Variability of Phytoplankton Distribution in Antarctic Waters

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ABSTRACT. The distribution, biomass, and productivity of phytoplankton in the Southern Ocean is briefly summarized in regard to coastal and pelagic regions and also to geographical features such as the major frontal systems. Pelagic waters show much less variability in phytoplankton distribution as compared to continental shelf waters. The marked intra-annual and inter-annual variability in phytoplankton distribution in coastal waters is illustrated from studies in the Bransfield and Gerlache Straits and in a large sampling grid around Elephant Island. This variability is discussed in regard to physical, chemical, and optical characteristics of the upper water column, with emphasis on factors that may limit the magnitude of primary production. Data from the Elephant Island region furnish strong evidence that availability of iron is a limiting factor for phytoplankton growth in the pelagic waters to the north of the continental shelf break. The variability in phytoplankton biomass in waters overlying the continental shelf, however, can not be ascribed to iron limitation. It is suggested that grazing pressure, for which we have very little data, may play an important role in controlling phytoplankton biomass distribution in coastal waters.

Key Words: chlorophyll-a, iron, limiting factors, phytoplankton, primary production

Introduction

The distribution and abundance of phytoplankton in Antarctic waters are often generalized into two major geographical zones - the deep pelagic waters north of the continental shelf break and the coastal waters overlying the continental shelf. In this paper chlorophyll-a (chl-a) concentrations are used as a proxy for phytoplankton cellular carbon, as the average ratio for phytoplankton cellular carbon/chl-a within the AMLR study area is usually close to 50 (Villafañe et al. 1993). Pelagic waters generally have low concentrations of chl-a and low rates of primary production (<0.4 mg chl-a m^{-3} and <0.2 g carbon fixed m^{-2} day^{-1}, respectively). Phytoplankton biomass in pelagic waters, however, often is enhanced considerably (>1.0 mg chl-a m^{-3}) near the Polar Front (Lutjeharms et al. 1985), in the vicinity of submarine mountain ranges (Hayes et al. 1984), in the wake of the retreating annual ice edge (Smith et al. 1988), and in mixing zones between different water masses (Helbling et al. 1993). Waters overlying the continental shelf, in contrast, are generally described as having relatively high chl-a concentrations (>1.0 mg chl-a m^{-3}) and correspondingly high rates of primary production (>1.0 g carbon m^{-2} day^{-1}; see El-Sayed 1988). There is, however, a great deal of variability in the distribution and abundance of phytoplankton in Antarctic waters, both spatially and temporally, and hence the above estimates for the summer period must be considered only as rough approximations.

As phytoplankton primary production provides the entire food base for higher trophic levels, it is important to better understand the processes involved in causing this variability of phytoplankton distribution. In the following sections, data from the long term (1989-present) U.S. Antarctic Marine

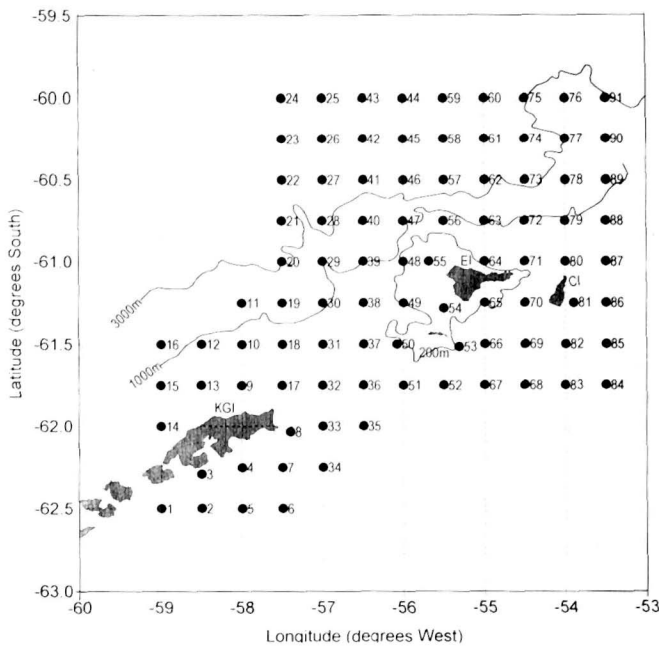*corresponding author (oholmhansen@ucsd.edu)

Fig. 1. Map showing the location of the 91 stations in the AMLR sampling grid. The continuous lines represent the 200, 1000, and 3000m depth contours. Waters flowing into this sampling area include (i) Drake Passage waters, from the west and northwest, (ii) Weddell Sea water from the east and southeast, (iii) Bellingshausen Sea water from the southwest, and (iv) Bransfield Strait waters from the south. KGI, King George Island; EI, Elephant Island; CI, Clarence Island.

Fig. 2. Concentration of chl-*a* at 5m depth throughout the AMLR sampling grid during cruises in Leg I and Leg II of 1993.

Living Resources (AMLR) program will be used to illustrate the variability that is found in phytoplankton distribution in the area around Elephant Island and to relate the variability to physical, chemical, and optical conditions in the upper water column.

Study Area

In order to acquire some insight into the factors affecting the distribution of phytoplankton, it is desirable to have repetitive sampling at a fairly large number of stations over an extended time period. An excellent data set for this purpose is that compiled by the AMLR program during the last eight years. The sampling grid (Fig. 1) includes both coastal and pelagic waters in an area of complex bottom topography. The circulation pattern in this region is also complex, with advection and mixing from four water masses (Drake Passage waters, Bellingshausen Sea water, Bransfield Strait water, and Weddell Sea water), each of which shows dis-
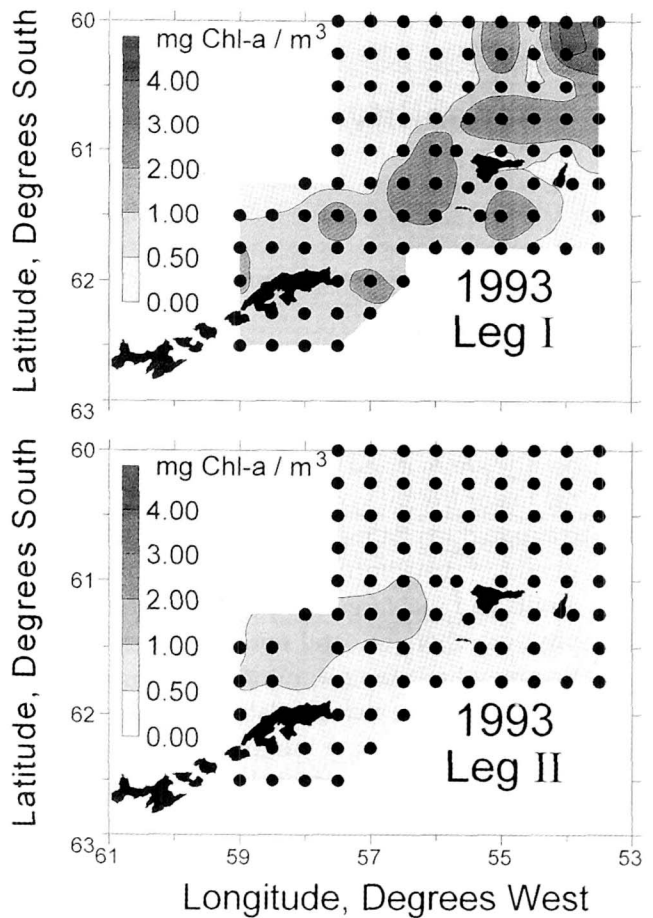
tinctive physical oceanographic properties (Niiler *et al.* 1991; Holm-Hansen *et al.* 1997). The stations shown in Fig. 1 were occupied two times each austral summer period: Leg I, generally during January, and Leg II, from early February to early March.

Chlorophyll-*a* Distribution

There has been considerable variation in phytoplankton distribution during each of the eight years of the AMLR program, but data from only two years (1993 and 1995) are shown (Figs 2 and 3, respectively) to illustrate both intra-annual and inter-annual variability. It is seen that phytoplankton abundance in 1993 was considerably higher during Leg I (mean was 0.88 mg chl-*a* m^{-3}) than during Leg II (mean was 0.30 mg chl-*a* m^{-3}). Not only was the reverse true in 1995, but the chl-*a* concentrations
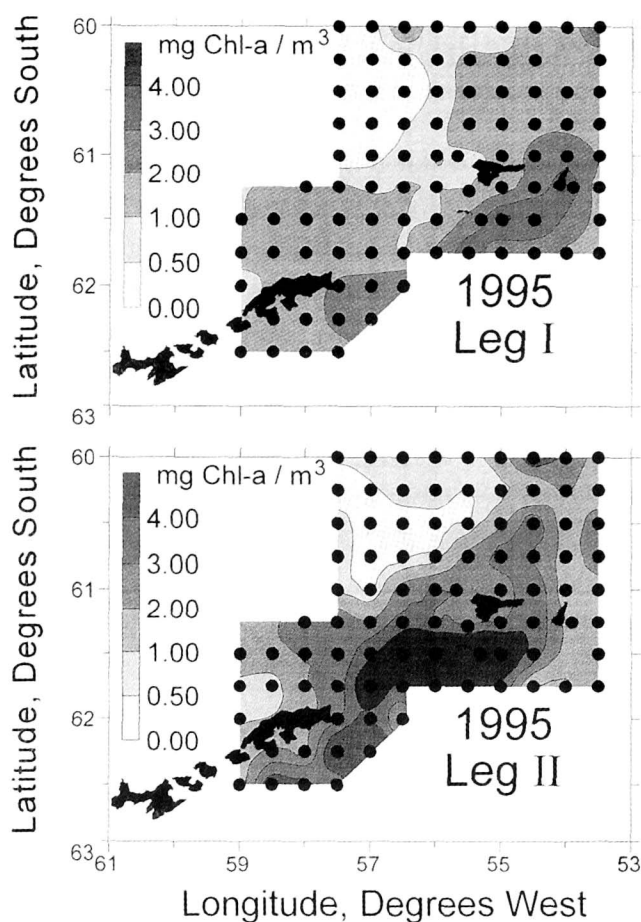
Fig. 3. Concentration of chl-*a* at 5m depth throughout the AMLR sampling grid during cruises in Leg I and Leg II of 1995.

Fig. 4. Chlorophyll-a concentrations in relation to water column stability (sigma-t) in three representative zones within the AMLR sampling grid. For extracted chl-*a* concentrations, use the scale (0 to 5) at the bottom of each figure; the continuous line shows chl-*a* concentrations as estimated by *in vivo* fluorescence (IVF) recorded by the *in situ* fluorometer attached to the CTD unit (use scale of relative units from 0 to 3 on the top of each figure).

were much higher (mean of 1.4 and 2.3 mg chl-*a* m^{-3} for Legs I and II, respectively) than in 1993. There are, however, a few characteristics of the chl-*a* distributions that seem be fairly consistent during each of the eight years of data. As can be seen from the representative data in Figs 2 and 3, chl-*a* concentrations are lowest in the northwest (Drake Passage waters; called zone A) and southwest (Weddell Sea waters; called zone B) corners of the sampling grid, with the highest concentrations being found in a broad region (called zone C) extending from King George Island to Elephant Island and to the northeast corner of the sampling grid.

As has been pointed out previously from studies in the Bransfield Strait (Holm-Hansen and Mitchell 1991), there is generally a good correlation between chl-*a* concentrations at 5 m depth and the integrated chl-*a* concentrations in the upper 100 m of the water
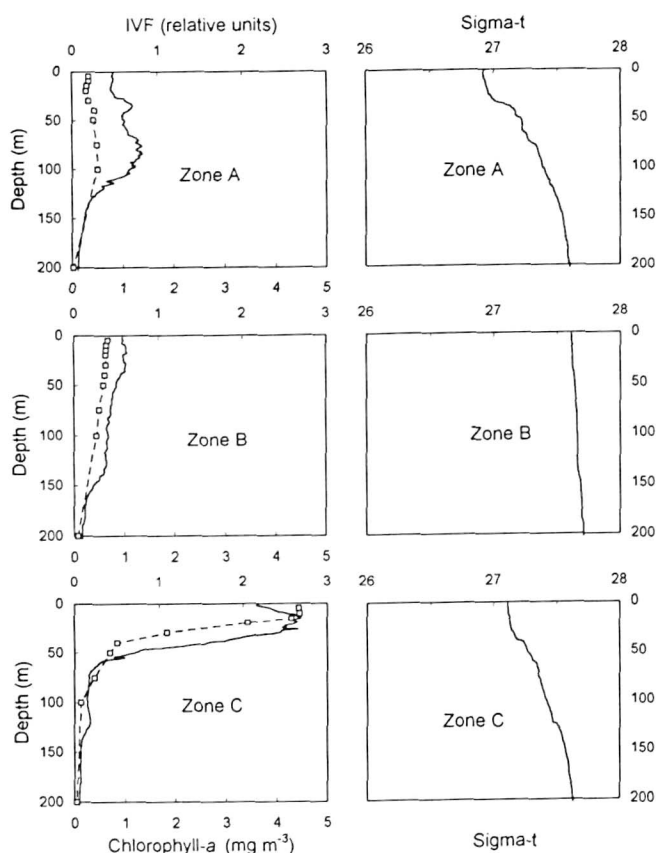
column. The integrated chl-*a* concentrations for Legs I and II in 1993 were 39 and 23 mg chl-*a* m^{-2} and in 1995 were 76 and 114 mg chl-*a* m^{-2}, respectively. Thus it is reasonable to discuss variability in phytoplankton abundance in Antarctic waters on the basis of chl-*a* values in surface waters. There is some variability in these estimates, however, caused by the consistently different profiles of chl-*a* in the upper water columns in zones A, B, and C. Data in Fig. 4 show that stations in zone A show a deep sub-surface chl-*a* maximum between 50-100 m, that stations in zone B have low chl-*a* values which decrease continuously with depth, and that chl-*a* concentrations at stations in zone C are high in surface waters and decrease rapidly with depth.

Factors Affecting Phytoplankton Distribution

The major environmental factors which are important in regard to abundance of phytoplankton in Antarctic waters (e.g., chl-*a* profiles in Fig. 4) are briefly discussed below. In order to relate these factors to the distribution of chl-*a* as noted in Figs. 2 and 3, the 91 stations in the sampling grid have been divided into the following three major groups based on temperature and salinity data in the upper 750 m of the water column: zone A, Drake Passage waters, found in the northwest region of the grid; zone B, stations in the eastern and southwest portion of the grid which are strongly influenced by Weddell Sea water; zone C, stations in the southern portion of the grid and in the region between zones A and B, which represent Bransfield Strait waters and mixing zones with waters from zones A or B.

Water column stability

The depth of the upper mixed layer (UML) will determine the mean solar irradiance which phytoplankton will experience as they circulate within the depth range of the UML. Thus the magnitude of the water density gradient, as well as the depth of the UML, is usually of much importance in regard to the maximum phytoplankton biomass that may develop (Holm-Hansen and Mitchell 1991; Sakshaug *et al.* 1991). However, the distribution of enhanced phytoplankton biomass in zone C, in contrast to the very low biomass in zone A , cannot be ascribed to differences in the depth of the UML (Fig. 4). It is seen that stations in zone A have the greatest change of density in the upper 200 m and also the shallowest UML. The least stable water columns are found in zone B, where there is no stable UML, but rather a slow and continuous increase in water density with depth. The profiles of water density at stations in zone C are intermediate between those for zones A and B, with a fairly stable and deep UML. The low phytoplankton biomass at stations in zone B may be due to cells sinking to deep waters, but the low biomass at stations in zone A cannot be

ascribed to instability of the upper water column.

Temperature

Although low water temperatures limit metabolic growth rates of phytoplankton (Eppley 1972), temperature would not limit the standing stock of phytoplankton unless other 'loss' factors caused the removal of phytoplankton. Water temperatures at the 91 AMLR stations generally range from close to 0°C (southeast region of sampling grid) to +3.0°C in Drake Passage waters. Antarctic phytoplankton grow well throughout this temperature range (Neori and Holm-Hansen 1982). If temperature were a limiting factor for phytoplankton standing stock in the AMLR area, the higher temperatures in zone A (about +3.0°C) should result in higher phytoplankton biomass than in the colder waters of zones B or C but the reverse is true, suggesting that temperature is not a critical factor to explain the variability in phytoplankton biomass.

Solar radiation

Although maximal incident solar irradiance will occur close to the solstice (Dec. 21), incident radiation remains quite high throughout the time period of the AMLR studies (e.g., the mean daily incident irradiance during Legs I and II each year average close to 620 and 480 μEinsteins m^{-2} second^{-1}, respectively). The depth of the euphotic zone (1% of incident irradiance) is at approximately 90 m throughout most of the AMLR sampling area. The irradiance levels in the upper 30-40 m of the upper water column exceed the irradiance needed to achieve maximal photosynthetic rates (about 100 μEinsteins m^{-2} second^{-1}) as described by Helbling *et al.* (1995). Changes in solar radiation thus cannot explain the temporal variability in phytoplankton abundance during Legs I and II as shown in Figs. 2 and 3.

Inorganic nutrients

The mean concentrations at 5 m depth of nitrate (N) in zones A, B, and C during 1991-1993 were 26.5, 28.3, and 27.4 μM, respectively (Silva *et al.* 1995). The corresponding values for phosphate (P) were 1.64, 1.85, and 1.84 μM and for silicic acid (Si) 37.6,

82.3, and 68.9 *μ*M, respectively. Although the silicic acid concentrations are significantly lower in zone A waters as compared to zone B and C waters, concentrations of N, P, and Si in all three zones are all in excess of growth-limiting concentrations.

Trace inorganic elements, however, may be implicated in causing some of the variability in phytoplankton distribution seen in Figs. 2 and 3. Martin *et al.* (1990a, b) have shown that concentrations of iron (Fe) are generally high in coastal waters, but very low and potentially growth-limiting in deep pelagic waters. Strong support for this hypothesis is furnished by the data of Helbling *et al.* (1991) who showed that there is no effect of adding Fe to water samples from zone C, whereas Fe additions to water samples from zone A results in much greater phytoplankton biomass within 4-10 days. Low Fe concentrations thus seem to be the reason that stations in zone A consistently have low phytoplankton biomass in surface waters and a slightly higher biomass at depths between 50-100 m. Studies in tropical waters have shown that such a deep chl-*a* maximum at depths corresponding to the nutricline is generally indicative of nutrient limitation in the overlying water (Kiefer *et al.* 1976).

Grazing pressure

All the factors mentioned above may influence the specific growth rates of phytoplankton cells, and hence the 'standing stock' at any one time. In contrast to this type of controlling factor for phytoplankton, grazing on phytoplankton by zooplankton represents direct removal of algal biomass without affecting specific growth rates. In order to evaluate the likelihood that grazing consumes a significant proportion of primary production, it is necessary to have data on the size, grazing rates, and feeding preferences for all protozoan and metazoan organisms. During the AMLR studies we obtain data only on the abundance of specific groups of nektonic organisms (usually restricted to krill and salps) which are sampled with nets of relatively large mesh size (minimum of 505 *μ*m), and hence we have no data on the biomass of microbial (<200 *μ*m) heterotrophs. As the food web in Antarctic waters is

generally dominated by nanoplankton (<20 *μ*m), the grazing on phytoplankton by the heterotrophic microbial organisms may be of greater importance than the losses due to larger nektonic organisms. We thus do not have the necessary data to evaluate the impact on phytoplankton biomass exerted by grazing heterotrophic organisms.

Discussion and Conclusions

Most phytoplankton studies in Antarctic waters report phytoplankton biomass (or chl-*a* concentrations) either in long transects or at a limited number of stations within a small area. It is difficult to document temporal phytoplankton variability with such sampling programs. The two long-term studies which have utilized a large number of stations within a reasonably sized sampling grid over many years are the RACER (Research on Antarctic Coastal Ecosystem Rates) program from the Bransfield and Gerlache Straits (Huntley *et al.* 1991) and the AMLR program around Elephant Island. Both of these studies have demonstrated that there is great variability in the distribution and abundance of phytoplankton, both temporally and spatially, within the sampling grids. The temporal variability in phytoplankton abundance noted in the RACER and AMLR programs does not support the generalized diagrams showing that seasonal abundance of phytoplankton more or less parallels seasonal incident solar irradiance (Heywood and Whitaker 1984) but rather lend support to the conclusion of El-Sayed (1988) that "...spatial variability (of phytoplankton biomass and primary production)...tends to overshadow the expression of seasonal differences."

From the above discussion of environmental factors that may be implicated in this variability, it seems that low Fe concentrations may be responsible for the very low biomass of phytoplankton in pelagic waters to the north of Elephant Island, which are in sharp contrast to the higher biomass encountered in Bransfield Strait waters. Results from the RACER program, however, also showed

dramatic variability in chl-*a* concentrations within a relatively small area of the Gerlache and Bransfield Straits (e.g., chl-*a* concentrations in surface waters ranged from 2.0 to >25 mg chl-*a* m^{-3} over a distance of 50 km). As these coastal waters supposedly have high Fe concentrations (Martin *et al.* 1990b), it is not likely that either major inorganic nutrient (N, P, Si) or Fe concentrations are responsible for this phytoplankton variability in coastal waters. The reasons for this variability in waters overlying the continental shelf remain an enigma, the solution of which will require better data on chemical constituents (e.g., other micro-elements) in the water as well as much better understanding of the structure and dynamics of the entire microbial food web.

Acknowledgements

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