

Phytoplankton biomass in Antarctic shelf zones: a conceptual model based on Potter Cove, King George Island

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Received 22 November 2000; accepted 19 June 2002

Abstract

Antarctic coasts are usually considered productive areas. However, some shallow coastal areas are known to be HNLC systems where even if favourable conditions for phytoplankton growth are apparent, phytoplankton biomass remains low. This study aims to analyse the processes that may modulate phytoplankton biomass in Antarctic shallow coastal environments. In situ phytoplankton production and growth experiments from Potter Cove (King George Island, Antarctica) are related to the prevailing oceanographic and meteorological conditions. A conceptual model has been developed, relating Antarctic phytoplankton growth during the spring–summer season to winds, sea-ice extent and the influence of the inland on the light-mixing regime. An attempt has been made to find the environmental threshold values for the factors controlling phytoplankton accumulation. The results from applying such a model suggest that, in spite of high nutrient concentrations, the combination of the time scale of the physical factors affecting both the radiation penetrating the water column and the depth of vertical turbulent mixing explain the low phytoplankton biomass values observed. Application of this model to other high-latitude areas (open ocean and coastal zones) is discussed.

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Keywords: Phytoplankton growth; Critical depth; Turbulent mixing; Conceptual model; Antarctica; King George Island; Potter Cove

1. Introduction

Except for some highly productive coastal or marginal ice environments (Karl et al., 1991), Antarctic waters, and especially their shallow areas, can show very low phytoplankton biomass and productivity (Hapter et al., 1983; Schloss et al., 1997, 1998)

with chlorophyll *a* rarely exceeding 3 mg m^{-3} (Clarke and Leakey, 1996). Different hypotheses have been suggested to explain the low biomass: grazing pressure (Walsh, 1976), light limitation related to deep mixing (Smith and Nelson, 1985) and lack of iron (Martin et al., 1990). Antarctic coastal waters are usually considered to be nutrient replete, except during local phytoplankton blooms in areas west of the Antarctic Peninsula (Moline and Prézelin, 1997) or close to the receding ice edge (Smith and Nelson, 1985). In shallow areas where little phytoplankton development is observed, both macro- and micronu-

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trient concentrations are usually high (Brandini and Rebello, 1994; Schloss, 1997) due to additional terrestrial inputs. In these shallow waters, light limitation (due to high turbidity, Schloss, 1997; Schloss and Ferreyra, 2002) and the strong mixing (consequence of the heavy winds) have been suggested to control phytoplankton (Brandini and Rebello, 1994; Schloss et al., 1997).

Although a variety of models simulating phytoplankton evolution have been constructed for other Antarctic zones (Mitchell and Holm-Hansen, 1991; Svansson, 1991; Sakshaug et al., 1991; Lancelot et al., 1991, 1993), to date, no model has been adapted to shallow coastal Antarctic areas.

This work presents a conceptual model with the aim of explaining the processes responsible for the low chlorophyll concentrations observed in some shallow Antarctic coastal areas. The temporal scale is restricted to the growth season (i.e., September to March) and the formulation is based on observations made in the Potter Cove system, a small fjord-like, low-chlorophyll environment located at King George Island. Hydrographic and phytoplankton data collection started in 1991. Here, data from field seasons corresponding to summer 1991–1992, years 1993, 1995 and 1996 will be analysed. Some of them have been already published (Klöser et al., 1993, 1994; Schloss et al., 1997; Schloss and Ferreyra, 2002), and all were presented in Schloss (1997). This relatively complete database allows the quantification of the threshold values for the processes and the time scales for the windows allowing or preventing phytoplankton growth and accumulation. The main parameterised processes are water column stratification, wind-induced turbulent mixing and light attenuation. In the model, these processes depend on a marked seasonality in light regime and sea-ice extent, strong winds and particles of terrigenous origin.

2. Methods

2.1. The Potter Cove system

Potter Cove is a small inlet in the southwestern end of King George Island (62°14'S, 58°38'W, South Shetland Archipelago, Fig. 1). Potter Cove is 4 km long and 2.5 km wide. A shallow sill (<30 m)

separates it into an inner and outer cove. The inner cove is characterised by soft sediments and shallower depth (<50 m) than the outer cove, where the bottom is mainly rocky and depths are around 100 m. It is adjacent to Maxwell Bay (Fig. 1), a 14 km long and 6 km wide opening, where maximum depth can reach 520 m. This bay connects to the Bransfield Strait. Circulation in Potter Cove is strongly influenced by the general circulation of Maxwell Bay (Roese and Drabble, 1998). In general, a cyclonic circulation has been identified, with efficient water renewal in the northern sector, where water from Maxwell Bay enters the Cove (Fig. 1). Freshwater input varies both seasonally and interannually. Two main creeks discharge into the cove, the Matias and the Potter Creeks. They exhibit different regimes, one being snowy and lacustrine, the other snowy and glacial (Varela, 1998). Drainage ranged between 0.03 and 0.11 m³ s⁻¹ in the Matias Creek and from 0.08 to 3.8 m³ s⁻¹ at Potter Creek (Varela, 1998). Suspended sediment discharges ranged between 0.04 and 15 kg m⁻³ (average=0.14 kg m⁻³), in correlation with air temperature; this is consistent with data from other glaciomarine environments that are subject to large influxes of sediment-laden meltwater (Leventer and Dunbar, 1985).

2.2. Sampling strategy

Intensive sampling at Potter Cove started in 1991 on time scales from daily to annual and hourly to weekly sampling frequency. Spatial variability was covered studying one site in the inner cove (E1) and one in the outer cove (E2) (Fig. 1). On three occasions (December 1995, January and February 1996), extensive hydrographic measurements were carried out in a grid. Although different instruments were used in the different seasons, all of them were intercalibrated. Meteorological variables such as wind speed and direction and incident photosynthetically available radiation (PAR) were measured at the meteorological park of the station by the Argentinean National Meteorological Survey and intercalibrated with an automated DL-LS2 station (Delta Logger, UK, calibration sheets were provided by the company). Water temperature was measured with an inversion thermometer, and salinity was determined with an induction salinometer Beckman RS9 in 1991–1992. During the other years, water salinity and temperature were

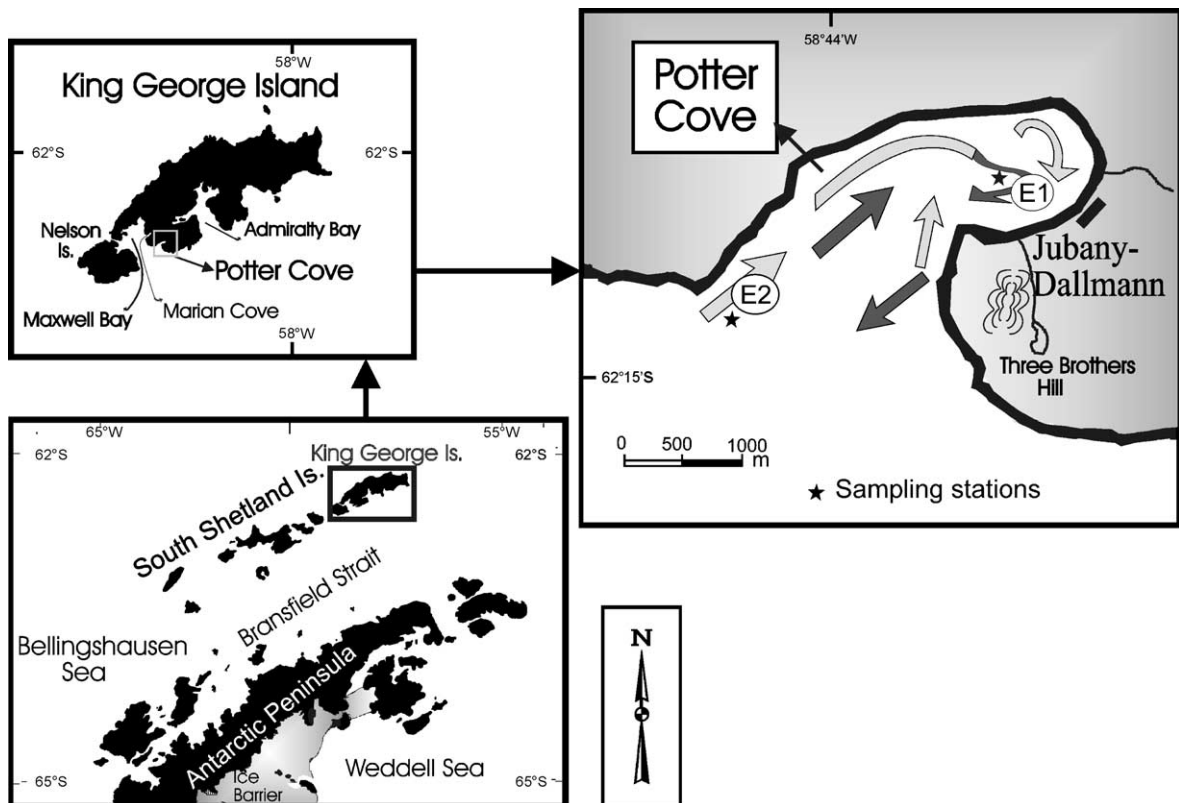


Fig. 1. Map showing the location of the Antarctic coastal shallow environment where the present study was conducted, Potter Cove, King George Island, South Shetlands and the areas adjacent to it. The arrows in the Potter Cove map represent a simplified circulation pattern of its waters (adapted from Schloss et al., 1997).

measured with a ME-ECO219 mini-CTD. PAR was measured using a Kahlsico 268WA310 underwater radiometer during the 1991–1992 campaign, and with LI-192SB and LI-193 sensors (Li-Cor, USA) added to an M&E Ecosonde CTD afterwards. Euphotic depth Z_e was considered where 1% of surface irradiance value was measured. A volume of 0.5–1 l seawater was filtered onto GF/F filters, and photosynthetic pigments extracted during 24 h in cold and dark conditions with 90% acetone and read on a Hitachi Perkin Elmer UV–VIS 139 spectrophotometer in 1991–1992, and a Shimadzu UV160A spectrophotometer thereafter. Correction for phaeopigments was done according to Strickland and Parsons (1972). Total particulated matter (TPM) was measured gravimetrically after filtering the samples through combusted preweighed Whatman GF/F filters. After filtration, filters were rinsed twice with distilled water

in order to remove salts, then dried 24 h at 60 °C, and weighed. Nutrients were measured on GF/F filtered water, on a Technicon II autoanalyzer.

2.3. Experimental studies

Results of experimental studies will be used in the conceptual model. Primary productivity measurements (photosynthetron method, Lewis and Smith, 1983) are described in Schloss (1997), Schloss et al. (1998) and Schloss and Ferreyra (2002). They were performed in summer 1991–1992 on waters from the inner and outer cove. Phytoplankton growth experiments are described in Schloss (1997), based on experiments done in spring/summer 1996, and also on water samples from the inner and outer cove, under ambient light and temperature-simulated conditions. Three 50-l aquaria were placed in a 200-l container

with circulating water pumped from the Cove. Light was screened with black neutral filters. Chlorophyll *a* has been measured as described above, on volumes varying from 1 to 0.2 l, and used as indicator of phytoplankton biomass. Nitrate has been additionally measured on 50-ml filtered samples. Results of these experiments are presented below.

2.4. Criteria to define phytoplankton growth

To measure phytoplankton growth and biomass accumulation, Sverdrup's (1953) critical depth Z_c

was taken into account. Z_c is the depth at which the vertically integrated rates of photosynthesis and respiration by the plankton are equal. We assume that phytoplankton accumulation is likely if $Z_c > Z_t$. Z_t (Denman and Gargett, 1983) is the root-mean square expected vertical displacement of a particle in the water column. It allows the estimation of the Lagrangian vertical displacement of a particle in a turbulent flow and can be used to obtain length scales for vertical displacement of phytoplankton as a function of time. It depends on a vertical eddy coefficient K_z , which in turn depends on N , the buoyancy frequency

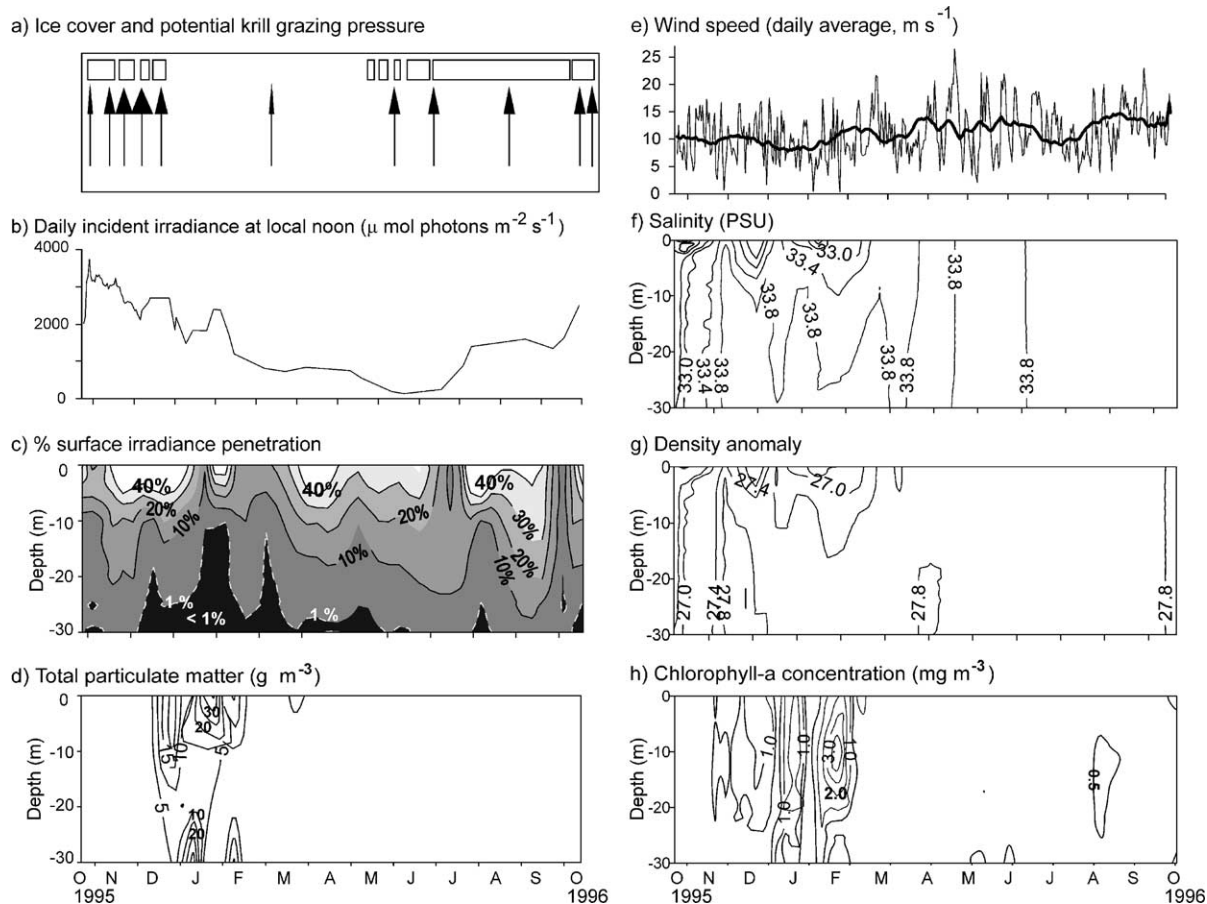


Fig. 2. Synthesis of the environmental information available for the Potter Cove area that has been used for the construction of the conceptual model. All data correspond to the period between October 1995 and October 1996. (a) Ice cover, represented by the squares, and potential krill grazing, represented by arrows. Note that the arrow's width changes, thicker arrows indicating heavier grazing pressure. (b) Incident irradiance (PAR) measured at local noon. (c) Calculated percentage of light penetrating the water column, at local noon. The white dashed line indicates the depth of the 1% light penetration, or Z_c . (d) Total particulate matter concentration at the different depths in the water column. (e) Daily average wind speed. (f) Vertical distribution of water salinity. (g) Vertical distribution of the density anomaly, σ_t , in the water column. (h) Vertical distribution of chlorophyll *a* concentration in the water column.

or Brunt–Väisälä frequency (a measure of the local stratification) and ε_v , the rate of dissipation of the wind-generated turbulent kinetic energy (TKE). TKE is directly related to the wind speed (see equations in Appendix A). Z_t was chosen instead of the depth of the upper mixed layer, Z_m , defined as the depth where the density gradient is maximal, which is more frequently used (Moline et al., 1997). The use of Z_t is preferable in windy coastal shallow environments because wind-generated turbulent eddies may overturn the water masses, moving phytoplankton up and down in the water column (Denman and Gargett, 1983). In this sense, Z_t covers not only the density field but also the time and/or the space scales of the vertical advection of phytoplankton by these eddies. Hence, it is a dynamic indicator of water column structure. It should be noted that sampling was only carried out when wind speeds were $< 10 \text{ m s}^{-1}$. Moreover, the use of Z_t would avoid a biased interpretation of water column dynamics since data were averaged for a long period.

Although daily average wind speeds were indeed generally $> 10 \text{ m s}^{-1}$, from September 1995 to March 1996, they generally decreased by noon allowing almost continuous daily sampling. Therefore, the values of some of the parameters presented in the model corresponding to the average of this period is considered, although all the 6 years data were used in its construction.

3. Results and discussion

Sea ice covered the waters in Potter Cove from 4 to 7 months each year (6.5 during the 1995–1996 period, Fig. 2a). Incident irradiance at local noon varied with the season (Fig. 2b) and light penetration in water (Fig. 2c) was influenced both by the ice cover and the amount of particles in the water column (Fig. 2d). The most conspicuous meteorological feature in the Potter Cove area during the present study was the wind speed (Fig. 2e). Therefore, wind-induced mixing heavily influenced the water column structure; in contrast, tidal-induced turbulent kinetic energy and mixing were not significant (Schloss, 1997). Fresh-water supply in spring (see salinity in Fig. 2f) formed either a thin low-density (Fig. 2g) surface mixed layer Z_m (Fig. 3a) or a continuously stratified water column.

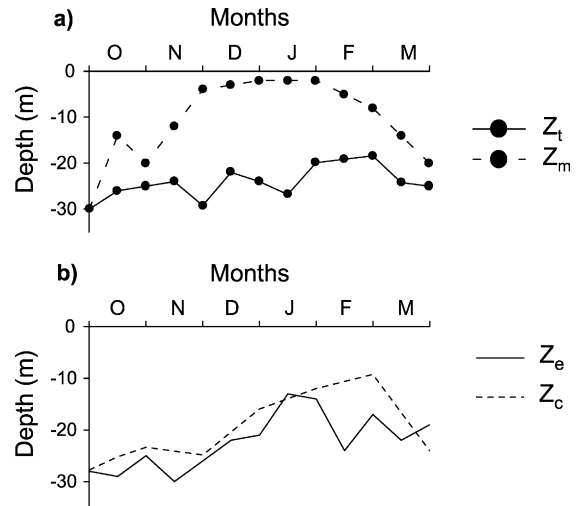


Fig. 3. (a) Comparison of the semimonthly averages of the mixed layer Z_m and the root-mean square expected vertical displacement depth of particles in the water column, Z_t , for the inner Potter Cove. (b) Comparison of the semimonthly averages of the euphotic and critical depths (Z_e and Z_c , respectively) for the inner Potter Cove.

However, winds generally eroded this stratification, and particles were mixed down to depths close to sea bottom (Fig. 3a). In the inner Potter Cove, calculated Z_c varied from 10 m in some summer days down to the sea bottom (or even more) in winter (Fig. 3b; Schloss et al., 1998). In general, the instantaneous Z_m depths measured were smaller than the wind influenced calculated Z_t , and Z_e and Z_c ; the latter were on average also smaller than Z_t , meaning that irradiance at the depths where cells are transported may not be adequate for phytoplankton growth. Chlorophyll *a* concentration usually ranged from undetectable to 1 mg m^{-3} and never exceeded 3.5 mg m^{-3} (Fig. 2h).

Although differences in primary production in E1 and E2 (Fig. 1) were in correlation with water column structure (Schloss and Ferreyra, 2002), no significant difference in average growth or production between the inner and the outer cove or between the spring and the summer seasons was found (Schloss et al., 1998). Average maximum photosynthetic rate P_{\max}^* was 1.09 (std: 0.042) $\mu\text{g C } (\mu\text{g chlorophyll } a)^{-1} \text{ h}^{-1}$; the photosynthetic efficiency α^* was 0.029 (std: 0.003) $\mu\text{g C } [(\mu\text{g chlorophyll } a)^{-1} \text{ h}^{-1}] \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, and E_k , the photoadaptation index, was $7.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Schloss et al., 1998), similar to values reported for other HNLC Antarctic environments (e.g.

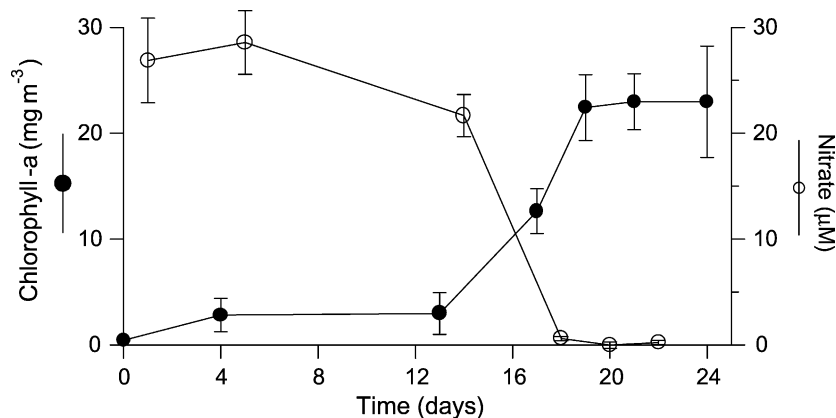


Fig. 4. Experimental determination of Potter Cove phytoplankton growth (expressed as chlorophyll *a* concentration) under environmental simulated light and temperature conditions. Nitrate time evolution is also presented.

Holm-Hansen and Mitchell, 1991). Experimental average doubling rates under simulated in situ conditions were $0.44 \text{ doublings day}^{-1}$ (Schloss, 1997), close to values reported for Antarctic phytoplankton (Spies, 1987; Sommer, 1989). Exponential growth started after 12–15 days of incubation (Fig. 4), reaching final biomass concentrations as high as 36 mg m^{-3} chlorophyll *a*. In this occasion, nutrients (especially NO_3) were depleted below detection after 16 days (Fig. 4), in agreement with observations made in other coastal Antarctic environments (Sakshaug and Holm-Hansen, 1986). These observations suggest that, for the time scale considered in this study, any combination of physical conditions favouring phytoplankton development in the natural environment would have to last for at least 12 days.

4. The conceptual model

4.1. Environmental factors considered influencing phytoplankton growth

Presence of phytoplankton cells in a specific water mass depends in part on grazing, advection, mixing, sedimentation, and/or resuspension. In polar marine environments, seeding from sea ice may be an additional cell source, although this contribution may be small (McMinn, 1996). Together, these processes determine the final yield of primary producers in a particular water body. In the model proposed here,

emphasis is put on the variables that directly affect phytoplankton production: the quantity and quality of incident irradiance (controlled by sea ice and particulate material), and the structure of the water column. Carbon dioxide, nutrients and trace metal concentration are not considered here because CO_2 is usually considered not to limit phytoplankton development (Riebesell et al., 1993), and no limitation of phytoplankton growth by macro- or micronutrients such as iron has been described in coastal Antarctic environments (Bidigare et al., 1996; Brandini, 1993). Particularly in Potter Cove, macronutrient concentrations were high (Table 1). The decrease in nutrients concentration from October to January is related to dilution by large meltwater supply (Lipski, 1982; Brandini and Rebello, 1994) and is not considered to limit phytoplankton growth at the model's time scale and is, therefore, not included.

Incident radiation defines the length of the growth season, and light penetrating the water column deter-

Table 1

Average nutrient concentrations (in μM) measured in Potter Cove (E1) at 5-m depth during the spring–summer season 1995–1996

	Nitrate	Phosphate	Silicate
October	26.43 (3.72)	3.20 (0.71)	50.76 (6.24)
November	17.20 (7.23)	2.33 (0.60)	41.46 (10.09)
December	14.86 (5.58)	2.05 (0.51)	44.12 (7.56)
January	13.75 (3.71)	2.07 (0.37)	42.36 (7.02)
February	15.27 (2.04)	2.01 (0.23)	47.00 (4.17)

Standard errors of means are presented in parentheses.

mines the energy available for photosynthesis. Water column stratification will delimit the depth at which photosynthetic cells are transported, and hence the radiation that they will receive during a given period. The central assumption of the conceptual model is that phytoplankton biomass in shallow coastal environments is primarily controlled by light availability and water column stratification which, in turn, are governed by freshwater runoff and winds (Fig. 5).

4.1.1. First subperiod (late September–early December)

At the start of the growth season (around September), when the solar zenith angle and day length provide an adequate light environment for photosynthesis (see Fig. 2b), other forcing factors have to be regarded as controls of phytoplankton development. The first factor considered in this model was ice cover, which can have both positive and negative effects on phytoplankton growth. The ice cover was usually present early in the growth season, on occasions reducing the available light by 90%, especially if the ice is also covered by snow, as known from other Antarctic areas (Buckley and Trodahl, 1987; Smith et al., 1996). Thus, a phytoplankton bloom could hardly start before ice has retired from the cove, or at least significantly melted. Ice melting also stimulates phytoplankton growth, by stratifying the water column. In the model in Fig. 5a, this situation is represented by the arrows that go out from the melt-water and the wind hexagons. It was evaluated that a situation with appropriate light conditions, stratified water column and low winds may have to remain at least for 12–15 days (as resulted from the growth experiments, Fig. 4) to enable phytoplankton accumulation in shallow environments like Potter Cove.

4.1.2. Second subperiod (early December to March): the riverine discharges

At this time, creek and riverine inputs, as well as subsurface drainage contribute to water column stratification. The riverine discharges also bring high loads of particulate matter (Varela, 1998). These transports are higher or similar to those from adjacent areas on King George Island (Pecherzewski, 1980). It has been shown that, especially for the upper 5 m of the water column during the summer months in Potter Cove, the attenuation coefficient, K_{PAR} , is strongly related to

total particulate matter (Schloss and Ferreyra, 2002). For high TPM loads (December 1995, see Fig. 2d), radiation penetrating the water column can be lower than that required for phytoplankton bloom development (Fig. 5a).

Again, phytoplankton development will depend on the 12-days time that the combination of the light and stratification conditions (given by the low wind intensities and the shallow pycnocline) described above remains adequate for cells' growth (Fig. 5a).

4.2. The parameters values

4.2.1. Light and stability conditions in the first subperiod

The seasonal PAR value assumed for phytoplankton to start growing (E_0) was $25 \text{ mol m}^{-2} \text{ day}^{-1}$ since this is an average value measured during the several seasons for early spring (September, average irradiance values can be found in Table 2). Once incident $\text{PAR} > 25 \text{ mol m}^{-2} \text{ day}^{-1}$, the radiant energy penetrating the water column has to be considered in order to estimate if it is enough for phytoplankton growth. The underwater threshold irradiance chosen in the present model for phytoplankton development was $37.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$. This value corresponds to the average saturation irradiance, E_k , of primary productivity measurements performed on Potter Cove phytoplankton (Schloss and Ferreyra, 2002). In the calculation of Sverdrup's Z_c , the irradiance value E_n at the compensation depth was equalled to E_k , following the criteria of Figueiras et al. (1994) and considering the similarity between our results and the estimations presented in Nelson and Smith (1991), who calculated Z_c considering $E_n = 35 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

The wind effect is quantified by ε_v , and the low salinity additions by the buoyancy frequency N . In the calculation of Z_t , several combinations of N and ε_v could lead to the Z_t values (calculated for 24 h) that allow phytoplankton growth, i.e., to a $Z_c > Z_t$ relation. Values chosen corresponded, for the buoyancy frequency, to the average for the first subperiod of the growth season $N = 7.4 \times 10^{-3} \text{ s}^{-1}$. For the average stability conditions during October and November, it has been estimated that, when average wind speeds are $< 4 \text{ m s}^{-1}$, wind-generated TKE will transport particles to depths above the critical depth Z_c and, in this way, favour phytoplankton development. Other

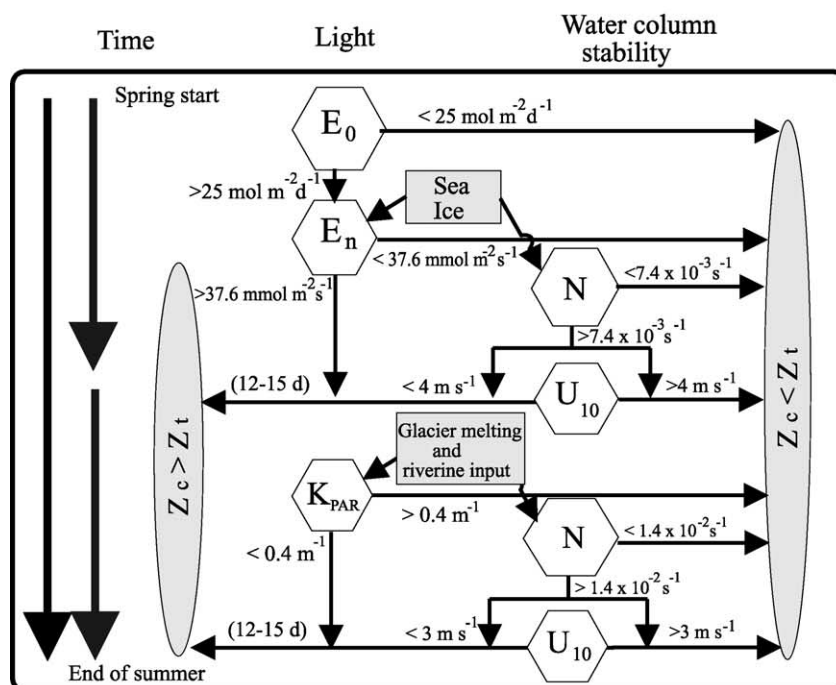
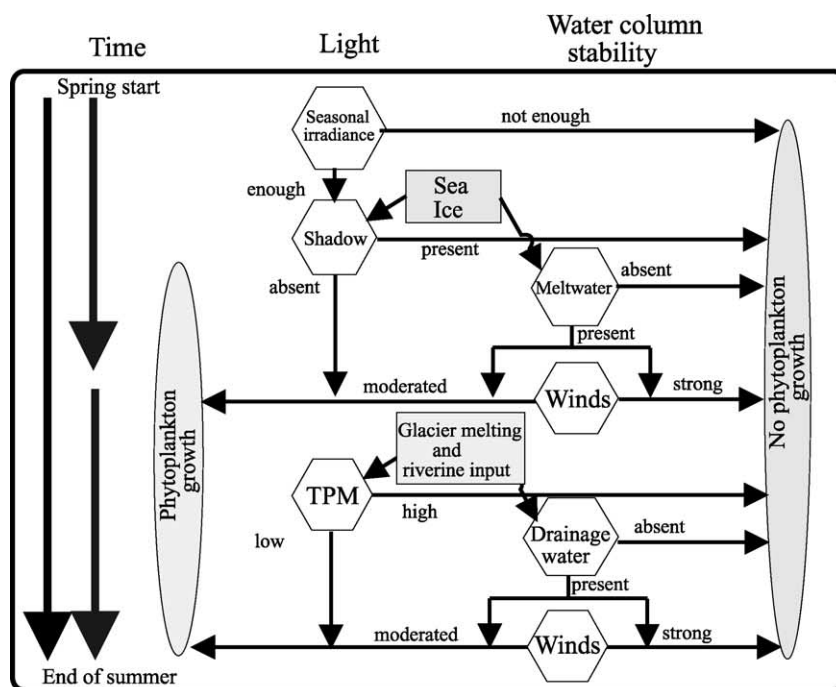


Table 2

Daily integrated PAR values, K_{PAR} (PAR extinction coefficient) for the water surface layer, Z_c and Z_t for Antarctic phytoplankton growth season

	PAR ($\text{mol m}^{-2} \text{ day}^{-1}$)	K_{PAR} (m^{-1})	Z_c (m)	Z_t (m)
September	25.76 (5.48)	0.22 (0.08)	36.57 (13.5)	38.2 (12.5)
October	37.96 (11.34)	0.43 (0.13)	23.35 (6.1)	71.0 (21.9)
November	41.35 (11.49)	0.44 (0.34)	24.85 (22.8)	29.2 (23.6)
December	37.93 (8.48)	0.63 (0.51)	15.92 (12.3)	33.7 (14.4)
January	30.27 (10.38)	0.67 (0.28)	11.95 (6.5)	19.9 (5.5)
February	25.49 (13.93)	0.73 (0.41)	9.23 (9.05)	18.4 (14.2)

Data correspond to monthly averages.

favourable combinations have indeed been observed, with higher than the average N values after ice melting (i.e., November 1991, Schloss et al., 1997). This means that even somewhat higher wind speeds would still be adequate for phytoplankton growth. These combinations, however, did not last for more than 2 or 3 days (Fig. 5a and b and Table 2).

4.2.2. Second subperiod

The light attenuation coefficient K_{PAR} was estimated and correlated with the TPM load (Schloss and Ferreyra, 2002). An average K_{PAR} of 0.4 m^{-1} was calculated for the upper 10 m of the water column as the limit that allows summer irradiance to penetrate the water column down to the depth particles could reach, assuming average winds. $K_{\text{PAR}} < 0.4 \text{ m}^{-1}$ values will then permit phytoplankton to develop in a well-irradiated environment, if $Z_t < Z_c$. Low K_{PAR} values have indeed been observed after ice retreat and before the massive stream inflow, and again at the end of the summer season, when land ice and snow have considerably melted so that flow streams are significantly reduced.

Water column structure presented an average $N = 1.4 \times 10^{-2} \text{ s}^{-1}$ due to the massive freshwater

input. No significant differences were found in the average wind speeds for the two subperiods considered here. However, since due to light limitation, Z_c was shallower during this second subperiod than during the first subperiod (Table 2), the wind speeds estimated to allow phytoplankton development were lower than earlier in the growth season. In this case, only wind speeds $< 3 \text{ m s}^{-1}$ allowed particles to remain at depths $< Z_c$.

Based on the abovementioned values, the conditions for phytoplankton development could be summarised as follows in the next section.

4.3. Temporal windows for phytoplankton development in Potter Cove

According to the light-mixing regime observed in Potter Cove, the first window of $Z_c > Z_t$ for > 12 –15 days could be found during the time span between the end of the sea–ice retreat and the beginning of the glacial melting (usually in December, Fig. 2d). Fresh-water supply is highly correlated with air temperature (Varela, 1998). Moreover, air temperature may also control the temporal extension between both events. Thus, low air temperature after sea-ice retreat may

Fig. 5. In the construction of the model represented in (a), it was hypothesised that light availability and/or water column stratification were the key factors affecting phytoplankton growth. In general, (a) and (b) have to be read like flux diagrams, considering the conditions that lead to phytoplankton growth (oval at the left part of the figure) or not (oval at the right side). In part (b) of the figure, threshold values for the most representative parameters have been added to the scheme. As mentioned above, the temporal scale considered in the conceptual model is phytoplankton growth season since it is the time of relevance for the calculation of the productivity in polar systems (Sakshaug and Holm-Hansen, 1984). This period potentially extends from September to March when the solar zenith angle and day length provide an adequate light environment to photosynthetic organisms. Time is represented in the model by the arrow at the left side of both (a) and (b). The temporal axis was, in turn, divided to represent two major events that are assumed to affect phytoplankton in shallow coastal environments in Antarctica. TPM: Total particulate material; E_0 : surface incident PAR; E_n : photocompensation irradiance; N : Brunt–Väisälä frequency; U_{10} : wind speed 10 m above sea surface; K_{PAR} : light attenuation coefficient; Z_c : Sverdrup's critical depth; Z_t : root-mean square expected vertical displacement depth of particles in the water column.

retard the freshwater supply and particulate matter input, affecting both water column stratification and light penetration. When combined with wind speed $< 4 \text{ m s}^{-1}$, this delay may allow phytoplankton accumulation, as it occurred at the end of November–beginning of December 1991 (Schloss, 1997). The second window may appear later in the growth season, when the materials transported by the creeks have been carried away or sedimented, some freshwater is still added to the waters in the cove and, again, winds remain low (in this case, $< 3 \text{ m s}^{-1}$) long enough. Such a combination of favourable conditions leading to chlorophyll concentrations of $3\text{--}4 \text{ mg m}^{-3}$ were observed from November 28 to December 4, 1991 (Schloss et al., 1997), and in February 1996 (Fig. 2h). Typical Antarctic phytoplankton species were generally found (i.e., *Corethron pennatum* (Grun.) Ostenfeld, *Thalassiosira antarctica* Comber, *Thalassiosira* spp.) on these occasions (Schloss, 1997). Benthic species (*Amphora* spp., *Gyrosigma* spp.) represented only a minor fraction, in contrast to similar areas (i.e., Admiralty Bay, King George Island, Brandini and Rebello, 1994).

5. Uncertainty of the chosen parameters—future sampling strategy

Z_c values present 66% variability, which is originated in the estimations of K_{PAR} . Variability in K_{PAR} estimations is 58%, and is mainly explained by the dependence of light attenuation not only on pigment concentration, but also on dissolved and, especially, on particulate material, which is very variable throughout the phytoplankton growth season as well as at the different depths in the water column (Fig. 2d). K_{PAR} variability may result in Z_c values varying between 37% and more than a factor of 2. Variability of daily-integrated PAR E_0 was around 28% (Table 2), mainly due to variable cloud cover, which led to 30–31% variability on Z_c . The use of daily-integrated PAR values in the calculation of Z_c is adequate since Potter Cove phytoplankton undergoes less than one division per day (Schloss, 1997). E_k was considered as equivalent to the photocompensation irradiance E_n in the calculation of Z_c . The variability in E_k , which resulted from the photosynthesis experiments, was 9%, and its effect on Z_c was only between 8.2% and

9.9%. The use of the average E_k value as E_n (as in Figueiras et al., 1994) may be an additional error source; actually, no information on E_n is available because investigations have not considered primary production with all the possible sources of cell losses. Ideally, such measurements should be considered in future works. As Platt et al. (1991) pointed out, the loss factor in Sverdrup's formulation should be interpreted in its widest sense to include all processes by which photosynthesis products are remineralised or removed from the mixed layer. In general, loss terms are the less known factors in the present formulation of the model. Grazing by macro- and microheterotrophs will have to be considered. Local, nonquantitative observations by divers indicated that the ice that covered Potter Cove usually also harboured small krill swarms (mostly juveniles), probably grazing on microalgae at the ice–water interface (Fig. 2a). In similar environments like Admiralty Bay, and after a period of wind relaxation, microheterotrophs could control phytoplankton biomass (Brandini, 1993). Antarctic zooplankton is mainly represented by krill. Yet, keeping krill grazing out of the conceptual model for the time considered here may not significantly affect the conclusions for several reasons. Zooplankton abundance in Potter Cove (especially that of krill) is low after the ice retreat (Elwers, personal communication), as it is in Admiralty Bay (Chojnacki and Weglenska, 1984). This kind of environments, on the other hand, does not seem to be favourable for hosting important krill stocks: birds and benthic fishes foraging activities prevent krill from being too close to water surface or to the water–bottom interface, respectively (Marschoff, personal communication). Moreover, no information is available on other zooplankton organisms' abundance, such as salps, which may be important grazers, with great effects at the ecosystem level, for they are regarded as top predators (Loeb et al., 1997). Consequently, phytoplankton abundance and species composition may be modified by the differential grazing preferences of both krill and salps. In other environments such as the Kerguelen area, it has been shown that grazing mainly determines the size of the stock of phytoplankton, controlling the collapse phytoplankton bulk (Pondaven et al., 1999).

Variability in the root-mean square expected vertical displacement of phytoplankton cells Z_t is similarly

influenced by the 60% variability in the measured wind speed and the 69% variability in the water column density gradient. Wind speeds did not vary significantly over the years. Average values ranged from $7.89 (\pm 3.89)$ to $9.43 (\pm 3.91) \text{ m s}^{-1}$, so that wind effects on Z_t (Fig. 6a and b) are not supposed to vary significantly in an interannual scale. Estimations on freshwater runoff volume are scarce and difficult to evaluate, and therefore uncertainty associated with this parameter is significant: not only does stream water entering the cove have to be considered, but also subsurface drainage; data on this last parameter are not available at all. However, an approximation can be done using the salinity and temperature data, which integrate the freshwater influxes into the sea. The average salinity and temperature values from the

various grids performed in the whole cove at different times of the spring–summer season have been included in the present estimations in order to minimise uncertainty.

Other factors affecting the model's results may be the ultraviolet B radiation effect on phytoplankton. Due to the seasonal stratospheric ozone depletion observed over the Antarctic continent and the surrounding waters, increasing UV-B radiation penetrates the water column. Spectral distribution measurements have recently started at Potter Cove and the preliminary data suggest that 99% of UV-B is absorbed in the first 2–3 m of the water column (Ferreira, personal communication), so that their effect would only be significant under calm weather conditions. Consequently, and taking into account the importance of

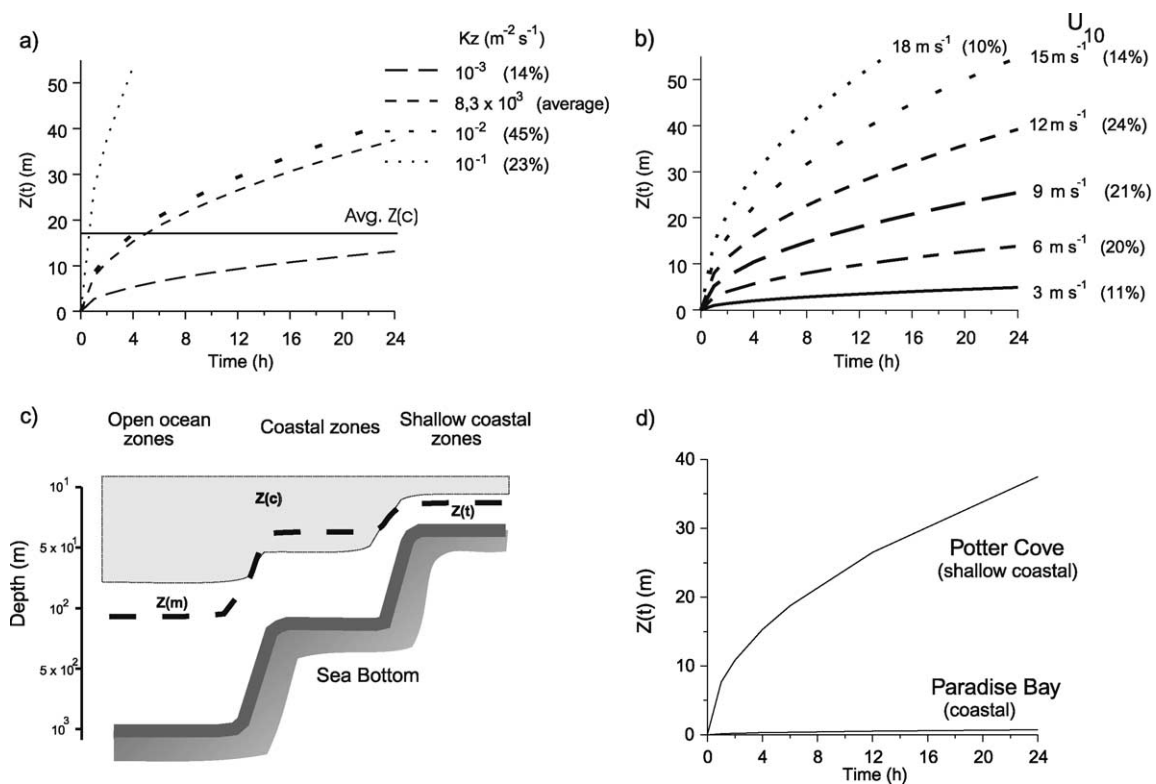


Fig. 6. (a) Calculated root-mean square expected vertical displacement (Z_t) of a phytoplankton organism up to a 24-h period for different values of vertical turbulent eddy coefficients K_z ; (b) Z_t for different wind intensities (considering average $K_z = 8.3 \times 10^{-3}$). (c) Relative positions of the Z_c (represented by the shaded area), Z_m and Z_t (dashed line) for different water column environments. It is considered here that the use of Z_m is adequate for open waters and coastal environments, while the use of Z_t is preferable in the shallow coastal ones. (d) Comparison of Z_t for the average wind and stability conditions in a shallow coastal environment, Potter Cove, and in a coastal one, Paradise Bay ($64^\circ 53'$, $63^\circ 53'$). Numbers in parentheses in (a) and (b) correspond to the frequencies of the observations in the Potter Cove area.

UV in this area, not only should PAR be regarded in Z_c evaluation in future studies, especially if long-term phytoplankton evolution is considered for these coastal areas. The information currently available is not enough to include it in the present model.

To validate and to use this model in a prognostic way for seasonal and interannual time scales, more information is needed. Information on zooplankton biomass in Potter Cove is scarce. However, studies on zooplankton composition and abundance are currently being undertaken in the frame of the plankton studies in Potter Cove. Similarly, grazing and other loss factors have to be estimated in order to adjust the photocompensation irradiance value. Other information that could significantly contribute to our understanding of the system would be related to heat fluxes, light spectral distribution and spectral light attenuation coefficients corresponding to the different fractions in the water column. At present, laboratory and fieldwork are currently being carried out in the frame of the studies of the impact of UV radiation on phytoplankton by taking high-quality light measurements in Potter Cove waters, especially during the spring season. This will reduce uncertainties associated to light availability for photosynthesis.

6. Spatial extrapolations

Application of the present conceptual model to other coastal regions of Antarctica may be conditioned by their environmental factors, such as topography and latitudinal position, which affect climate conditions. The relations between the optics and the mixing of the water column in the Antarctic Ocean lead to different situations like those depicted in Fig. 6c. For example, high wind intensities are a common feature in the low-pressure ring surrounding the Antarctic continent, except in some locally protected areas. Strong winds will mainly influence phytoplankton growth where the critical depth is shallow (see Fig. 2), resulting in unfavourable relations between Z_c and the expected depth of particle vertical displacement, Z_t (like the one generally found in Potter Cove). These places are expected to present low phytoplankton biomass during the overall growth season, as it happens, for example, in the adjacent Marian Cove (Fig. 1) (Yang, 1990). In deeper (>100 m) coastal areas west of the Antarctic

Peninsula, where average wind speeds are relatively low (around 2 m s^{-1} , like Paradise Bay, $64^\circ 53'S$, $63^\circ 53'W$, Ferreyra, 1995) (see Fig. 6d for comparison), Sverdrup's critical depth Z_c is not compared with Z_t , but with the mixed layer depth, Z_m , since depth of vertical turbulent mixing is very shallow. In these areas, the mixed layer depth is mainly controlled by freshwater runoff, which creates a relatively shallow pycnocline (Ferreyra, 1995; Moline and Prézélin, 1997). Thus, Z_m is frequently shallower than Z_c . This situation leads to a development of large phytoplankton blooms ($>25 \text{ mg m}^{-3}$ chlorophyll, Ferreyra, 1995; see review in Smith et al., 1996). Furthermore, in a broader scale like the open ocean areas in Antarctica (the Weddell Sea, for example), very deep Z_m result in a relation between the mixed and the critical depths that is usually not favourable for phytoplankton growth, as it is the case of the Circumpolar Current waters (Mitchell et al., 1991).

Considering the so-called top-down phytoplankton control, modifications in ice temporal and/or spatial extension may change grazing pressure by altering the relative composition of the zooplankton community, from krill-dominated zooplankton assemblages to salp-dominated ones (Loeb et al., 1997). This suggests that the changes that may happen in the future as a consequence of temperature increase (due to global climate change associated to CO_2 increase) could not only lead to changes in phytoplankton biomass and production in coastal Antarctic systems, but also in phytoplankton species composition. The use of the present model as a predictive tool will be possible once the model is validated with the data that are continuously being acquired at Potter Cove.

7. Conclusions

The present conceptual model allows the quantification of the growth of phytoplankton in an Antarctic shallow coastal environment. In this system, physical processes appear to be the main factors controlling phytoplankton accumulation. Physical limitation to phytoplankton growth can be represented by the relation between the critical depth Z_c and the expected depth of particle vertical displacement Z_t , which is a better descriptor than Z_m for these windy, shallow coastal environments. Furthermore, cell growth will

be evident not only whenever the combination of physical conditions leads to $Z_c > Z_t$ situations, but when this combination lasts for at least 12–15 days, to allow accumulation of phytoplankton. The growth season can be divided in two subperiods. In the first one, the water column stratification and the light environment are greatly influenced by the presence of sea ice. The incident irradiance E_0 has to be $>25 \text{ mmol m}^{-2} \text{ day}^{-1}$ and the photocompensation irradiance $E_n > 37.6 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$, and stability, expressed as $N > 7.4 \times 10^{-3} \text{ s}^{-1}$, combined with wind speeds (U_{10}) $< 4 \text{ m s}^{-1}$. If all these conditions are present, phytoplankton growth may happen, as observed in November–December 1991. During the second subperiod, riverine discharges control both water column structure and light penetration in the water, therefore being K_{PAR} (the light attenuation coefficient) the critical parameter; growth has been considered to proceed if $K_{\text{PAR}} < 0.4 \text{ m}^{-1}$. N in this subperiod is higher, and for $N > 1.4 \times 10^{-2} \text{ s}^{-1}$ value, $U_{10} < 3 \text{ m s}^{-1}$ are necessary to maintain the adequate conditions for phytoplankton growth, as observed in February 1996. The unfavourable Z_c/Z_t condition led to a generally low phytoplankton biomass in shallow coastal environments such as Potter or Marian Cove, in spite of high inorganic nutrient concentrations. Although the $Z_c > Z_t$ criteria applies well to shallow coastal environments, the use of Z_m is still preferable in coastal environments like the western Antarctic Peninsula, where the relation among both estimators is favourable for phytoplankton accumulation during the spring–summer season. In open polar oceans, where Z_m is generally $>100 \text{ m}$, this relation is again unfavourable most of the time and therefore contributes to explain the low phytoplankton biomass observed in these environments.

Acknowledgements

We would sincerely like to thank all the persons working with us in the field during the years 1991–1996, both scientists and logistics. Our special thanks also to the personnel from the Alfred-Wegener-Institut (AWI), who shared equipment and results with us in the frame of the Argentinean–German Cooperation at Jubany-Dallmann in Potter Cove, Antarctica. Thanks also to R. Sánchez, D. Boltovskoy and to an

anonymous referee for the judicious comments that helped us to improve the manuscript.

Appendix A

Z_c = critical depth, as modified by Nelson and Smith (1991) is:

$$Z_c = \frac{0.8 \cdot 11.57 \cdot \sum E_0}{E_n \cdot K_{\text{PAR}}}$$

where 0.8 is an optical correction factor, $\sum E_0$ is the time-integrated PAR for a 24-h period (in $\text{mol m}^{-2} \text{ day}^{-1}$), 11.57 converts them in $\mu\text{mol m}^{-2} \text{ s}^{-1}$, E_n is the irradiance at the compensation depth (the depth where net phytoplankton growth equals zero, in $\mu\text{mol m}^{-2} \text{ s}^{-1}$), and K is PAR attenuation coefficient, in m^{-1} .

To calculate vertical displacement of cells Z_t (Denman and Gargett, 1983), which is function of time and the wind generated turbulent kinetic energy, the equation used was

$$Z_t^2 = 2K_z t,$$

for t = time (in s) and $K_z = (\text{m}^2 \text{ s}^{-1})$ is the turbulent vertical diffusion coefficient (Mann and Lazier, 1991):

$$K_z = 0.25 N^{-2} \varepsilon_v$$

where N = Brunt–Väisälä frequency, which is defined as

$$N = \left[\frac{g}{\rho} \left(\frac{\partial \rho}{\partial z} \right) \right]^{\frac{1}{2}}$$

with $\rho_{(\text{water})}$ = average water density ($1.0277 \times 10^3 \text{ kg m}^{-3}$ in our study); $\partial \rho$ = density is the difference between two water masses (in kg m^{-3}), ∂z = depth is the difference among those water masses (in m) and ε_v = rate of dissipation of the TKE due to the winds is given by

$$\varepsilon_v = \frac{\rho_{(\text{air})}}{\rho_{(\text{water})}} \frac{C_{10}}{H} K_w U_{10}^3$$

where C_{10} = drag coefficient for the winds at 10-m height = 1.3×10^{-3} , H = depth of the water column

in m, K_w = correction factor for the winds at surface = 4×10^{-2} (Pingree et al., 1978) and U_{10} = wind speed at 10 m above sea level.

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