THE ANNUAL CYCLE OF TEMPERATURE, CHLOROPHYLL AND MAJOR NUTRIENTS AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS, 1969–82

A. Clarke, L. J. Holmes *and* M. G. White

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Abstract. Temperature, salinity, chlorophyll, nitrate, nitrite, phosphate, silicate and ammonia were measured approximately monthly at two sites in Borge Bay, Signy Island, between 1969 and 1982. Salinity showed no seasonal variation apart from occasional slightly lower surface values caused by melt water. Temperature showed a small seasonal variation, from about −1.8 °C in winter to roughly +0.3 °C in summer (February). Sea ice was present for an average of 140 days each year, though there was great year to year variation. In winter chlorophyll levels were very low. The bloom started in late November and peak chlorophyll biomass in January occasionally reached over 40 mg/m^3. The bloom then declined rapidly, usually reaching winter levels once more in March. Winter levels of nitrate, phosphate and silicate were high, and all showed extensive depletion during the bloom. Nitrite was present at low levels but also decreased during summer. Ammonia levels were very variable, although they generally increased during summer. The size of the summer bloom varied greatly between years, and the annual minimum concentration of nitrate, phosphate and silicate depended on the size of the bloom. Comparison with other Southern Ocean data indicates that in inshore areas phytoplankton blooms are typically more predictable and intense than in offshore waters.

Introduction

The pattern of seasonal variation in phytoplankton standing crop and production is of fundamental significance to the marine ecosystem. The availability of phytoplankton determines the ecology of both benthic and pelagic herbivores, and this influence permeates the higher levels of the food web (Clarke, 1988).

Between 1969 and 1982 regular measurements of temperature, salinity, chlorophyll and the major nutrients (N, P and Si) have been made approximately monthly at two sites close to the British Antarctic Survey base at Signy Island. In this paper we present a summary of these data and discuss year to year variations.

Materials and Methods

Sampling sites

Signy Island (60° 42′ S, 45° 36′ W) is part of the South Orkney Islands, situated in the maritime Antarctic. A description of the climate is given by Holdgate (1967). The British Antarctic Survey base is sited on the edge of Factory Cove, a small inlet off Borge Bay (Fig. 1). Borge Bay consists of a series of inlets and shallow embayments covering about 2 km^2. The maximum depth is roughly 30 m and the mean depth is about 10 m. There is free exchange of water between Borge Bay and the Orwell Bight since the bay entrance is unrestricted and has no underwater sill. The bottom varies from rock to fine sand and the nature of the substratum largely determines the distribution and abundance of benthic plants (Richardson, 1980). In winter the sea is covered by fast ice up to 1 m thick for between 70 and 241 days (data for the period

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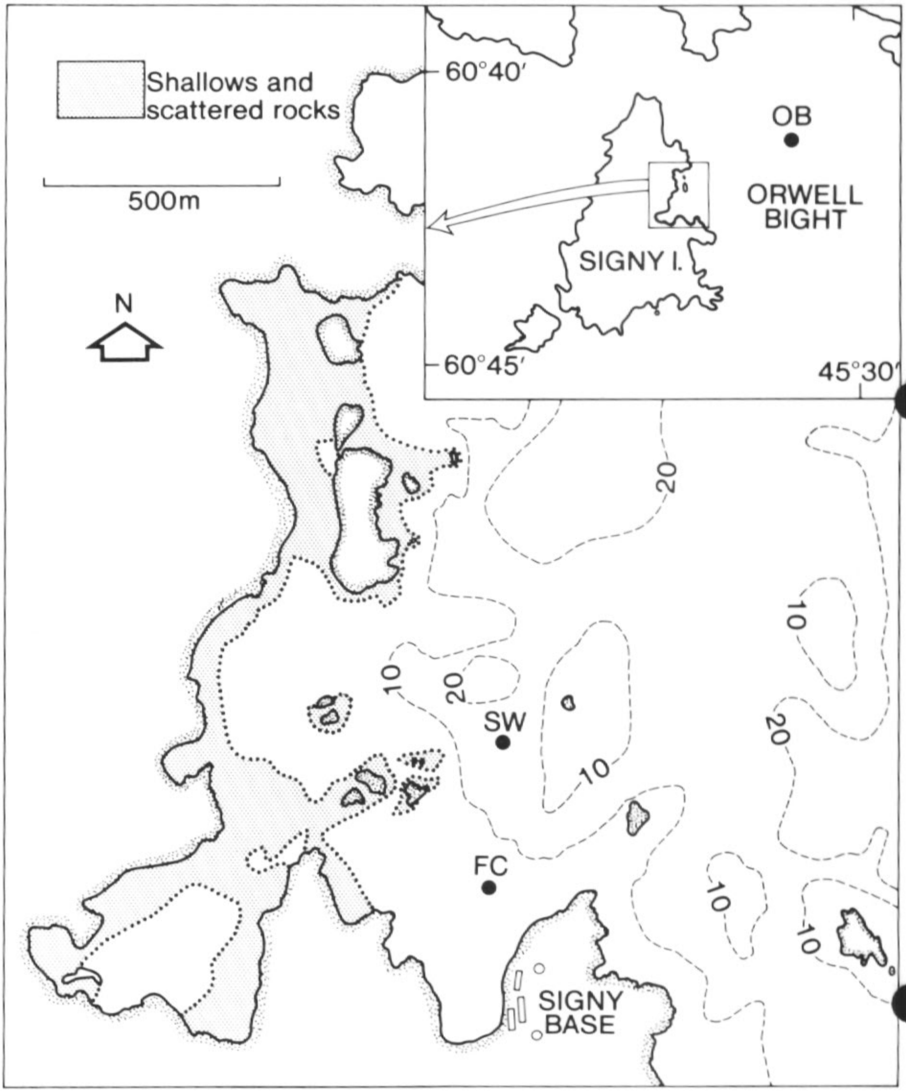

Fig. 1. Map of Borge Bay, Signy Island showing the location of the sampling sites (●) used in this study. FC, Factory Cove; OB, Orwell Bight ('Normanna'). Also shown is the sampling site (Small Rock) used by Whitaker (1982) and a one-year sediment trap study (SW).

1957–72: White, 1977), and pack ice may be present at almost any time when fast ice is absent.

Water samples were taken from two sites. The first (Factory Cove) was in the inner part of Borge Bay where the depth is a little under 10 m. Samples were taken at depths between 5 and 7 m; these data have been pooled and termed 6 m. Less frequently shallower samples were also taken at 2 m. The second, deeper water, site was in the Orwell Bight, in 40 m of water. This site has traditionally been referred to as 'Normanna'; however since it is actually some way from Normanna Strait (which separates Signy Island from Coronation Island to the north), this potential confusion has been avoided here by referring to the site as Orwell Bight. When weather permitted samples were taken from 2, 10 and 30 m depth. The location of both sampling sites is shown in Fig. 1.

Sampling and analysis

Water samples were taken with high density polyethylene NIO (National Institute of Oceanography) water bottles. Between 1 and 4 litres of water were collected from each depth to ensure sufficient sample for chlorophyll analysis. Samples were transferred to the laboratory in wide-mouthed polythene screw-top bottles, and bottles were always rinsed out with a small volume of water from the relevant sample before the bulk of the sample was introduced. Analyses were usually completed within 24 h of sampling. Summer samples were taken from a small dinghy or the base [illegible]nch. In winter samples were taken through a hole cut in the fast ice.

Temperature was measured with fully protected Watanabe reversing thermometers mounted on the water bottles. A minimum of 15 min was allowed for equilibration at the relevant depth and on return to the base thermometers were held for at least one hour in the (unheated) aquarium room on the base before being read. Either two or three thermometers were used for each determination and the mean value recorded.

For the measurement of phytoplankton chlorophyll *a* water samples were filtered onto Whatman GF/C glass fibre filters, the volume filtered depending on the season. The filters were then ground and extracted into cold acetone as described by Strickland and Parsons (1965, 1972). Salinity, orthophosphate, nitrate, nitrite and reactive silicate were assayed in the filtered seawater according to Strickland and Parsons (1965, 1972). Ammonia was determined initially by the phenolhypochlorite technique of Solorzano (1969) and later using the modification of this procedure described by Liddicoat and others (1975).

Absorbances were read on a Pye SP-600 spectrophotometer using 1- or 4-cm path-length cuvettes. Cell to cell and reagent blanks were incorporated in all analyses, and the assays were calibrated by spiking replicate samples with known amounts of the nutrient being analysed. All nutrient data have been expressed as mg-atoms/m^3, which is numerically identical to μg-atoms/litre and, for these nutrients, also to mmol/m^3 or μM (micromolar).

Data analysis

The water sampling programme started in 1969 with measurements of temperature and salinity. Assay of chlorophyll and the major nutrients was begun in 1971/72 and by the termination of the programme in March 1982 a total of 1056 samples had been analysed. Coverage was fairly evenly spread over the years except for particularly intense sampling in 1972–73, which was the period of Whitaker's study of primary productivity in Borge Bay (Whitaker, 1982).

Although samples have been taken in all months of the year, coverage has not been even (Fig. 2). In Factory Cove relatively fewer samples were taken in the period February to June than at other times. This seasonal variation was significant ($\chi^2 = 24.22$, $P < 0.05$) and reflected the difficulty of sampling in some years during late summer or early winter when unconsolidated pack ice can prevent both boating and snowmobile travel. Fewer data were available for the deeper water Orwell Bight station but the monthly coverage was more consistent ($\chi^2 = 6.17$, $P > 0.05$, Fig. 2).

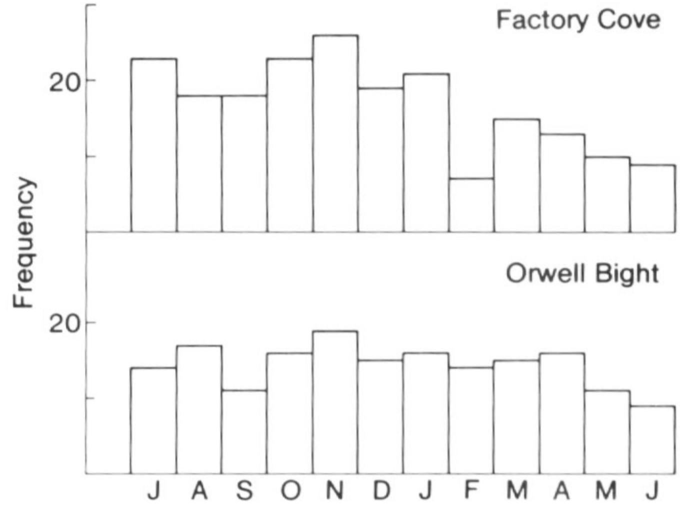

Fig. 2. Frequency histogram of all temperature data, pooled by month of observation, for the Factory Cove and Orwell Bight stations, Signy Island, 1969–82. Factory Cove data are for 6 m ($n = 202$) and Orwell Bight data for 10 m ($n = 173$).

The data presented in this paper have been obtained by nine different marine assistants. These analysts were working at Signy without direct supervision and although extended periods of overlap between successive assistants (usually four to six months) assured a reasonable continuity, it is likely that analytical precision and accuracy will have varied from year to year. The full extent of this variance cannot be determined, but examination of the raw data in the laboratory notebooks indicates that the overall precision of the various measurements is of the order:

Temperature	±0.02 °C	Phosphate	±0.04 mg atom/m^3
Salinity	±0.02	Nitrate	±0.07 mg atom/m^3
Chlorophyll	±0.02 mg/m^3 (below 1 mg/m^3)	Nitrite	±0.04 mg atom/m^3
	±0.04 mg/m^3 (1–10 mg/m^3)	Silicate	±4.0 mg atom/m^3
	±0.1 mg/m^3 (above 10 mg/m^3)	Ammonia	±0.2 mg atom/m^3

For initial analysis data were pooled by month, and data for each depth at both stations analysed using both the GENSTAT (Rothamsted Experimental Station, Herts, UK) and MINITAB (Pennsylvania State University) statistical packages. Following this initial analysis, year to year comparisons were undertaken for selected variables, using unpooled data.

RESULTS

Preliminary analyses indicated that when all data were pooled by month there were virtually no detectable differences in the seasonal patterns of all variables between the various depths at both sites. Two data sets were therefore selected for detailed examination, namely 6 m depth in Factory Cove, and 10 m depth in Orwell Bight. These were the most complete data sets at each site.

The month to month variation in all parameters at both sites was examined by one-way analysis of variance (ANOVA). All but two of the measured variables showed significant seasonal variation (temperature, chlorophyll, phosphate, nitrate all $P < 0.001$; nitrite, silicate both $P < 0.05$). The exceptions were salinity and ammonia which showed no seasonal variation at either site (both $P > 0.05$).

The overall mean salinity was 33.91 (SD 0.46) at 10 m in Orwell Bight and 33.87 (SD 0.37) at 6 m in Factory Cove. It might be expected that lower salinities would be detected in surface waters associated with melting ice. However, the mean salinity at 2 m depth in Orwell Bight was 33.84 with the lowest value recorded being 32.34. Clearly the effects of terrestrial run-off, melting of sea ice *in situ* and percolation of water from melting snow through tide cracks do not extend below the top 2 m. In addition, fast ice in Borge Bay tends to break up and blow out during spring bad weather rather than melt *in situ*.

Temperature

The seasonal variation in monthly mean temperature at the two sites is shown in Fig. 3. At both sites the lowest temperatures were reached in August, −1.76 °C at

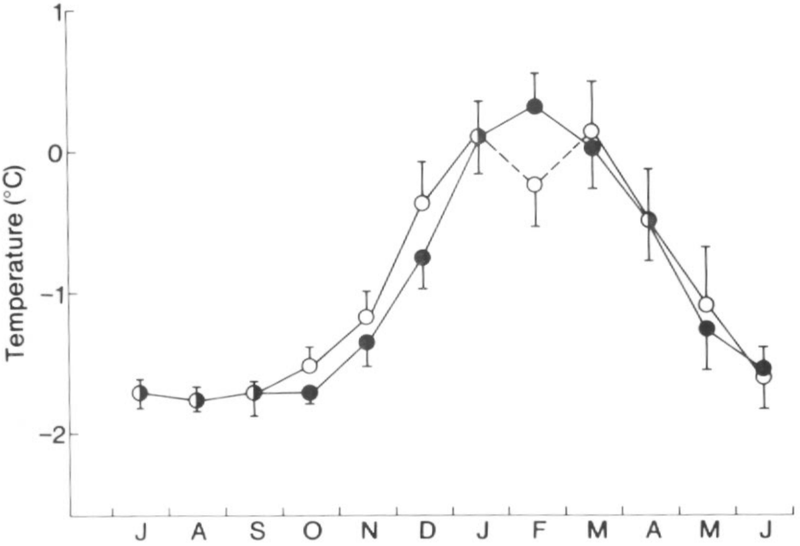

Fig. 3. Seasonal variation in seawater temperature (°C) at 6 m in Factory Cove (○) and at 10 m in Orwell Bight (●). Data are presented as mean ± 95 % confidence intervals for all data pooled by month. For clarity only one error bar is shown for each site. Coincident means are shown by ◑. The total number of observations at each site were 202 at Factory Cove (range 7–26 observations per month) and 173 at Orwell Bight (range 9–19 observations per month). In this and all subsequent summary plots, the year has been shown from July to June so that the austral summer is shown complete. Note dashed lines connecting data for February in Factory Cove to adjacent points (see text).

10 m in the Orwell Bight, and −1.78 °C at 6 m in Factory Cove. In Factory Cove temperatures started to rise in September/October, reaching +0.1 °C in January and +0.14 °C in March. These points were separated by a value of −0.24 °C in February, which represented a strange dip in summer temperature (Fig. 3). Since February was represented by only seven data points (Fig. 2) this dip was assumed to be an artefact.

The rise in seawater temperature at 10 m in Orwell Bight lagged behind that in Factory Cove by 10–15 days, reaching a maximum of +0.31 °C in February. The decline in temperature in late summer and early winter was virtually identical to that in Factory Cove. The earlier rise in temperature at the shallower site presumably reflects the smaller mass of water to be heated by incoming solar radiation, and possibly warming by bottom sediments.

The equilibrium freezing point of seawater depends on the salt content and for waters of salinity 34.8 would be about −1.8 °C (Sverdrup and others, 1942). Nevertheless there were six individual observations (three for each station) of temperatures below −1.9 °C. The coldest observations were −2.03 °C in June at Orwell Bight and −2.15 °C in August at Factory Cove. In addition, three observations below −2 °C were made at 2 m depth in Orwell Bight (the lowest being −2.26 °C in June). This suggests that the observations may be real and were due to temporarily undercooled seawater associated with very low air temperatures and the formation of sea ice. Littlepage (1965) reported four measurements of seawater temperature below −2 °C from McMurdo Sound in July 1961, and collated scatte[illegible] data for other sites in Antarctica.

Sea ice

The duration of fast ice in Borge Bay varied greatly from year to year. Between 1969 and 1982 it ranged from 59 days (1977) to 230 days (1973); the mean duration was 141 days (SD 57 days, equivalent to a coefficient of variation (CV) of 40 %, Table I). This is very similar to the data summarized for 1957–72 by White (1977), which gave a mean duration of 149 days. These two data sets overlap between 1969 and 1972 but the data for fast-ice duration do not always agree. This is because the criteria used to decide on the date when surface ice can be regarded as solid differs between observers and also between people extracting information from sea-ice records. In

Table I. Fast-ice cover and summer temperature rise, Borge Bay, Signy Island, 1969–82. Data for ice cover refer to the preceding winter (that is for the austral summer 1971/72 season, ice cover data refer to the 1971 winter)

			Temperature			
	Fast ice		*Factory Cove*		*Orwell Bight*	
Season	*Duration*	*End*	*Start*	*Duration*	*Start*	*Duration*
1969/70	127	269	328	131	—	—
1970/71	113	248	288	219	—	—
1971/72	63	249	336	138	—	—
1972/73	208	344	348	—	354	117
1973/74	230	340	—	—	355	149
1974/75	163	303	—	—	321	173
1975/76	145	304	325	—	325	218
1976/77	147	305	320	223	322	217
1977/78	59	250	—	—	347	178
1978/79	89	274	341	155	341	195
1979/80	—	—	—	—	352	123
1980/81	216	352	—	—	359	121
1981/82	184	330	—	—	339	—
1982/83	90	300	—	—	—	—

All dates are presented as Julian day (day number). Duration of summer temperatures is that period for which seawater temperature was above −1 °C.

—, Data not available.

this study, a solid ice cover was assumed to be formed once either 10/10ths pack ice covered the area of Borge Bay, or fast ice sufficiently solid to walk upon had formed *in situ*. The differences between the two studies are, however, minor and the overall picture is very similar.

A much more extensive data set is available for Factory Cove. Here the date for the start of the period of fast ice was taken as that date on which the surface ice was sufficiently strong to support the weight of a man. The end of the fast ice was that date on which the ice blew out. These criteria are different again from those applied to Borge Bay but the overall pattern was remarkably similar. For 38 years between 1947 and 1986 the mean duration was 140 days (SD ± 50 days, CV = 35%). The average date of fast-ice formation was 1 June (SD ± 24 days), and the average date of blow-out was 18 October (SD ± 37 days). The earliest date of walkable sea ice was 14 April (in 1949), the latest date of ice break-up was 26 December (in 1966).

Clearly there is little difference in the annual pattern of sea ice between Factory Cove and the more extensive and open area of Borge Bay. This is in part because the arrival of pack ice in Borge Bay is usually the factor which allows the surface of Factory Cove to freeze. Furthermore, the ice from both areas tends to leave at about the same time (though clearly the ice in Factory Cove cannot leave before that covering Borge Bay). The slight difference in the timing of the increase of seawater temperature between the Factory Cove and Orwell Bight sites cannot therefore be due to differences in the duration of ice cover.

Overall the mean annual pattern is one of sea ice covering the area for about 140 days every year but with very great year to year variation. Just how large is this year to year variation in fast ice cover can be seen from Fig. 4. This diagram has been modified from that in White (1977) by altering slightly the overall duration of fast ice for the years 1959 and 1969–72. (Again these alterations reflect the different criteria used to define solid fast ice in the various studies.) In some years, for example 1959 and 1972, fast ice was present for a long period with no breaks and grew to a thickness of over a metre. In other years, notably 1960, 1967 and 1968, the sea ice repeatedly broke up and reformed. These differences are of considerable significance to the underlying biological communities since sea ice influences light transmission and water column stability. When sea ice is present the underlying water is very stable and most of the particulate matter sediments out. If the sea ice breaks out wind-induced turbulence can once more turn over the water column and resuspend bottom material.

Chlorophyll

The seasonal variation in the standing stock of chlorophyll *a* at the two stations is shown in Fig. 5. In Factory Cove winter levels were very low, with a minimum monthly mean of 0.23 mg/m^3 in July. The lowest individual observations in June, July and August were 0.02, 0.06 and undetectable (< 0.001). There was a very slight increase in chlorophyll during September and October. The bloom then started in November, climbed very rapidly during December and peaked in January. The peak value attained during the bloom varied greatly from year to year, resulting in wide confidence intervals on the mean. In Factory Cove the mean peak chlorophyll concentration between 1972 and 1979 was 19.3 mg/m^3, with 95% confidence intervals of 14.5–24.2. Peak chlorophyll values for the individual years varied much more widely than this, however, with overall maxima for December, January and February being 30.5, 50.9 and 22.4 mg/m^3 respectively. These are very rich blooms indeed and are considerably more intense than typical open-water (pelagic)

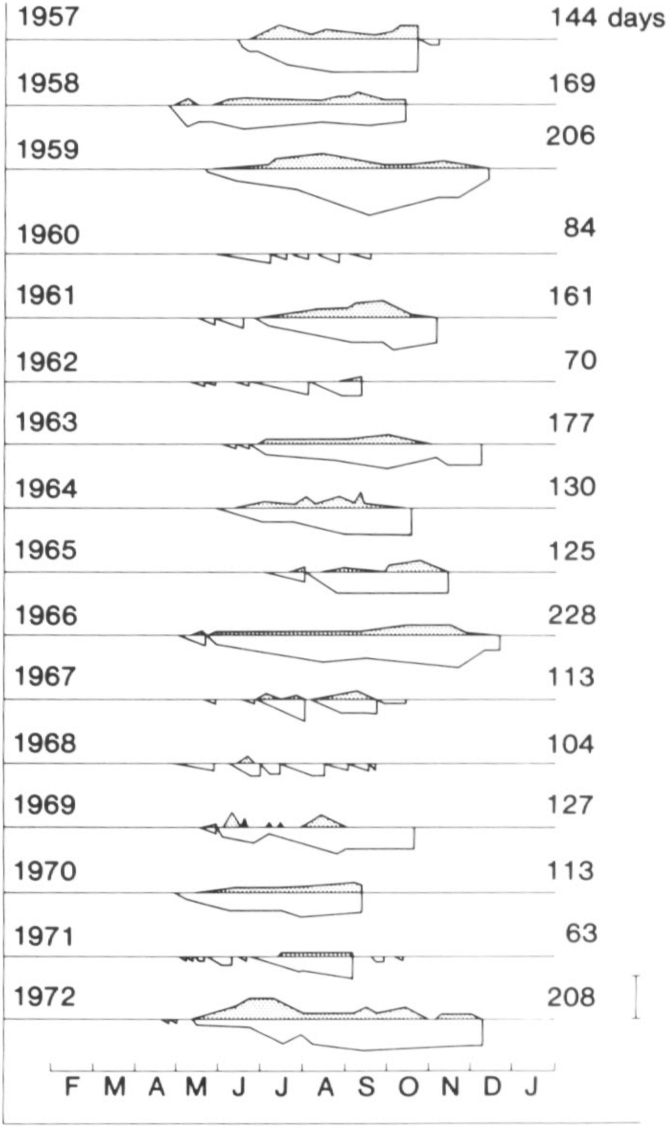

Fig. 4. Fast ice development in Borge Bay, Signy Island, 1957–72. The year of the observations is shown on the left, and the duration of fast ice (days) on the right. The bar represents 1 m, with snow (stippled) shown above the horizontal and ice shown below the horizontal. Redrawn from White (1977), with slight modifications to the data for 1959, and 1969–72 (see text).

chlorophyll concentrations which are usually 8–10 mg/m^3 (Sakshaug and Holm-Hansen, 1984). After January the bloom declined rapidly, reaching levels below 1 mg/m^3 in April.

The seasonal pattern at Orwell Bight was similar to that in Factory Cove although chlorophyll levels were systematically lower. Monthly mean levels in winter were 0.10, 0.10 and 0.09 mg/m^3 for July, August and September respectively. Individual levels below the limit of detection (< 0.001 mg/m^3) occurred during July, September and

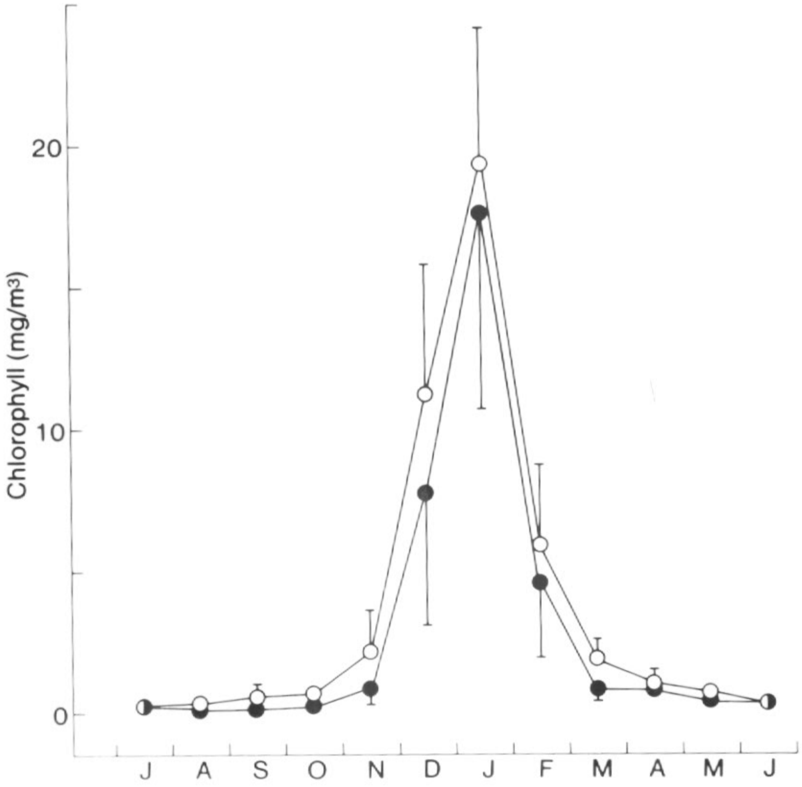

Fig. 5. Seasonal variation in the standing crop of chlorophyll *a* retained by a GF/C filter (mg/m³) at Signy Island. Data are presented as mean ± 95 % confidence intervals for all data pooled by month; where no error bar is shown it is less than size of symbol. Data are for 6 m in Factory Cove (○, total of 233 observations, range 12–29 per month) and 10 m in Orwell Bight (●, total of 162 observations, range 8–21 per month). Coincident means are shown ◑. Note that the zero level has been displaced vertically for clarity.

tober. Chlorophyll levels increased in November, and the bloom developed rapidly uring December reaching a peak in January, declining through February and March to typical winter levels in April. As in Factory Cove there was considerable year to year variation in the intensity of the bloom, leading to wide confidence intervals.

The overall mean picture (Fig. 5) suggests that, as with temperature, the bloom started on average about 15 days earlier in Factory Cove than in Orwell Bight. However, if the data for individual years are compared (Table II) then the mean dates of initiation of the bloom are almost identical. In Factory Cove between 1972 and 1979 the mean starting date of the bloom was 29 November (SD ± 9.6 days); in Orwell Bight it was 1 December (SD ± 25 days). There are also strong correlations between the two sites in the peak concentration reached and time-integrated biomass (Table II; Spearmann rank correlation, $r_s = 1.0$ for peak concentration, $r_s = 0.86$ for biomass, both $P < 0.05$).

Macronutrients

The seasonal pattern of phosphate concentration at the two sites is shown in Fig. 6. At both the Factory Cove and Orwell Bight sites monthly mean winter levels were

Table II. Duration and intensity of phytoplankton blooms, Borge Bay, Signy Island, 1972–82. (A bloom was defined as a chlorophyll concentration above 1 mg/m^3.)

Season	*Date of start (Julian day)*	*Duration (days)*	*Peak concentration (mg/m^3)*	*TIB (mg-days/m^3)*
Factory Cove				
1972/73	347	118	37.5	1068
1973/74	325	150	38.3	2014
1974/75	333	106	18.6	1107
1975/76	319	98	50.9	1887
1976/77	321	188	13.7	677
1977/78	338	95	3.0	191
1978/79	336	92	6.5	224
1979/80	336	127	24.2	1427
Orwell Bight				
1972/73	347	133	35.4	1435
1973/74	324	112	41.3	1954
1974/75	330	109	26.8	1161
1975/76	291	107	41.6	1416
1976/77	307	170	14.5	696
1977/78	339	67	2.8	130
1978/79	363	34	5.7	146
1979/80	(339)	(100)	28.2	1347
1980/81	331	118	2.8	291
1981/82	4	41	2.2	77

TIB, time integrated biomass derived by trapezoidal integration. Data in parentheses have been derived by interpolation (see text).

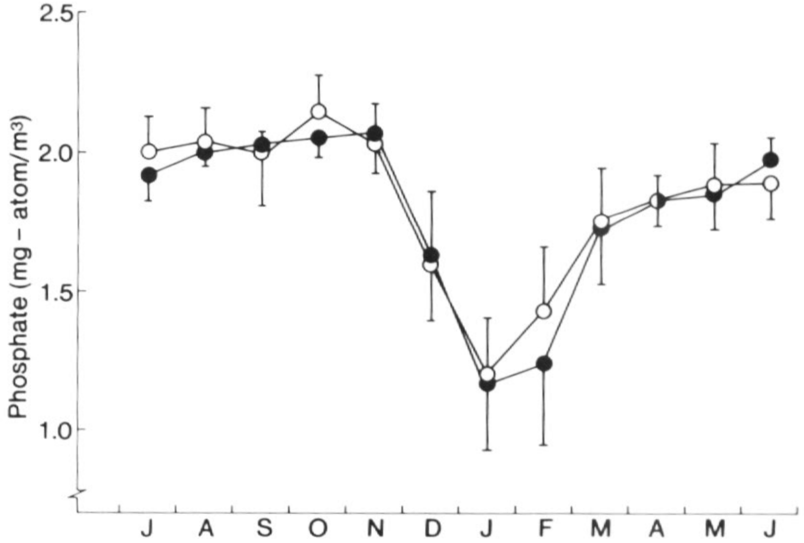

Fig. 6. Seasonal variation in the concentration of orthophosphate (mg-atom/m^3) at Signy Island. Data are presented as mean ± 95 % confidence intervals. Data are for 6 m in Factory Cove (○, total of 227 observations, range 13–27 per month) and 10 m in Orwell Bight (●, total of 161 observations, range 9–19 per month). Coincident means are shown ◑.

quite high, roughly 2 mg-atom/m³. Once the bloom started developing in November, phosphate levels dropped rapidly to a mean annual minimum of around 1.2 mg-atom/m³.The actual minimum reached varied from year to year, resulting in wide confidence intervals. From January phosphate levels started to rise rapidly, reaching 1.7–1.8 mg-atoms/m³ in March but then rising only slowly to the peak winter levels in September/October. The pattern of depletion of phosphate was similar at the two sites. However the late summer rise in phosphate levels occurred earlier in Factory Cove than in Orwell Bight, although the confidence intervals were wide.

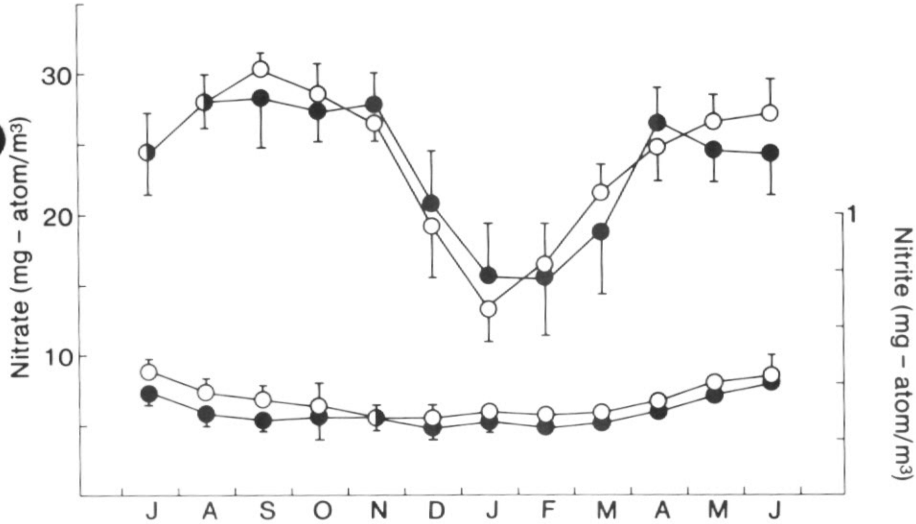

Fig. 7. Seasonal variation in the concentration of nitrate and nitrite (mg-atom/m³) at Signy Island. Data are presented as mean ± 95 % confidence intervals. Data are for 6 m in Factory Cove (○, total of 195 nitrate observations, range 10–26 per month, and 200 nitrite observations, range 11–26 per month) and 10 m in Orwell Bight (●, total of 155 nitrate observations, range 9–19 per month, and 162 nitrite observations, range 10–19 per month). Coincident means are shown ◑.

A similar pattern was shown by nitrate (Fig. 7). The highest monthly mean levels, 28–30 mg-atom/m³, were reached in late winter but once the bloom started in November nitrate levels decreased rapidly to a mean annual minimum of between 13 and 16 mg-atom/m³ in January. As with phosphate there was a relatively rapid increase in nitrate during summer and a more gentle increase, at least in Factory Cove, during early winter. Again as with phosphate the return to winter levels appeared to start earlier in Factory Cove than in Orwell Bight.

Nitrite was present at much lower levels than nitrate, 0.2–0.4 mg-atom/m³. The seasonal pattern was one of a gentle decline in the monthly mean level of nitrite towards a mean minimum level in summer and an equally gentle return to peak mean levels around mid-winter (Fig. 7). Despite the relatively small scale of this variation one-way ANOVA of the individual data for each site indicated that these changes were statistically significant (both $P < 0.05$).

The seasonal pattern in ammonia concentration (Fig. 8) was difficult to interpret. The precise measurement of ammonia in seawater is not easy and during the course of this investigation (1972–80) two different (but related) techniques have been used. Initially the method of Solorzano (1969) was used, but this was eventually replaced

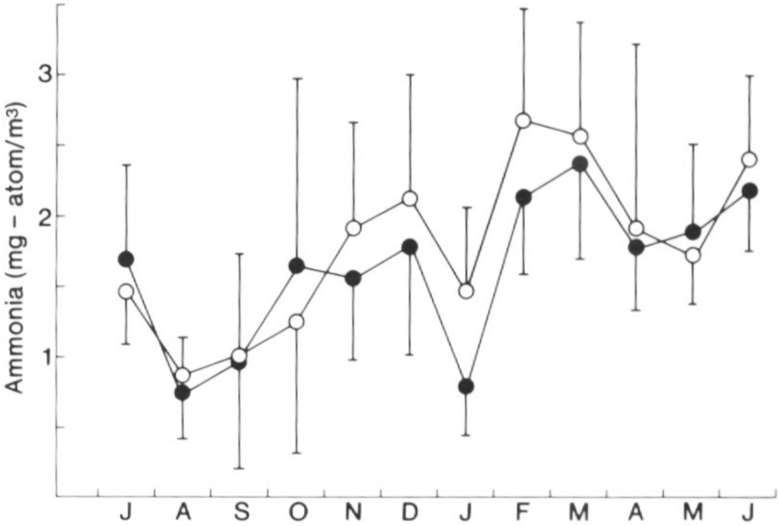

Fig. 8. Seasonal variation in the concentration of ammonia (mg-atom/m^3) at Signy Island. Data are presented as mean ± 95 % confidence intervals. Data are for 6 m in Factory Cove (○, total of 170 observations, range 9–22 per month) and 10 m in Orwell Bight (●, total of 139 observations, range 7–16 per month).

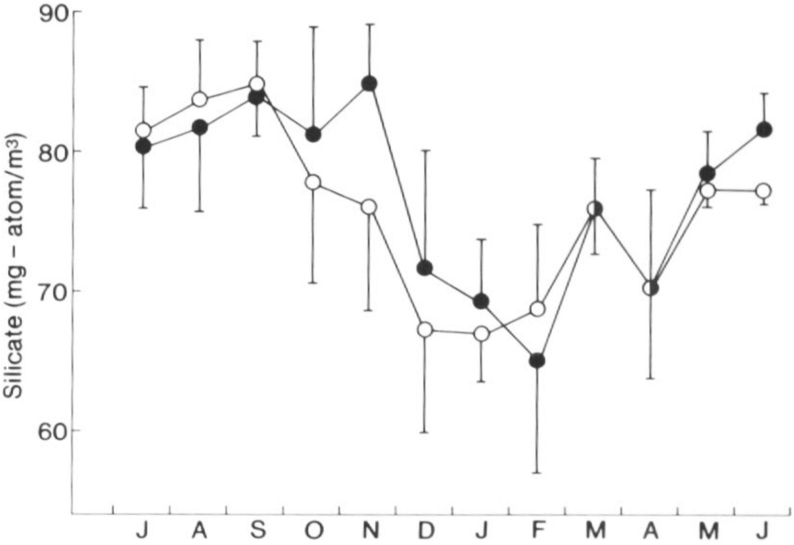

Fig. 9. Seasonal variation in the concentration of reactive silicate (mg-atom/m^3) at Signy Island. Data are presented as mean ± 95 % confidence intervals. Data are for 6 m in Factory Cove (○, total of 190 observations, range 11–24 per month), and 10 m in Orwell Bight (●, total of 159 observations, range of 10–19 per month).

by the modified protocol described by Liddicoat and others (1975). Despite the care taken during analysis, an initial scatter plot of the raw data for each site showed many points of dubious validity. All data > 6 mg-atom/m^3 were excluded as obviously erroneous but the remaining data set still contained a great deal of analytical variance. As a result the confidence intervals were wide and seasonal variation not quite significant (one-way ANOVA, $0.10 > P > 0.05$ at both sites). In most years the ammonia concentration increased from below 1 mg-atom/m^3 to about 2 mg-atom/m^3 during the summer. The decrease in January was surprising but it did occur in both Factory Cove and Orwell Bight (Fig. 8). This was followed by a sharp increase in ammonia level to almost 3 mg-atom/m^3 in late summer.

Silicate levels were high in winter, with a maximum monthly mean value of about 85 mg-atom/m^3 in September (Fig. 9). These values are indicative of Weddell Sea water. During the summer, silicate levels fell to a mean annual minimum of about 65 mg-atom/m^3. Silicate then increased through the winter. Unlike phosphate (Fig. 6) and nitrate (Fig. 7), the patterns of decrease in silicate level appeared to differ between the two sites. In Factory Cove, silicate started to fall as early as September and had reached a minimum by December. It would thus appear that silicate was being utilized before the phytoplankton bloom got underway. Nitrate also showed some indication of depletion starting in September at the Factory Cove site (Fig. 7), but phosphate did not. At the Orwell Bight site depletion of silicate did not start until November, and continued until February. The whole cycle at Orwell Bight thus appeared to be about two months behind that in Factory Cove, although this delay was not matched by the annual patterns of chlorophyll, phosphate or nitrate.

DISCUSSION

Data collected between 1969 and 1982 at two inshore sites at Signy Island have revealed an annual pattern of a small seasonal change in temperature together with a sharp and intense summer bloom accompanied by a depletion of macronutrients in the water column. Two features of this picture are of particular ecological interest, namely the extent of year to year variation and the degree of nutrient depletion during blooms.

Year to year variation in bloom size

The standing stock of chlorophyll *a* at 10 m depth at the Orwell Bight station between 1971 and 1981 is shown in Fig. 10. There were clearly considerable year to year variations in the intensity and duration of the bloom.

For calculating summary data a bloom was defined somewhat arbitrarily as any chlorophyll concentration above 1 mg/m^3. The start of the bloom was estimated by linear interpolation between the last sampling date when the concentration was below 1 mg/m^3 and the first when the concentration exceeded this level. The end of the bloom was estimated by linear interpolation in the reverse direction. The start of the bloom in the 1979/80 summer could not be estimated by this technique because a long period of pack ice prevented sampling at the relevant time. The start was therefore estimated by extrapolating back to 1 mg/m^3 using the mean rate of increase in chlorophyll biomass observed in 1972–76. The data for 1979/80 have therefore been plotted with broken lines in Fig. 10, and given in parentheses in Table II. Sampling difficulties may also have lead to a slightly early estimate for the start of the 1975/76 bloom, but this has not been corrected or adjusted. The overall size of the bloom was calculated as time-integrated biomass (TIB) by trapezoidal integration; the units are therefore mg-days/m^3.

Between 1971 and 1982 peak chlorophyll standing crop varied from 2.2 to 41.6 mg/m^3 and integrated biomass (TIB) varied by a factor of 25, from 77 to 1954 mg-days/m^3 (Table II). The duration of the bloom varied from only 41 days in 1981/82 to 170 days in 1976/77.

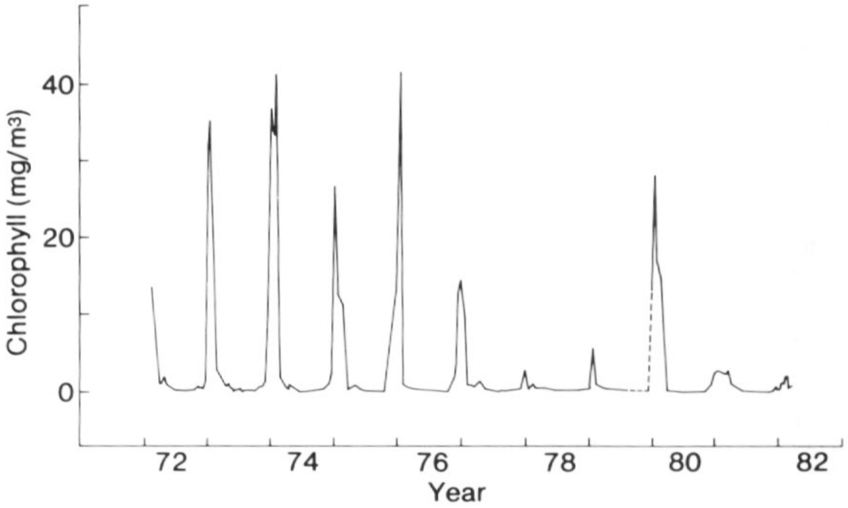

Fig. 10. Variation in standing crop of chlorophyll (mg/m^3) retained by a GF/C filter, at 10 m depth, Orwell Bight, Signy Island, between 1972 and 1982. Note that the zero level has been displaced vertically for clarity. Weather and ice conditions prevented sampling in late 1979, so data have been interpolated on the basis of the mean pattern in 1972–76 (see text). The interpolated data are shown by ---.

Table III. Correlation between bloom size (time integrated chlorophyll biomass, TIB: mg-days/m^3) and selected environmental parameters

Parameter	*n*	Pearson *r*	*P*
Fast ice			
Duration (days)	8	0.357	NS
Date of breakout	8	0.410	NS
Seawater temperature > −1 °C			
Date of onset	9	0.005	NS
Duration (days)	8	0.184	NS
Mean wind speed (knots)			
October	9	−0.316	NS
November	9	−0.742	< 0.05
December	9	−0.470	NS
January	9	−0.782	< 0.05

n, number of data point; *r*, correlation coefficient; *P*, probability of this result (for *n*-2 degrees of freedom; null hypothesis, $r = 0$); NS, not significant ($P > 0.05$).

All analyses exclude data for 1976/77 (see discussion of nutrient depletion in text), although including these data did not alter the significance of any result.

These variations in bloom characteristics are of enormous ecological significance. Many marine invertebrates have their biology coupled very tightly to the pattern of primary productivity (White, 1977; Clarke, 1988). Clearly 1972/73 to 1976/77 were five consecutive 'good' years; these were followed by two 'poor' years in 1977/78 and 1978/79. The next year produced a good bloom, but was followed by a poor bloom and a very poor bloom in 1982/83. For organisms dependent directly on the phytoplankton bloom, or which release planktotrophic pelagic larvae into the water column, there will clearly be significant year to year variation in growth rate, survival and recruitment.

It is not clear what factors govern whether the bloom is large or small in any given year. Taking the data for Orwell Bight shown in Fig. 10, there was no significant correlation of total integrated biomass with the date of ice breakout, duration of winter fast ice, the timing of the summer temperature rise or the length of time that seawater temperatures were above −1 °C (Table III).

Phytoplankton blooms do not appear to be nutrient-limited in the Southern Ocean (Heywood and Whitaker, 1984; Sakshaug and Holm-Hansen, 1984; Priddle and others, 1986). Furthermore although nutrient depletion might conceivably set an upper limit to bloom intensity or duration, it seems unlikely that this mechanism can be responsible for the observed year to year variation. It is generally agreed (see for example Priddle and others, 1986) that physical factors such as wind-induced turbulence are likely to be important factors regulating phytoplankton growth in the Southern Ocean. Certainly blooms are associated with the enhanced vertical stability produced by melting ice at the ice-edge (Sakshaug and Holm-Hansen, 1984), and at an inshore site in Admiralty Bay, Kopczynska (1981) found that an increase in algal numbers always followed a period of calm days. It is possible that years with only slight blooms are those with particularly windy conditions at key times.

This hypothesis was tested by examining the wind-speed data for October to January in the relevant years. There was no significant relationship between the size of the bloom and mean wind speed in October or December, but there were significant negative correlations between bloom total integrated biomass (TIB) and mean wind speed in November and January (Table III, Fig. 11). Significantly, these are respectively the months when the bloom starts and peaks. These data thus suggest

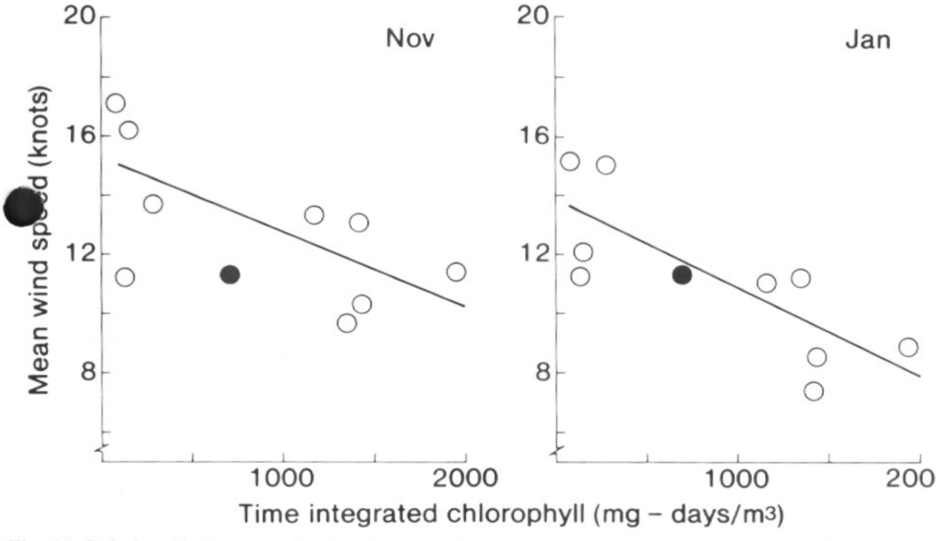

Fig. 11. Relationship between the time integrated chlorophyll biomass, TIB (mg-days/m^3) and monthly mean wind speed (knots) for November and January. Chlorophyll data are for the Orwell Bight station at 10 m depth (○), 1972–81; data for the 1976/77 season (●) have been excluded from the analyses (see discussion of nutrient depletion). Regression lines shown were fitted by least squares: November, $y_1 = (-2.54 \times 10^{-3})\, x_t + 15.28$; January, $y_t = (-2.91 \times 10^{-3})\, x_t + 13.73$. (Both lines are significant fits: $P < 0.05$.)

that wind-induced turbulence is an important factor influencing the size of the phytoplankton bloom in inshore waters in Antarctica.

Year to year variation in bloom timing

A particularly detailed study of the chlorophyll bloom at Signy Island was undertaken in 1972 and 1973 by Whitaker (1982) at a site between the stations at Factory Cove and Orwell Bight, which he termed the Small Rock station (Fig. 1). Since the seasonal cycles at Factory Cove and Orwell Bight are generally very similar, comparison with the intermediate Small Rock site is reasonable. Comparison of the annual pattern of the bloom at Small Rock (Whitaker, 1982) and that in Fig. 10, with the averaged picture in Fig. 5 shows that the averaged picture exaggerates the duration of the bloom. This is because the averaged picture is blurred by year to year variations in the timing of the bloom. Thus the mean annual pattern shown in F[illegible] 5 suggests that the bloom will have a standing stock of 1 mg/m^3 or greater for 155 days. During the period 1972/73 to 1981/82 (Table II) the mean duration of the bloom at Orwell Bight was actually 99 days (SD = 42 days). For Factory Cove the average picture suggests a bloom length of 150 days, due mainly to the slow autumn return to winter levels below 1 mg/m^3. Between 1972/73 and 1979/80 the mean duration was actually 122 days (SD = 33 days).

Like the intensity of the bloom, the timing of the spring increase is of crucial ecological importance (for example to invertebrates releasing eggs which will hatch into planktotrophic larvae). Whitaker (1982) commented that in the period of his study 'phytoplankton growth began abruptly during the first two weeks in December'. In years with small blooms it is very difficult to determine the start of the bloom with any precision. For the six good blooms observed in Factory Cove, the date when chlorophyll levels reached 1 mg/m^3 ranged from 14 November to 12 December, a span of only 28 days. For seven blooms observed in Orwell Bight the range was wider, from 17 October to 12 December, a range of 56 days. The range is increased by the data for 1975/76, when an inability to sample may have been responsible for the extrapolated date for the start of the bloom being too early (see Fig. 10 and earlier discussion).

The reason for the year to year variation in the timing of the bloom, small as it is, is unclear. There is no correlation with either the date of ice breakout, or the date of onset of the summer temperature rise (both $P > 0.05$). It is possible that, like the [illegible] of the bloom, the timing is related to the wind at critical periods but the data to test this are lacking.

Nutrient depletion

As phytoplankton growth proceeds, nutrients are removed from the seawater. Although the very high initial levels of nutrients mean that Southern Ocean phytoplankton are rarely, if ever, nutrient limited, substantial depletion of nutrients does occur, especially where sedimentation represents a significant loss of material to the benthos.

A traditional means of examining data for evidence of nutrient depletion is to look for any relationship between chlorophyll standing stock and nutrient concentration measured together (see examples in Priddle and others, 1986). In the Southern Ocean such relationships are at best weak, and often nonexistent. Pooling all data for the Orwell Bight station does reveal relationships between chlorophyll and nitrate,

Table IV. Relationships between chlorophyll concentration and nutrient depletion, Orwell Bight, Signy Island, 1972–82

Variables					% of		
Dep	*Ind*	*b*	*SEb*	*Intercept*	*% of variance explained*	*n*	*F*
All data pooled, untransformed							
NO_3	Chl	−0.423	0.064	24.58	0.23	148	43.3
PO_4	Chl	−0.035	0.003	1.89	0.49	152	141.6
SiO_3	Chl	−0.548	0.108	79.00	0.15	147	25.8
All data pooled, transformed to $\log_e$							
$\ln(NO_3)$	ln (Chl)	−0.124	0.024	2.94	0.15	148	26.2
$\ln(PO_4)$	ln (Chl)	−0.121	0.014	0.44	0.34	152	80.1
$\ln(SiO_3)$	ln (Chl)	−0.040	0.008	4.30	0.13	147	23.1
Yearly mean data, untransformed*							
MinN	TIB	-7.98×10^{-3}	2.19×10^{-3}	20.17	0.61	9	13.1
MinP	TIB	-7.26×10^{-4}	9.08×10^{-5}	1.84	0.89	9	64.0
MinS	TIB	−0.012	0.004	65.21	0.49	9	8.6

NO_3, PO_4 and SiO_3 all in mg-atom/m^3; MinN, MinP, MinS are minimum levels of nitrate, phosphate and silicate recorded in each season. Chl, chlorophyll (mg/m^3); TIB, time integrated chlorophyll biomass (mg-days/m^3).

All regressions were fitted by least squares. *b*, regression coefficient; SE, standard error; *n*, number of data points.

* 1976/77 data ignored (see discussion of nutrient depletion in text).

phosphate and silicate, but these are very weak (Table IV). However, a simple linear regression is not an appropriate analysis because the long winter period means that the distribution of chlorophyll values is highly skewed. A logarithmic transformation improves the distribution of chlorophyll values, but does not improve the fit.

These are better relationships than have generally been found for open water in the Southern Ocean (see Priddle and others, 1986 for examples) although a recent study of phytoplankton entrained within an eddy has revealed a strong negative correlation between chlorophyll *a* biomass and silicon concentration (Heywood and Priddle, 1987). The slightly improved fit observed in inshore waters is because chlorophyll blooms are more intense there, resulting in lower nutrient levels and hence a wider spread in values of both parameters being used in the regression. Nevertheless a linear regression of matched pairs of variables measured together in the same sample is not an appropriate statistical procedure for demonstrating nutrient depletion (or lack of it). This is because of the differing time scales over which the parameters vary. When the bloom is growing, chlorophyll levels are increasing and at the same time nutrient levels are decreasing; as a result there will be a close inverse relationship between the two variables. When the bloom collapses, however, chlorophyll levels decrease rapidly but nutrient levels recover much more slowly. Thus low chlorophyll levels can be associated with both high and low nutrient levels, distorting the relationship.

An alternative approach is to examine the relationship between overall bloom size (as time integrated chlorophyll biomass in mg-days/m^3) and the minimum nutrient levels observed in that season. Data for nitrate and phosphate at the Orwell Bight station are shown in Fig. 12. These data show a tight inverse relationship for both nutrients, which confirms that the small blooms observed in the late 1970s and early 1980s were real for they were associated with only slight nutrient depletion. The only exception was the 1976/77 season when an intermediate size bloom was accompanied by relatively intense nutrient depletion. Examination of the sampling records for this

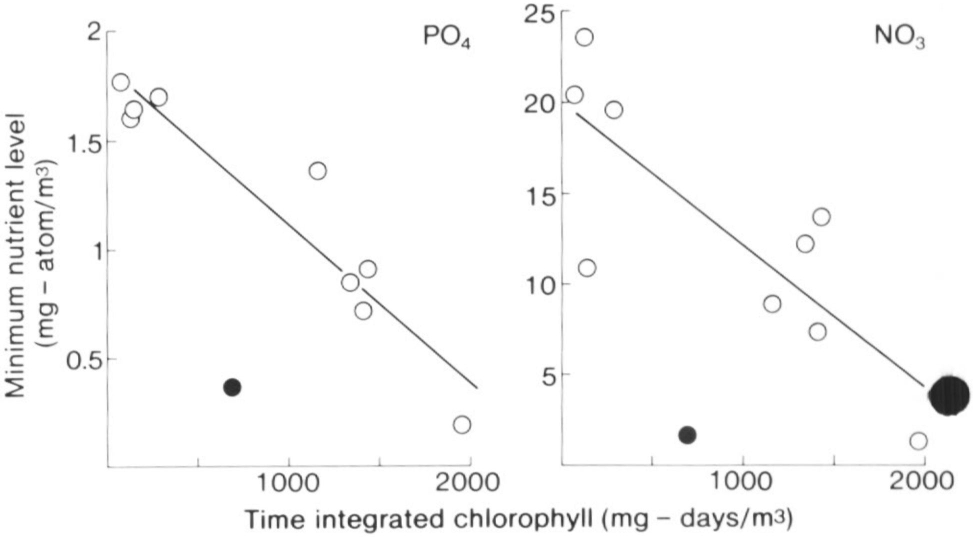

Fig. 12. Relationship between time integrated chlorophyll biomass, TIB (mg-days/m^3) and the minimum nitrate and phosphate levels (mg-atom/m^3) observed during the same year. Data are for Orwell Bight station at 10 m (○), 1972–81; data for the 1976/77 season (●) have been excluded from the analyses. Regression lines shown were fitted by least squares: Phosphate, $y_i = (-7.257 \times 10^{-5})\, x_i + 1.836$; Nitrate, $y_i = (-7.976 \times 10^{-4})\, x_i + 20.167$. (Both lines are significant fits, $P < 0.05$.)

season suggests that gaps in the sampling may have resulted in the peak of the bloom being missed. Data for this season were therefore excluded from the analyses. Overall the results show strong nutrient depletion in years with intense phytoplankton blooms, with the correlation being particularly strong for nitrate, less so for phosphate and poor for silicate.

Comparison of the time integrated chlorophyll biomass with the peak chlorophyll concentration observed (Table II) suggests that detectable nutrient depletion will occur once chlorophyll standing stocks exceed about 10 mg/m^3. Since this is above the concentrations generally observed in the Southern Ocean away from inshore areas (Priddle and others, 1986; von Bodungen, 1986) then it should be expected t[illegible] relationships between instantaneous measures of chlorophyll and nutrients in these areas should be poor.

Generally measurements in the Southern Ocean have provided little evidence for nutrient exhaustion (that is depletion of nutrients to the point at which they limit phytoplankton growth). However in the Weddell Sea, Jennings and others (1984) found marked nutrient reduction which they ascribed to the presence of an intense bloom associated with the ice-edge. Using a number of assumptions concerning utilization of nutrients by Antarctic phytoplankton, Jennings and others estimated the primary production required to produce the observed reduction in nutrient concentration. Estimates from nitrate, phosphate and silicate agreed well. In Table V similar conversion factors have been applied to the nutrient depletion rates observed in Orwell Bight. The estimated rates of carbon fixation calculated from nitrate and phosphate agree well (16.1 and 19.1 mg/m^3/day) but that from silicate is only about one third of these. However, all values are considerably less than those measured by Whitaker (1982) at the Small Rock site, which ranged from about 350 mg/m^3/day in December to 13 in March. These data were taken in the 1972/73 season which had a strong bloom, whereas the data in Table V are calculated from an average of data

Table V. Estimates of primary productivity from nutrient depletion, Orwell Bight, Signy Island

		Nutrient depletion ($\mu mol/m^3$)		*Carbon fixation (mg/m^3)*	
Nutrient	*Atomie ratio*	*($\mu mol/m^3$)*	*days*	*mg/day*	*mg total*
Nitrate	C:N 6.6	0.203	60	16.08	965
Phosphate	C:P 106	0.015	60	19.08	1145
Silicate	C:Si 2.5	0.220	90	6.60	594

Nutrient depletion rates were estimated from the periods of rapid depletion only, November to January (nitrate, phosphate) or November to February (silicate).

Carbon fixation was calculated from N and P using the Redfield ratio (C:N:P, 106:16:1 in atomic terms) and from Si using the factor devised by Jennings and others (1984). Total carbon fixation rates are [illegible]culated for the period of nutrient depletion only.

for 1972–82 and hence would be lower. Nevertheless, the magnitude of the difference suggests that estimates of primary production from nutrient depletion underestimate actual carbon fixation rates.

Although phytoplankton growth removes nitrate from the water column, there is some evidence that ammonium is the preferred form of nitrogen for Southern Ocean phytoplankton (Koike and others, 1986; Priddle and others, 1986). Dissolved free amino acids may also be important sources of nitrogen (Flynn and Butler, 1986). Against this must be set the fact that the concentration of nitrate is generally an order of magnitude greater than that of ammonia. It has been suggested that primary production may be divided into 'new' and 'regenerated' production, fuelled respectively by nitrate and ammonia (Smetacek and Pollehne, 1986). Nitrate uptake may thus be used as a measure of new production, that is the increase in phytoplankton biomass. The mean winter maximum and mean summer minimum nitrate concentrations at Orwell Bight during the period of this study were respectively 28.34 and 15.78 mg-atom/m^3. The nitrate utilized during the bloom thus averaged 12.56 mg-atom/m^3. Taking the Redfield ratio (C:N:P) to be 106:16:1 in atomic terms, the C/N ratio is thus 6.625 and this predicts a carbon production of 999 mg/m^3 during the bloom. Assuming the C/Chlorophyll ratio to be 30, the [illegible]edicted mean peak chlorophyll concentration during the bloom would be 33.3 mg/m^3. The actual mean value observed was 15.5 mg/m^3. A similar calculation for Factory Cove gives predicted and observed peak chlorophyll concentrations of 45.1 and 19.3 mg/m^3 respectively. These discrepancies suggest that the value of 30 for the C/Chlorophyll ratio may be too low. C/Chlorophyll ratios were calculated for the six years with good blooms (peak > 10 mg/m^3) in Orwell Bight using the carbon production estimated from nitrate depletion and the observed peak chlorophyll concentration. The mean value was 49.1, with a standard deviation of 12.5.

It would thus appear that rates of carbon fixation are underestimated by calculations from the rate of nutrient depletion, whereas peak standing crop biomass is overestimated by calculation from overall nutrient depletion.

Comparison with other areas

The seawater data set for Signy Island is unique in that it is the only continuous such set for any site in Antarctica. This makes comparison with other studies difficult.

Krebs (1938) measured chlorophyll *a* at 3 m depth in Arthur Harbour, Anvers

Island from July 1972 to November 1974. He observed a spring bloom in November and a second (summer) bloom in December/January. There was also equivocal evidence for late autumn (fall) bloom in February/March. Peak chlorophyll concentrations were about 12 mg/m^3 in December 1972 and 26 mg/m^3 in December 1973. These values are comparable with those observed in Borge Bay. The presence of two or three separable blooms is, however, somewhat different from Borge Bay. The species composition was recorded at the same time, and this gave clear evidence of distinct spring, summer and autumn (fall) blooms. In Borge Bay only in 1973/74 was there any indication of more than a single peak; in all other years there was only a single chlorophyll peak. It would be interesting to see further data from Arthur Harbour to judge whether this site differs consistently from Borge Bay.

At McMurdo Sound in 1961/62, Bunt (1964) found a single phytoplankton bloom which started in early December, reached a peak of about 35 mg/m^3 chlorophyll *a* in late December and declined to about 15 mg/m^3 by early January. Detail[illegible] measurements showed that the increase in standing crop was accompanied by changes in the phytoplankton species composition. In 1962/63 the bloom was later, with lower maximum chlorophyll concentrations and a delayed appearance of *Phaeocystis*.

The study by Kopczynska (1981) at King George Island only covered part of a single season, as did that of Rawlence and others (1987) at McMurdo Sound. The latter study found chlorophyll concentrations up to 30 mg/m^3 in tide cracks, comparable with the water-column concentrations found by Bunt (1964). Japanese studies at Syowa station have also concentrated on primary production close to sea ice and seasonal coverage has been patchy.

In the open ocean chlorophyll levels tend to be lower, bloom concentrations typically reaching only 8–10 mg/m^3 (Sakshaug and Holm-Hansen, 1984). A seasonal picture has been produced by Hart (1942) and more recently by El-Sayed (1984). These show a much smoother rise and fall in chlorophyll concentration than is seen at inshore sites such as Arthur Harbour or Borge Bay. In part this may be due to the smoothing effect of combining data from different sites and seasons referred to above. Also open water chlorophyll maxima are more sporadic in both time and space (Priddle and others, 1986). Although the mechanisms regulating open-ocean production are only imperfectly understood (Priddle and others, 1986) it is likely that prolonged decreased turbulence, and hence increased water column stability, may be part of the reason why inshore blooms are so much more intense than th[illegible] offshore.

Future studies

Collection of the data analysed in this paper ceased in April 1982. It is clear that regular monitoring of the inshore marine environment at Signy has provided extremely valuable ecological information. It is intended to restart data collection from the 1988/89 season, modifying some of the techniques in the light of the analyses presented here. In particular recent studies have shown that an important fraction of the chlorophyll biomass is in the nanoplankton (El-Sayed and Weber, 1985), although at least part of this may be due to intact chloroplasts released from damaged diatom cells (Gieskes and Elbrachter, 1986). Future studies will therefore involve size-fractionation of the chlorophyll biomass. Attention will also be directed at better defining the relationship between bloom size and nutrient depletion, establishing the year to year variation in bloom size and predictability, and documenting changes in species composition.

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