NOTE

Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago (Southern Ocean)

R. Perissinotto[1,2], C. M. Duncombe Rae[1], B. P. Boden[1], B. R. Allanson[1]

[1] Southern Oceans Group, Department of Zoology, Rhodes University, 6140 Grahamstown, South Africa
[2] Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

ABSTRACT· Relationships between phytoplankton production and biomass and upper ocean stability and mixing depth were analysed using data obtained on 3 cruises to the Prince Edward Islands. Bloom concentrations of chlorophyll a occurred over a wide range of mixed layer depths, from 20 to 130 m. A relatively low percentage of total biomass variance was accounted for by the degree of vertical stability. Conversely, the dominant source of variation responsible for observed differences in the meso-scale distribution of production variables (integrated production rate and photosynthetic capacity) was strongly related to the vertical structure of the water-column. It is suggested that the high levels of freshwater run-off from the islands are retained in the inter-island region by an anticyclonic eddy field. This would result in a local increase in vertical stability with consequent enhanced primary production.

The continuous upwelling at the Antarctic Divergence results in the Southern Ocean having the highest known nutrient levels for pelagic ecosystems (Sakshaug & Holm-Hansen 1984, Priddle et al. 1986). In spite of the high growth potential which characterizes the local primary producers (Holm-Hansen 1985), the phytoplankton production and biomass range far below the levels expected from the nutrient concentrations. The paradox of oligotrophic, or plankton-poor, nutrient-rich waters requires an examination of the processes limiting phytoplankton production to levels of only a few percent of growth potential.

Considerable attention has recently been given to the distribution of water temperature, incident radiation and nutrients in the Southern Ocean (Holm-Hansen et al. 1977, Jacques 1983, LeJehan & Treguer 1983, Tilzer et al. 1985, Tilzer & Dubinsky 1987). However, the distribution of these features over large areas is too uniform for them to explain the spatial distribution of phytoplankton production and biomass at all scales (Fogg 1977, Holm-Hansen et al. 1977, Sakshaug &

Holm-Hansen 1984). In particular, it has been suggested that the small- and meso-scale dynamics of phytoplankton productivity in the Southern Ocean may be regulated by the physical structure of the water-column and by the grazing pressure of herbivorous zooplankton (Hasle 1969, El Sayed 1984, Priddle et al. 1986).

Using data collected on 3 occasions in the vicinity of the Prince Edward Islands (47° S, 38° E; Fig. 1), we examine the relationship between phytoplankton production and biomass and upper ocean stability and mixing depth.

Eighty-three stations were occupied in the area by SA 'Agulhas': 15 stations in April/May 1982, 26 in April/May 1983 and 42 in April/May 1987 (Fig. 2). At each station casts were made using a Neil Brown Mk III conductivity-temperature-depth probe (CTD) and discrete measurements of chlorophyll a concentration were obtained by the spectrophotometric method (SCOR/UNESCO 1966). At 42 stations integrated primary production rates,

$$\Sigma P = P_{max} \cdot z_{0.1},$$

where P_{max} = maximum potential photosynthetic rate and $z_{0.1}$ = 10 % light depth, were estimated by onboard incubation (Gargas et al. 1976, Allanson et al. 1981). Sixteen incubation flasks were inoculated with a solution of 4 μCi $NaH^{14}CO_3$/100 ml. This series was incubated for 4 h under a light regime set up by an array of neutral density filters with transmission values of 50, 25, 15, 10 and 5 % of the incident light. Two bottles were exposed to 100 % of the incident light flux from the bank of Phillips Daylight fluorescent tubes and a tin foil backing was used to increase the light to 150 % for another 2 bottles. The last 2 bottles were wrapped in tin
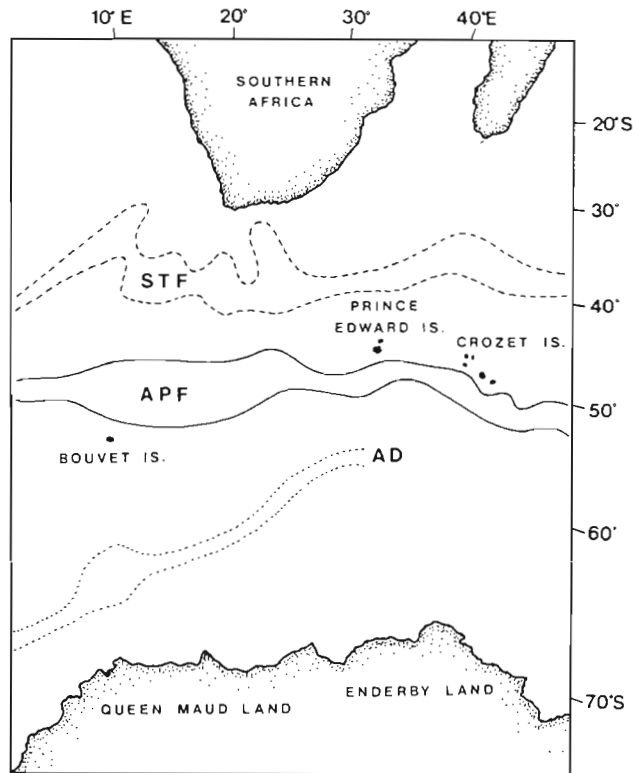
Fig. 1. Position of the Prince Edward Islands and of the main frontal systems south of Africa (redrawn after Lutjeharms 1985 and Hofmann 1985). STC: Subtropical Convergence; APF: Antarctic Polar Front; AD: Antarctic Divergence

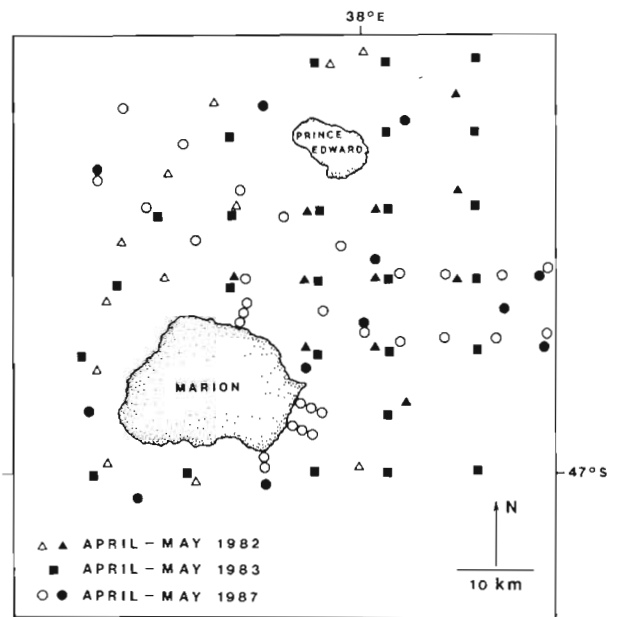Fig. 2. Station positions on the 3 cruises to the Prince Edward Islands. Open symbols indicate stations where only CTD casts and chlorophyll a determinations were made. Closed symbols represent stations where primary productivity estimates were made in addition to the CTD casts and chlorophyll a determinations

foil to determine the amount of ^{14}C taken up by passive diffusion and which had absorbed onto the surfaces of the phytoplankton. Phytoplankton photosynthetic capacity, P_m^B, was calculated by normalizing the maximum potential photosynthetic rate to chlorophyll a concentration (Platt et al. 1980). The depth of the surface mixed layer was assumed to be where a pycnocline of 0.03 kg m^{-3} occurred within 10 m (Priddle et al. 1986). Vertical stability was estimated for the upper 100 m of the water column using the stability parameter

$$E = \alpha \, (dT/dz + \Gamma) - \beta ds/dz \quad [m^{-1}],$$

where α = thermal expansion coefficient; dT/dz = vertical temperature gradient; Γ = adiabatic lapse rate; β = expansion coefficient for salinity; and ds/dz = vertical salinity gradient.

Non-linear regression analysis (Table 1; Fig. 3) showed that several phytoplankton characteristics were significantly related (p $\leq$ 0.05) to the physical structure of the water column. Surface chlorophyll a concentration was correlated with vertical stability during 1982 and 1983 but not during 1987. Negative correlation of chlorophyll a with mixed layer depth was

also significant on 2 of the 3 occasions (1982 and 1987). This pattern was also found for chlorophyll a integrated over the water-column where this was available. The amount of variance explained (R^2) by these relationships ranged from 11 to 40 % of the total (Table 1).

The spatial distribution of phytoplankton biomass is often dominated by local hydrodynamic effects and can account for the lack of consistency in these regressions and the relatively low percentage of variance explained. Small- and mesoscale variations in chlorophyll a concentrations would be the result of physical processes causing accumulation and dissipation of phytoplankters rather than of in situ growth, a hypothesis which is supported by similar results reported for other areas of the Southern Ocean (Weber & El Sayed 1985, Priddle et al. 1986).

According to the hypothesis developed by Sverdrup (1953), the critical depth, Z_{crit}, at which water-column photosynthesis equals the integrated respiration, must be greater than the mixed layer depth for phytoplankton blooms to develop. As the critical depth in the Southern Ocean is generally deeper than the usual summer mixed layer ($Z_{crit} > 100$ m), it is now widely accepted that Sverdrup's hypotheses cannot explain the low phytoplankton production of these waters (Jacques 1983, Priddle et al. 1986, El Sayed 1988) However, turbulence within the euphotic zone must play an important role in regulating the photosynthetic

Table 1. Significant non-linear regressions of phytoplankton biomass and production versus vertical stability and mixed layer depth

Dep. variable (Y)	Indep. variable (X)	Cruise	Model fit	Prob. level	Variance expl.
Surface chl a	Stability	1982	$Y = 4.4 \times 10^{-5} X^{1.01}$	$p = 0.0138$	$R^2 = 0.408$
Surface chl a	Stability	1983	$Y = 3.9 \times 10^{-5} X^{0.80}$	$p = 0.0013$	$R^2 = 0.393$
Surface chl a	Mixed layer depth	1982	$1/Y = -1.70 + 0.05 X$	$p = 0.0343$	$R^2 = 0.321$
Surface chl a	Mixed layer depth	1987	$Y = \exp(0.89 - 0.01 X)$	$p = 0.0181$	$R^2 = 0.145$
Integrated chl a	Stability	1983	$Y = 62.6\ X^{0.48}$	$p = 0.0352$	$R^2 = 0.194$
Integrated chl a	Mixed layer depth	1987	$Y = \exp(5.19 - 0.01 X)$	$p = 0.0423$	$R^2 = 0.112$
Primary production	Stability	1983	$Y = 0.21\ X^{0.96}$	$p = 0.0001$	$R^2 = 0.716$
Primary production	Stability	1987	$Y = 0.37\ X^{0.66}$	$p = 0.0503$	$R^2 = 0.377$
Primary production	Mixed layer depth	1983	$1/Y = -0.02 + 8.63 X$	$p = 0.0320$	$R^2 = 0.178$
Photosyn. capacity	Stability	1983	$Y = 1.00\ X^{0.29}$	$p = 0.0009$	$R^2 = 0.416$
Photosyn. capacity	Mixed layer depth	1983	$Y = \exp(2.08 - 0.01 X)$	$p = 0.0005$	$R^2 = 0.412$
Photosyn. capacity	Stability	1987	$Y = 0.04\ X^{0.95}$	$p = 0.0003$	$R^2 = 0.819$
Photosyn. capacity	Mixed layer depth	1987	$Y = \exp(4.25 - 0.04 X)$	$p = 0.0203$	$R^2 = 0.509$

activity of phytoplankton. When the mixed layer depth exceeds the euphotic depth ($Z_{mix} > Z_{eu}$) phytoplankton remain in the aphotic zone during part of the day. Thus, the carbon balance would be shifted towards increasing respiratory losses following the relation: $K = Z_{eu}/Z_{mix} (P - R)$, where K is the daily net growth rate, P the diurnal photosynthetic carbon accumulation and R the nocturnal respiratory carbon losses (Tilzer & Dubinsky 1987). If $Z_{mix} < Z_{eu}$, the daily production will increase and, for constant Z_{eu}, the shallower the mixed layer the higher the production. It has been reported (Holm-Hansen & Foster 1981) that phytoplankton blooms in the Southern Ocean (with chlorophyll a concentrations > 1.5 mg m^{-3}) occur predominantly in conjunction with a shallow mixed layer and Sakshaug & Holm-Hansen (1984) suggest that a pycnocline depth of 50 m may be the maximum depth allowing blooms to occur.

Although phytoplankton biomass in the Southern Ocean generally reflects the variation in primary production (Burkholder & Mandelli 1965, Holm-Hansen et al. 1977), the results of the investigations at the Prince Edward Islands indicate that most of the biomass variance is not accounted for by the degree of vertical stability. On all 3 occasions bloom concentrations of chlorophyll a were observed over a wide range of mixed layer depths, from 20 to 130 m. We suggest, therefore, that biomass (as chlorophyll a) may not be a suitable variable to be used in small- and meso-scale analysis of the relationships between local phytoplankton variations and the vertical structure of the upper ocean.

More consistent results can be expected on considering the distribution of primary production or appropriate algal physiological indicators, such as maximum photosynthetic rate or in vivo fluorescence, which are good indicators of the rate of vertical mixing in the

water-column (Lewis et al. 1984). Our data (Table 1) show that integrated primary production was significantly related to stability in April/May 1983 and April/May 1987, when production data were available. The correlation between productivity and mixed layer depth was significant only for the 1983 data set. Strong and consistent relationships were found between the photosynthetic capacity, and the stability and mixed layer depth (Fig. 3).

These relationships would suggest that the dominant source of variation responsible for the observed difference in local phytoplankton photosynthesis is the physical structure of the water-column. During 1987 stability explained over 80 % of the total variance of phytoplankton photosynthetic capacity.

At the Prince Edward Islands recurrent phytoplankton blooms associated with high photosynthetic rates are found mostly over the shallow saddle between the 2 islands (Allanson et al. 1985, Boden 1988). This region has also been shown to be characterized by the presence of an anticyclonic eddy field (Allanson et al. 1985, Perissinotto & Duncombe Rae unpubl.). Freshwater run-off of the high rainfall on the islands (mean 210 mm mo^{-1}; South African Weather Bureau, pers. comm.) retained between them by the eddy, is shown by Duncombe Rae (in press) to decrease significantly the density of the mixed layer, thereby increasing its stability over the saddle compared to the surrounding ocean.

Similar dynamics may prevail around most of the Subantarctic islands where run-off may contribute substantially to elevated phytoplankton production. This is a form of island mass effect that could play a far-reaching role in the general economy of the entire ecosystem.

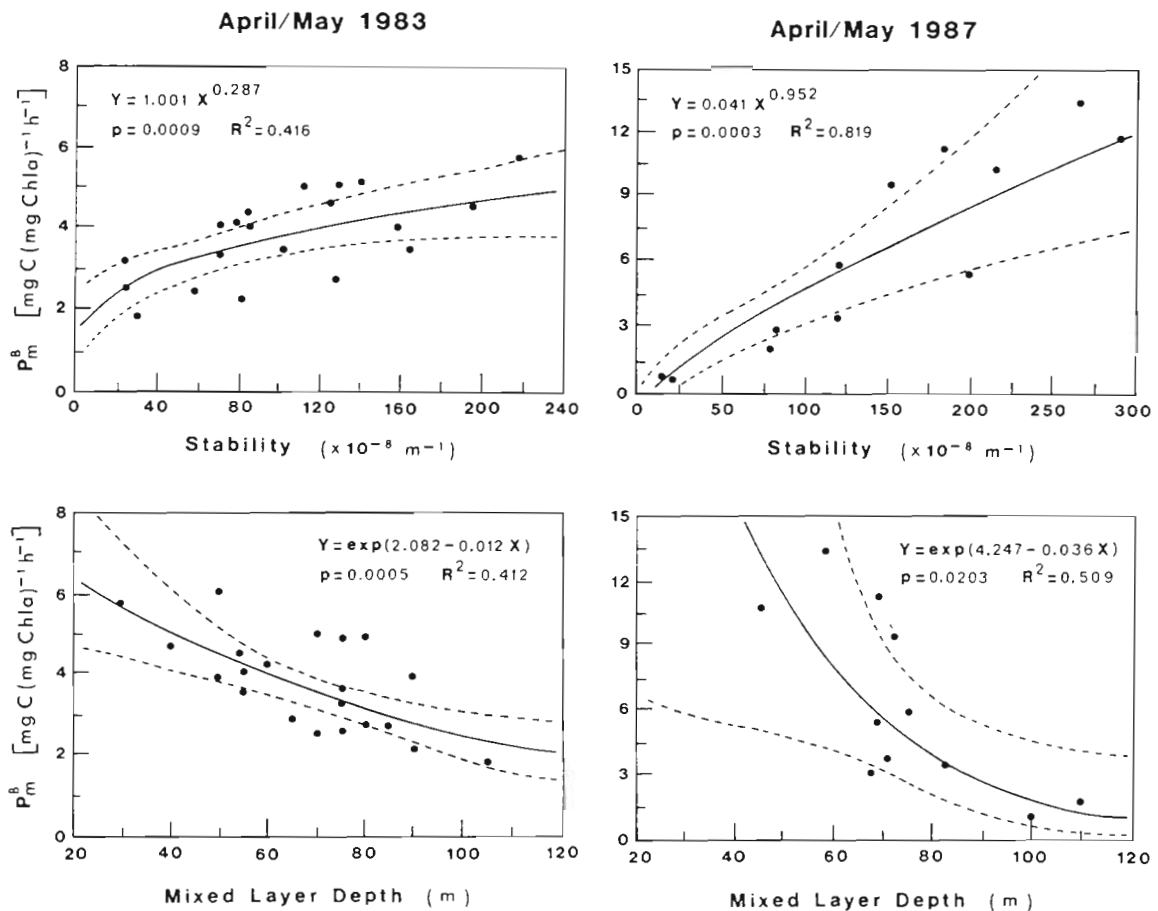Ice-melt around the Antarctic continent also affects the vertical stability of the water-column by increasing

April/May 1983

April/May 1987

Fig. 3. Non-linear regressions of phytoplankton photosynthetic capacity (P_m^B) versus vertical stability and mixed layer depth. Dashed lines represent 95 % confidence limits

the buoyancy of the surface layer. Although in this case the source of freshwater input is different compared to that at the Prince Edward Islands, a similar effect, with enhancement in phytoplankton production, seems to occurr (Smith & Nelson 1985, Nelson et al. 1987).

LITERATURE CITED

Allanson, B. R., Boden, B. P., Parker, L. D., Duncombe Rae. C. M. (1985). A contribution to the oceanology of the Prince Edward Islands. In: Siegfried, W. R., Condy, P. R., Laws, R. M. (eds.) Antarctic nutrient cycles and food webs. Springer, Berlin, p. 38–45

Allanson, B. R., Hart, R. C., Lutjeharms, J. R. E. (1981). Observations on the nutrients, chlorophyll and primary production of the Southern Ocean south of Africa. S. Afr. J. antarct. Res. 10/11: 3–14

Boden, B. P. (1988). Observations of the island mass effect in the Prince Edward archipelago. Polar Biol. 9: 61–68

Burkholder, P. R., Mandelli, E. F. (1965). Carbon assimilation of marine phytoplankton in Antarctica. Proc. natn Acad. Sci. U.S.A. 54: 437–444

Duncombe Rae, C. M. (in press). Physical and chemical marine environment of the Prince Edward Islands (Southern Ocean) during April/May 1987 S. Afr. J. mar Sci. 8

El Sayed, S. Z. (1984). Productivity of the Antarctic waters – a reappraisal. In: Holm-Hansen, O., Bolis, L., Gilles, R. (eds.) Marine phytoplankton and productivity. Springer, Berlin, p. 19–34

El Sayed, S. Z. (1988). Seasonal and interannual variabilities in Antarctic phytoplankton with reference to krill distribution. In: Sahrhage, D. (ed.) Antarctic Ocean and resources variability. Springer, Berlin, p. 101–119

Fogg, G. E. (1977). Aquatic primary production in the Antarctic. Phil. Trans. R. Soc. London B279: 27–38

Gargas, E., Nielsen, C. S., Lonholdt, J. (1976). An incubator method for estimating the actual daily plankton algal primary production. Wat. Res. 10: 853–860

Hasle, G. R. (1969). An analysis of the phytoplankton of the Pacific Southern Ocean: abundance, composition and distribution during the Brotegg expedition, 1947–1948. Hvalråd Skr. 52: 1–168

Hofmann, E. E. (1985). The large-scale horizontal structure of the Antarctic Circumpolar Current from FGGE drifters. J. geophys Res. 90: 7087–7097

Holm-Hansen, O. (1985). Nutrient cycles in Antarctic marine ecosystems. In: Siegfried, W. R., Condy, P. R., Laws, R. M. (eds.) Antarctic nutrient cycles and food webs. Springer, Berlin, p. 6–10

Holm-Hansen, O., El Sayed, S. Z., Franceschini, G. A., Cuhel, G. L. (1977). Primary production and the factors controlling phytoplankton growth in the Southern Ocean. In: Llano,

G. A. (ed.) Adaptations within Antarctic ecosystems. Smithsonian Institution, Gulf Publ. Co., Houston, Texas, p. 11–50

Holm-Hansen, O., Foster, T D. (1981). A multi-disciplinary study of the Eastern Scotia Sea. Antarctic J. U.S. 16: 159–160

Jacques, G. (1983). Some ecophysiological aspects of the Antarctic phytoplankton. Polar Biol. 2: 27–33

LeJehan, S., Treuger, P. (1983). Uptake and regeneration Δ Si/ Δ N/ Δ P ratios in the Indian sector of the Southern Ocean. Polar Biol. 2: 127–136

Lewis, M. R., Horne, E. P. W., Cullen, J. J., Oakey, N. S., Platt, T. (1984). Turbulent motion may control phytoplankton photosynthesis in the upper ocean. Nature, Lond. 311: 49–50

Lutjeharms, J. R. E. (1985). Location of frontal systems between Africa and Antarctica: some preliminary results. Deep Sea Res. 32: 1499–1509

Nelson, D. M., Smith, W. O. Jr, Gordon, L. I., Huber, B. (1987). Early spring distributions of density, nutrients and phytoplankton biomass in the ice-edge zone of the Weddell/ Scotia Sea. J. geophys. Res. 92: 7181–7190

Platt, T., Gallegos, C. L., Harrison, W. G. (1980). Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. J. mar Res. 38: 687–701

Priddle, J., Hawes, I., Ellis-Evans, J. C., Smith, T. J. (1986).

Antarctic aquatic ecosystems as habitats for phytoplankton. Biol. Rev. 61: 199–238

Sakshaug, E., Holm-Hansen, O. (1984). Factors governing pelagic production in polar oceans. In: Holm-Hansen, O., Bolis, L., Gilles, R. (eds.) Marine phytoplankton and productivity. Springer, Berlin, p. 2–34

SCOR/UNESCO Working Group 17 (1966). Determination of photosynthetic pigments in seawater UNESCO Monographs on oceanographic methodology, 1. UNESCO, Paris

Smith, W. O., Nelson, D. M. (1985). Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science 227: 163–166

Sverdrup, M. U. (1953). On conditions for the vernal blooming of phytoplankton. J. Cons. int. Explor Mer 18: 287–295

Tilzer, M. M., Dubinsky, Z. (1987). Effects of temperature and day-length on the mass-balance of Antarctic phytoplankton. Polar Biol. 7: 35–42

Tilzer, M. M., Elbrachter, M., Gieskes, W. W., Beese, B. (1985). Light-temperature interactions in the control of photosynthesis in Antarctic phytoplankton. Polar Biol. 5: 105–111 .

Weber, L. H., El Sayed, S. Z. (1985). Spatial variability of phytoplankton and the distribution and abundance of krill in the Indian sector of the Southern Ocean. In: Siegfried, W. R., Condy, P. R., Laws, R. M. (eds.) Antarctic nutrient cycles and food webs. Springer, Berlin, p. 284–293

This note was submitted to the editor