Journal of Marine Systems, 4 (1993) 289–301
Elsevier Science Publishers B.V., Amsterdam

Seasonal variation of algal growth conditions in sheltered Antarctic bays: the example of Potter Cove (King George Island, South Shetlands)

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(Received October 10, 1992; revised and accepted May 11, 1993)

ABSTRACT

Wind, air temperature, surface irradiance, light penetration into the water, salinity and water temperature have been recorded from mid November to mid February in Potter Cove, King George Island. Results are compared with published data on requirements for growth of Antarctic macroalgae. The investigated season showed two distinct periods: Early summer lasted until end of December with comparatively cold temperatures, unstable water column and deep penetration of light; late summer started in early January and was characterized by reduced salinity due to meltwater discharge and high turbidity due to suspended sediments. Meltwater influence did not sufficiently change salinity to be responsible for the frequently noted paucity of macroalgal communities in sheltered bays. Shading by suspended sediments was equally considered to be of minor importance, as macroalgae have their optimal growth phase from September to December. During this period, light penetration and depth distribution of macroalgae coincide perfectly. From these results, a general review on depth limitation of macroalgae by light conditions is derived.

Introduction

Antarctica harbours a rich and unique flora of macroalgae, which is particularly well developed in the Antarctic Peninsula region and the islands of the Scotia Arc (Skottsberg, 1962; Papenfuss, 1964; DeLaca and Lipps, 1976; Moe and DeLaca, 1976; Lamb and Zimmerman, 1977; Ramirez, 1982; Etcheverry, 1983; Heywood and Whitaker, 1984; Lüning, 1990; Zielinski, 1990). This is rémarkable, as the benthic vegetation has to withstand several unfavourable environmental conditions. Many comments have especially been made about the various effects of ice (Neushul, 1965; Dayton et al., 1970; Arnaud, 1974; DeLaca and Lipps, 1976; Moe and DeLaca, 1976; Gruzov, 1977; Zamorano, 1983; Picken, 1985; Dayton, 1989). From that, sheltered locations might be expected to be favourable habitats for macroalgal communities. However, macroalgal flora was noted to be very poor in protected inner bays (DeLaca and Lipps, 1976; Moe and DeLaca, 1976; Dhargalkar et al., 1988; Kirkwood and Burton, 1988; Zielinski, 1990; Rauschert, 1991). The following factors have been considered to be responsible: Salinity reduction by meltwater (DeLaca and Lipps, 1976; Kirkwood and Burton, 1988), reduced penetration of light due to shading by phytoplankton blooms (Moe and DeLaca, 1976; Hastings, 1977; Clarke et al., 1988; Gilbert, 1991; Drew and Hastings, 1992), reduced light penetration due to suspended sediments (Moe and DeLaca, 1976; Hastings, 1977; Pecherzewski, 1980; Jonasz, 1983; Zielinski, 1990), shortening of the growing season due to prolonged ice cover (Moe and DeLaca, 1976; Zielinski, 1990; Drew

0924-7963/93/$06.00

and Hastings, 1992). Of these factors, the shading effect either by phytoplankton or suspended sediments touches an old (Zanefeld, 1966) and as yet unresolved (Dayton, 1990; Wiencke, 1990b) problem: Antarctic macroalgae have been repeatedly reported from great depths (Table 1), down to more than 700 m (Zanefeld, 1966; Zanefeld in: Balech et al., 1968). Less spectacular records give approximately 25 m to 40 m in the Low Antarctic region and 15 m to 25 m from the High Antarctic. Most records, however, are not met by available data on light penetration (Table 1). While euphotic layers (level of 1% surface light) of over 80 m have been measured in Antarctic off-shore waters (Balech et al., 1968; Wensierski and Wozniak, 1978; Stramski and Montwill, 1982; Gieskes et al., 1987), coastal waters, where macroalgae grow, are considerably less transparent (Table 1). Although several species of macroalgae are known to grow at less than 1% of incident irradiance (0.44%: Wiencke, 1990a, b), recalculated limits of the euphotic zone at approximately 28 m in inshore waters and 53 m in off-shore waters (Wiencke, 1990a) still are not appropriate. To get a better insight into the ecology of Antarctic sublittoral vegetation, a multidisciplinary research program on coastal ecology has been performed in Potter Cove, King George Island. In this context, we report here on the variability of temperature, salinity and underwater light cli-

TABLE 1

Comparison of reported depth limits of macroalgae with depth of the euphotic zone (expressed as 1% of surface irradiance) at various regions of the Antarctic. Months of light measurements are also given

area	depth limit	reference	1% level	month	reference
Signy Island	25– 30 m	Richardson, 1979	14.5 m	II–IV	Drew, 1977
King George Isl.:					
–Admiralty Bay	90–100 m	Zielinski, 1981, 1990	40 m	III	Stramski and Montwill, 1982
–Ezcurra Inlet	20– 60 m	Zielinski, 1990	24 m	XII–III	Dera, 1980; Olszewski, 1983
			25 m	XII–III	Wozniak et al., 1983
–Ardley Cove	30 m	Gruzov and Pushkin, 1977			
–Fildes Strait	25– 30 m	Rauschert, 1991			
Robert Island	15 m	Etcheverry, 1983			
Hope Bay	80– 90 m	Bellisio et al., 1972			
Palmer Archip.:					
–Melchior Isls.	> 50 m	Bellisio et al., 1972	17 m	?	El-Sayed, 1968
–Bismarck Strait	25 m	Zamorano, 1983			
–Arthur Harbor	33– 40 m	DeLaca and Lipps, 1976	7 m	?	El-Sayed, 1968
–Gerlache Strait	60– 80 m	Castellanos, 1973	7–20 m	XII–II	Bienatti et al., 1975
East Antarctic:					
–East Ongul Isl.	10 m	Nakajima et al., 1982			
–Enderby Land	25 m	Gruzov and Pushkin, 1977			
–Ellis Fjord	29 m	Kirkwood and Burton, 1988			
–Haswell Isls.	15 m	Gruzov, 1977			
	25 m	Propp, 1970			
–Adelie Coast	70 m	Arnaud, 1974			
Ross Sea:					
–Balleny Isls.	> 300 m	Zanefeld, 1966			
–Victoria Land	> 300 m	Zanefeld, 1966			
–McMurdo Sound	18 m	Miller and Pearse, 1991	≈ 24 m	XII	Miller and Pearse, 1991

mate, as well as implications on growth conditions of benthic macroalgae.

Material and methods

Investigation area

Potter Cove is a tributary inlet close to the entrance of Maxwell Bay, one of the two big fjords at King George Island (Fig. 1). The cove is divided into mouth and inner part. The mouth area is bordered by steep slopes in the north and by a broad intertidal platform in the southeast. The bottom of the mouth area lies between 100 m and 200 m. The inner part is not deeper than about 50 m and barred by a sill of about 30 m depth. The southern shore is a sandy beach, where three creeks debouch into the cove. The biggest one forms a small delta immediately at the margin of the glacier. Another creek runs from Barton Peninsula, passing only rocky ground. Glacier cliffs reach the cove in the north and east. The glacier is supported by bedrock until its terminus and therefore does not produce icebergs. Usually, a clock-wise circulation is present, which may be interrupted by easterly gales (Klöser et al., in press, a). On hard substrates, the upper sublittoral is covered by a dense vegetation of the phaeophytes *Desmarestia anceps* and *D. menziesii*, which is replaced by fields of *Himantothallus grandifolius* below 25 m and in areas of frequent ice impact (Klöser et al., in press, b). In the inner cove, soft bottom colonized by a diverse community of sessile animals is found (Klöser et al., in press, b).

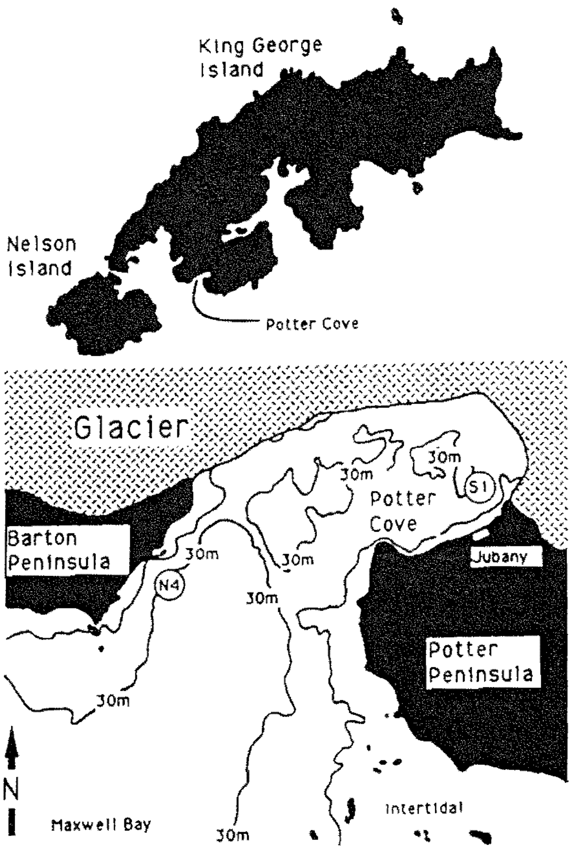

Fig. 1. Map of Potter Cove and its location on King George Island. Contour lines indicate extension of the intertidal and depth of 30 m. Stations N4 and S1 are marked.

Working procedure

Investigations started at November 15, 1991, and ended February 15, 1992. Two sites were chosen as permanent stations (Fig. 1), at which light penetration into the water column, water temperature and salinity were recorded. Hydrographical data were gained using a CTD, type "M and E Ecosonde". Underwater photon flux was measured with a Li-193SB spherical quantum sensor, which is sensitive in the range of 400 to 700 nm (approximately Photosynthetically Active Radiation: PAR). Irradiance was also measured continously on land close to the shoreline (PAR). Maximum and minimum values for half-hourly periods were recorded as well as integral values, which were added up for daily integrals. Measurements on land started only at December 28, 1991, for logistic reasons. Other basic wheather data were provided by the Servicio Meteorológico de la Fuerza Aérea Argentina.

Results

Surface irradiance

During the investigation period, the sky has been almost permanently clouded with an average of 6.8 oktas cloud cover (1 okta is the eighth part of the observable sky). Less than 6 oktas were noted only in 13 out of 156 registrations between December 1 and February 16. Most frequent cloud types have been altostratus or stratus. Cloud cover could be translucient at times, allowing sunlight to penetrate, and causing a very irregular pattern of irradiance (Fig. 2). Although the highest daily total photon fluence rate was observed shortly after the summer solstice (123 mol/m^2/d) and the lowest (27 mol/m^2/d) close to the end of the investigation period (Fig. 3), variation in irradiance masked the seasonal pattern considerably.

Remarks on hydrography

Water temperature rose from about −1.2°C in November to about +1.0°C in early February. Higher temperatures only episodically occurred in shallow surface layers of reduced salinity. Salinity remained above 34.00 PSU (Practical Salinity Unit: UNESCO, 1981) until end of December, when meltwater discharge increased. Maximal reduction of salinity in January and February yielded values between 31.00 and 32.00 PSU. During that period, high amounts of sediments were introduced into the southern part of the cove, resulting in visible coloration of the surface water (Fig. 4). Stratification was absent or weakly developed until end of December. But even under maximal meltwater influence in January and February, stratification remained unsta-

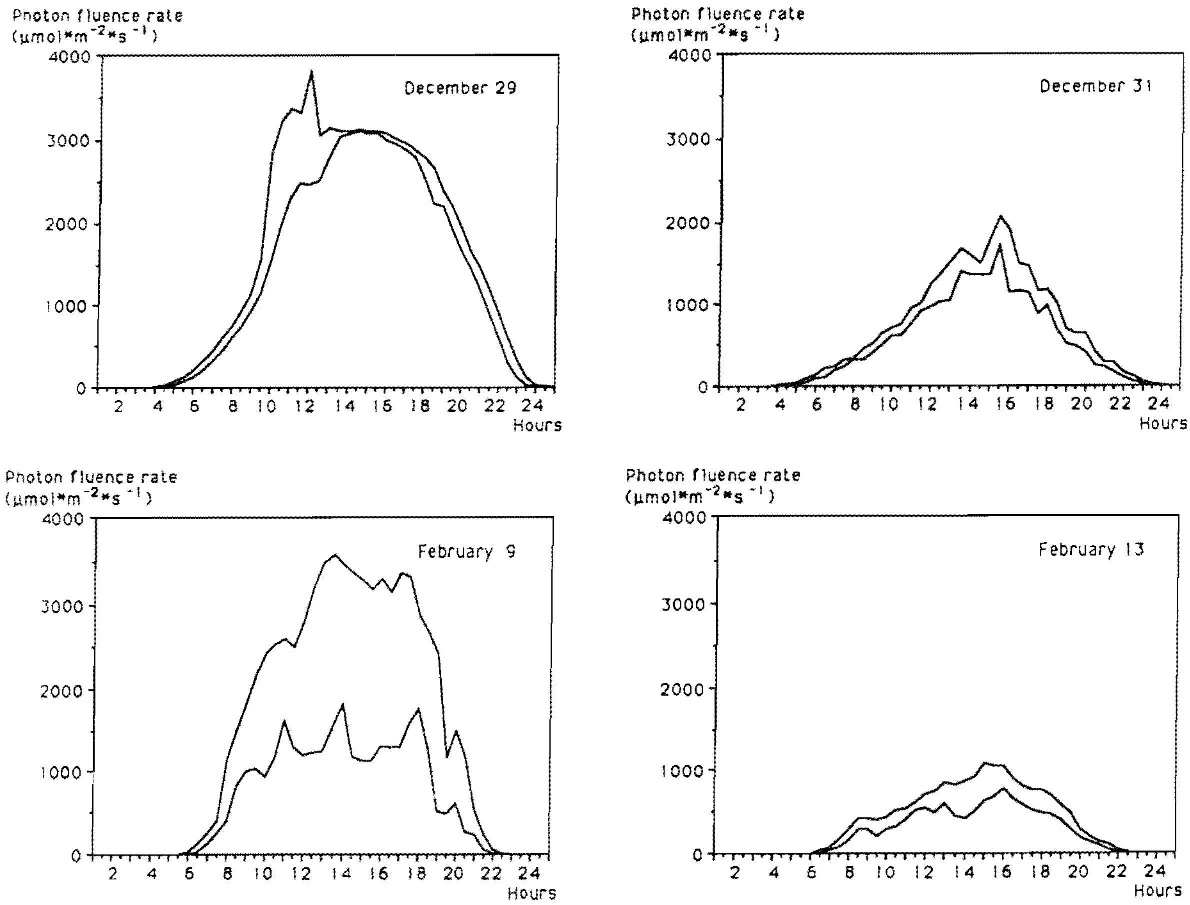

Fig. 2. Selected examples of daily irradiation curves (PAR) at Station Jubany: days with high (a and c) and low (b and d) irradiance from the beginning (a and b) and the end (c and d) of the period of measurements (December 28, 1991 to February 14, 1992). Upper lines indicate maximum, lower lines minimum values of instantaneous irradiance in half-hourly intervals. At December 29, the sky cleared up during the morning. Maximum values from these hours are in excess of those from clear sky at noon. This is due to a light trapping mechanism by multiple reflection at the clouds' lower surface and the glacier ice (Franceschini, 1968, 1977; Dera, 1980). The same process explains the high maximum values at February 9, a day of scattered cloud cover. December 31 and February 13 have been days with low stratus overcast and fog.

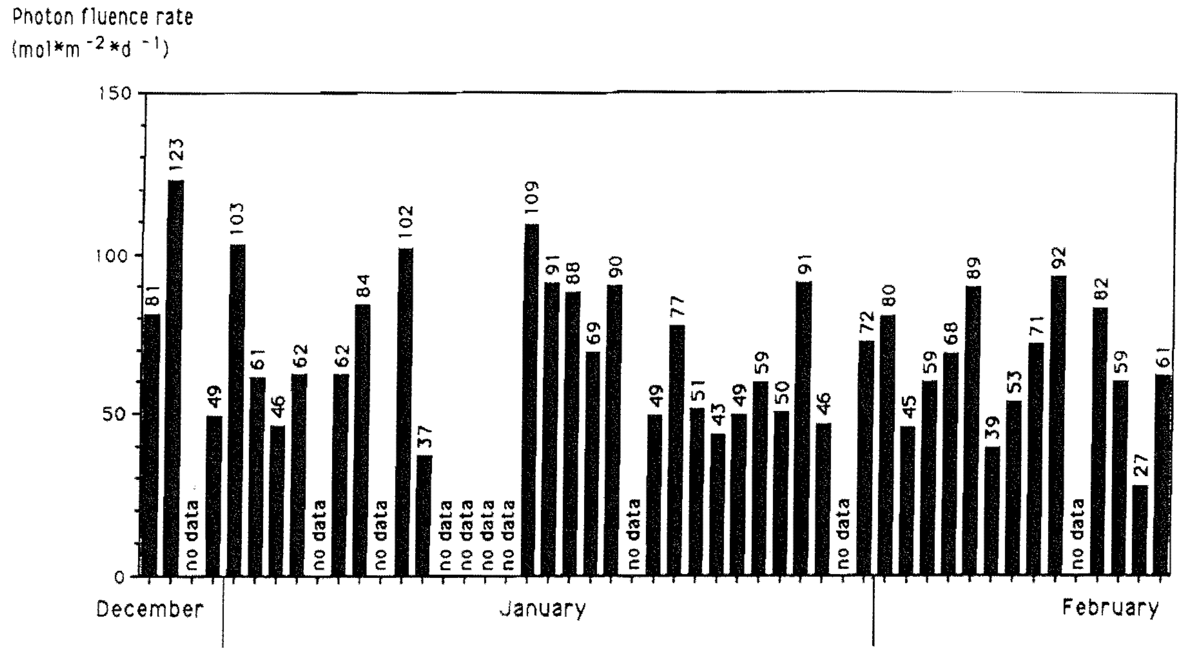

Fig. 3. Total daily photon flux (PAR) from December 28, 1991 to February 14, 1992, at Station Jubany. Values are integrated data from continous records, of which examples are given in Fig. 2. These measurements had to be interrupted, if the probe was needed for underwater measurements.

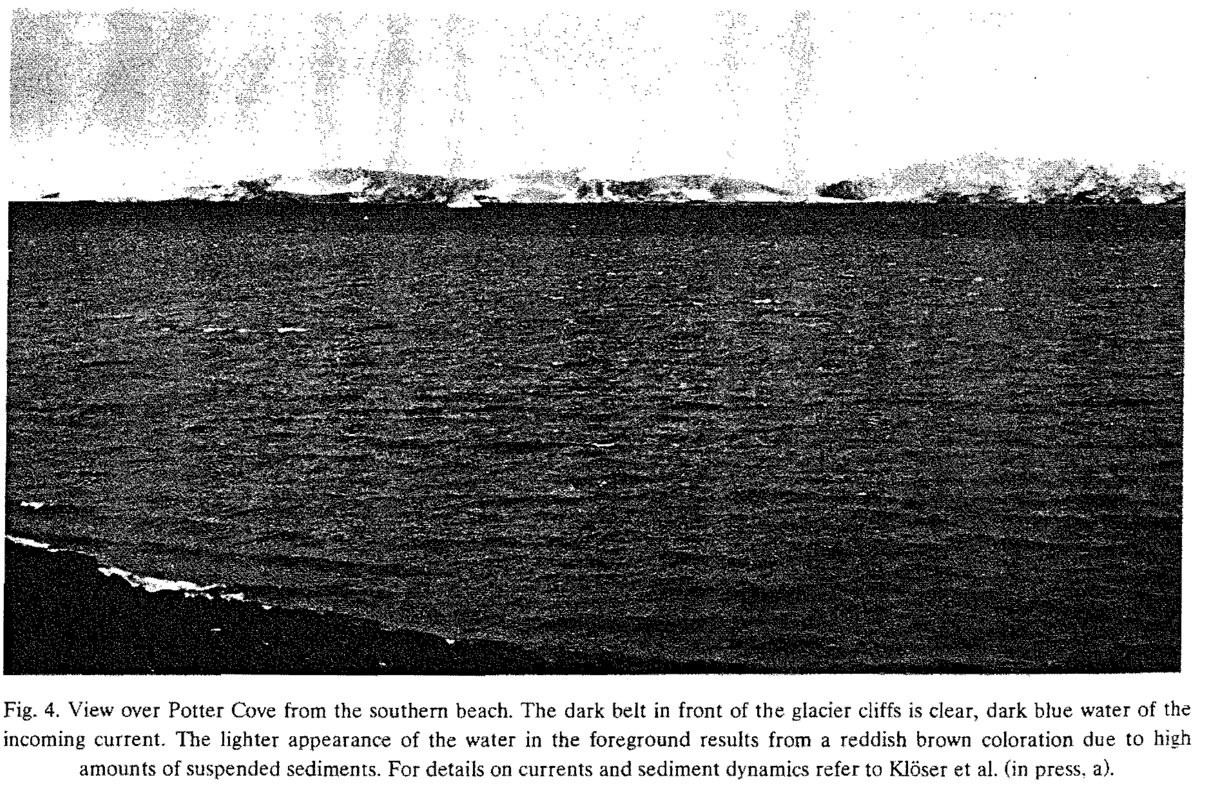

Fig. 4. View over Potter Cove from the southern beach. The dark belt in front of the glacier cliffs is clear, dark blue water of the incoming current. The lighter appearance of the water in the foreground results from a reddish brown coloration due to high amounts of suspended sediments. For details on currents and sediment dynamics refer to Klöser et al. (in press, a).

ble, as evidenced by upwelling events due to storms (Fig. 5).

Water transparency

Until end of December, water transparency was similar on station N4 and S1, with conditions resembling Jerlov's water type III. In January and February, however, conditions differed markedly on both stations (Fig. 5). While station N4 was only slightly affected, light penetration was limited to a few meters at station S1 coincident with increasing discharge of meltwater and suspension of sediments (Figs. 4, 5b). An easterly gale caused an upwelling event around January 20, thereby completely exchanging the water of the cove and allowing light to penetrate deeper for some days (Fig. 5b).

Discussion

Summerly increases of water temperature to 2.5°C (Presler, 1980), 2.81°C (Szafranski and Lipski, 1982), 3.41°C (Kowalewski and Wielbinska, 1983) and 5.30°C (Rakusa-Suszczewski, 1980) have been reported in Admiralty Bay, and to 2.05 in Maxwell Bay (Hong et al., 1991). In Potter Cove, water temperature did not rise up to +2.0°C

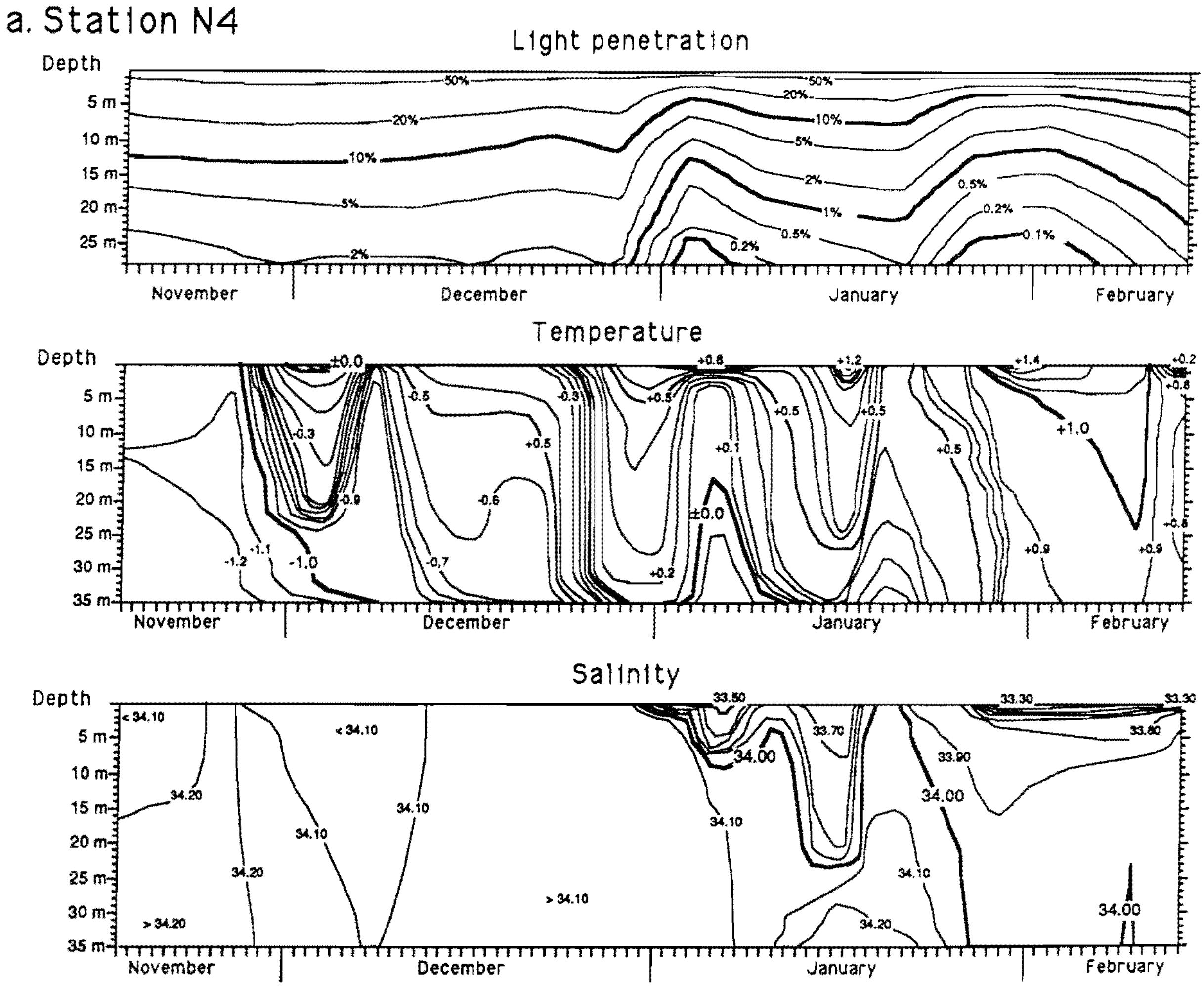

Fig. 5. Time series of light penetration, temperature and salinity in the upper water layers for the period from November 15, 1991 to February 13, 1992 at permanent station N4 (a) and S1 (b). Station N4 was located at the northern shore of the Potter Cove mouth area (Fig. 1), where comparetively clear, blue water prevailed (Fig. 6), while station S1 was located at the southern shore of the inner cove within the usual occurrence of the sediment-laden, brown water.

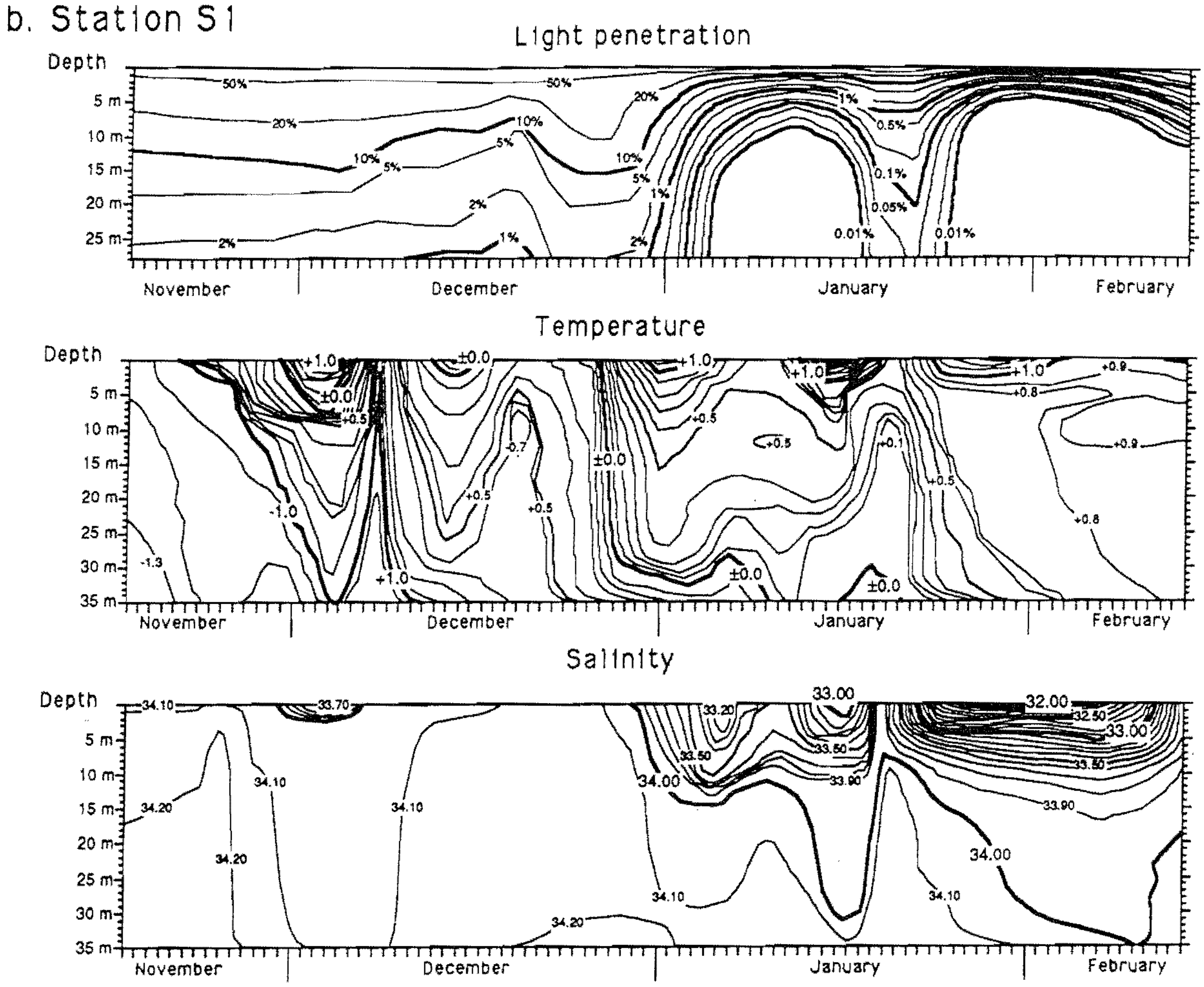

Fig. 5 (continued)

during the whole summer, which is coincident with measurements in Marian Cove (Chang et al., 1990; Hong et al. 1991). Whether this difference is due to different local climate or to interannual variability, cannot be answered. For the moment, alterations of macroalgal communities by specific responses to temperature variability may not be expected in Potter Cove.

Effects of salinity reduction on macroalgal community structure are neither evident in Potter Cove, as meltwater discharge rarely dropped salinity values below 32.00 PSU (Fig. 5). Literature reports on strong salinity reductions in other Antarctic fjords and inlets suggest, that less than one meter of the upper water layer should be affected anyway (Nakajima et al., 1982; Szafranski and Lipski, 1982; Krebs, 1983; Kirkwood and Burton, 1988; Tucker and Burton, 1988). Nevertheless, a sublittoral community dominated by *Palmaria decipiens* has been reported from Long Fjord (Dhargalkar et al., 1988), Marian Cove (KORDI, 1988, 1989) and unspecified sites along the Antarctic Peninsula (DeLaca and Lipps, 1976), which according to the latter authors is indicative to enhanced freshwater influence. However, *Palmaria decipiens* also was found to be very abundant in full salinity on outlying shores being subject to strong ice abrasion (Neushul, 1965; Klöser et al., in press, b). Thus, the species seems to be an opportunist, which may become dominant after exclusion of competitors by various ecological stresses. Therefore, a profound effect of meltwater on sublittoral macroalgal communities still needs confirmation.

Light climate changed drastically in the course of the summer. Compared with literature data from Low Antarctic regions (Table 1), similar or even lower depth levels of 1% of surface irradiance have been measured at both permanent stations during late summer (Fig. 5). It should be noted, that all measurements cited in Table 1 have been taken in late summer, from December to March. During these months, high concentrations of phytoplankton (Hastings, 1977; Krebs, 1977, 1983; Ferreyra and Tomo, 1979; Clarke et al., 1988; Gilbert, 1991; Drew and Hastings, 1992) or suspended sediments occur (Warnke et al., 1973; Dera, 1980; Pecherzewski, 1980; Jonasz, 1983; Griffith and Anderson, 1989; Drew and Hastings, 1992; Klöser et al., in press, a).

Our measurements indicate far deeper penetration of light prior to late December. Although the depth of the 1% level exceeded the length of our cable (Fig. 5), comparison of our data with depth profiles of downwelling irradiance provided by Jerlov (1978a, b) justifies to expect the position of the 1% level in a depth of about 35 m. This roughly coincides with the distribution of macroalgae in the mouth area of Potter Cove (Klöser et al., in press, b). Of the few Antarctic macroalgae, which have been investigated so far, the mostly dominant perennial phaeophytes (Hastings, 1977; Dieckmann et al., 1985; Wiencke, 1990a; Drew and Hastings, 1992) and the rhodophyte *Palmaria decipiens* (Wiencke, 1990b) have their main growth phase from September to December with greatly reduced activity in late summer. The often noted paucity of macroalgal vegetation in shallow bays may therefore not be due to high water turbidity in summer. This hypothesis is corroborated by the observations on the circulation in Potter Cove, which results in a flow of the sediment-laden water along the outlying shore of the Potter Peninsula eastwards (Klöser et al., in press, a), thereby shading the most diverse algal communities found in the whole study area (Klöser et al., in press, b). Thus, the only readily apparent detrimental effect associated with suspended sediments seems to be their deposition as thick layers of mud, which are unsuitable for macroalgal colonization (Zielinski, 1990).

We do not know at present, whether the scenario outlined above is representative for other years or other locations. Our values of air temperatures in December 1991 are lower than other reported data from King George Island, while those for January 1992 fall in range of other data sets (Table 2). From this, an earlier onset of turbid meltwater discharge may be expected in other years. The window, which is open to macroalgal growth in early summer, may further be cut short in warmer years: During the investigation period, no phytoplankton bloom was observed in Potter Cove (Schloss et al., unpubl.). Weak phytoplankton development was also ob-

TABLE 2

Air temperature data from various years and locations on King George Island

area/period	December				January			
	max.	mean	min.	reference	max.	mean	min.	reference
Admiralty Bay								
1977/1978	+7.6	+0.5	−3.3	Presler, 1980	+8.0	+2.1	−1.4	Nowosielski, 1980
1978/1979	+8.2	+1.2	−6.7	Nowosielski, 1980	no data			
Marion Cove								
1988/1989	+10.4	+0.5	−5.2	Lee et al., 1990	+8.1	+1.5	−3.3	Lee et al., 1990
1989/1990	+6.6	+1.4	−2.7	Lee et al., 1990	+7.6	+2.3	−6.3	Lee, 1990
Potter Cove								
1991/1992	+4.5	+0.2	−2.8	Klöser et al., in press, a	+7.2	+2.5	−2.0	Klöser et al., in press, a

served in other coastal areas (Warnke et al., 1973; Platt, 1979; Hapter et al., 1983; Clarke et al., 1988; Yang, 1990). This is not considered to be a constant feature, but rather a result of interannual variation (Clarke et al., 1988). In comparatively warm years, stratification of the water column may already be present as early as mid of November and favour early phytoplankton blooms (Krebs, 1977; Ferreyra and Tomo, 1979; Krebs, 1983; Clarke et al., 1988; Gilbert, 1991).

In colder years, on the other hand, prolonged duration of the ice cover may inhibit growth of macroalgae for considerable periods. On Signy Island, the date of fast ice break-up varied between early September and late December in the period from 1957 to 1972 (Clarke et al., 1988). No similar data set is available for King George Island, but high variability in ice cover was noted as well: In Admiralty Bay, no closed ice cover occurred at all in 1983 (Ligowski, 1987), while in other years ice cover may persist locally until January (Zielinski, 1990).

Although it is to be expected, that the seasonal development of macroalgae will be synchronized with the seasonal variation of environmental conditions (Lüning and tom Dieck, 1989), little is known about the triggering factors. According to present knowledge, the most abundant Antarctic macroalgae are "seasonal anticipators", which most probably respond to daylength (Wiencke, 1990a, b). However, if the algae should be able to compensate for shifts of favourable periods, they would need triggers, which act earlier in warmer years and later in colder years.

In conclusion, conditions in sheltered bays are far from uniform, and it is not well understood at

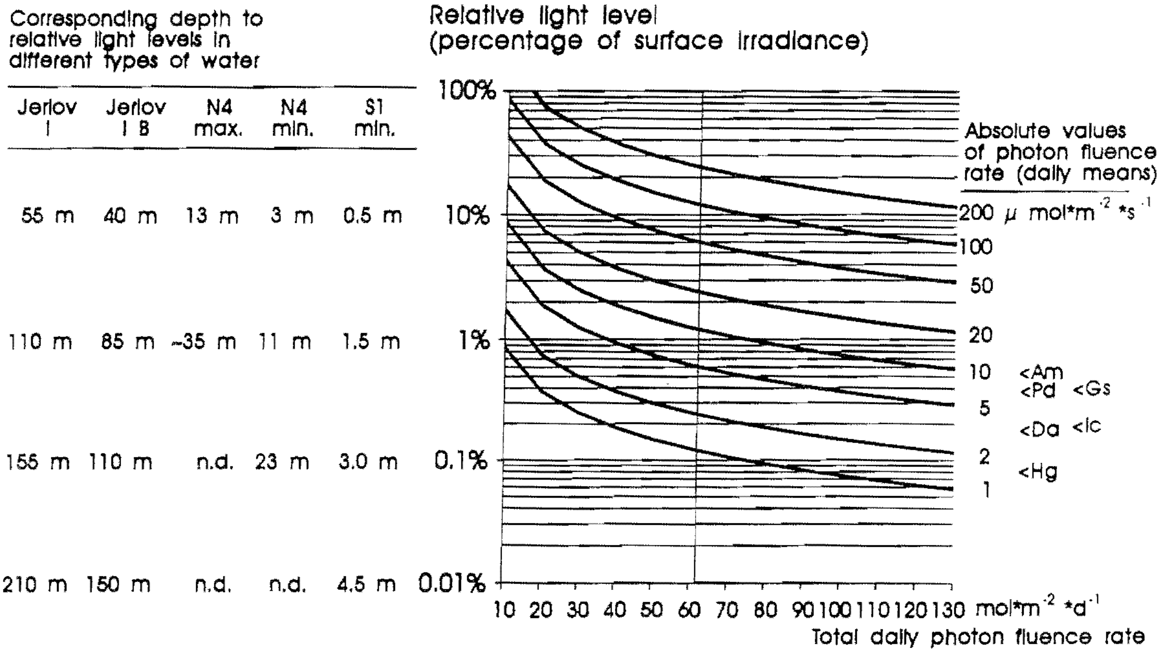

Fig. 6. Conversion table for relative and absolute light data: The figure gives mean daily photon flux at different levels of percentage of surface irradiance (ordinate) in relation to total daily surface irradiance (abscissa). Values in the abscissa cover the range of data given in Fig. 4; the median is indicated by a vertical line. Note, that the absolute values represented by the curves do not represent discrete instantaneous values, but values averaged over the day. These averages are directly comparable to compensation points of various Antarctic macroalgae (Wiencke et al., 1993), which have been determined in experiments of 4 to 6 weeks duration (C. Wiencke, pers. commun. 1992). These compensation points are indicated (A.m. = *Ascoseira mirabilis*, D.a. = *Desmarestia anceps*, H.g. = *Himantothallus grandifolius*, G.s. = *Gigartina skottsbergii*, P.d. = *Palmaria decipiens*, I.c. = *Iridaea cordata*). In addition, depth positions of relative light levels in various types of water are indicated at the left side of the figure.

present how they modify macroalgal communities. Shading by suspended sediments, at least, does not seem to play a major role. In the period important for algal growth, no disagreement between light penetration and depth distribution of macroalgae has been found in this study. This calls for some general comments on the depth limits of macroalgae. For the sake of comparability, we argued with the level of 1% of surface irradiance. However, depth limits for algae should be defined by a critical value in absolute terms, the compensation point. For example, at 0°C water temperature, the compensation point of *Himantothallus grandifolius* is reached at a daily mean photon fluence rate of 1.6 μmol/m^2/s, which so far seems to be the lowest value demonstrated in Antarctic macroalgae (Wiencke et al., 1993). If this value is related to the range of daily sums of surface irradiance, the compensation point will already be reached close to the 1.5% level on very dull days, approximately at the 0.1% level on very bright days and close to the 0.2% level on median conditions (Fig. 6). To which percentage of surface irradiation macroalgae may be able to descend, thus obviously depends on local average wheather conditions. While an almost continous cloud cover seems to be typical for King George Island (Dera, 1980; Nowosielski, 1980; this study), locations close to the Antarctic Peninsula mainland get a higher amount of bright sunny days (Farman and Hamilton, 1978). Therefore, in order to establish a maximum estimate of macroalgal depth limits, we may use the 0.1% level as a critical value. The depth position of the critical level of illumination in turn is highly dependent on the attenuation of light in different types of water (Jerlov, 1976; Fig. 6). If we use an extrapolated version of Jerlov's tables (Lüning and Dring, 1979), we get an ultimate depth limit of 155 m, down to which Antarctic macroalgae would be able to grow under conditions of constantly excellent wheather and extremely clear water (Jerlov's water type I). Thus, reports on macroalgae growing in depths of 300 m to more than 700 m (Zanefeld, 1966; Zanefeld in: Balech et al., 1968; Wagner and Zanefeld, 1988), which still find support in recent literature (Dayton, 1990), may safely be ruled out as dislodged and deposited material. Even dredge samples containing fresh material still attached to some stones (Wagner and Zanefeld, 1988) must not be considered as proof for autochtonous growth, as macroalgae may well be lifted together with their anchoring stone by high water turbulence (Gilbert, 1984; Ayup-Zouain and Dillenburg, 1988; Klöser et al., in press, b) and dropped again under calm conditions. It may be noted, that Arnaud (1974) also retrieved macroalgae from depths in excess of 300 m, but rejected them as being deposited material after statistical analysis of his collection, and accepted only samples from depths less than 70 m as autochtonous.

Normally, conditions will not be as extraordinarily favourable as assumed above. In Potter Cove, combination of the more appropriate limit of 0.2% of surface irradiance for macroalgal growth with the maximum transmission experienced in this study (December data at station N4: Fig. 6a) results in a depth limit of only 40 m, which is sufficient to explain our records of macroalgae (Klöser et al., in press, b). In close vicinity, however, Zielinski (1981, 1990) reported depth limits for macroalgae between 90 m and 100 m in central Admiralty Bay. Under prevailing wheather conditions, this would require Jerlov's water type I B (Lüning and Dring, 1979). Whether such clear water really exists in this deep fjord, needs to be confirmed.

Acknowledgements

We gratefully acknowledge the help of Pablo Ljungberg and Oscar "Picurú" Alvarenga in the field work. The Servicio Meteorológico Nacional de la Fuérza Aereá Argentina provided basic data for the description of the wheather. The crews of the German ship *Polarstern* and the Argentinian ship *Almirante Irizar* provided well-organized transport. Expedition preparations would not have been completed in time without the help of Susanne Wenck and Christina Langreder. Valuable comments have been given by Dr. Ad Huiskes and Dr. Christian Wiencke. The first author wants to thank the Stichting Onderzoek der Zee for generous granting and the Alfred-Wegener-Institute for taking the costs of the expedition.

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