Island, in June 1908 (Mawson, 1916). Lakes Dingle, Stinear, Deep and Chub, Vestfold Hills, appear to have freezing points close to the ambient mean winter temperature of −17° C. Lakes Dingle and Stinear usually freeze over from July to November but the ice often consists of a slushy mixture of ice crystals and snow (McLeod, 1964*a*).

In general, the most important factors are mean depth and water volume, and most water bodies freeze solid. The deeper lakes on Ross Island freeze to depths of over 6 m. and retain a thick ice cover over all but shallow peripheral areas during the summer (David and Priestley, 1914). Snow cover may prolong the frozen period in some areas but no information is available. Ablation/evaporation rates are high during the summer (Rusin, 1959) and small pools with limited sources of melt water may dry up (Armitage and House, 1962). The permanently frozen surface of Sunk Lake lies 6 m. below sea-level probably as a result of ablation (David and Priestley, 1914).

Summer conditions parallel those recorded for water bodies in the "oases" and are determined by solar radiation and the temperature of inflowing water (Armitage and House, 1962). Temperatures as high as 16° C have been recorded in pools and shallow lakes which thaw out completely (David and Priestley, 1914). Although the volcano Mount Erebus is still active, there are no reports of any lake on Ross Island being heated by geothermal sources.

Practically no information is available on the optical properties of the ice cover and waters of lakes and pools in these areas. Members of the British Antarctic Expedition reported that the ice of certain lakes was extremely clear and that benthic algae could be seen through it (Murray, 1910*b*; David and Priestley, 1914). The work of Goldman and others (1963) clearly indicates that the waters of some shallow Ross Island lakes and pools are very transparent; algae are limited by high light intensities.

Lakes and pools of the Antarctic Peninsula and adjacent islands

This region includes the South Shetland Islands and the South Orkney Islands, the southern groups along the Scotia Ridge (Fig. 1). The earliest fresh-water biological collections were made in this region (Hooker, 1847) and collections and general narratives from the numerous subsequent expeditions indicate that there is a relatively rich fresh-water flora and fauna (de Mann, 1904; Murray, 1906; Fritsch, 1912*a*, *b*; Gain, 1912; Carlson, 1913; Harding, 1941; Bryant, 1945). A recent paper by Corte (1962) on the algae of lakes in the Hope Bay area was the first to include details of the fresh-water environment. A comprehensive programme of limnological studies is now being carried out on Signy Island, South Orkney Islands, and detailed descriptions of lakes and pools have been published (Heywood, 1967*a*, *b*, 1968; Goodman, 1969).

Geography and geology

The Antarctic Peninsula, the South Shetland Islands and the South Orkney Islands extend in an arc, north-north-east from lat. 73°25′ to 60°40′S., between long. 72°00′ and 44°30′W. Physiographically the region is very varied. The Antarctic Peninsula has a backbone formed by a high (2,000 m. in the south), narrow, ice-clad central plateau and mountains. The west coast is a typical ice-cliffed fjord coast, whereas the greater part of the east coast is bordered by an ice shelf of varying width (Adie, 1964). The islands are alpine although they rarely attain great heights. Large areas of lowland, particularly along the western coastline of the Antarctic Peninsula and on the islands, are ice-free and become snow-free during the summer months. The geology is complex (Adie, 1964) with many granite and diorite intrusions. The bedrock of the valleys is covered by moraines and, in recently active volcanic areas, scoria. Numerous lakes and pools lie in the lowland areas. The physiography of the region suggests that the majority of basins are of glacial origin but others could have been formed by volcanic and tectonic action. Hawkes (1961) reported lake basins of volcanic origin on Deception Island, South Shetland Islands. Lake basins in the Hope Bay area, Antarctic Peninsula, and on Signy Island, South Orkney Islands, are of glacial origin and have been further deepened by moraines. Lakes, so far examined, are small; the largest, Lake Boeckella at Hope Bay, has a surface area of 4 km.^{2} with a maximum recorded depth of only 6 m. Lake 12, a 0·02 km.^{2} cirque lake on Signy Island, has a maximum recorded depth of 15 m. Bryant (1945) found only shallow pools in the Marguerite Bay area, Antarctic Peninsula.

Climate

The climate of the Antarctic Peninsula region is milder than most continental coastal areas because the marine influence is dominant and the continental influence is at a minimum. Holdgate (1964) has described this region as the "maritime Antarctic". The climate is largely determined by the interaction of the cold air mass over the ice-bound Weddell Sea and the warmer air mass over the Bellingshausen Sea. Consequently, isotherms and isohyets follow the line of the Scotia Ridge at least as far south as the Antarctic Circle. The mean summer (December–February) temperatures for the west coast and adjacent islands of the Antarctic Peninsula are near or slightly above freezing while the east coast, like the continental coast, has summer mean temperatures below freezing. There is a difference of only 3 deg. in the annual

TABLE IV. PHYSICAL AND CHEMICAL PROPERTIES OF LAKES IN THE ANTARCTIC PENINSULA REGION

Location	*Date*	*Depth* (m.)	*Temp.* (°C)	*pH*	*Conductivity* (μmho)	Na^+ (p.p.m.)	K^+ (p.p.m.)	Mg^{++} (p.p.m.)	Ca^{++} (p.p.m.)	Cl^- (p.p.m.)	$SO_4^=$ (p.p.m.)	$PO_4^{\equiv}$ (p.p.m.)	NO_3^- (p.p.m.)	*Total solids* (p.p.m.)	*Reference*
Hope Bay															
Boeckella	Summer	—	—	6·6	—	—	—	—	—	14·00	—	—	—	—	Corte, 1962
Esperanza	Summer	—	—	6·6	—	—	—	—	[illegible]	8·00	—	—	—	—	Corte, 1962
Flora	Summer	—	—	6·6	—	—	—	—	[illegible]	10·00	—	—	—	—	Corte, 1962
Signy Island															
Lake 2	29 Jan. 1964	3·0	4·1	6·7	—	—	—	3·1	3·6	44·00	6·0	0·013	0·07	—	Heywood, 1968
Lake 5	29 Jan. 1964	2·0	5·1	6·9	—	—	—	2·0	2·7	29·50	4·3	0·007	0·04	—	Heywood, 1968
Lake 6	29 Jan. 1964	1·5	5·6	7·1	—	—	—	1·3	2·1	17·50	1·6	0·002	0·03	—	Heywood, 1968
Lake 7	27 Feb. 1964	2·0	2·9	6·9	—	—	—	3·9	4·8	48·00	5·5	tr	0·04	—	Heywood, 1968
Lake 10	28 Feb. 1964	2·0	3·8	7·1	—	—	—	5·4	12·5	61·00	15·0	0·160	9·03	—	Heywood, 1968

tr Trace.

mean temperature of Signy Island (lat. 60°43′S., long. 45°38′W.; −4° C) and Stonington Island (lat. 68°11′S., long. 67°01′W.; −7° C). The few records suggest that precipitation may be as little as 10 cm./yr. in the Weddell Sea and this rises to above 40 cm./yr. along the west coast of the Antarctic Peninsula and on the South Shetland and South Orkney Islands. The maximum amount is still relatively small but the annual mean relative humidity of the oceanic winds is high (approximately 80 per cent) and evaporation/ablation rates are correspondingly low. Large amounts of snow accumulate during the winter and, on the west coast of the Antarctic Peninsula and on the islands, produce copious amounts of water during summer thaws. The annual mean cloudiness of much of the region is very high (approximately 87 per cent) and the amount of solar radiation received is curtailed severely. Few radiation records are available but it is probably true to say that because of cloudiness, most areas north of the Antarctic Circle in this region receive little if any more solar radiation than areas subject to periods of polar night.

Weathering

The rate and form of soil formation differs considerably from that occurring in the continental areas. In the ice-free lowland areas, frost wedging and nivation is extensive. Wind erosion and salt wedging have not been recorded and presumably play only minor roles. The mechanical break-down of rock by frost action on Signy Island, South Orkney Islands, has been investigated in some detail (Holdgate and others, 1967). The process is proceeding rapidly and solifluction is affecting the upper layers of the ground on a large scale (Chambers, 1966*a*, *b*, 1967). Holdgate and others (1967) suggested, after observing colour changes in the mineral soil and the presence of secondary clay minerals, that some active chemical weathering occurs. This was later confirmed by the field work of Northover (Allen and Northover, 1967; Northover and Allen, 1967; Northover and Grimshaw, 1967). Therefore, soluble salts are probably readily available to most lakes and pools in the Antarctic Peninsula region.

Vegetation

Extensive stands of moss and small stands of the phanerogams *Deschampsia antarctica* and *Colobanthus quitensis* grow in many lowland areas in this region (Longton, 1967). The abundance of terrestrial vegetation in this region of Antarctica is most certainly due to the relatively mild climate, with abundance of water during summer and insulation by snow cover against severe low temperatures and high winds during winter. The richness of the flora, in terms of species, probably reflects two main factors. First, the northern part of the region lies relatively close to the cold temperate zone of South America, a source area for species suitable for the colonization of recently deglaciated areas. Secondly, the region has the most extensive and diverse range of edaphically favourable ice-free habitats in Antarctica.

The terrestrial flora contributes important amounts of organic material to the lakes on Signy Island (Heywood, 1967*b*, 1968, 1970*a*) and probably to most lakes in the region.

Lakes and pools

Chemical properties. All the lakes and pools so far examined in the region (Table IV) contain fresh water. Work on Signy Island clearly indicates that wind-borne sea spray is the major source of ions in the coastal lowlands (Heywood, 1968; Goodman, 1969). The mineral content is generally low because most water bodies receive copious amounts of melt water during the early spring thaw and sufficient water during the summer to compensate for any loss through evaporation. Virgin mineral soil on Signy Island has a high base-rich calcium and sodium content (Holdgate and others, 1967). Leaching of calcium appears to have raised the calcium: chloride ratio in the lakes above that of sea-water, and additional calcium from marble outcrops promotes and maintains the slightly higher ratios found in certain lakes. Experimental work by Goodman (1969) has suggested that the ratios of certain ions in coastal pools on Signy Island differ from the expected sea-water ratios because of differential rates of leaching of inorganic ions in snowdrifts during thaw periods. Similar processes may be responsible for the unexpected ratios of ions measured in lakes and pools in other areas (p. 45).

Signy Island lakes and pools also receive important amounts of nutrient salts and organic matter from animal wastes. A. J. Horne (personal communication) measured radionitrogen assimilation in the alga, *Nostoc commune*, associated with moss stands on Signy Island and concluded that it may contribute a considerable amount of the nitrogen recorded from streams which flow through moss (Heywood, 1968). Ions from all these sources are probably available to most water bodies in the Antarctic Peninsula region.

Extraction of water molecules in the formation of ice cover is mainly responsible for the remarkable increase (often 100 per cent) observed in the concentration of major ions during the winter in Signy Island lakes which, though shallow, do not freeze solid (Heywood, 1968). The oxygen concentration falls rapidly under the ice cover, presumably through biological activity, and for most of the winter conditions are almost anaerobic in the lower levels. Oxygen loss is parallelled by an increase in carbon dioxide which lowers the pH. Preliminary investigations suggest that the cycling of chemicals is similar to that in the hypolimnetic zone of typical eutrophic lakes.

Physical properties. Snow cover is the most important factor governing both the depth to which most lakes on Signy Island freeze and the duration of ice cover. Snow insulates the water against the ambient temperature and prevents warming by solar radiation. Precipitation during early winter in the South Orkney Islands is frequently associated with high winds which prevent accumulation. The snow-free period coincides with the period of minimum solar radiation and the heat loss from the lakes may be high. As winter proceeds, however, lighter winds allow the rate of snow accumulation to increase. Subject, therefore, to the complex interaction of wind, temperature and weather in a region of complicated weather patterns (Pepper, 1954), the snow cover, and therefore ice cover, of these lakes varies considerably from year to year. The effect of close proximity to snow and ice fields (p. 41) is also clearly seen in some lakes. Maximum recorded ice thickness varies from 1 to 2 m. and duration from 8 to 12 months.

Water temperatures during the summer on Signy Island are determined by solar radiation and the temperature of inflows. The high mean cloudiness of the area (Table I) limits the effect of solar radiation, and therefore water bodies of corresponding depth and size are colder than in some of the continental areas, all other factors being equal (recorded lake temperatures, Signy Island 0–6° C (ambient mean summer temperature +0·1° C), Ross Island and Schirmacher Ponds 0–8° C (ambient mean summer temperature −5·6° and −2·0° C, respectively)).

The temperature and ice-cover regimes observed on Signy Island are probably typical of most lakes in the Antarctic Peninsula region. Corte (1962) reported that in November 1958, Lakes Boeckella, Esperanza and Flora at Hope Bay were covered with 1·70, 1·75 and 3·00 m. of ice, respectively. The lakes did not open completely that summer although they did so in other years. These lakes receive melt water from the ice and snow of Mount Flora. Lake Flora, with the thickest ice cover, is nearest the permanent ice line and also receives water from a nearby glacier. Kroner Lake on Deception Island received heat from geothermal sources. It did not freeze over completely during the winter and a maximum temperature of 10° C was recorded during the 1963–64 summer (Stanley and Rose, 1967). This lake disappeared during the recent volcanic eruptions. Other lakes in the South Shetland and South Sandwich Islands may also receive geothermal heat.

Observations on Signy Island indicate that the degree of transparency varies widely from lake to lake in the Antarctic Peninsula region according to the amount of allochthonous matter received from moss banks, bird colonies and seal wallows. On Signy Island the mean transmission of visible light per metre varies from 19 to 85 per cent. Corte (1962) merely recorded that the waters of the Hope Bay lakes are clear.

The Signy Island lakes form a valuable link between those of cold temperate South America, sub-Antarctic South Georgia and continental Antarctica.

Flora and fauna

Although collections have been made since as early as 1839–43 (Hooker, 1847), biological information is extremely limited. The reason is three-fold. First, most collections have been made by non-specialists (often non-scientists) and microscopic animals and phytoplankton are more difficult for the amateur to see, capture and preserve than benthic algal felts. For example, geomorphologists, geologists and glaciologists have together provided a reasonable picture of water bodies in the Schirmacher Ponds "oasis" as environments and have collected benthic algal felts which have subsequently been described. But no information is available on the phytoplankton or fauna of these lakes and pools. Secondly, in the absence of planned limnological programmes, specialists have usually concentrated on one plant or animal form, publishing little comment, if any, on other members of the community. Thirdly, time has often been limited to a few weeks or even days. Consequently, the species list for an area is more likely to reflect the thoroughness of collecting than the actual flora and fauna present. Ecological and physiological information is generally non-existent. It is obvious, however, that numerous organisms are able to colonize the extremely harsh environment of the Antarctic lakes and pools.

Flora. Most lakes and pools support rich benthic algal communities, usually in the form of felts, but the phytoplankton appears to be poor. The main characteristic of the flora is the dominance of Myxophyceae, which often form over 70 per cent of the species present. Oscillatoriaceae, which have the greatest adaptability to adverse conditions of all algae, are the most important family. Fritsch (1912*b*) suggested that sheets of filamentous Myxophyceae are breeding places for the bulk of the algal flora. Myxophyceae, Chlorophyceae and Bacillariophyceae form the epiphytic vegetation, for another characteristic of the flora is a rapid decrease of the Conjugatae, the commonest members of temperate algal floras, with increase in latitude. Hirano (1965) has given a comprehensive review of literature dealing with the systematics and distribution of all the algae, and a list of species.

After examining the ratio of endemic to cosmopolitan species in the diatom floras of Ross Island and several east Antarctic coastal areas, Fukushima (1970) concluded that the Antarctic element became dominant between lat. 68° and 77°S. He inferred that the correlation with latitude is direct, and synonymous with increasing severity of environment.

In most areas, the dominant and component species of the algal communities vary from one water body to another. There are indications that salinity is probably a major factor governing distribution. Fukushima (1962, 1964) and Zaneveld (1969) recognized Bacillariophyceae and Myxophyceae associations correlated with various salinities. *Navicula muticopsis* and *Microcoleus lyngbyaceus* are dominant in the really fresh waters (Cl′ up to 123 mg./l.) examined and a *Nitzschia* sp. and *Calothrix parietina* or *Microcoleus vaginatus* in very saline waters. West and West (1911) suggested that high salinities inhibit the growth of green algae. Marine and brackish algal species are often found in Antarctic inland waters (Carlson, 1913) but the salinities in certain lakes appear to inhibit the growth of all algae. Although 11 species of Myxophyceae, 11 species of Bacillariophyceae (mainly marine) and five species of Chlorophyceae have been recorded in the very saline Green Lake, Ross Island, numbers are low, all are free-floating and no felts are developed.

Many other factors are probably also involved in determining species composition. On the Ongul Islands, Chlorophyceae (particularly *Ulothrix*) dominate the flora in running water, and Bacillariophyceae (*Hantzschia*) areas of wet silt, which freeze every night during the summer (Fukushima, 1961).

A low nutrient content may be responsible for the poor flora of the large, permanently frozen lakes in the south Victoria Land dry valleys (Goldman, 1964). Likens (1964) found *Schizothrix calcicola* growing in distinct, narrow parallel trails extending 4 m. into Lake Vanda. He concluded that distribution was determined by very small melt-water streams carrying nutrients into the lake. Wille (1902) attributed the poverty of the algal flora of the Wilhelm II Coast to nitrogen deficiency.

The adverse factor in Lakes Bonney and Vanda is unlikely to be the light regime under the persistent ice cover which in any case is absent from the peripheral areas in the summer. Experiments in temperate latitudes have shown that algae can photosynthesize in light intensities down to 1 per cent of surface insolation (Rodhe, 1962; Rodhe and others, 1966). The photic zone in Lakes Bonney and Vanda is therefore very deep. Goldman and others (1967) found phytoplankton densities of 10^5–10^6 organisms per litre in these lakes. Most of the plants, coccoid blue-greens (*Synechocystis*) and phytoflagellates (*Ochromonas* and *Chlamydomonas*), are less than 20 μm. in size. Goldman and his co-workers suggested that either flagella or small size are probably necessary to prevent the phytoplankton from sinking in the absence of wind-generated turbulence and that the suspension of organisms on pycnoclines may also serve to keep the phytoplankton in suspension. Wilson and Wellman (1962) discovered a concentration of algae, thought to be benthic in origin, at the level of the upper monimolimnion. This is a very stable, almost isotonic environment, receiving about 1,000 cal. cm.$^{-2}$ yr.$^{-1}$ mostly in the blue part of the spectrum and all during the summer months, and having a temperature of 7·8° C. Although provisionally identified as *Phormidium* with a few *Chroococcus* and *Anabaena*, the material has since been described as containing an atypical form of *Lyngbya musicola*, two species of *Chlorella*, an encysted *Chlamydomonas* and *Gloeotrichia contracta* (Goldman and others, 1967). The convection cells discovered by Ragotzkie and Likens (1964) in Lake Vanda are probably important in maintaining the phytoplankton in suspension, particularly the 100 μm. units of *Phormidium* (? *Lyngbya*) found there. Baker (1967) found a maximum of free-floating algae occurring in a convection cell deep in Lake Miers.

Lakes in the Bunger Hills and the Schirmacher Ponds oases, with similar light regimes to those of Lakes Bonney and Vanda, have a rich benthic flora to depths of at least 35 m. (Vyalov and Sdobnikova, 1961; Simonov and Fedotov, 1964; Aleshianskaya and Bardin, 1965; Lavrenko, 1966). Bacteria, algae and a moss, *Bryum korotkevicziae* (Savich-Lyubitskaya and Smirnova, 1959), form a thick shiny felt in the Bunger Hills lakes. There is apparently strong intra-community competition; the moss develops better in the deeper water where it is not smothered by the algae. Several mosses* are associated with algae in the Schirmacher Ponds lakes (Savich-Lyubitskaya and Smirnova, 1964).

While carrying out a brief limnological reconnaissance in the Marguerite Bay area of the Antarctic Peninsula, Bryant (1945) noticed that species of *Protococcus* or allied forms were usually the first algae to appear in temporary pools. Yellow-green filamentous species were found after 2 weeks, followed by blue-green and gelatinous thalloid types. No further work on colonization has been carried out.

Preliminary ecological and production studies on algae have been undertaken in Ross Island and south Victoria Land dry valleys lakes. Armitage and House (1962) found that the net production of oxygen varied from 0·029 to 0·057 mg. l.$^{-1}$ hr.$^{-1}$ (corresponding to rates of carbon production of 326–1,008 mg. m.$^{-3}$ day^{-1}) during a 2 day investigation of phytoplankton production in the shallow Skua and Coast Lakes, Ross Island, using the "light and dark bottle" technique. They also obtained evidence of light inhibition during the period of maximal light intensity, a phenomenon later investigated by Goldman and others (1963) in diel studies on Skua and Alga Lakes using radiocarbon methods. The diel rates of carbon fixation were completely out of phase with light intensity, the effect being more pronounced at the surface (5 cm.) than at depth (50 cm.). By exposing the plankton to incident light passing a graded series of neutral-density filters, a maximum rate was found at 0·10 langley min.$^{-1}$ (20 per cent of incident photosynthetic light at noon during the period of the investigation, 9–15 January 1962. Phytoplankton from Alga Lake was more adapted to high light intensities than phytoplankton from the more productive and much more turbid Skua Lake. Goldman and his co-workers pointed out that this is understandable since the mere presence of higher algal concentrations in Skua Lake will lead to self-shading. The phytoplankton production in Skua Lake is almost ten times greater per unit area than that found in Alga Lake and the seasonal phytoplankton bloom is comparable in production to those recorded in temperate waters. The differences in production appear to be indicative of the relative amounts of nutrients available in the two lakes; Skua Lake receives effluent from a skua colony. Goldman and his co-workers suggested that "The transparency decrease and high standing crop produced by the bloom in Skua Lake are probably responsible for the relatively great absolute efficiency of the Skua Lake phytoplankton. The beneficial shading effect resulting from the bloom conditions would be self-reinforcing. The ability to develop dense populations rapidly would seem to be of

* Mosses were found in the troughs of many Signy Island lakes during a recent (1970–71 austral summer) Scuba diving survey (Heywood and Light, unpublished data). The mosses grew in isolated patches on rocks except in one lake where they formed a continuous stand over the bottom (5–13 m. depth). There was evidence of competition with algae but the limiting factor, most apparant during this preliminary survey, was ice scour.

considerable advantage in shallow environments exposed to light of inhibitory intensities. However, one such bloom population would distribute its benefits to the whole photosynthetic community, and as a result any selective evolutionary force would operate at the community rather than the interspecific level."

Studies on the crustacean populations of the Signy Island lakes have provided circumstantial evidence of phytoplankters being similarly inhibited by high light intensities (Heywood, 1967*a*, 1970*a*, *b*). Peaks of sexual activity and larval blooms occur while the lakes are ice-covered in April/May and October/November; periods of reasonable day length when the ice cover is snow-free and approximately 1–10 per cent of incident radiation is reaching the water. The phytoplankters are presumably able to maintain station at any level where light conditions are good in the relatively non-turbulent water. During the summer the phytoplankters are unlikely to remain in the optimum light zone for any useful period of time because the lake waters are completely and continually stirred by strong winds (the mean wind speed during the summer is normally more than 6·7 m. sec.$^{-1}$).

High levels of summer carbon production have been obtained for benthic algae. Goldman and his co-workers on Ross Island suggested that the benthic algal felts may be well adapted to conditions of high light intensity, surface cells specializing for light absorption and removal of inhibitory intensities and wave-lengths. Alga Lake felt had a particularly noticeable orange, carotenoid-rich surface layer, which strongly supports the view that carotenoids serve a protective function for the whole periphyton community. They found that this was not the result of active carotenoid build-up but rather of selective chlorophyll destruction. Between 10 January and 16 February 1962, the carotenoids had increased considerably in the surface layer relative to the underlying green layers. However, the total pigment content per gram of tissue was one-third lower in the surface layer than in the underlying layers. The variation in carotenoid content of the Alga and Skua Lake algal felts reflects the relative degree to which they are sheltered from solar radiation by phytoplankton. When subjected to inhibiting light conditions in the laboratory, the production of carbon was 50–100 per cent higher in the Alga Lake felts than in the Skua Lake felts.

The benthic felts on Signy Island also appear to be of two distinct layers. Preliminary studies indicate that differences in appearance and texture may result from a light intensity-dependent variation in dominant myxophycean species. Certainly more than a selective break-down of pigments under harmful light intensities appears to be involved.

The importance of periphyton production is clear. In 1961–62, it was about three times the phytoplankton production in the highly turbid Skua Lake, and over 20 times as great in Alga Lake, Ross Island (Goldman and others, 1963). Production rates 25 times greater than that of phytoplankton in the overlying water have been recorded in the lake waters of Signy Island (in a paper in preparation by Horne and Fogg; cited by Fogg and Horne, 1970).

The combined production of periphyton and phytoplankton in the Ross Island lakes ranged from 2 to almost 5 g. C m.$^{-3}$ day^{-1} during the 1961–62 summer. These are very high rates for any latitude. Goldman (1970) pointed out, however, that "the summer growing season is very short and its intensity is partly the result of there being continuous light".

Recorded primary production in Lakes Bonney and Vanda, south Victoria Land dry valleys, is extremely low, rates of light fixation varying from 0·24 to 8·00 mg. C m.$^{-3}$ day^{-1} for plankton in the main water body and from 0·5 to 10 mg. C m.$^{-3}$ day^{-1} for plankton in the shallow peripheral areas (Goldman and others, 1967). The primary factors limiting photosynthesis appear to be temperature and availability of nutrients. Maximum production was recorded below 50 m. in Lake Vanda where both temperatures and nutrient concentrations were highest but light intensity was below 1 per cent of surface incident light.

The effect of temperature increase upon photosynthetic uptake in inhibited plankton indicated that the photoplankton species in Alga and Skua Lakes, Ross Island, were extremely responsive to heat ($Q10$, 4–14° C$\simeq$7) and also tolerant of heat greatly in excess of that normally experienced. The effect of increased temperature on benthic photosynthesis was smaller ($Q10$, 4–14° C$\sim$2). Goldman and others (1963) pointed out that in these lakes solar heating regularly produced high temperatures within the algal felts to which the photosynthesizing cells must be tolerant, and suggested that this is why they are less sensitive than the phytoplankton to the high experimental temperatures. Fogg and Horne (1970) pointed out the biological significance of the phenomenon. At high light intensities, photosynthesis is temperature-dependent with a $Q10$ of 2 to 3. Consequently, the gain of heat by the absorption of solar energy could have important effects on metabolic rates. They showed by calculation that the temperature differences that can arise in this way are negligible for the plankton algae but probably significant for the benthic algae. They recorded temperature differences between the algal felt and overlying water of 1–2·3 deg. in Signy Island lakes and concluded that the absorption of solar energy is an important factor contributing to the success of the benthic algae.

Even in lakes and pools (or sub-lacustrine shelf area) which are frozen solid, the algal felt may receive sufficient solar energy to melt the ice immediately surrounding it and to permit photosynthesis. The bubbles of oxygen so produced lift the felt off the rock. Some pieces eventually break away and slowly move to the surface as heat absorbed melts the overlying ice. Murray (1910*a*) first observed this phenomenon in Clear and Coast Lakes, Ross Island, and recent reports have been published by Wilson (1965), Komarek and Ruzicka (1966) and Zaneveld (1969).

High dark fixation rates in Lakes Bonney and Vanda, south Victoria Land dry valleys, suggest that heterotrophy is important in the main water body. Fixation of carbon at the expense of an organic energy source may be the means by which the plant community survives the months of darkness. Baker (1967) has suggested that algae living under a harsh light regime deep in Lake Miers, south Victoria Land dry valleys, may also survive the low summer light intensities and the 6 months of winter darkness by heterotrophically assimilating dissolved organic substances. The organic material might be extracellular products produced during photosynthesis in the summer by plants living in surface waters and littoral regions. Horne and Fogg (in a paper in preparation; cited by Fogg and Horne, 1970) found by radiocarbon experiments that phytoplankton released between 23 and 40 per cent of total fixed carbon in extracellular products in the Signy Island lakes. The periphyton released only 0·4 per cent but, because of the difference in production rates, the actual amounts released were approximately the same. Fogg and Horne (1970) thought that heterotrophic uptake by algae in complete darkness is unlikely and suggested that what may occur is photo-assimilation, the direct assimilation of organic substances under very low light intensities using photochemically generated high-energy phosphate and hydrogen donors.

The seasonal formation of a relatively thick ice cover may have side effects which are extremely beneficial to the production potential of a lake. Freezing-out of water molecules probably raises the concentrations of soluble organic compounds to levels at which algae can use them in photo-assimilation. Also, the gradual concentration of inorganic nutrient salts is probably equivalent, in effect, to the spring circulation in temperate lakes, enabling a burst of photosynthetic activity to occur in both benthic and planktonic flora as soon as the snow cover clears and the irradiation increases. This could be of particular importance in lakes where the external supply of nutrient salts is low.

Holm-Hansen (1963*b*) has established cultures of benthic algae from Lake Vanda, and shown experimentally that Antarctic algae are cold-adapted and have a higher viability after freezing than temperate forms. The Myxophyceae, which showed the greatest survival, were filamentous species which normally grew in soil or attached to the substratum in fresh water. This is expected since these are the forms most likely to be subjected to repeated freeze-thaw cycles.

Meyer and others (1962) isolated only four bacteria (as yet unidentified), a yeast and a yeast-like organism from the littoral areas of Lakes Vanda and Bonney. Goldman and others (1967) also found low concentrations of bacteria throughout the main water body of Lake Vanda but observed high concentrations at 20 m. depth in Lake Bonney. They did not suggest any reason for this phenomenon. Fungi in Lake Vanda appear to prefer high temperatures and high chloride concentrations. Sugiyama and others (1967) found that the number of fungal strains increased with depth and were particularly numerous in the bottom sediments where the temperature was +25° C. The zone of bacteria in Lake Bonney may therefore be determined by temperature; it lies just below the region of maximum temperature. However, Stanley and Rose (1967) were able to show that bacteria, yeasts and fungi in lakes and pools on Deception Island, South Shetland Islands, were psychrophilic.

Bacteria and yeasts form a unique aerobic community in Don Juan Pond, south Victoria Land dry valleys, a body of water 13·7 times as saline as sea-water (Meyer and others, 1962). No growing algae were present. Three types of bacteria (*Bacillus megaterium*, *Micrococcus* sp. and *Corynebacterium* sp.) and a yeast (*Sporobolomyces*) have been grown in laboratory culture. The organisms are very adaptable in laboratory culture, growing in a range of media, over a wide range of salt concentrations and temperatures. Yet in nature the organisms are not found in less saline waters adjacent to Don Juan Pond.

Barghoorn and Nichols (1961) found sulphate-reducing bacteria (*Desulfovibrio*) in the bottom muds of a small pond, salinity 3·8 times that of sea-water. The bacteria induce the precipitation of iron sulphide by sulphate reduction. Decaying filamentous algae, diatoms and other microplankton are quoted as energy sources for the bacteria.

Fauna. Protozoa, Rotifera, Tardigrada, Nematoda and sometimes Gastrotricha, Turbellaria and Annelida (Enchytraeidae) are found wherever there are benthic algal felts (Bryant, 1945 (Antarctic Peninsula); Dougherty and Harris, 1963 (south Victoria Land dry valleys); Heywood, 1967*a* (South Orkney Islands); Korotkevich, 1958 (Bunger Hills and Vestfold Hills "oases"); Murray, 1910*b*; Dillon and others, 1968 (Ross Island)). Bryant (1945) also found a bryozoan, *Calloporina* sp., in a pool only 6 in. [15 cm.] deep. Although papers on only the Protozoa and Tardigrada of the Ongul Islands pools have been published (Morikawa, 1962; Hada, 1967), Protozoa (69 spp.), Rotifera (13 spp.), Tardigrada (6 spp.), Nematoda (3 spp.) and Gastrotricha (1 sp.) have been found in wet moss on the nearby Langhovde hills (Sudzuki, 1964). It is logical to assume therefore that the fauna of the pools is equally diverse.

Communities are poor in species compared with temperate regions, but each species may be numerically very strong. Numbers are determined by the luxuriance of the algal felts. Several authors have commented upon the remarkable abundance of the bdelloid rotifer *Philodina gregaria* which often covers the floors of pools in blood-red patches 15 cm. or more in diameter and one individual thick. *Adineta grandis* (Rotifera) was also extremely numerous in the distinct fauna found by Murray (1910*d*) in the very saline Green Lake on Ross Island.

Crustacea complete the fauna in several regions. *Acanthocyclops mirnyi* (Copepoda, Cyclopoida) and larval harpacticoid copepods have been collected from lakes in the Bunger Hills, and these copepods and a cladoceran, *Daphniopsis studeri*, have been collected from lakes in the Vestfold Hills (Borutskiy and Vinogradov, 1957; Korotkevich, 1958; Akatova, 1964). Lakes and pools on the Antarctic Peninsula and adjacent islands have been colonized by at least ten species: *Branchinecta gaini* (Anostraca); *Pseudoboeckella poppei*, *Pseudoboeckella silvestri*, *Parabroteas sarsi* (Copepoda, Calanoida); *Harpacticus furcatus* (Copepoda, Harpacticoida); *Macrothrix hirsuticornis*, *Alona rectangula*, *Ilyocryptus brevidentatus* (Cladocera); *Cypridopsis frigogena*, *Eucypris* sp. (Ostracoda) (Harding, 1941; Heywood, 1967*a*).

Pioneer field studies on the fauna were carried out by Murray (1910*d*), who worked on the Rotifera of Ross Island. He found that in the dormant state adult rotifers are remarkably tolerant of adverse conditions. Specimens survived repeated freezing and thawing over periods of several months and temperatures as low as −40° C. (*Philodina gregaria* survived after being subjected to −78° C for many hours.) They lived for a month in sea-water and in much more saline solutions, and became active immediately they were transferred to fresh water. Some *Adineta grandis* even survived temperatures of + 100° C. Rotifers also survived being dried by ablation and transportation through the tropics to the United Kingdom. They subsequently revived within 1 hr. of being moistened. There has been no further work along these lines. Recent attempts to establish cultures of *Philodina gregaria* (Rotifera) and *Hypsibius arcticus* (Tardigrada) have met with limited success (Dougherty, 1964*a*, *b*). An apparently unsuitable culture medium produced a progressive deterioration of stock. Studies of maturation time and fecundity indicated, however, that in favourable summers both species could reproduce prolifically.

A preliminary study of the fresh-water Crustacea on Signy Island has been completed. The anostracan *Branchinecta gaini* dominates the nektobenthos of many lakes during the summer. The copepod *Pseudoboeckella silvestri* is present in the nektobenthos of all lakes and most pools. The adult and late larval forms of these species feed mainly off the myxophycean mat epiflora and associated detritus. The smaller larvae form a nektoplankton. A larger copepod, *Parabroteas sarsi*, preys on all life stages of *Pseudoboeckella silvestri*. It may also eat the smaller larva of *Branchinecta gaini*, and the cladocerans *Macrothrix hirsuticornis*, *Alona rectangula* and *Ilyocryptus brevidentatus*, which have also colonized all the lakes. Although nektobenthic in habit, *Macrothrix hirsuticornis* and *Alona rectangula* are found at all levels during the summer because they are swept from the bottom by wind-generated currents. *Ilyocryptus brevidentatus* is a large benthic form which crawls over and within the myxophycean mat and organic debris. The Cladocera are presumably feeding on the myxophycean mat epiflora and on decomposing algal detritus. *Cypridopsis frigogena* and *Eucypris* sp. (Ostracoda) complete the nektobenthos in three of the lakes. *Cypridopsis frigogena* is an active swimmer and a scavenger. It may well play a role in the community complementary to that of *Parabroteas sarsi* (Heywood, 1967*a*).

Reasons for the sporadic distribution of the anostracan and the ostracods are not known. *Branchinecta gaini* has colonized a 30 cm. by 60 cm. by 10 cm. puddle draining into a lake in which the animal has never been observed. The crustaceans have not colonized the streams on Signy Island, but individuals are being continually swept out of the lakes and into the sea.

Branchinecta gaini overwinters in the egg stage. Hatching occurs in late winter, a period of probable high phytoplankton activity (p. 51). Hutchinson (1967, p. 562) suggested that the stimulus required to promote the hatching of resting anostracan eggs is a lowering of osmotic pressure at the egg surface. For eggs frozen in pools and on the shelf area of lakes on Signy Island this change is probably brought about by the return of the liquid medium when the ice thaws at the rock/ice interface. The stimulus for eggs in deeper water is probably the dilution of the surrounding medium with melt water. In lake populations, sexual maturity is attained in approximately 3 months. It is not known whether females produce more than one clutch of eggs. Adults of both sexes vary in size and this may reflect either the amount of food available during the individual period of growth (see below) or post-reproductive stage moulting. The average life span for *Branchinecta gaini* is approximately 6 months in the lakes. The populations die out shortly after the lake surface freezes. The life cycle is accelerated in the pools, presumably because of the higher temperatures, and the life span may be as short as 3 months (Heywood, unpublished data).

Although *Parabroteas sarsi* and *Pseudoboeckella silvestri* have the faculty to overwinter in the egg stage, they appear to do so only in pools, which freeze solid, and one lake, polluted by effluent from a seal wallow, where the oxygen content falls to zero (all the crustacean species overwinter in the egg stage in this lake). Both appear to breed continuously in other lakes and most life stages are present throughout the year. However, there are two clear peaks of sexual activity. These occur in early and late winter, producing the largest numbers of nauplii during the periods probably favourable for high phytoplankton activity (p. 51). The nauplii of *Parabroteas sarsi* feed on the nauplii of *Pseudoboeckella silvestri* and the activities of the two species are naturally synchronous. More detailed study has revealed that availability and perhaps type of food are the main factors affecting lake populations of *Pseudoboeckella silvestri*, controlling maturation rates, longevity, body size and fecundity (Heywood, 1970*b*).

All the cladocerans overwinter as both adults and resting eggs. Only subitaneous eggs are produced during early summer. Ephippial eggs appear in mid-summer and by late summer are carried by most gravid females. No males have been found so the ephippial eggs are probably pseudosexual. The number of clutches produced by each female is not known. Gravid females vary considerably in size but this could reflect differences in available food supply or differences between ex-ephippial and ex-subitaneous generations as well as post-reproductive moulting. Old females die off in early winter leaving small populations of young, presumably ex-subitaneous, juveniles which slowly mature during the winter. Recruitment of ex-ephippial juveniles probably occurs during late winter before the lakes open. The stimulus for hatching could be a lowering of osmotic pressure at the egg surface, increase in oxygen tension or increase in irradiance (Heywood, unpublished data).

Very few specimens of the ostracods have been obtained and no details of their biology are known.

DISCUSSION

Although the climate in all regions of Antarctica is extremely rigorous, the severity of the environment in the lakes and pools varies considerably. Highly saline pools and temporary pools are exceptionally severe environments in which colonizing organisms must withstand either high osmotic pressures or desiccation (or both) and temperatures below −40° C. In other lakes the growing season is severely curtailed by either the water body freezing solid or snow cover reducing the irradiance below that required for photosynthesis. Nevertheless, these lakes can support large populations of a few species of Crustacea.

But there are also in the same regions fresh-water lakes in which the environment is extremely equable although they are permanently ice-covered. Aridity and high prevailing winds prevent snow cover throughout the year, and light conditions are probably favourable for photosynthesis at all times other than the polar night (2–4 months). The ice cover cuts out harmful ultra-violet light and insulates the water against low ambient temperatures. Solar radiation heats the water and temperatures therefore fluctuate slowly over only 4 or 5 deg. Other, shallower, lakes are open during the summer and water temperatures fluctuate over 6–8 deg. During the open period, phytoplankters appear to be adversely affected by high light intensities but, when ice-covered, these lakes too are snow-free and receive a considerable amount of solar radiation at intensities favourable for photosynthesis. In both types of lake, the benthic flora flourishes during the long periods it is not encased in ice. The aridity of the region does not affect these lakes adversely because either local topography promotes the formation of snowdrifts or they receive copious amounts of melt water during the summer from glaciers or icefields. These types of lake which have been described from the Schirmacher Ponds and the Bunger Hills "oases" presumably also occur in the fringe areas of the south Victoria Land dry valleys and in particularly wind-swept areas of the continental coastal region and the Antarctic Peninsula region. The fresh upper layers of water in Lakes Bonney, Fryxell and Vanda, south Victoria Land dry valleys, would probably be as productive as these fresh-water lakes were it not for nutrient salt deficiences. The majority of temperate lakes can be considered more severe environments than these lakes in the sense that organisms in them must be tolerant of a far wider range of variation of each environmental factor.

The review of Antarctic limnology clearly shows that in general the low ambient temperatures do not affect the aquatic environment directly but indirectly by controlling precipitation. This influence is dominant, however, and it seems unwise for Dunbar (1968) to have concluded that temperature is one of the least important factors in the development of polar ecosystems. Low temperatures were directly responsible for past glaciation and are therefore indirectly responsible for the youth of the ecosystem. Low temperatures are ultimately responsible for the poor development of the soil, the lack of nutrient salts and the limited growing season.

Before determining which features of Antarctic lakes are unique, characteristically polar or merely typical of oligotrophic conditions, it is necessary to compare briefly the inland-water ecosystems of the two polar regions.

Limnological research in the Arctic is also of recent origin and available information is limited. A recent review of the Arctic lake ecosystem by Kalff (1970) dealt mainly with three studies on plankton primary production carried out in northern Alaska (Hobbie, 1962 (Lakes Peter and Schrader); Kalff, 1965 (tundra pools)) and northern Sweden (Holmgren, 1968 (Lake Nedre Laksjön)). Useful background information on Arctic inland waters has been published by Amrén (1964*a*, *b*) on Spitsbergen, Frey and Stahl (1958) on Southampton Island, Livingstone and others (1958) on northern Alaska, McLaren (1964) and Oliver and Corbet (1966) on Ellesmere Island, Røen (1962) on Greenland, and Swartz (1966) on east central Alaska. Considerable research has been carried out in Scandinavia but this has been mainly on cold-temperate and sub-Arctic lakes. Further information may be available in the Russian literature but this has not been reviewed.

Although information is limited, it is clear that the inland-water ecosystems differ considerably between the polar regions and that this is due to differences in physiography and in the periods of time that have elapsed since deglaciation. The Arctic is essentially a large ocean surrounded by fringes of large continents, whereas the Antarctic is centred on an ice-clad continent surrounded by the largest unbroken oceanic area on Earth. The Arctic Ocean is a positive source of heat for a large part of each year and a warm current, the North Atlantic Drift, penetrates north beyond the Arctic Circle. The surrounding continents also warm up considerably during the summer and are then a further source of heat. By contrast the Antarctic continent is a negative source of heat throughout the year. Approximately 90 per cent of solar energy is re-radiated back into the atmosphere. Antarctica is the world's highest continent (mean elevation 2,000 m.) and the difference in elevation alone would result in the mean annual temperature of Antarctica being 12 deg. colder than that of the Arctic, were all other factors equal. The general climatic effects are that, although winters in the polar regions are of equal severity, they are of longer duration in Antarctica, and summers are considerably warmer in the Arctic, for comparable latitudes. Ice-free areas in the Arctic have been deglaciated for a far longer period than in most cases in Antarctica, and soil formation is comparatively well advanced. Since there are no sea barriers to the dispersal of living organisms in the Arctic, a rich terrestrial vegetation has spread north, encouraged by the relatively warm summers, and even flourishes as far north as Ellesmere Island (lat. 76°–83° N.) (Oliver and Corbet, 1966). The following description of the Alaskan coastal plain (approximately lat. 69°–71° N.) contrasts sharply with that of any Antarctic ice-free area.

> "The area around Point Barrow, and extending inland about 100 miles [160 km.], is a flat, water-soaked plain on which thousands of ponds, lakes, lagoons, and widely meandering streams present a landscape of monotonously low relief—about one-half of the surface being covered with water during the summer season . . . . During the summer the soil thaws to a depth of 1 to 3, or sometimes 4 feet. Below these levels, except beneath deep streams and lakes, the sub-strata are perennially below freezing temperatures. Thus, all biological activity on and in the soil is confined to the thin blanket of the 'active layer', that portion of the soil that thaws in summer. Winter temperatures drop to, or a little below, 50° Fahrenheit below zero [−45° C]. Air temperatures in the summer rarely go above 55° Farhenheit above zero [+12·5° C].
>
> "The tundra is carpeted with a dense growth of low perennial vegetation, composed mostly of prostrate shrubs, herbs, grasses, sedges, mosses, and lichens. The ponds, lakes and wet surface of the soil support a large number of algae. Thousands of birds nest on the tundra, myriads of insects and mites inhabit the peaty 'active layer', and populations of such mammals as lemmings, foxes, weasels, and shrews occur in varying numbers near Point Barrow. Farther inland, particularly in the rolling foothills of the Brooks Range (between 68° and 69°N.), such additional mammals as the barren-ground grizzlies, caribon, arctic squirrels, voles, wolves, marmots, and wolverines occur." (Wiggins, 1953)

These considerable differences in geography, topography and development of the terrestrial ecosystem are reflected in the inland water bodies, which in the Arctic are numerically far greater than in Antarctica. They are also morphologically more diverse and there are numerous streams and rivers. The lakes and pools appear to be mainly of glacial origin or are thaw lakes, formed from the melting of large masses of ground ice (Black and Barksdale, 1949) a type not found in Antarctica. Hattersley-Smith and others (1970) have concluded that lakes at the heads of certain fjords in northern Ellesmere Island are the result of glacial overdeepening followed by post-glacial uplift, a process responsible for several known Antarctic lakes.

Physical conditions within the Arctic inland water bodies are largely determined by the snow cover and available descriptions of its effect on light, and temperature regimes (Hobbie, 1962; Holmgren, 1968) parallel those for lakes on Signy Island. During the summer, however, temperatures between 10° and 16° C are attained by the surface waters of even large Arctic lakes, presumably reflecting warmer ambient temperatures, lower cloud amounts and greater heating of inflowing water compared to Antarctic conditions. Many pools and lakes, particularly in Alaska, receive large amounts of humic material and their waters are highly coloured and therefore have an increased capacity for absorbing solar radiation. Kalff (1965) reported that a small pond near Point Barrow had a lower albedo than surrounding areas of grass, moss and soil. Because of the high surface-water temperatures, summer stratification may occur in Arctic lakes but it is prevented in many by prevailing high winds. Pools and lake surface waters are frozen for periods of 7–9 months. Longer periods are exceptional. Lake Hazen (lat. 81°50′ N., long. 71°00′ W., Ellesmere Island) is glacier-fed and has a maximum recorded depth of 280 m. Temperatures in this lake rarely exceed 3° C and the surface is not always ice-free in summer (McLaren, 1964). This is clearly the effect of morphology and site, factors unique to the lake, and not of general regional factors such as climate. Nearby Skeleton Pond (lat. 81°50′ N., long. 71°30′ W.), with a surface area of 1·5 ha. and a maximum recorded depth of 3·5 m., is almost isothermal at 10–11° C during most of the summer. Some of the northern Ellesmere Island lakes recently examined by Hattersley-Smith and others (1970) retain their ice cover throughout some years. These lakes have similar temperature profiles to Lake Bonney in south Victoria Land dry valleys, Antarctica, with maxima occurring at depths between 10 and 15 m. As in Lake Bonney (and Lakes Vanda and Fryxell), the upper layers in the Ellesmere Island lakes are virtually fresh but below this there is a gradual rise in salinity towards the bottom where the concentration is approximately the same as sea-water. Hattersley-Smith and his co-workers inferred from this that the saline water in the lakes is relict sea-water and concluded that inflowing fresh water from spring run-off has completely replaced the sea-water at the surface and diluted it for a further 30–40 m. by a process of diffusion. They attributed the heating at depth to solar radiation.

The concentration of chloride ions and high salinities does not dominate discussions on the chemical properties of Arctic inland waters as it does in Antarctic limnology. Only a relatively small number of Arctic lakes and pools lie close enough to the coast to be seriously affected by ions of marine origin. Calcium and bicarbonate ions predominate in most of the inland pools and lakes examined in the Alaskan and Canadian Arctic (Livingstone and others, 1958; Oliver and Corbet, 1966). The nature of the surrounding terrain has more influence on the chemical composition of apparently all inland waters in the Arctic than it does in the Antarctic. High salinities caused by ablation/evaporation have not been observed in the Arctic. Although precipitation amounts are low, and pools decrease in size and even dry up during the summer, the almost pure surface water from spring melt is sufficient to refill completely the basins of temporary ponds and to replenish the permanent ponds and tarns. The drying-up process is even reversed by the melting of permafrost on Ellesmere Island. Oliver and Corbet (1966) reported:

> "By 1 Aug. the active zone is approaching its maximum thickness and particularly in the lower areas is saturated with water. On long slopes of porous material the lateral movement of this water becomes concentrated in streams such as those from the talus slopes of Mt. McGill. This saturation of the active zone by permafrost melt not only prevents the area from being completely arid and provides water for the plants, but it also contributes to the chemical composition of the ponds."

This phenomenon may be common in the Arctic.

The biota of all the Arctic lakes and pools so far examined is richer and more diverse than that found in the Antarctic. The bedrock of the basins is generally covered with silt and organically rich mud. Most lakes and pools have an emergent vegetation of grasses, sedges, lilies, and other macrophytes such as *Potamageton* spp. and *Ranunculus* spp. form under-water meadows in the littoral zone. However, in the larger lakes there may be a noticeable lack of well-developed vegetation in the 0–2 m. zone. Livingstone and others (1958) suggested that this may be caused by the scouring action of ice which often forms ridges of silt 4–5 m. high along the lake shores. The moss *Drepanocladus* is a major component of the benthic flora in many pools.

The algal flora is rich in species and there appears to be no invariable reduction in number of species with latitude. Variation in numbers recorded appears to reflect the intensity of sampling and the environmental conditions in particular lakes (Kalff, 1970). The composition of the algal floras of the polar regions differs in two important respects. The Myxophyceae, exceedingly dominant in the Antarctic, are unimportant in the benthic and planktonic Arctic flora. The Conjugatae, rare in Antarctica, are generally abundant in the Arctic. Kalff (1965) recorded few species of Conjugatae in certain pools on the Alaskan coastal plain. Investigations have not been carried out to determine the reasons for these differences. Suggested reasons for the abundance of Myxophyceae in the Antarctic (Hirano, 1965) and their paucity in the Arctic (Kalff, 1970) partly conflict. Hirano attributed the success of the Myxophyceae in Antarctica to their simple life cycle, their ability to reproduce asexually, and their ability to thrive under oligotrophic conditions. Kalff took the more generally accepted view that the Myxophyceae require nutrient-rich waters which are apparently rare in Arctic regions. Hutchinson (1967), while concluding that the detailed requirements for Myxophyceae are "far from clear", strongly supported an earlier suggestion by Provasoli that sodium ions are important. Sodium ions are far more abundant in Antarctic than in Arctic lakes. The abundance of Conjugatae in the Arctic is probably due to their preference of waters rich in humic material (p. 56). The distribution of both forms may ultimately be explained by their relative abilities to survive dispersal across wide oceanic areas. The Myxophyceae may thrive in Antarctica under what would normally be considered minimal nutrient conditions because of limited competition from other benthic forms such as Conjugatae.

In both regions, nannoplankters dominate the phytoplankton. Kalff (1970) suggested that this reflects extreme oligotrophy. The high surface to volume ratio of the nannoplankton is likely to facilitate the uptake of nutrients and growth factors from the generally nutrient-poor waters.

Conditions for primary production in lakes and pools are essentially similar in both polar regions. The period for photosynthesis is restricted by the polar night and snow cover. Some Arctic phytoplankters are adapted to low light intensities and blooms can occur under ice in late winter/early spring. Hobbie (1962) recorded maximum production in early spring beneath ice in Lakes Peters and Schrader, Brooks Range, northern Alaska. McLaren (1964) found the rate of plankton primary production in Lake Hazen, Ellesmere Island, too low for measurement by the "light-dark bottle" technique. He deduced from this and other indirect evidence that primary production occurred largely before the ice cover melted. However, in other lakes there are also phytoplankters with a higher light optimum and a further "bloom" frequently occurs during the summer (Holmgren, 1968; Kalff, 1970).

Winter conditions do not permit photosynthesis and yet an appreciable number of phytoplankters are known to survive this period without any resting stages (Hobbie, 1962; Holmgren, 1968). After reviewing the limited information, Kalff (1970) concluded that Arctic lake phytoplankton may rely on a variety of mechanisms to survive the winter—phagotrophy, utilization of stored cell material and photo-assimilation of organic substrates under very low light intensities.

Rates of primary production in Arctic lakes recorded so far indicate that the sampled lakes are considerably less productive than most oligotrophic lakes of the north temperate zone (Kalff, 1970). The prime reason is the short growing season, but nutrient deficiency also limits production during the summer. In some Alaskan tundra ponds, the major deficient ion is phosphate (Kalff, 1965). Reasons commonly given for nutrient poverty in Arctic lakes are the relatively poor development of the soil, the restriction of chemical and biological weathering to the short summer, the low rate of break-down of organic matter in the soil and the relatively restricted sub-surface drainage. Loss of available nutrients also occurs through chelation in Arctic lakes rich in humic material (Kalff, 1965). Nutrient deficiency is probably a common factor in Antarctic lakes since the above factors, with the exception of chelation, are even more apparent here. It has already been shown that nutrients are limiting in one lake on Ross Island (Goldman and others, 1963) and in another in the south Victoria Land dry valleys (Likens, 1964).

The fresh-water fauna of the Arctic is considerably richer than that of Antarctica and includes representatives of the Protozoa, Rotifera, Tardigrada, Nematoda, Annelida (Enchytraeidae), Mollusca (Gastropoda), Arthropoda (Crustacea, Insecta) and Vertebrata (Pisces). The number and abundance of species is in most cases directly determined by the level of primary production. Holmgren (1968) recorded 21 species of Rotifera, 17 species of Crustacea and three species of fish in Nedre Laksjön (lat. 68°21′N., long. 18°49′E.), a productive lake, by Arctic standards, in Swedish Lapland, but McLaren (1964) only found two species of Rotifera, one species of Crustacea and one species of fish in the ultra-oligotrophic Lake Hazen (lat. 81°50′N., long. 71°00′W.) on Ellesmere Island. Fish are generally found only in lakes that are deep enough to have a considerable body of water under the ice in winter, presumably because of their oxygen requirements, but they have been found in small pools which freeze solid during the winter (Livingstone and others, 1958). These occasional occurrences are generally attributed to accidental colonization during the melt period when fish may be swept out of the lakes in which they have overwintered. Stomach contents clearly indicate that insect larvae form the most important food source during summer, the period of most rapid fish growth (Kalff, 1970). The zooplankton standing crop in most lakes is low but Crustacea may be a very important fish food during the winter.

Differences in environmental factors are not sufficient to account for the considerable variation in the richness of the fresh-water biota of the two regions. The poorer biota of

Antarctica must largely reflect isolation and the youth of the ecosystem. Antarctica is separated from other continents by vast stormy seas. The prevailing winds and surface sea currents move out from the continent and therefore colonizing organisms are most probably transported by birds on muddied feet or trapped in feathers. With one exception, all Antarctic birds are marine and are unlikely to cover vast areas of sea without settling on the water to feed or ride out a storm. Few fresh-water organisms are likely to survive this treatment. Therefore, the source of fresh-water organisms for most areas of Antarctica is most likely to have been a relict biota in adjacent islands. The cladoceran found in the Schirmacher Ponds, Bunger and Vestfold Hills has previously been reported from Iles Kerguelen and Marion Island (Brehm, 1954). The copepod genus *Pseudoboeckella* has a similar discontinuous circum-Antarctic distribution (Brehm, 1936; Sewell, 1956). The richer biota of the Antarctic Peninsula region probably reflects the proximity of the cold temperate zone of South America, a source area of species suitable for colonizing polar lakes. Difficulties of dispersal are probably the main reason why no crustacean appears to have yet colonized the truly fresh-water lakes in the McMurdo Sound area. The south Victoria Land dry valleys have been ice-free for much longer than the Schirmacher Ponds, Bunger and Vestfold Hills; therefore time is not the dominant factor. Similarly, variations in the ratio of endemic to cosmopolitan algae, recorded between the McMurdo Sound area and areas of coastal east Antarctica, are more likely to be function of dispersal difficulties and of environmental conditions in particular lakes than one of latitude which Fukushima (1967, 1970) suggested. The implication that increase in latitude is symonymous with increase in severity of aquatic environment is clearly not correct.

Differences in the biology of the Arctic and Antarctic Crustacea so far studied may reflect the relative complexity of the biocoenoses. Most of the Arctic calanoid copepods and cladocerans form univoltine populations and overwinter in the egg stage (Hutchinson, 1967, p. 599, 668–69). The resting egg stage is probably obligatory because of inter-specific competition. This factor appears to be of minor importance in the Signy Island lakes.

In his recent dissertation on the development of polar ecosystems, Dunbar (1968) presented a valuable critical review of theories on the ecological control of species diversity and a theoretical model of the mechanism of the evolution of the ecological system. It appears that selective forces have resulted in two pressures which are conflicting. Adaptation to oscillating environmental factors favours large populations of few species, whilst development towards greater ecological stability tends towards proliferation of species. The former effect predominates in polar regions and Dunbar concluded that "the question to be resolved is whether enough time has elapsed since the Pliocene–Pleistocene climatic change to allow ecological saturation to have been reached in the higher latitudes, that is, whether the ecological systems of the polar and subpolar regions are in fact saturated". Dunbar marshalled evidence, taken entirely from the marine biota, to suggest that the growth of diversification is in its infancy. He conceded that the evidence is not conclusive. Polar environments are so varied that it seems unwise to use evidence from one to make generalizations about them all. Antarctic terrestrial and fresh-water ecosystems are probably immature in comparison with temperate ecosystems, because of the severe restrictions on the rate of colonization imposed by isolation. But it seems equally likely that diversity in Arctic terrestrial and fresh-water ecosystems is near the limits imposed by the unfavourable physical factors and potential organic productivity. Furthermore, these conditions are unlikely to become more favourable, and may well become less so should further glaciation occur.

The environments of the highly saline pools and the temporary pools are peculiar to Antarctica, for if high salinities and high evaporation rates are phenomena common to all deserts, extremely low temperatures are not. Also, the "sea inlets" of the Schirmacher Ponds area appear to be unique. But the environments found in Antarctic lakes are not even confined to polar regions. Cold monomictic regimes have been found in small lakes associated with glacier margins, snowfields or fed by short melt streams, in the central European Alps, Himalayas and Andes. Temperature regimes similar to those found in most Arctic lakes, with a summer maximum below 10–15° C are even encountered in lakes in the Cairngorm Mountains, Scotland, and presumably in many other temperate-zone mountain lakes. Similarly, the surface waters of these lakes may be frozen for 6 months or longer. Perennially frozen lakes have been reported from the Andes (Loffler, unpublished data; quoted by Hutchinson, 1957,

p. 462). The amount of light available in polar lakes is restricted by the polar night and snow cover. In continental and mountainous cold temperate regions, where the amount of precipitation is considerably higher, the thicker snow cover will probably be equally effective. Therefore, phytoplankters in many of these lakes may receive insufficient light for measurable photosynthesis for periods as long as those encountered in polar lakes. Low nutrient levels are typical of all rocky oligotrophic lakes and, since these occur most frequently in mountainous areas in temperate regions, are often found in lakes subject to the harsh conditions described above. Nutrient levels could be lowest in these temperate lakes because high annual precipitation causes a rapid turnover of lake waters. Ectogenic meromixis is a phenomenon also found in other climatic zones and the anomalous temperature curves caused by the solar heating of chemically stratified lakes are well known (Hutchinson, 1957, p. 479; Anderson, 1958). The phenomenon is exploited commercially in Norway and Israel.

There is, however, one outstanding feature common to all Antarctic inland waters: the simplicity of their ecosystems. Throughout the whole continent the fresh-water biota is restricted by environmental factors, isolation and the brevity of the time since deglaciation. Consequently, the trophic structure within the ecosystem and the interspecific relationships are relatively simple.

CONCLUSION

This review clearly indicates the need for basic, comprehensive research programmes in all areas of the continent. Antarctic lakes and pools are closed systems for most of each year and are apparently affected by fewer external influences than lakes in lower latitudes. Studies of these habitats with their restricted environmental variables and inter-specific relationships may reveal basic ecological principles more readily than studies elsewhere. Limnological studies, with terrestrial studies, will also throw light on the development of recently deglaciated areas. In evaluating the biological information, however, the isolation factor must always be considered, for the rate and nature of colonization by living organisms are greatly different from those which have occurred and are occurring in the Northern Hemisphere.

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