Seasonal and Interannual Variabilities in Antarctic Phytoplankton with Reference to Krill Distribution

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Summary. The spatial and temporal variabilities in the distribution of Antarctic phytoplankton biomass, based primarily on data collected by the author and other investigators during the past 25 years, are summarized. Mesoscale seasonal and interannual variabilities in phytoplankton distribution and abundance in the Drake Passage/Scotia Sea, the Bransfield Strait/Elephant Island, and the Ross Sea are examined. The general picture that emerges is one of great variability of the phytoplankton biomass and primary production. This spatial variability (up to two orders of magnitude) tends to overshadow the expression of seasonal differences. The time of peak phytoplankton abundance varies from year to year. Seasonal variability is much more pronounced than any interannual variability.

Of the several factors thought to cause spatial and temporal variability in Antarctic phytoplankton, three factors, namely, nutrient salts, water column stability, and grazing are discussed. The relationship between phytoplankton and krill remains as one of the vexing problems in Antarctic marine ecosystem studies. For better understanding of phytoplankton/krill interrelationships, future studies must resolve finer spatial scales and include time-course measurements to examine underlying mechanisms. Recommendations for future research are discussed.

1 Introduction

The study of Antarctic marine phytoplankton has a long and almost uninterrupted history that dates back nearly a century and a half to the *Erebus* and *Terror* expedition (1839–43). This history continued with the celebrated expeditions of the *Challenger* (1872–76), *Antarctica* (1895), *Belgica* (1897–99), *Valdivia* (1898–99), *Southern Cross* (1899–1900), *Gauss* (1901–03), *Scotia* (1902–04), *Pourquoi Pas?* (1908–10) and the *Discovery* investigations (1925–39) (see El-Sayed 1987 for review). Thanks to the extensive investigations carried out on board the USSR *Ob* and *Vitiaz*, the USNS *Eltanin*, the Argentinian *San Martin* and *Islas Orcadas*, the French *Commandant-Charcot* and *Marion Dufresne*, and the numerous Japanese and other ships throughout the 1960's and 1970's, a large amount of useful data on the geographical and temporal distributions of phytoplankton standing crop and on the magnitude of primary production in the circum-Antarctic waters was obtained (Klyashtorin 1961; Ichimura and Fukushima 1963; Mandelli and Burkholder 1966; El-Sayed 1967, 1968; Fukuchi 1980; Fukuchi and Tamura 1982).

The extensive investigations carried out during FIBEX (First International BIOMASS Experiment 1980–1981) and SIBEX (Second International BIOMASS Experiment 1983–84 and 1984–85) have greatly enriched our data base with regard to the phytoplankton and their primary consumers (zooplankton, especially krill). Although we now have a fair body of knowledge on phytoplankton distribution, abundance, and productivity in the waters surrounding Antarctica, we still have a poor understanding of the factors that regulate phytoplankton production in this area. We know, for instance, very little of the life history, physiology, behavior, and population dynamics of even the most common components of Antarctic phytoplankton, and whether they are well adapted to their environment is still a matter of controversy (Holm-Hansen et al. 1977; El-Sayed and Taguchi 1981). Moreover, the low levels of phytoplankton standing crops and primary production that are characteristic of most of the oceanic regions are puzzling in view of the high inorganic nutrient concentrations reported from these waters.

This chapter reviews the subject of spatial distribution of the phytoplankton biomass and productivity based primarily on data collected at 780 stations by the author and other investigators in the circum-Antarctic waters during the past 25 years (Fig. 1). The mesoscale seasonal and interannual variabilities in phytoplankton distribution and abundance in the three best-studied areas of the Southern Ocean, namely, the Bransfield Strait/Elephant Island, the Drake Passage/Scotia Sea, and the Ross Sea are discussed. The factors thought to govern the spatial and temporal variabilities of Antarctic phytoplankton, in light of data collected during the last decade, are also reviewed. In this review, the pelagic primary producers are featured, leaving the discussion of ice-algae to other contributors to this seminar (see Smith et al. this Vol.).

2 Data Limitations

Despite the large amount of data collected by the author and others since the early 1960's, both the geographical

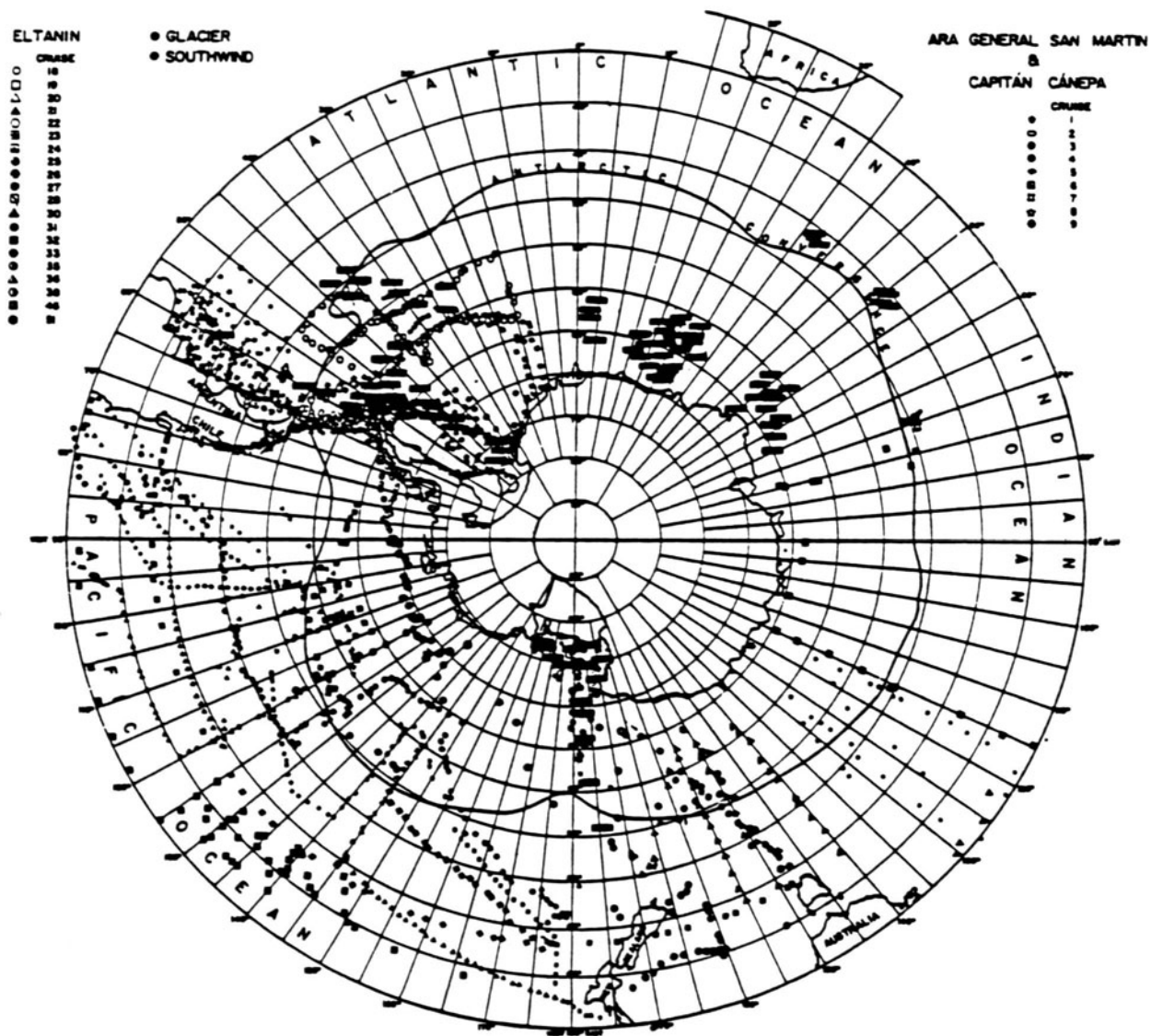1 Department of Oceanography, Texas A & M University, College Station, Texas 77843, USA

Fig. 1. Distribution of data on phytoplankton biomass and primary productivity discussed in the text. Stations occupied between 1976 and 1987 are indicated with ➡

and temporal coverage of the data is far from complete because of the vastness of the Southern Ocean. Heywood and Whitaker (1984) remind us that observations of standing crop and productivity rates have been made in isolation, both in time and space, as dictated by logistics and the workload of research vessels rather than by the biology of the flora. Most of the expeditions to the Southern Ocean have been limited to the periods of austral spring and summer, thus covering only part of the annual growth cycle, and giving us an incomplete picture of seasonal variability. Moreover, current methods and techniques have many limitations and have changed or been modified during the past two decades, thus making it difficult to compare results. Such limitations should be borne in mind, especially when comparing data obtained from various sources.

3 The Marine Environment

Before details about spatial and temporal variabilities of Antarctic phytoplankton are discussed, it is important to understand the unique physical/chemical settings of the Antarctic seas, since these strongly affect the biology, distribution, and abundance of the planktonic organisms.

The Southern Ocean is an upwelling system whose large-scale physical oceanography is dominated by the Antarctic Circumpolar Current. The unique features of this system are: the presence of pack ice around the continent and the seasonal waxing and waning of the pack-ice zone; the variability of the light regime that alternates between perpetual dankness in winter and continuous daylight during the summer; the extensive cloud cover; the stormy weather; and the Circumpolar Current, which connects
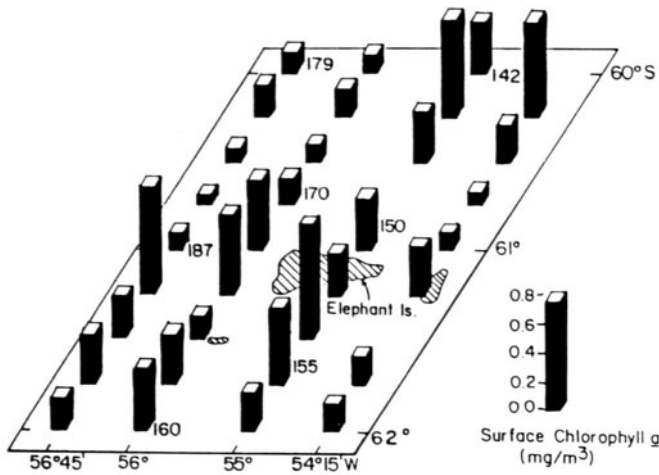
Fig. 2. Distribution and abundance of surface chlorophyll a in waters in the vicinity of Elephant Island during November 1984. (Data from Weber and El-Sayed 1986)

circum-Antarctic waters into a single system, the Southern Ocean, through the transport of nutrients and plankton. The Antarctic organisms have developed their characteristic features in response to the physical/chemical environments, and these are precisely the unique environmental parameters that present a paradox of considerable scientific interest, as is discussed later.

4 Spatial Distribution of Phytoplankton Standing Crop

4.1 Surface Distribution of Chlorophyll a

The bulk of the phytoplankton data shows chlorophyll concentrations in the range of 0.1 to 1.0 mg/m^3, with a mean value of 0.5 mg/m^3 (Saijo and Kawashima 1964; El-Sayed and Mandelli 1965; El-Sayed 1970; Fukuchi 1980). Within the confines of such low values, there is pronounced geographical variability in chlorophyll a concentration, even over relatively small spatial scales. This is clearly shown by the marked spatial heterogeneity of the phytoplankton biomass around Elephant Island (Fig. 2). Similar observations are also reported for around South Georgia (Priddle et al. 1986b), where the highest values of phytoplankton biomass were associated with stations off the northwest of the island and the lowest chlorophyll levels were located to the southeast. Priddle and his coworkers are essentially correct in stating that this patchiness around South Georgia (240 × 180 nm grid) reflects in a microcosm the distribution of phytoplankton throughout the Southern Ocean.

In contrast to the generally low standing crop of phytoplankton in oceanic regions, elevated biomass levels are reported from inshore waters, e.g., west of the Antarctic Peninsula and the Gerlache Strait (El-Sayed 1968), in the

southern Ross Sea (El-Sayed et al. 1983), near the Kerguelen and Heard Islands (El-Sayed and Jitts 1973); off the Crozet Archipelago (El-Sayed et al. 1979), and in the inshore waters of Signy Island (Horne et al. 1969). Exceptionally high values (i.e., in excess of 25 mg/m^3) were reported by Mandelli and Burkholder (1966) during a phytoplankton bloom near Deception Island. Elevated values in phytoplankton standing crop and primary production in Antarctic coastal waters and in the vicinity of Antarctic and Sub-Antarctic islands have been attributed to the so-called island-mass effect (El-Sayed et al. 1964; El-Sayed and Jitts 1973; Nast and Gieskes 1986). However, increased concentrations of inorganic salts cannot be invoked here, as is usually the case in tropical or temperate waters, since these nutrients, as discussed later, are in abundant supply.
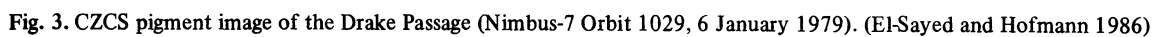
Phytoplankton blooms also occur near the edge of the seasonally retreating pack-ice (El Sayed and Taguchi 1981; Smith and Nelson 1985; Nelson et al. 1987). The most extensive and richest of such blooms occurred in the southwestern Weddell Sea (El-Sayed 1971a). This bloom, composed entirely of the diatom Thalassiosira tumida, covered an area 15 000 km^2, with chlorophyll concentrations of up to 190 mg/m^3.

In addition to inshore waters and the ice edge zone, high chlorophyll concentrations have been frequently associated with frontal structures such as the Polar Front (Allanson et al. 1981; El-Sayed and Weber 1982; Yamaguchi and Shibata 1982; Lutjeharms et al. 1985; Bidigare et al. 1986) and the Weddell/Scotia Confluence (Bidigare et al. 1986; Nelson et al. 1987).

In recent years, the advent of remote sensing has added a new and powerful tool to the study of geographical variability of phytoplankton biomass. Such variability is graphically documented in a satellite (Nimbus 7 Coastal Zone Color Scanner) image from the region of the Polar Front in the Drake Passage (Fig. 3). This image is a striking example of the interaction of mesoscale physics and phytoplankton biomass (El-Sayed and Hofmann 1986). The phytoplankton-poor waters of the Drake Passage and the cold core rings are clearly visible. The image further shows generally low pigment values in the Polar Front, a region of relatively high pigment concentration squeezed between bands of low pigment concentration. Pigment values north of the Polar Front are also generally low, but isolated regions of concentrations in excess of 0.1 mg Chl a/m^3 are observed. The reasons for these enhanced concentrations are unknown.

4.2 Vertical Distribution of Phytoplankton Biomass

The vertical distribution of phytoplankton biomass (in terms of chlorophyll a) generally exhibits maximum values at subsurface (50–70 m) depths. Following these maxima, there is a gradual decrease in the chlorophyll values to a depth of 200 m (Fig. 4), below which chlorophyll con-

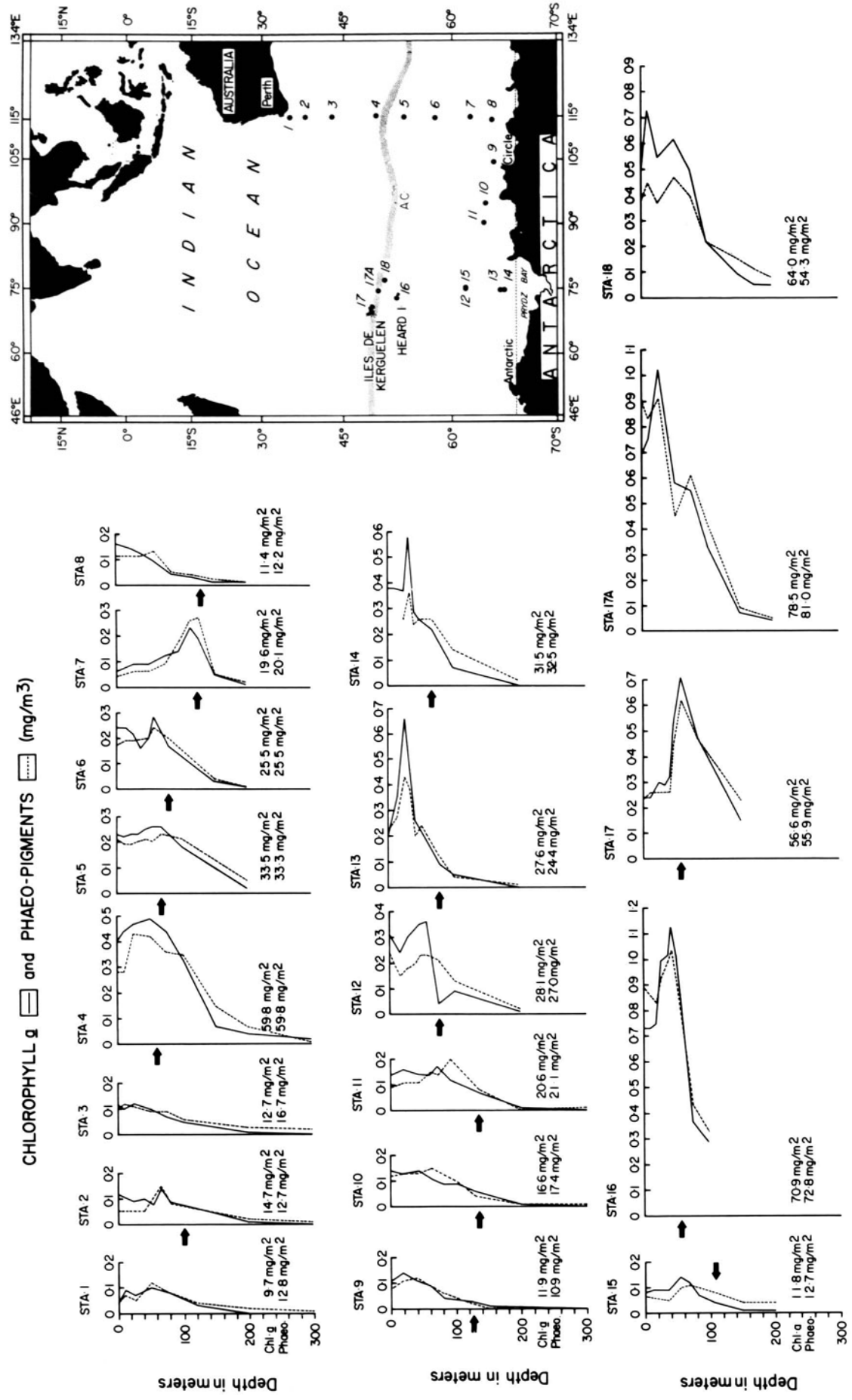**Fig. 3.** CZCS pigment image of the Drake Passage (Nimbus-7 Orbit 1029, 6 January 1979). (El-Sayed and Hofmann 1986)

Fig. 4. Vertical distribution of chlorophyll a and phaeopigments (mg/mg³) at stations occupied during *Eltanin* Cruise 46. Position of arrows indicate depth of euphotic zone. (El-Sayed and Jitts 1973)

centration is usually negligible (El-Sayed 1970; El-Sayed and Turner 1977; El-Sayed and Weber 1982). It is not uncommon for substantial amounts of chlorophyll to be found below the euphotic zone (i.e., below the depth to which 1% of surface light penetrates).

4.3 Spatial Distribution of Primary Production

The magnitude of primary production is a function of the phytoplankton biomass and the growth rates. Therefore, it is not surprising that most primary productivity data (estimated by the ^{14}C uptake method of Steemann Nielsen 1952) from the Southern Ocean show good correlation with the distribution of the phytoplankton standing crop. For instance, low values of primary production are reported for the Drake Passage, the Bellingshausen Sea, and in the oceanic waters in general. The open-ocean system has rates of production typical of oligotrophic regions (< 0.1 g C/m^2/day). On the other hand, high values are often found in coastal regions and in the vicinity of Antarctic and Sub-Antarctic islands. For example, El-Sayed (1968) recorded 3.2 g C/m^2/day in the Gerlache Strait; Mandelli and Burkholder (1966) reported 3.62 g C/m^2/day near Deception Island; and Horne et al. (1969) found a peak productivity of 2.8 g C/m^2/day in the inshore waters of Signy Island in the South Orkney Islands. Such values, which are comparable to those from the upwelling systems off Peru, southeast Arabia, Somalia, and southwest Africa, have no doubt perpetuated the belief in the proverbial "richness" of the Antarctic waters.

4.4 Vertical Distribution of Primary Production

As to the vertical distribution of primary productivity in the circum-Antarctic waters, maximum photosynthetic activity generally occurs at depths corresponding to between 50 and 10% of surface light intensity, corresponding to a photosynthetically available radiation (PAR) between 500 and 100 μE/m^2/s (von Bodungen et al. 1986). Carbon fixation, has been measured in samples from well below the classical euphotic zone. For example, El-Sayed and Taguchi (1981) and El-Sayed et al. (1983) report that primary production below the euphotic zone in the Ross and Weddell Seas was nearly one-fourth of the total production in the water column. However, in other studies, ^{14}C uptake below the euphotic zone did not exceed 5 to 10% of that in the entire water column (El-Sayed and Jitts 1973; El-Sayed and Weber 1982).

5 Seasonal Variability of Phytoplankton Biomass and Primary Production

As to the seasonal variability in the distribution of phytoplankton, unfortunately, there is a relative dearth of long-term phytoplankton data from any of the Antarctic regions. In this respect Antarctic biological oceanographers are not as fortunate as, for example, their British counterparts, who have long-term data records for the North Sea and the English Channel from as early as the 1920's (Cushing 1966; Russell et al. 1971; Southward 1974, 1980), or their American colleagues, whose California Cooperative Oceanic Fisheries Investigation (CALCOFI) spans nearly 40 years (Brinton and Reid 1986).

The problem is further complicated by the fact that seasonal cycles based on data from single stations, or from single depths, may not be representative. For example, deep chlorophyll maxima will be missed entirely if surface samples are used to reconstruct the seasonal cycle of phytoplankton biomass (Harris 1986). Further, large-scale advection may also modify the seasonal cycle as observed at a single point if the seasonal biomass cycle differs between water masses. Such complications should be kept in mind when examining the seasonal variability of phytoplankton biomass in the Bransfield Strait and neighboring waters, which are noted for their complex hydrographic structure (Stein this Vol.; Sievers and Nowlin this Vol.).

Despite the nonquantitative methods used by Hart (1934, 1942), his is still the most complete data set on seasonal variability of Antarctic phytoplankton to date. Hart demonstrated that the onset of the period of maximum production changes from early spring to late summer or early fall with increasing latitude (Fig. 5). He was able to show that the period of maximum production decreased in duration with increasing latitude and, further, that annual differences in the hydrographic conditions could affect the timing and magnitude of these peaks and the species that are active during the period. Hart's observations have been corroborated by the observations of many investigators. Figure 5 illustrates the marked resemblance between El-Sayed's (1970) observations and those Hart made in "the Northern Zone".

In this section we will discuss the seasonal and interannual variabilities of the standing crop of phytoplankton in the Drake Passage/Scotia Sea region, the Bransfield Strait and contiguous waters, and the Ross Sea. We will discuss how these data fit into the generally accepted patterns of geographical and seasonal productivity of the Antarctic waters. Again, it is worth repeating (cf. Introduction) that seasonal biomass cycles cannot be adequately defined by mounting three or four cruises between austral spring and late summer in such large bodies of water as the Scotia Sea or the Bransfield Strait. Further, it is widely recognized that in order to describe the physicochemical fluctuations that drive year-to-year variations in the phytoplankton biomass, it is necessary to have very long data sets, covering at least 20–30 years.

5.1 Drake Passage/Scotia Sea Region

The two cruises of the ARA *Islas Orcadas* (Cruise 17 — 2. September–14. October 1978 and Cruise 19 — 22. Feb-
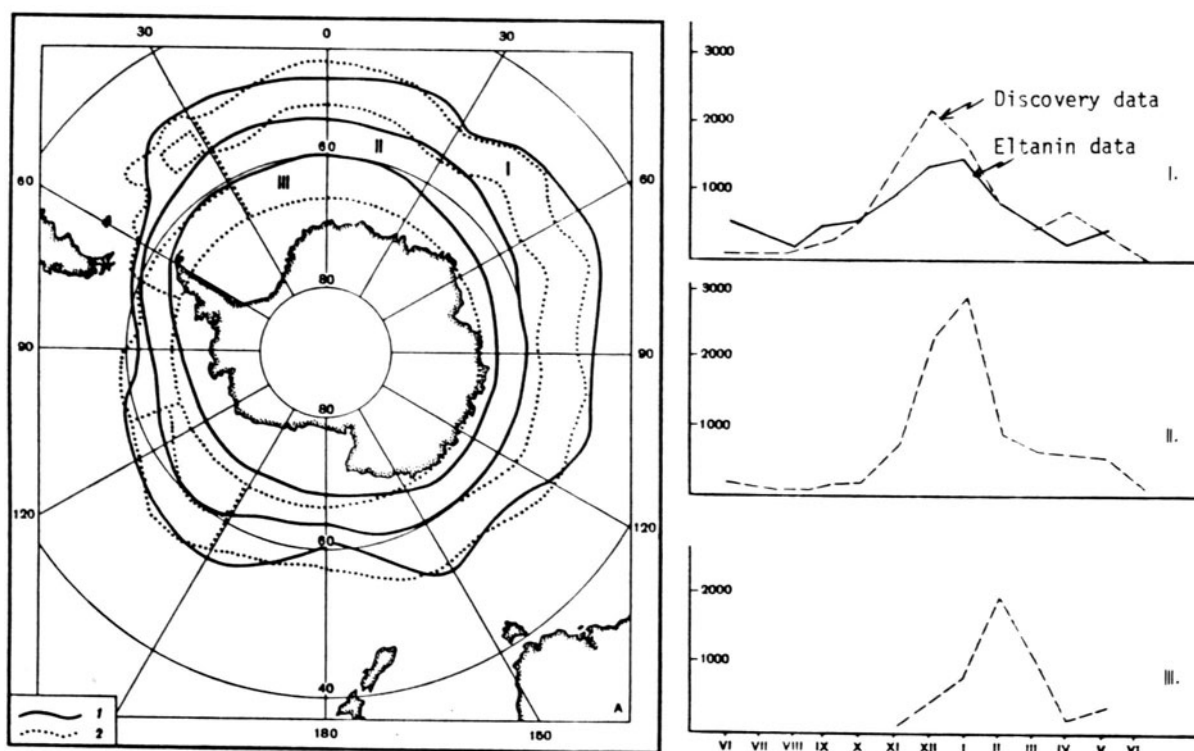
Fig. 5. Seasonal variation in plant pigment concentrations with latitude in the Southern Ocean. (Hart's 1942 *Discovery* data). *Eltanin's* chlorophyll a data are plottet for comparison (El-Sayed 1971a). *1* Northern Zone (ca. 50°–55°0.50'S); *II* Intermediate Zone (ca. 55°–66°00'S); *III* Southern Zone (above 66°00'S). (After Voronina 1984)

Fig. 6. Cruise tracks of the *Islas Orcadas* Cruise 17 and 19 in the Southwest Atlantic and the Scotia Sea. (El-Sayed and Weber 1982)

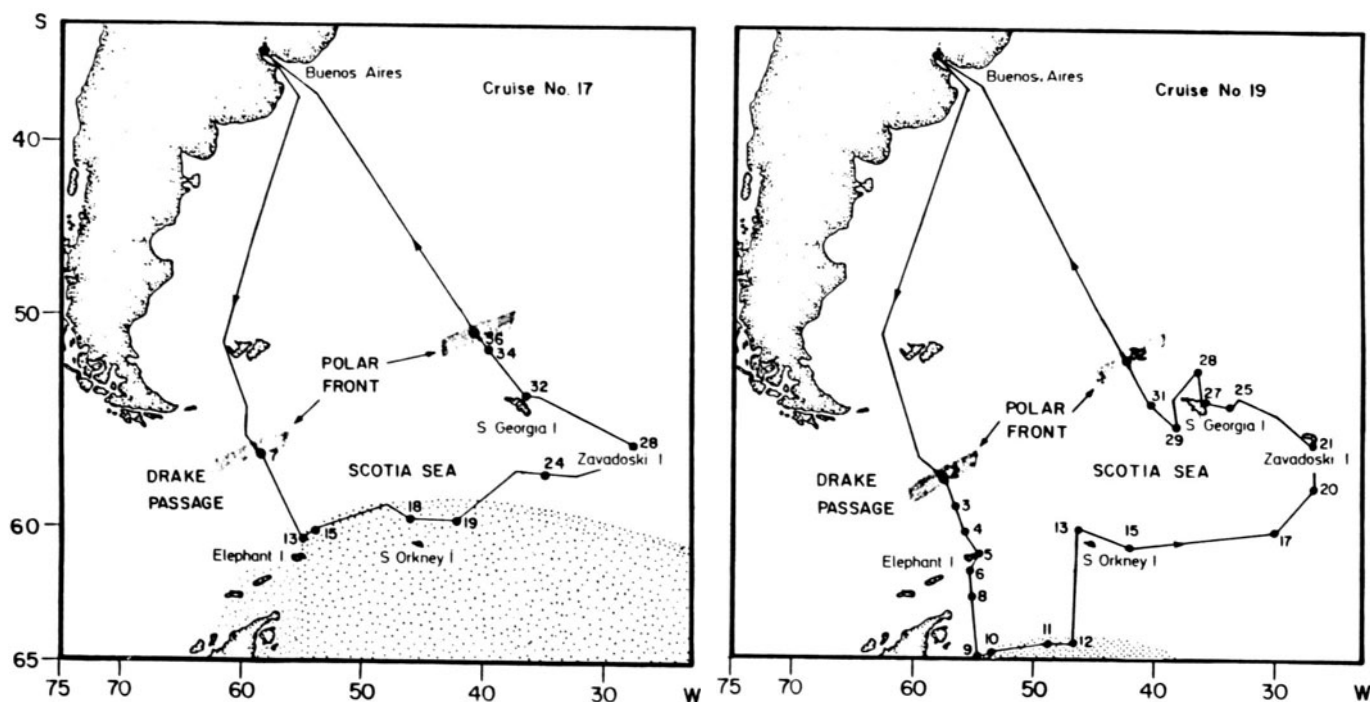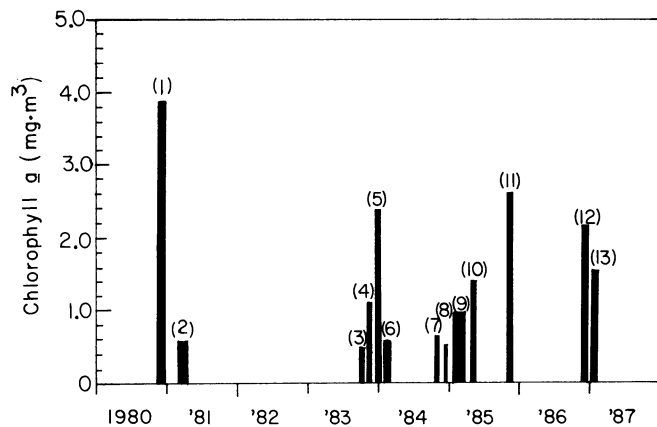Fig. 7. Seasonal distribution of chlorophyll a in the Bransfield Strait between 1980 and 1987. (For explanation of numbers shown see Table 1)

ruary–9. April 1979) had as their major objectives the studies of the biological productivity and the metabolic activities of selected Antarctic organisms at two different seasons, namely late winter/early spring and late summer/ early fall. Study of the seasonal variability was made possible by occupying stations along nearly identical cruise tracks (Fig. 6).

The general picture that emerges from the investigation carried out during the two cruises of the ARA *Islas Orcadas* (see El-Sayed and Weber 1982 for details) is one of great variability of the phytoplankton biomass and primary productivity between low values, typical of oligotrophic waters, and high values characteristic of eutrophic regions. *This spatial variability (up to two orders of magnitude) tends to overshadow the expression of seasonal differences.*

Surprisingly, when discrete and integrated values for primary productivity, chlorophyll, and phaeopigments, at all stations occupied in or south of the Polar Front during

Cruises 17 and 19·are compared, only the phaeopigment values are significantly different. When stations from the two cruises are paired on the basis of geographical location, two stations from the late winter/early spring cruise have order of magnitude higher values of chlorophyll a and primary productivity than the corresponding stations from the late summer/early fall cruise. However, in considering all of the paired stations, values for chlorophyll and productivity from Cruise 17 appear randomly larger or smaller than values measured during Cruise 19. *Thus, temporal variability is clearly discernible at small spatial scales but is easily masked when comparing mean values of chlorophyll and productivity from large areal regions.* It should be noted that maximum phytoplankton biomass and productivity have been observed to occur in December (Hart 1942) in the area studied, indicating that the lack of significant differences between seasonal values may be due to the timing of the cruises, which fall on both sides of the vernal austral peak (see Fig. 5).

5.2 Bransfield Strait and Contiguous Waters

In Fig. 7 we compare surface chlorophyll a concentrations measured between 1980 and 1987 in the Bransfield Strait during the cruises of the West Germany's *Polarstern* and *Walther Herwig*, Chile's *Itsumi*, Poland's *Professor Siedlecki*, and Brazil's *Professor Besnard*. Dates, number of stations occupied during these cruises, and average surface chlorophyll values are given in Table 1. It is noted that chlorophyll a concentrations in the Bransfield Strait are generally high when compared to average oceanic values for the Southern Ocean. It should be realized that data averaged over the periods and geographic ranges of individual cruises will conceal significant small-scale spatial and temporal differences. Also, it is risky to compare

Table 1. Sources of data on average surface chlorphyll a concentrations (mg/m^3) in the Bransfield Strait and Elephant Island region during 1980–1987. (n) = number of stations

Number[a]	Investigator	Dates	Chlorophyll a values					
			Bransfield Strait			Elephant Island		
			Mean	(n)	Median	Mean	(n)	Median
1	von Bodungen (1986)	Nov. 20–Dec. 14, 1980	4.63	(14)	3.83	2.44	(2)	2.44
2	Lipski (1981)	Feb.–Mar. 1981	0.77	(21)	0.53			
3	Gieskes and Elbrächter (1986)	Oct. 24–Nov. 16, 1983	0.28	(17)	0.25	0.29	(33)	0.19
4	von Bodungen (1986)	Nov. 26–Dec. 21, 1983	2.20	(9)	1.18	1.94	(1)	1.94
5	Lipski (1985)	Dec. 1983–Jan. 1984	2.91	(33)	2.37	1.00	(7)	0.35
6	Kutner (pers. commun.)	Jan. 21–Feb. 9, 1984	0.51	(19)	0.37	0.21	(7)	0.15
7	Weber and El-Sayed (1986)	Nov. 21–Dec. 4, 1984	0.93	(7)	0.60	0.32	(39)	0.27
8	von Bodungen (pers. commun.)	Jan. 6–12, 1985	1.52	(3)	0.51	0.95	(1)	0.95
9	Kutner (pers. commun.)	Jan. 27–Mar. 15, 1985	4.64	(20)	0.85	0.29	(10)	0.27
10	Elbrächter (pers. commun.)	Mar. 20–Apr. 5, 1985	3.07	(15)	1.20	1.57	(33)	0.80
11	von Bodungen (pers. commun.)	Nov. 15–28, 1985	2.44	(13)	2.50			
12	Weber and El-Sayed (in prep.)	Jan. 2–19, 1987	2.44	(11)	2.09	1.24	(36)	1.01
13	Ochocki (pers. commun.)	Jan. 26–Feb. 22, 1987	1.46	(27)	1.52	0.91	(12)	0.66

[a] Corresponds to Numbers in Figs. 7 and 8.

average values from different cruises if the proportions of neritic and oceanic stations are different. Recognizing these caveats, we nevertheless suggest that this limited data set shows seasonal variability in chlorophyll a values within individual study years. Within a given year, average chlorophyll values differ by an order of magnitude, depending on the month of sampling. However, the period of peak phytoplankton abundance varies considerably from year to year. For the 5 years of observation, highest chlorophyll values occurred anywhere between November (1980) and March (1985). Considering the large month-to-month differences, interannual variability in the phytoplankton standing stock appears to be small in the Bransfield Strait.

5.3 The Elephant Island "Box"

For the past several years, West German scientists have been studying, on an almost annual basis, an area of 36 000 km^2 around the Elephant Island (referred to as the Elephant Island Box, see Fig. 2). This area, deliniated by 60°–62°S and 54°15′–56°45′W, was covered with a grid of 36 stations along 4 meridional transects, 45 nm and 60 nm apart. The distance between stations on each transect is 15 nm. One objective of this mesoscale investigation was to assess the phytoplankton and krill standing stocks in the study area in an effort to improve our understanding of the macroscale processes.

Average results from the Elephant Island investigations are given in Table 1 and plotted in Fig. 8. Chlorophyll values in this region are, with few exceptions, similar to typical values (< 0.5 mg/m^3) reported for oceanic waters, and thus much lower than the Bransfield Strait values. As in the case for the Bransfield Strait, approximate order of magnitude differences in chlorophyll concentrations are noted within individual years, and the period of peak phytoplankton abundance also varies from year to year. Again, seasonal variability is much more pronounced than any interannual variability.
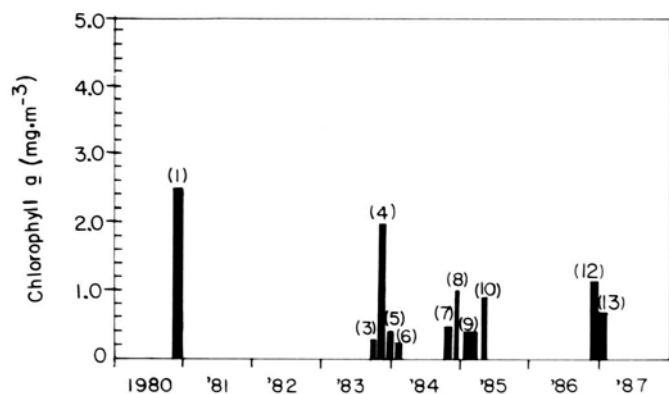
5.4 The Ross Sea

The average surface chlorophyll values for the USNS *Eltanin* Cruises 27 (January/February 1967) and 51 (January/ February 1972) and USCGC *Glacier* (December 1977/ January 1978) for all the stations occupied south of the Antarctic Circle in the Ross Sea are plotted in Fig. 9. Based on these three data sets (collected at approximately the same time of year), interannual variability of phytoplankton biomass in the Ross Sea is minimal (less than a factor or two). Unfortunately, seasonal data are not available for this region.

Fig. 8. Seasonal distribution of chlorophyll a in the Elephant Island Box between 1983 and 1987. (For explanation of numbers shown see Table 1)
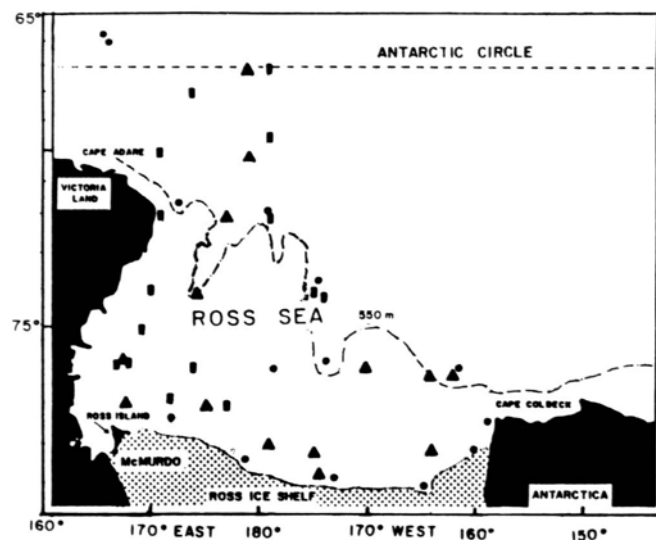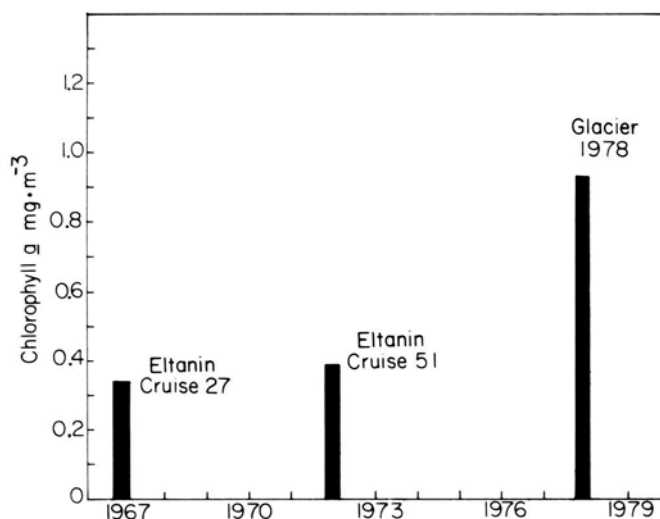

Fig. 9. Seasonal distribution of surface chlorophyll a in the Ross Sea during the austral summers of 1967, 1972 and 1977/78. Position of stations occupied are shown in *inset* below

6 Factors Governing the Distribution and Productivity of Antarctic Phytoplankton

Since the publication of Hart's (1934 and 1942) works, the factors governing the distribution and productivity of Antarctic phytoplankton have occupied the attention of several investigators (see Fogg 1977; Jacques 1983; Heywood and Whitaker 1984; Sakshaug and Holm-Hansen 1984; Priddle et al. 1986a; El-Sayed 1987 for reviews). Of the numerous physical, chemical, and biological factors that might limit the productivity of Antarctic marine phytoplankton, large-scale variation in radiation climate, water column stability, nutrients, and grazing are generally concluded to be the most important. Unfortunately, the evidence provided by investigators is often contradictory and unsubstantiated. In this section we will discuss three of these factors: nutrient salts, water column stability, and grazing, and the possible effects that each has on spatial and temporal distributions of Antarctic phytoplankton.

6.1 Nutrient Salts

The numerous observations of the nutrient salts in Antarctic waters clearly show that these salts generally exceed phytoplankton requirements (Hart 1942; Holm-Hansen et al. 1977; El-Sayed 1984; Hayes et al. 1984; Heywood and Whitaker 1984). Even at the peak of phytoplankton growth, the concentration of nutrient salts remains well above limiting values (El-Sayed 1971a). Thus, it is unlikely that these nutrient salts are sufficiently low at any one time to become limiting factors to phytoplankton growth. Priddle et al. (1986b), using multivariate analysis to examine interrelationships between phytoplankton and environmental variables around South Georgia, found a relatively strong, inverse relationship between phytoplankton biomass and the concentrations of a combination of dissolved nutrients. They observed that the diminution of the total nutrient pool by phytoplankton growth was clearly demonstrated, although no single nutrient could be identified as being important in determining phytoplankton variation.

With regard to trace elements, Jacques (1983) and Hayes et al. (1984) carried out enrichment experiments using Zn, Mo, Co, Mn, and Fe, and showed that these are not limiting factors. However, it is possible that organic factors, e.g., vitamin B_{12} and thiamin (see Carlucci and Cuhel 1977) may alter the species composition of the phytoplankton without changing the overall rate of primary production. It is also possible that the availability of trace elements/micronutrients may be altered by meltwater from the pack ice and icebergs, thus affecting the productivity or species composition of the water in their vicinity.

6.2 Water Column Stability

Braarud and Klem (1931), Gran (1931), and Sverdrup (1953) were among the early investigators to draw attention to the importance of the stability of the water column in controlling primary production and, hence, phytoplankton biomass. The length of time that phytoplankton cells remain within the euphotic zone depends, in part, on the extent of vertical mixing. Sverdrup (1953) showed theoretically that phytoplankton blooms will occur only when the depth of the mixed layer is less than the critical depth. The critical depth in the Southern Ocean is generally between 130–200 m (Jacques and Minas (1981). This is deeper than the usual summer mixed layer (60–95 m, Jacques and Minas 1981; 60–160 m, Priddle et al. 1986b; 12–48 m, Miller and Monteiro this Vol.), which generally corresponds to the depth of the euphotic zone. Such data imply that Sverdrup's critical depth hypothesis cannot explain the low phytoplankton production (Jacques 1983). However, turbulence within the euphotic zone may play a significant role in preventing large increases in phytoplankton biomass. Sakshaug and Holm-Hansen (1984) report that for ten stations in the Scotia Sea where chlorophyll a was > 2 mg/m^3, the pycnocline was located at 20–40 m. They speculate that 50 m may be the maximum pycnocline depth for a bloom to develop. Thus, the presence of an homogeneous (i.e., isothermal) water column reaching to depths of 50–100 m during most of the year hinders the development of blooms and contributes to the low primary production of Antarctic waters. In this respect, it is interesting that the *Discovery* investigations found that the depth to which wind action was generally effective in overturning the water column in the open ocean ranged from 60–80 m, especially after storms. Heywood (1984) observed the discontinuity layer at 112 m after a 2-day storm in latitude 56°S (in the sector between 20° and 30°E), and Nast and Gieskes (1986), reported a deep mixed layer (to 200 m) north of Elephant Island as a result of high wind forces.

Bottom topography may, on a regional basis, play an important role in inducing vertical mixing. This was first suggested by Hart (1934) and corroborated by the findings of El-Sayed and Jitts (1973) at Station 12 (61°35'S, 75°12'E) of the *Eltanin* Cruise 46 which lies in proximity to the Banzare Bank. This station was noted for its extremely high standing stocks of phytoplankton and zooplankton. A 1.0-m No. 3 zooplankton net towed vertically from 500 m to the surface yielded 3600 ml of wet volume that was predominantly composed of the diatom species *Thalassiothrix antarctica*.

The vertical stability induced by meltwater has also been suggested as a significant process in initiating and sustaining near-ice blooms. According to this suggestion, the low salinity of meltwater contributes to the stability of the near-ice water column, thus helping to retain the phytoplankton near the surface and promoting a bloom. Corroborative evidence that this mechanism is important in the initiation of ice-edge blooms in the Antarctic is furnished by Jacobs and Amos (1967), El-Sayed (1971a), Smith and Nelson (1985) and Nelson et al. (1987). Thus,

the high phytoplankton standing stock (up to 190 mg Chl a/m³) recorded in the 1968 bloom in the southern Weddell Sea (El-Sayed 1971a) may have been due to a strong pycnocline produced by the melting of ice at the edge of the Filchner Ice Shelf.

Further, low vertical stability of the water column has been implicated by several investigators as a factor contributing to a low standing crop of phytoplankton in the region of the Polar Front (Hart 1942; Hasle 1956; El-Sayed and Mandelli 1965). However, as noted earlier, higher-than-average values of chlorophyll a and primary productivity have also been noted in the vicinity of the Polar Front (Allanson et al. 1981; El-Sayed and Weber 1982; Yamaguchi and Shibata 1982; Lutjeharms et al. 1985; Bidigare et al. 1986). Allanson et al. (1981) postulate that the Polar Front may be characterized, at the sea surface, by a divergence rather than a convergence. Thus, the physical complexity of this frontal system (Amos 1984) must be examined more closely before we can decide whether the variability in phytoplankton standing crop and primary production at the Polar Front stations can be explained in terms of stability or instability of the water column, or if other factors must be invoked.

6.3 Grazing

To date, much of the importance given to grazing has been by default. That is, the generally low phytoplankton biomass of Antarctic waters cannot be otherwise accounted for, therefore grazing pressure has been assumed to play an important limiting role. In examining the role of grazing in controlling Antarctic phytoplankton biomass and productivity, attention generally focuses on the Southern Ocean krill, *Euphausia superba*, which constitutes a significant (but not necessarily the most abundant) portion of the Antarctic zooplankton biomass (Holdgate 1967; Brinton and Antezana 1984) and serves as a key link between marine primary producers and top predators. Although *E. superba* is regarded by some investigators as the dominant herbivorous species in the Antarctic waters, one should not overlook the significance of two other main components of Antarctic zooplankton (i.e., salps and copepods) as important herbivores affecting phytoplankton density.

The seasonal rise and fall of the krill population appears to lag behind that of the phytoplankton biomass. This is demonstrated in Fig. 10, where mean (and median) concentrations of surface chlorophyll a and mean values of krill abundance for the Bransfield Strait/Elephant Island region are plotted by month. Krill abundance values include data from 1977 to 1985 (Siegel this Vol.), while phytoplankton data were collected between 1980 and 1987.

Early investigators observed that areas of high krill concentration are usually noted for their low standing crop
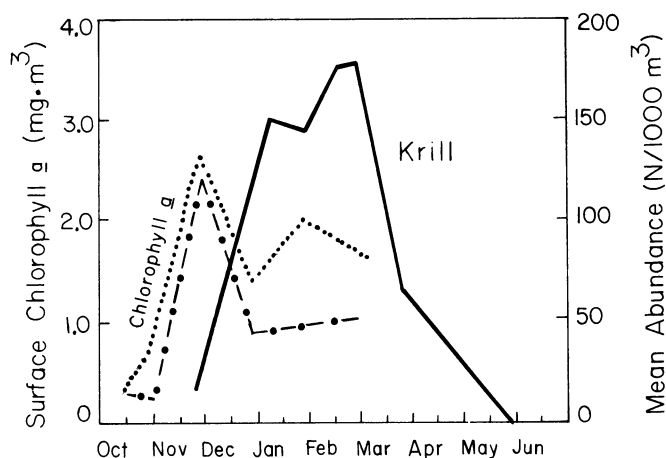

Fig. 10. Mean monthly abundance of krill (N/1000 m³) for the Bransfield Strait/Elephant Island region (Siegel 1987). Also shown are monthly mean (· · · ·) and median (— · —) values of surface chlorophyll a (mg/m³) for October–March (1980–1987)

of phytoplankton (Hardy and Gunther 1935; Hart 1942). Polish (Rakusa-Suszczewski 1982) and Chilean (Uribe 1982) investigators found that areas of dense krill concentration in the central parts of the Bransfield Strait exhibited low chlorophyll a values at the surface (<0.5 mg/m³) and in the water column (<50 mg/m²). According to Uribe (1982), the poverty of the phytoplankton was due not to nutrient limitation but most likely to intensive krill feeding. Figure 11, taken from Nast and Gieskes (1986), demonstrates the inverse relationship between phytoplankton and krill in the waters around Elephant Island during early November 1983. Similarly, an inverse relationship was observed with time when an area north of the Elephant Island was sampled prior to and during the occurrence of a super swarm of krill (Holm-Hansen and Huntley 1984). The phytoplankton biomass was very high in January (633 mg Chl a/m² at Station 16), but had been reduced more than tenfold (55 mg Chl a) by March (Fig. 12). On the other hand, the very low zooplankton biomass in January was replaced in March by a dense swarm of furcilia, which extended for 200 km. Paden et al. (1981) reported a chlorophyll a concentration of 3 mg/m³ upstream of the Elephant Island krill swarm, while downstream, chlorophyll a values were only about 10% of those upstream.

It should be pointed out that coincidence of high phytoplankton standing crop and high krill density has also been reported (Weber and El-Sayed 1985; Mujica and Asencio 1983). Nast and Gieskes (1986) conclude that: "Whereas the negative correlation between chlorophyll a and krill abundance seems to be valid in the mesoscale, a positive correlation between the high krill mass in the Scotia Sea and enhanced phytoplankton food sources may also exist."
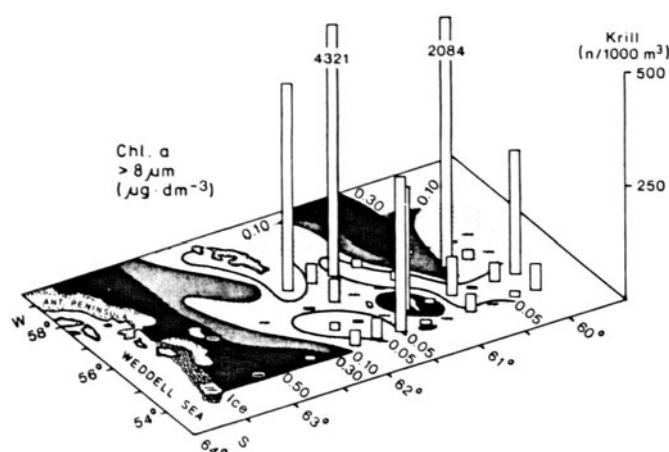
Fig. 11. Surface distribution of chlorophyll a in particles <8 μm (mg/m^3) around Elephant Island, November 1983. (Nast and Gieskes 1986)

7 Phytoplankton/Krill Distributional Relationships

Although grazing pressure has been proposed as a factor that controls the abundance of Antarctic phytoplankton, it was only recently (during the 10 February–20 March 1981 cruise of the S.A. *Agulhas*) that the availability of phytoplankton data taken concurrently with acoustic estimates of krill biomass has allowed, perhaps for the first time, a statistical examination of the distributional relationship between these two important components of the ecosystem (Weber and El-Sayed 1985). Because of the

significance of the *Agulhas* results to our understanding of the phytoplankton/krill distributional relationship, we will discuss them in some detail.

The waters surveyed during the *Agulhas* cruise were entirely within the Antarctic Zone except for the southernmost section near the continent, which lay within the Continental Water Mass (Fig. 13). Thus the discussion relates to an open-ocean region of the Antarctic where frontal mixing and bottom topography play a very limited role in determining phytoplankton and krill distribution patterns. Surface seawater temperature over the entire study area varied only between −2° and +2°C. Temperatures during any single daytime transect were always within ±0.2°C of the transect mean. Extracted chlorophyll a concentrations were low, averaging only 0.12 mg/m^3. The detected krill biomass was concentrated in 1034 aggregations, having a mean diameter of only 13 m (Hampton 1985).

Station data were examined statistically using simple correlation, multivariate regression, and canonical correlation analyses. Parameters considered include chlorophyll a, phaeopigments, primary productivity, nutrient concentrations, light, temperature, salinity, sigma-t, water column stability, and krill. Krill parameters were estimated acoustically and included (a) mean krill density (g/m^2), (b) number of swarms, (c) mean radius of swarms, and (d) the maximum swarm biomass. Each of these krill parameters was evaluated for the 10 km before and after each station. In the simple correlation matrix (Table 2) chlorophyll a is correlated (positively) more strongly with maximum swarm biomass than with any other variable. In both the multiple regression and canonical correlation analyses, the
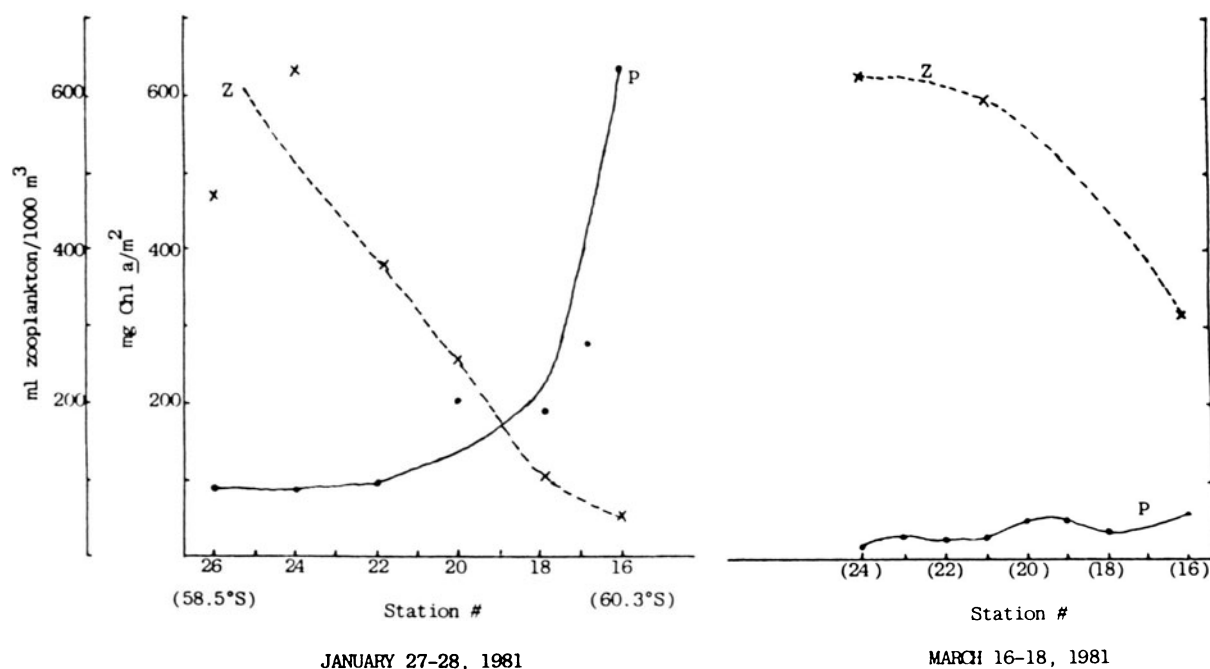

Fig. 12. Total zooplankton biomass and chlorophyll a in the upper 200 m of the water column of a north-south transect to the northwest of the South Orkney Islands. The same stations were sampled during January and again during March 1981. The cruise track lay close to longituide 46°30'W. (Holm-Hansen and Huntley 1984)

Fig. 14. Horizontal profiles of integrated krill density (g/m²), surface in vivo fluorescence (relative units), and surface seawater temperature 0°C) from the 6 March 1981 transect of the *Agulhas* cruise. Both the original (– – – –; *right-hand scale*) and detrended (———; *left-hand scale*) data are plotted. (Weber et al. 1986)
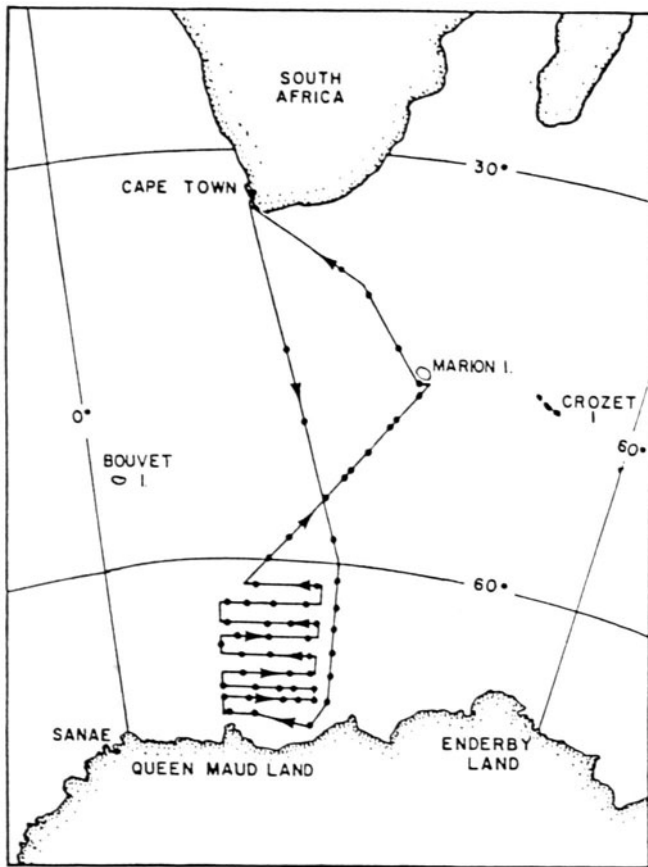

Fig. 13. Cruise track of the M.V. S.A. *Agulhas* during FIBEX, February–March 1981. (Weber et al. 1986)

relation between phytoplankton biomass and maximum swarm biomass remains strongly positive. On the other hand, although the simple correlation between chlorophyll a and mean krill density is positive, an inverse relationship is noted when other parameters are statistically held constant via multivariate regression. Although the absence of time course measurements makes interpretation difficult, it appears that krill are somehow cueing in on areas of local phytoplankton abundance. Hampton (1985) suggests that the larger swarms may have been nonfeeding aggregations that were migrating or foraging. In support of the conclusion of Meyer and El-Sayed (1983) concerning the size-dependent selectivity of krill feeding, the amount of phaeopigments relative to net chlorophyll concentration is correlated positively with each of the four krill parameters in the multiple regression models.

Representative continuous profiles of integrated krill biomass, surface in vivo fluorescence and surface seawater temperature from a single daytime transect are shown in Fig. 14. Three- to fivefold differences in in vivo fluorescence values over the course of the daily transects (79–245 km) suggest strong, though fairly large-scale phyto-plankton patchiness. In contrast, krill exhibit intense patchiness over very short scales.

Interrelationships between the krill, phytoplankton, and the physical environment were examined by applying the techniques of power spectral analysis to the suite of continuous daytime profiles of acoustically derived krill biomass, surface in vivo fluorescence and seawater temperature as functions of spatial scale are similar, suggesting that the distributional patterns of phytoplankton biomass are largely determined by physical processes. However, consistent coherence between the fluorescence and krill profiles suggests that predator-prey interactions are also important in determining patterns of phytoplankton distribution.

8 Discussion

Patterns of spatial and temporal variabilities in Southern Ocean phytoplankton distribution, abundance, and productivity are complex. As a whole, there is considerable heterogeneity in the distribution of the phytoplankton density and a great difference between the low values of phytoplankton biomass and primary productivity in oceanic regions and the high values of the inshore waters. This geographical variability tends to overshadow the expression of seasonal differences as the analysis of the data collected during Cruises 17 and 19 of the ARA *Islas Orcadas*

Table 2. Simple correlation coefficients for all pairs of phytoplankton, krill, and physicochemical variables. Only r values ≥ 0.25 (with P-values ≤ 0.05) are included. (Weber and El-Sayed 1985)

	Temp.	Salinity	Sigma-t	DO	Silicate	Nitrate	Latitude	Stabil-ity	Max fons	Nano prod	Net prod	Nano AT	Nano Chl	Net Chl	Nano phago	Net phago	Nano AN	Net AN	Net AN
Light	0.38	-0.40	-0.43							0.30							0.39		
Temp.		-0.62	-0.74		-0.44	-0.31	-0.83	-0.44							-0.36	-0.45			0.36
Salinity			*0.98*	-0.57	0.53	0.55		-0.38		-0.25					0.58	0.50			-0.45
Sigma-t				-0.53	0.56	0.54	0.39								0.57	0.53			-0.44
DO					-0.32	-0.34									-0.58	-0.48			0.38
Phosphate					0.30	0.29	-0.52	-0.35		-0.26									-0.25
Silicate						0.60	0.44												-0.29
Latitude								0.39											0.39
Integ. krill					-0.49				0.66					0.48	0.47				
Mn radius									0.50			0.50							
Nano AT								0.46	*0.60*		0.25		0.49	0.41	0.70			0.34	0.41
Net AT		0.41	0.39	-0.26		0.26			*0.60*			0.32	0.58	0.60		0.30	-0.37	-0.31	0.33
Nano EC																			-0.26
Nano Chl	-0.35	0.44	0.52			0.31			*0.73*					0.63	0.40		-0.39	-0.28	0.28
Net Chl		0.26	0.26						*0.80*						0.36		-0.28	-0.33	0.47
Nano Phaeo						0.48			*0.60*							0.67	-0.28	-0.26	*-0.76*
Net Phaeo						0.32												0.58	*0.39*
Nano AN		-0.36	-0.36							0.69								0.36	
Net AN											0.59								0.35
Nano pig rat						-0.30													0.35

clearly demonstrated. Although the open ocean regions are noted for their impoverished phytoplankton standing crop and low productivity, the fact that they constitute 12 times the combined neritic and upwelling areas explains why they supply the bulk of primary production of the Southern Ocean (Heywood and Whitaker 1984).

The seasonal variability of the phytoplankton biomass is just as complicated as that of the spatial variability. Although it is nearly half a century since Hart's (1942) publication (see Fig. 6) and despite the growing interest in recent years in the study of all aspects of Antarctic phytoplankton, our knowledge of the seasonal variation of Antarctic phytoplankton is still limited. As was pointed out earlier, observations from single stations, or from single depths, may not be representative of a body of water. Further, average seasonal values could be misleading in that they conceal temporal or spatial variability, or both. Further, because of the scarcity of data from open waters during late austral fall and winter, it is difficult to construct a complete year-round picture of the seasonal variability or to describe the physicochemical fluctuations which drive seasonal and year-to-year variations in phytoplankton biomass.

Although much useful information on the physiological ecology of phytoplankton has been gathered during the last two decades, it is humbling to state that an explanation of the factors which govern phytoplankton distribution and production has continued to defy sceintific inquiry. Investigators are confounded by the fact that the ocean south of the Polar Front contains a circumpolar phytoplankton population living in a fairly uniform environment with sufficient light for photosynthesis (at least during the austral spring and summer), that is more or less adapted to cold temperature and has access to abundant nutrient salts, and yet that population is not only patchy, but its density is very low, approaching that of oligotrophic regions. The nutrient levels should be able to support a phytoplankton biomass of at least 25 mg/m^3 chlorophyll a (Holm-Hansen and Huntley 1984). However, Antarctic phytoplankton seldom achieve the high growth rates suggested by the high nutrient levels, except for occasional blooms of phytoplankton such as those reported by El-Sayed (1971a), Mandelli and Burkholder (1966), and others.

In seeking an explanation for the spatial variability in primary production, Fogg (1977) contends that variability in the waters south of the Polar Front cannot be accounted for by differences in incident radiation, water temperature, or concentrations of nitrate, phosphate, and silicate, as each of these parameters has similar values over the entire area in question. After noting that environmental factors act synergistically, Priddle et al. (1986a) conclude that "no one single factor is likely to be identified as ecologically important from a subjective comparison of species and environemental data, even though this method may be effective over large time- and space-scales (e.g., Hart 1942)."

We are still left with the puzzling questions as to why phytoplankton biomass achieves only a fraction of its potential and why such a small part of the Antarctic Ocean is highly productive, while its vast expanses are much less productive. While Sverdrup's (1953) theory of critical depth is essentially sound, it cannot, by itself, provide sufficient explanation of this paradox, as Jacques (1983) has clearly shown. Perhaps an explanation lies in considering light limitation mediated by variation in vertical mixing. To test this hypothesis we need to enlist the cooperation of the physical oceanographers to clarify once and for all the relationship between vertical mixing and primary production. The results of this joint effort could have global implications considering the vast areas in the world ocean where such study is relevant.

Such cooperation may also yield an explanation of the generally enhanced production during most of the production season in the waters off the Antarctic Peninsula and around the Antarctic and Sub-Antarctic islands. This island effect is generally explained in temperate and tropical waters by the input of nutrients from depth as a result of turbulence around the islands (Simpson et al. 1982). In the Antarctic, on the other hand, the nutrients are in abundant supply at the surface, so that turbulence-induced variations in the light regime may provide the answer for the above paradox.

Study of the phytoplankton/krill distributional relationship still remains one of the most vexing problems in marine Antarctic ecosystem studies. Although many hypotheses/explanations have been advanced to elucidate the observed inverse and coincident relationships, for the most part they remain unconvincing or unsubstantiated. Despite its limitations, we feel that the investigation of Weber et al. (1986) of the spatial variability in surface in vivo fluorescence carried out simultaneously with krill assessment by the hydroacoustic method is a step in the right direction.

The positive coherence observed in their study between phytoplankton and krill agrees with the spectrally derived positive correlations between phytoplankton and zooplankton in the Mediterranean Sea and over Georges Bank (Mackas 1977) and in the North Pacific (Star and Mullin 1981), but is in contrast to the inverse correlation found between phytoplankton and zooplankton in the North Sea (Mackas 1977; Mackas and Boyd 1979). Moreover, the positive correlation between in vivo fluorescence and krill biomass observed at scales of 2–20 km is in contrast to the negative correlations usually reported between these two entities on the basis of random, discrete samples separated by much larger distances (Hardy and Gunther 1935; Hart 1942; Witek 1979; Witek et al. 1982; Rakusa-Suszczewski 1982; Uribe 1982; Weber and El-Sayed 1985; Nast and Gieskes 1986).

As a result of their investigation, Weber et al. (1986) identified several problems in the study of phytoplankton/krill relationships that need further elucidation. The most critical need is to resolve finer spatial scales, that is hundreds

of meters instead of kilometers. In terms of interpreting results, the most serious problem in their data set stems from the fact that in vivo fluorescence values yield estimates of surface phytoplankton concentrations, while acoustic estimates of krill density give water column values integrated from near-surface to a depth of 100 m. During the day, krill were generally concentrated near the top of the thermocline at a depth of 40–60 m; whereas at night they were found near the surface and could not be detected acoustically (Hampton 1985). Although there is a fair correlation between surface and integrated water column values of chlorophyll, the different sampling strategies for krill and in vivo fluorescence result in an implicit time lag between these two parameters. Moreover, the lag period varies as a function of the time of sampling. Thus, the use of daytime transects (necessary because the downward-looking acoustics could not "see" nighttime surface concentrations of krill) confounds temporal and spatial variability. Side-scan sonar (which was not available on the *Agulhas* cruise) could adequately sample the upper water column and thus provide reliable nighttime acoustic estimates of krill.

These nighttime estimates, together with simulatneous records of surface in vivo fluorescence, could then be analyzed by cross-spectral analysis without having the contend with the problem of implicit temporal variability. Additional advantages of using nighttime transects would be the relatively larger signal-to-noise ratio for the in vivo fluorescence, as well as a decrease in the amount of data manipulation necessary to detrend the profiles.

The application of multivariate regression and power spectral analysis procedures to the suite of data obtained during the *Agulhas* FIBEX cruise (Weber and El-Sayed 1985; Weber et al. 1986) has generated several hypotheses concerning phytoplankton/krill interrelationships. In order to test these hypotheses, future studies must resolve finer spatial scales and include time-course measurements in order to examine the underlying mechanisms.

9 Conclusions and Recommendations

Despite more than 50 years of intensive field work in the Southern Ocean and the expenditure of millions of dollars, we are still unable to answer some of the most fundamental questions in Antarctic marine ecology, for example, why is such a small part of the Antarctic Ocean so much more productive than its vast expanses? However, now researchers more than ever before realize that the distribution and abundance of Antarctic phytoplankton and the rates of primary production are intimately related to the physical oceanographic processes of horizontal circulation and vertical mixing. These relationships operate on time scales ranging from hours to months and over spatial scales of meters to hundreds of kilometers.

Until recently, primary productivity studies have often consisted of piecemeal projects directed at problems of specific interest to individual investigators and limited in scope to localized areas and short time periods. Although data from such projects provide a wealth of information relevant to the localized areas at the time of study (the Elephant Island "Box", for example), we still lack an overall description of the productivity of the Southern Ocean. This seriously limits our ability to assess the significance of the results of many individual research projects and perpetuates the considerable uncertainties regarding estimates of the overall primary production of the Southern Ocean. The unavoidable lesson learned from half a century of Antarctic marine research is that the field season in the Southern Ocean is too short and the logistic support is too expensive for ship-based studies ever to provide a proper perspective of the productivity of the marine ecosystem. Continued application of conventional research techniques and sampling strategies will no longer advance our quest for better understanding of the temporal and spatial variabilities of the biota of the Southern Ocean. Bold, imaginative new approaches are needed in the way we study the Southern Ocean ecosystem. I offer a few suggestions as to the directions our research should take in the next decade.

Research satellites have demonstrated a remarkable ability to measure ocean variables (e.g., sea surface temperature, sea-ice concentrations and ocean color). Measurements made with the Coastal Zone Color Scanner (CZCS) on the Nimbus-7 satellite launched in 1978 have shown that we can now estimate chlorophyll concentrations and thus infer the amount and distribution of the phytoplankton over large areas of the oceans. Now that the CZCS sensor is no longer operational, NASA is investigating the deployment of a satellite-borne Ocean Color Imager (OCI) in 1990. The primary goal of OCI will be to measure visible and near-infrared ocean radiance in order to derive chlorophyll concentrations as an estimation of ocean productivity. The OCI program will be aimed at providing a new "global" perspective of the distribution, abundance, and variance of phytoplankton in the ocean. Such satellite-based data could enhance understanding of phytoplankton dynamics on space and time scales that have so far eluded quantitative investigations, thus providing fundamental new information on Southern Ocean biology, biogeochemical fluxes, and the complex interactions of phytical and biological processes.

A second technological achievement in recent years is the successful use of moored instruments to obtain long-term (months to years), uninterrupted records of currents, temperature, and fluorescence measurements. Here again we should take advantage of this new technology to advance our knowledge of the scales and intensity of both biological and physical processes and to gain an understanding of the causes behind the seasonal and interannual fluctuations of the phytoplankton.

Finally, there is a great need to organize the widely scattered body of knowledge on Antarctic phytoplankton distribution and abundance collected during the past 25 years into an atlas form. Similar efforts have been made by our physical oceanography colleagues (e.g., Wyrtki's 1971 Indian Ocean Atlas, Bainbridge's 1980 Atlantic GEOSECS Atlas, and more recently, Gordon and Molinelli and Baker's 1982 Southern Ocean Atlas). In the latter, the enormous wealth of data on the physics and chemistry of the Southern Ocean is neatly summarized and attractively displayed. Although we cannot aspire to match the quantity of data contained in the physical oceanographic atlases, nonetheless the rapidly growing data set on Antarctic productivity is currently being collated into a Southern Ocean Productivity Atlas. Upon completion, the productivity atlas will be useful in establishing correct overall patterns of Southern Ocean productivity and in providing background information against which spatial and temporal variations in phytoplankton data can be interpreted.

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