THE PHYSIOLOGY OF PHOTOSYNTHESIS AND RESPIRATION IN SOME ANTARCTIC MARINE ALGAE

By EDWARD A. DREW*

ABSTRACT. Scientific opinion on the suitability of polar seas for growth of benthic marine algae ranges from those who consider conditions ideal for very good and deep growth to those who postulate the need for partially heterotrophic nutrition to account for growth under very poor photic conditions.

Laboratory experiments to assess the photosynthetic ability of one green, four brown and eight red algae at various light intensities indicate that net carbon fixation in these Antarctic species was limited by the low water temperature (about 0° C), whilst field measurements of water clarity in the summer growing season showed consistently turbid water with the calculated light-compensation depth for most species in the region of 10 m.

These plants showed no obvious adaptations to the extreme conditions of their environment, having chlorophyll contents very similar to their temperate counterparts and photosynthesis and respiration rates also similar to winter-adapted temperate species. It is therefore unlikely that they can grow autotrophically at great depths in the area of this investigation. Although it is not suggested that the Signy Island algae occur at depths where heterotrophic nutrition must be postulated for their existence, the evidence available lends more support to the hypothesis of restricted growth potential than to the reports of living algal material growing attached at depths greatly in excess of 100 m. elsewhere in the Southern Ocean.

LIFE in the Antarctic is based on the productivity of the cold oceans, since the land masses are covered with ice and snow except for a few places where mosses and small accumulations of peat may occur. Sea birds, seals and whales feed on the Crustacea which graze the phytoplankton in the upper illuminated water layers. However, macroscopic benthic algae are also widespread, even beneath fast sea ice (Neushul, 1965; Delepine and others, 1966; Zaneveld, 1966), and they often attain considerable dimensions. Despite this, there is considerable divergence of opinion amongst algologists about the suitability of polar seas for the growth of autotrophic seaweeds, for some such as Zaneveld (1968) considered the exceptional clarity of the open ocean waters of the Antarctic to be ideal for colonization to depths of 600 m. from which he dredged apparently healthy material attached to stones. On the other hand, Wilce (1967) proposed that Arctic benthic algae must be at least in part heterotrophic in their nutrition because they could not obtain sufficient light during the short polar summer to account for their growth, especially as summer insolation also causes ice melt and accompanying turbidity of the sea with resultant reduction in light penetration.

The major factors controlling the growth of attached marine algae in polar regions are probably substrate suitability, light energy, water temperature, interspecific competition, herbivorous grazing, ice scour and various forms of physical attrition due to rough seas. If algae manage to become established in a particular habitat, then light energy and water temperature are probably of paramount importance in determining growth rates. As such plants are able to adjust rapidly to different light regimes and temperatures (Gessner, 1970), it is necessary to know the rates of photosynthesis and respiration which they can achieve under the prevailing environmental conditions before their productive potential under polar conditions can be realistically assessed. In order to determine the degree of physiological adaptation of these plants, it is also important to know their overall tolerances of extremes of illumination and increased water temperature.

Apart from a few published light measurements in polar seas (Zaneveld, 1966; Wilce, 1967), very little quantitative work has been done on the problem of benthic algal growth in such an extreme environment. In order to obtain some fundamental physiological data about polar algae, a series of experiments was carried out to quantify rates of photosynthesis and respiration in a number of common Antarctic species under a range of light intensities and at water temperatures between 0° and 30° C. The results are presented in this paper and are discussed

* Gatty Marine Laboratory, St. Andrews, Fife, Scotland.

both in terms of the potential autotrophic growth rates in the Antarctic environment and also in comparison with similar species found in temperate waters.

Site, Materials and Methods

The marine environment

This work was carried out at the Signy Island station of the British Antarctic Survey, situated at lat. 60°43′S., long. 45°38′W. in the South Orkney Islands and thus well within the Antarctic Convergence which delimits Southern Ocean conditions from, at that longitude, the South Atlantic Ocean. Sea temperature varies between +2° and −2° C, and is below 0° C for more than half the year. Sea ice up to 1 m. thick, with additional snow cover, can occur between May and November for variable periods each year. Water turbidity is relatively high during the ice-free summer period due to phytoplankton blooms and glacial melt water, as well as sediment stirred up by rough seas; in winter under-ice visibility can increase to over 30 m. from a summer value of 1–10 m.

In addition to low water temperature and high turbidity in summer, stormy seas are frequent with occasional hurricane conditions, and the abrasive action of small icebergs in the shallow sub-littoral, an attritional factor of frequent occurrence, is further aggravated under these conditions. Intertidal ice scour is widespread in winter and the intertidal flora is therefore very reduced. Details of this and of sub-littoral algal growth, which can be prolific, have been reported by Price and Redfearn (1968).

The algae used

The benthic marine algae of Signy Island form a sub-littoral vegetation surprisingly similar to that of the British Isles at first sight, although the dominance of certain species endemic to the Antarctic, such as *Phyllogigas* and *Ascoseira*, the increased importance of *Desmarestia* species and the absence of *Laminaria* forests belies this similarity on further inspection. The following algae were investigated in this study:

Chlorophyta	*Monostroma hariotii* Gain
Phaeophyta	*Ascoseira mirabilis* Skott.
	Desmarestia anceps Montagne
	D. ligulata (Lightfoot) Lamour.
	Phyllogigas grandifolius (A. & E. S. Gepp) Skott.
Rhodophyta	*Gigartina apoda* J. Ag.
	Iridaea obovata Kutz.
	*Leptosarca simplex** A. & E. S. Gepp
	Myriogramme mangini (Gain) Skott.
	Plocamium secundatum (Kutz.) Kutz.
	Porphyra umbilicalis (L.) Kutz.
	Porphyra sp.†
	Pseudophycodrys sp.‡

All these algae, except the *Porphyra* sp. and *Iridaea*, were collected in the upper 10 m. of the sub-littoral by SCUBA diving. *P. umbilicalis* grew on the sides of large boulders totally

* This corresponds to *Leptosomia simplex*, a name applied in error by Kylin and widely used in recent papers on Antarctic algae.

† A very thin membraneous alga found epiphytic on *Iridaea* in the very shallow sub-littoral and not previously recorded at Signy Island.

‡ Not yet identified with certainty. May correspond to *Phycodrys antarctica*, stated by Zaneveld (1966) to be a dominant species in the Ross Sea.

immersed at low tide, whilst *Iridaea* and the unidentified *Porphyra* sp. were collected from shallow pools on intertidal boulder-strewn flats.

The data presented in this paper were obtained from laboratory experiments carried out during February–April 1975, the second half of the austral summer. Prior to experimentation, the algae were kept in dimly illuminated aquarium tanks supplied with flowing sea-water at ambient sea temperature and were never kept more than 24 hr. before use.

Measurement of photosynthesis and respiration

All measurements of photosynthesis and respiration reported in this paper were made using the Winkler chemical method to determine changes in dissolved oxygen caused by the metabolic activities of pieces of algal tissue inside sealed glass bottles. 4 cm.^{2} discs were used except in the case of the *Desmarestia* sp. and *Plocamium* whose growth forms necessitated use of 5 cm. sections of healthy branches. The areas of these latter samples were measured graphically at the end of experiments whilst, for the purposes of later calculations, the volumes of all tissue samples were measured by displacement. Tissue dry weight was determined using identical tissue samples which had not been exposed to the Winkler chemicals (as experimental material was during analysis) which was found to cause a significant reduction in retained dry weight ($<$40 per cent). The incubation bottles were 28 ml. nominal capacity glass Universal containers with plastic screw caps fitted with rubber liners to facilitate injection of Winkler reagents according to the method described by Drew and Robertson (1974); for calculation purposes it was necessary to record the actual volumes of all the experimental bottles which varied between 25·0 and 31·5 ml. but were mostly around 29 ml. The highest rates of photosynthesis recorded reduced the inorganic carbon content of the enclosed sea-water by 10 per cent, whilst the oxygen content was not reduced by more than 10 per cent in dark respiration experiments other than some with *Ascoseira* tissue which had a very high respiration rate and consumed about 25 per cent of the available oxygen in some experiments.

The incubation apparatus used is shown in Fig. 1. Light energy up to 15 mW cm.$^{-2}$ visible radiation (400–700 nm.) was provided by a 1,500 W tungsten halide floodlight tube, and water temperature was maintained between $+0·5°$ and $+1·5°$ C with flowing sea-water taken directly from the sea except when elevated temperatures were required (see below). The same cold water flow was used to cool the glass-bottomed water bath placed between the light source and the incubation bath to absorb the heat produced by the lamp. The spectral characteristics of the light within this apparatus are shown in Fig. 2.

Since the incubation bottles were completely filled with water, agitation by the usual reciprocating shaker mechanism would not have caused appreciable water movement within the bottles, thus allowing development of diffusion shells deficient in nutrients and dissolved gases around the tissues. Therefore, the bottles were oscillated through an angle of about 60° about an axis perpendicular to their long axis in mechanically driven trays at a rate of 60 oscillations min.$^{-1}$, which induced continuous movement of the enclosed water around the tissue discs which were wedged firmly between the walls of the bottles (unless insufficiently rigid when they too moved continuously), and were arranged perpendicular to the direction of illumination. Control experiments showed that this water movement was essential for maximum photosynthesis rates, as illustrated in Fig. 3, although its effect on respiration rates was negligible and in some cases caused slight reduction.

Light intensities within the incubation apparatus were varied by placing different numbers of layers of Cinemoid plastic neutral density filter No. 60 over different groups of bottles. One, two or three layers were used, transmitting 30, 9 and 2·7 per cent of incident light, respectively. Dark respiration bottles were wrapped in aluminium foil and also placed in the oscillation trays. Water controls were not wrapped (the sea-water used in these and the incubation bottles was filtered and the oxygen content remained unchanged during the

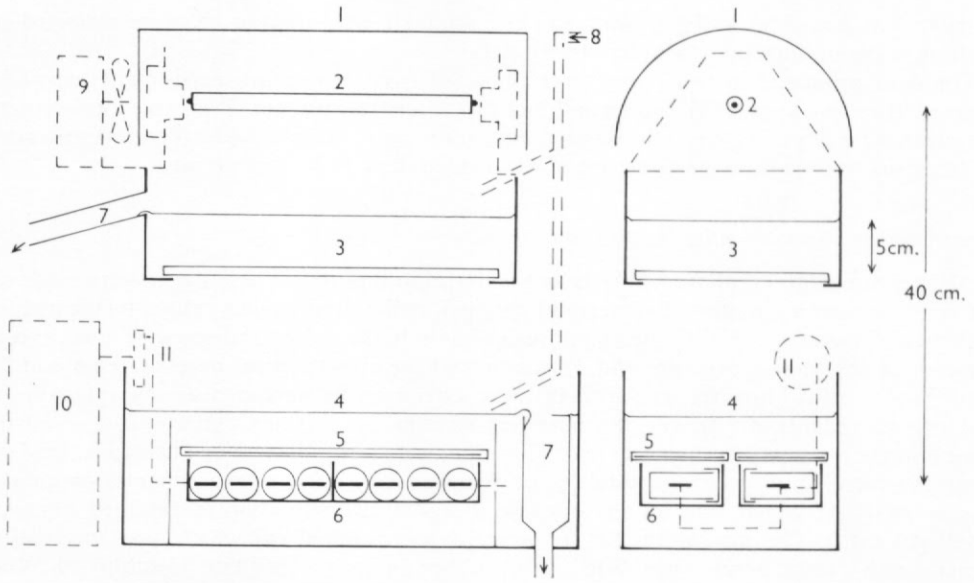

Fig. 1. Diagram of incubation apparatus (front and side elevations to show disposition of items; not intended as a construction drawing).
1. Removable reflector; 2. 1,500 W tungsten halide lamp; 3. Heat-filter water bath with Perspex bottom; 4. Incubation bath (heated water can be re-circulated here); 5. Neutral density filters; 6. Oscillation trays plus incubation bottles and tissue discs; 7. Large diameter overflow to waste/re-circulation; 8. Cold sea-water inflow; 9. Cooling fan; 10. Oscillation motor; 11. Oscillation mechanism.

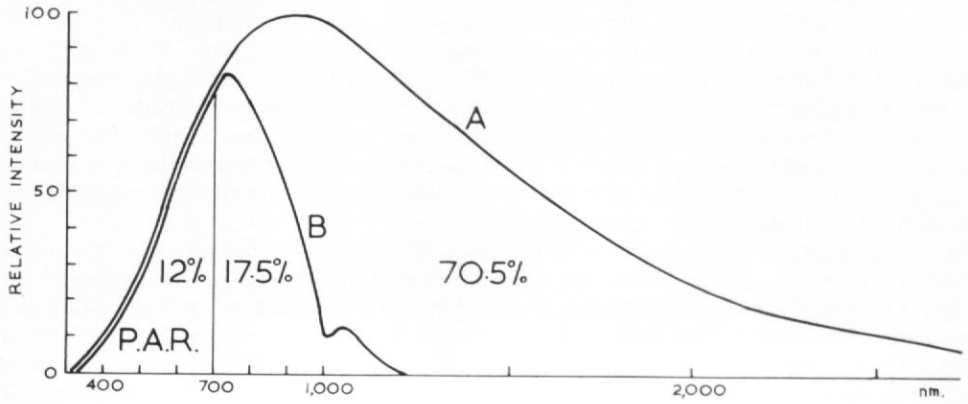

Fig. 2. Spectral characteristics of light within the incubation apparatus.
A Total emission from tungsten halide lamp with quartz envelope at 3,000° K.
B Portion transmitted through 6 cm. of water.
P.A.R. Photosynthetically active radiation (12 per cent of total emission).

duration of the experiments) and were either oscillated or kept in the bottom of the water bath according to available space. It was possible to incubate four bottles under each light regime, and usually three light and one dark bottle were placed in each compartment, giving three replicates of each light treatment and four replicate dark respiration measurements per experiment; experiments were of 1 hr. duration or occasionally 2 hr. It was possible to inject the first two Winkler reagents into all 20 bottles from such an experiment within 5 min. of the

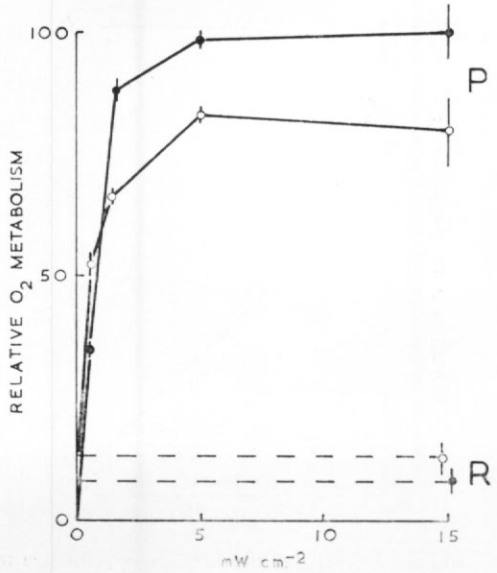

Fig. 3. Effect of bottle oscillation on oxygen exchange in *Leptosarca*.
—●— Oscillated at 60 oscillations min.$^{-1}$.
—○— Static.
P Net photosynthetic O_2 production in light.
R Respiratory O_2 consumption in dark.

end of the incubation, thereby minimizing further metabolism before the tissues were killed by the very high pH and anaerobic conditions produced by the reagents.

Prolonged pre-treatment of tissues at elevated temperatures was carried out in buckets of sea-water either in rooms on the research base at the appropriate temperatures or in constant-temperature heated water baths. For use as incubation medium at temperatures above ambient sea temperature, sea-water was warmed in bulk in a water bath for 15 min. This would not allow total equilibration of dissolved gases at the higher temperatures but no problems such as subsequent release of gas bubbles in the incubation bottles were encountered. During photosynthesis and respiration measurements at elevated temperatures, the flow of cold sea-water through the incubation bath was replaced by water re-circulated through a constant-temperature water bath maintained within $\pm 0{\cdot}5°$ C of the desired incubation temperature.

Difficulties with Ascoseira

Difficulties were experienced with Winkler titrations of water from experiments with *Ascoseira*. If left for more than a few seconds after the addition of the sulphuric acid reagent which releases iodine into solution, the subsequent titration end point came very early and a deep yellow solution remained. The rapid reduction of titration values with increased delay after addition of this reagent is shown in Fig. 4. The yellow solution remaining was the same colour as the original iodine solution but less dense and it gave no reaction with further starch indicator or sodium thiosulphate. It is possible that a soluble compound from the *Ascoseira* tissue was irreversibly complexing the iodine in solution making it unavailable for titration, thereby causing the very low results, but not giving the intense colour change of the iodine–starch complex. This difficulty was partially overcome by using a very rapid and consistent titration procedure which gave useable results with most of the *Ascoseira* treatments, although more difficulty was experienced with the higher-temperature experiments and some results from titrations with unacceptably deep yellow end points were rejected. No such

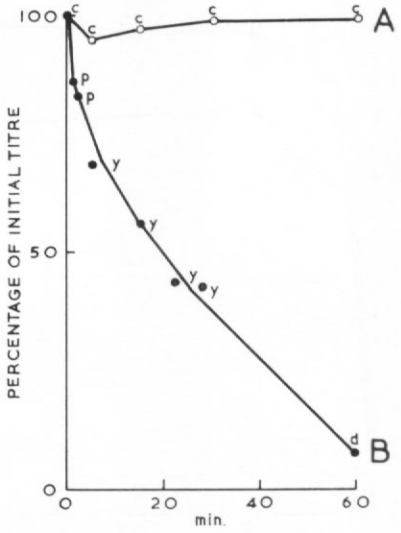

Fig. 4. Effect of delay between addition of reagents and titration in *Ascoseira* treatments.
A Reagents I and II added initially—addition of sulphuric acid delayed but titration carried out immediately after that.
B Reagents I and II and sulphuric acid added initially—delay after acid addition and before titration.
End-point colours: c clear; p very pale yellow; y distinctly yellow; d deep yellow.

difficulty was experienced with the other Antarctic algae investigated or with the many temperate and Mediterranean algae used in similar experiments.

Expression of results

Values for changes in oxygen content from those of control bottles without tissue were converted to μg. carbon metabolized, using the relationship 1 μl. O_2 equivalent to 0·54 μg. C. This assumes photosynthetic and respiratory quotients of unity which, in view of the range of metabolic substrates known to occur in such algae, may lead to overestimation of carbon metabolized by up to about 10 per cent in some cases.

Rates of photosynthesis are expressed as apparent net carbon assimilation (which may be negative in low light) and gross photosynthesis can be computed by summation of values for carbon metabolized in light and dark bottles. Since this approach takes no account of either possible depression of dark respiration rates by light or of photorespiratory oxygen uptake and carbon loss, which may be several times greater than dark respiration in some plants (Zelitch, 1971), such values for "gross" photosynthesis must be treated with caution.

Determination of chlorophyll content of thalli

Known areas of algal thalli were ground with sand in chilled methanol until all green pigmentation was removed into solution. Total chlorophyll was then calculated from the value for optical density of the solution (after centrifugation) at 665 nm., measured in an SP 600 spectrophotometer. The formula used was taken from Vollenweider (1974) with a correction for the use of methanol rather than acetone as the solvent from Marker (1972).

Measurement of irradiance

Ambience irradiance at depths down to 10 m. in the sea, at various times of day at the sea surface and also in the incubation apparatus, was measured using a light meter similar to that

described by Drew (1971) but modified to measure total visible irradiance directly by use of Cinemoid filters Nos. 9 and 17 to give a flat spectral response to the selenium photocell between 400 and 650 nm. The light reaching the photocell was attenuated by various numbers of layers of Cinemoid neutral density filter No. 60 beneath the opal Perspex cosine light-collecting surface in order to keep within the linear range of the photocell and to keep the micro-ammeter reading on scale (50 μA f.s.d.). Readings taken under-water were increased by 25 per cent to take account of the immersion effect on such irradiance detectors. The filter and detector unit was removable from the meter housing to facilitate measurements in confined spaces such as the incubator bath.

Results

Photosynthesis and respiration at ambient sea temperature

The rates of apparent net photosynthesis for the 13 species investigated at various levels of irradiance are shown in Figs. 5 and 6. These experiments were carried out at ambient summer water temperature (+1° C). In most cases the maximum rate of photosynthesis was achieved at between 1 and 2 mW cm.$^{-2}$ irradiance whereafter the dark reactions of photosynthesis were presumably the limiting factor rather than light availability. Maximum net photosynthesis rates for the different species ranged from 3·2 to 8·8 μg. C cm.$^{-2}$ hr.$^{-1}$; certain species such as *Myriogramme* and *Pseudophycodrys* showed consistently low rates of light-saturated photosynthesis but most species gave values between 6 and 8 μg. C cm.$^{-2}$ hr.$^{-1}$. There was little indication of photo-inhibition of any of these species at the highest light intensity which was equivalent to about 30 per cent full sunlight.

Data for dark respiration rates are also set out in Figs. 5 and 6. Values for all the red algae fell in the range 0·5–1·4 μg. C cm.$^{-2}$ hr.$^{-1}$; the *Desmarestia* sp., at 0·7–0·8 μg., had lower respiration rates than *Phyllogigas* and *Monostroma* (1·8–2·1 μg. C), whilst values for *Ascoseira* were particularly high at 5·4 μg. C cm.$^{-2}$ hr.$^{-1}$ on average for the various experiments with that species.

Individual points on these graphs and the others in this paper represent the mean of two or three replicates of the light treatments and four replicates for dark respiration; the vertical bars represent the range of values obtained for individual incubation bottles. In order to facilitate comparison with data by some authors quoted in terms of photosynthesis or respiration per unit weight of tissue, the average density of thallus samples of the species investigated is set out in Table I as mg. dry tissue cm.$^{-2}$ and also as specific lamina area (SLA; cm.^{2} mg.$^{-1}$).

Table I. Average thallus density and specific lamina area

Species	*Thallus density* (mg. cm.$^{-2}$)	*SLA* (cm.^{2} mg.$^{-1}$)
Monostroma	2·1	0·48
Ascoseira	11·3	0·09
Desmarestia anceps	5·8	0·17
D. ligulata	3·3	0·30
Phyllogigas	14·8	0·07
Gigartina	24·4	0·04
Iridaea	13·2	0·08
Leptosarca	3·6	0·28
Myriogramme	2·8	0·36
Plocamium	2·7	0·37
Porphyra umbilicalis	1·8	0·56
Porphyra spp.	1·2	0·83
Pseudophycodrys spp.	3·5	0·29

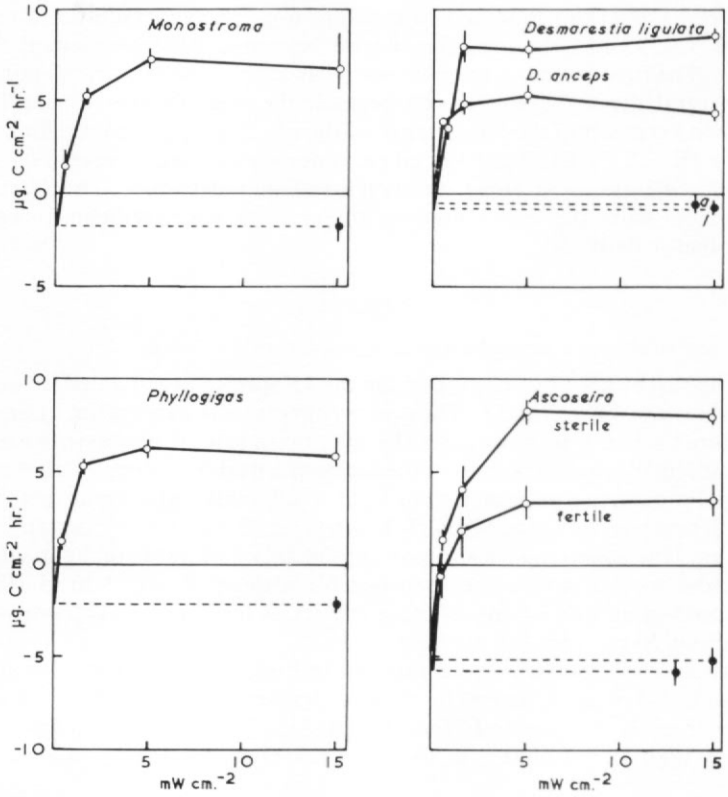

Fig. 5. Apparent net photosynthesis and respiration in *Monostroma* and four brown algae at various light intensities and at +1° C.
——○—— Photosynthesis.
——●—— Respiration.

Photosynthesis and respiration at elevated temperatures

The effect of water temperatures up to 30° C on photosynthesis and respiration rates during 1 hr. exposures of *Ascoseira*, *Desmarestia anceps*, *Leptosarca* and *Phyllogigas* tissue is shown in Fig. 7. Respiration rates continued to rise rapidly in all four species up to the maximum temperature used. However, there was a well-defined temperature optimum for photosynthesis in these plants, occurring between 15° and 20° C, whereafter photosynthesis decreased rapidly. *Ascoseira* was unusual in that its "peak" at 15° C was only slightly higher than the rate at 1° C, whereas the other species at least doubled their rates of photosynthesis at the maximum and *Leptosarca* showed a four-fold increase to 27·7 µg. C cm.$^{-2}$ hr.$^{-1}$ apparent photosynthesis.

Although the data in Fig. 7 suggest that these algae could survive in waters considerably warmer than those enclosed within the Antarctic Convergence, it is important to remember that prolonged exposure to elevated temperatures may have a greater effect on metabolic processes than the 1 hr. exposures described above. *Phyllogigas*, an alga endemic to the Antarctic and therefore possibly most susceptible to the damaging effects of high temperatures, was exposed to temperatures up to 26° C for up to 6 hr. in order to investigate this feature. Data in Fig. 8 show that, although even the highest temperature had no immediate effect on respiration rates after 6 hr. pre-treatment, 6 hr. at 18° C was sufficient to inactivate photosynthesis, whereas 6 hr. at only 3° C cooler (15° C) had no apparent deleterious effect. This

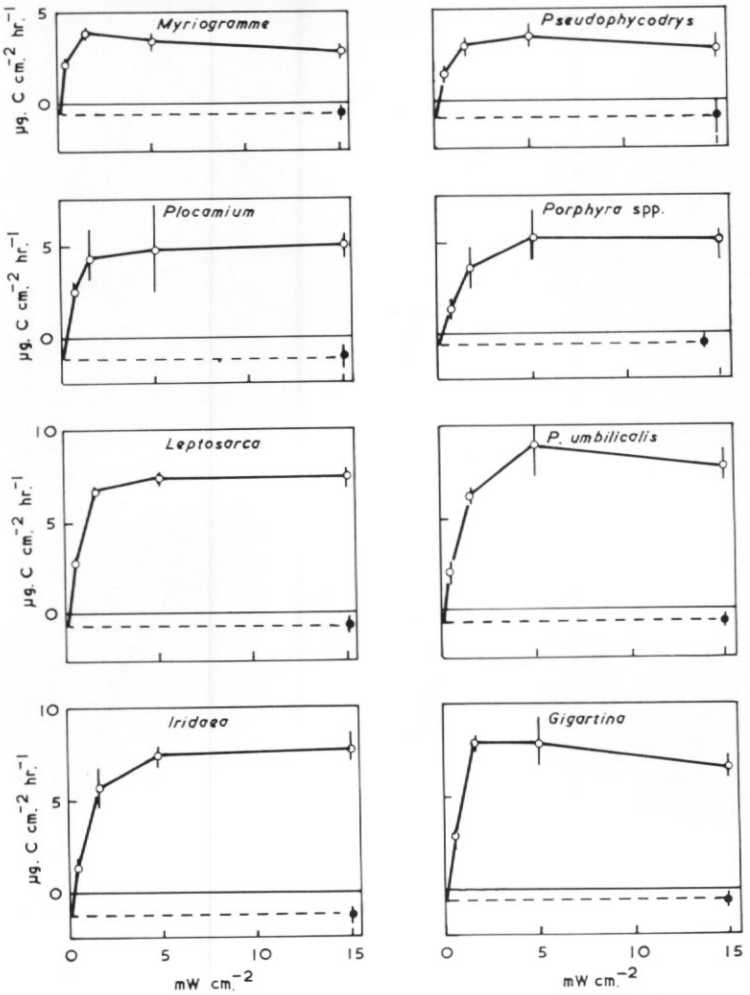

Fig. 6. Apparent net photosynthesis and respiration in eight red algae at various light intensities and at +1° C.
——○—— Photosynthesis.
——●—— Respiration.

indicates a very sharply defined temperature of inactivation for photosynthesis in this species and in fact only 3 hr. at 18° C was equally effective.

The effect of pre-treatment at 15° C on both *Ascoseira* (also endemic) and *Phyllogigas* was investigated further and data in Fig. 9 show that these two species continued to photosynthesize rapidly at 15° C after up to 6 hr. pre-treatment, although *Ascoseira* returned to a somewhat lower rate of photosynthesis when replaced in water at 1° C. Changes in the contribution of dark respiration to total carbon metabolism also occurred during pre-treatment of *Ascoseira* at 15° C, further evidence that this alga is slightly more temperature sensitive than *Phyllogigas*.

Photosynthesis is apparently more temperature sensitive than respiration in *Phyllogigas* and the inactivation induced by 6 hr. at 18° C was not reversible during a subsequent 17 hr. period at 1° C (Fig. 8b). Although no immediate deleterious effects on respiration were manifest at any temperature up to 26° C for 6 hr., serious disturbance of respiratory metabolism and of the

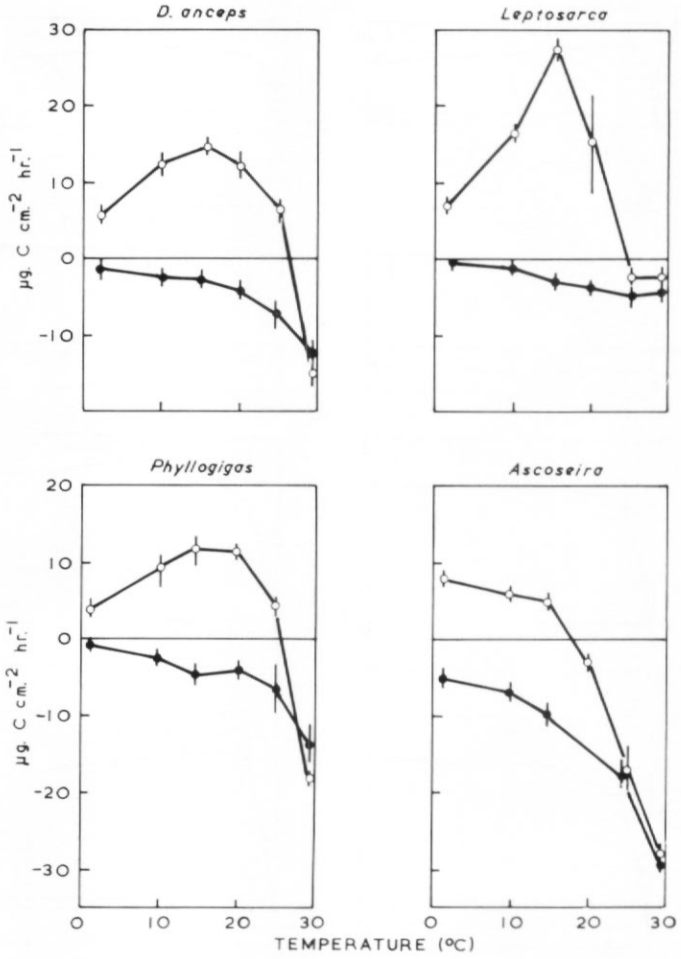

Fig. 7. Apparent net photosynthesis and respiration at elevated temperatures in four algae.
——○—— Photosynthesis.
——●—— Respiration.

tissue in general occurred as low as 18° C. Two features of these disturbances, not detected at lower temperatures, were:

i. Failure of the respiration rate to return to the normal low level when the tissue was replaced in water at 1° C (Fig. 8a), and
ii. Changes in tissue colour and texture when returned to 1° C for 17 hr. in the dark, when the tissue became more rigid and a dark brown colour due to accumulation of coloured material (possibly phenolic) in the cells just below the epidermis as illustrated in Fig. 10.

The 26° C pre-treated tissue did not develop the dark coloration during 17 hr. "recovery" but was flaccid, slightly green in colour and had a very low respiratory rate suggesting a moribund condition.

Thallus chlorophyll content

In order to assess any adaptation of these Antarctic algae to low light and cold seas by increase in photosynthetic pigment content, the total chlorophyll content, on an area basis,

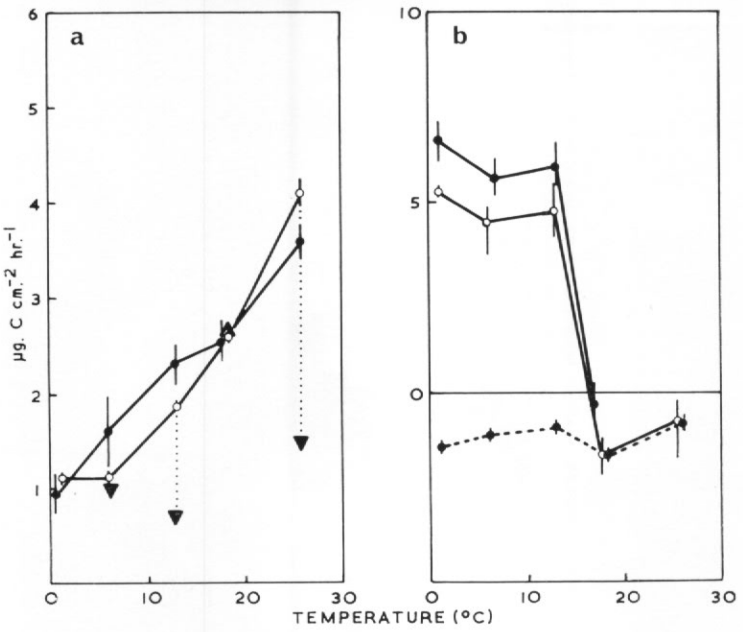

Fig. 8. Effect of pre-treatment at elevated temperatures on apparent photosynthesis and respiration in *Phyllogigas*.

a. Dark respiration.
—●— 0 hr. pre-treatment } measured at pre-
—○— 6 hr. pre-treatment } treatment temperature.
⋮ ▼ Returned to +1° C after 6 hr. pre-treatment.

b. Apparent photosynthesis (measured at +1° C, 15 mW cm.$^{-2}$).
—●— 6 hr. pre-treatment.
—○— 6 hr. pre-treatment followed by 17 hr. "recovery" at +1° C.
– – ● – – Dark respiration of "recovered" material at +1° C.

was determined for nine of the species used in photosynthesis experiments; the results are set out in Table II. The red algae and *Monostroma* all had lower chlorophyll contents than the more massive brown algae. Also shown in Table II are comparable data for the temperate massive brown algae *Laminaria hyperborea* and *L. digitata* which have similar chlorophyll contents to *Ascoseira* and *Phyllogigas*. Equivalent data for comparison of the red algae on an area basis are not available in the literature and the considerable range of thallus structure in this group makes comparison on a weight basis difficult; the data included in the table for two Mediterranean algae suggest that the Antarctic species have a relatively high chlorophyll content on a weight basis.

Submarine irradiance

The light-energy profile shown in Fig. 11 represents submarine irradiance conditions on a typically overcast summer day measured close inshore with water turbidity quite low for the period February–April 1975. Nevertheless, water clarity only just exceeds that of Jerlov (1951) type 5 coastal water and thus emphasizes the poor photic conditions normally found in the shallow sub-littoral in this region in summer, with the depth for 1 per cent of surface irradiance on this occasion at 14·5 m. The profile was measured at mid-day on 27 March 1975 and the surface irradiance data shown in the inset of that figure indicate that, even on an unusually sunny day (7 April 1975), surface irradiance was only twice that on the day of the profile measurements.

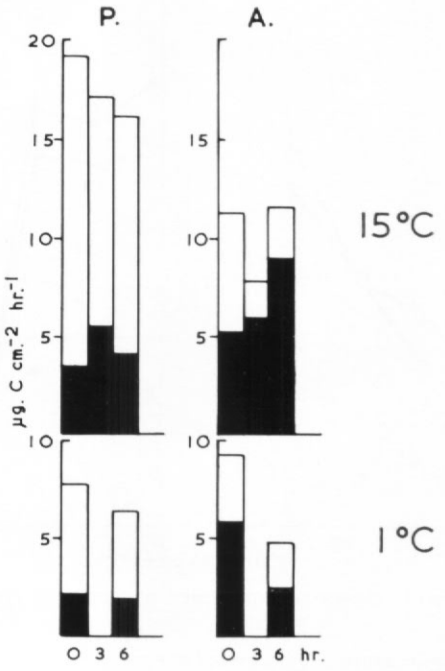

Fig. 9. Effect of up to 6 hr. pre-treatment at 15° C on photosynthesis and respiration in *Phyllogigas* and *Ascoseira*.

P *Phyllogigas*. 15° C Measured at that temperature.
A *Ascoseira*. 1° C Measured at that temperature.
"Gross" photosynthesis { □ Apparent photosynthesis. ■ Dark respiration.

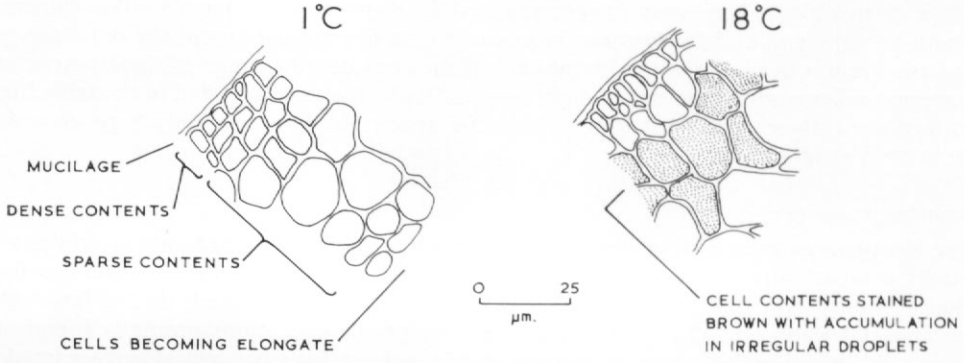

Fig. 10. Sections through *Phyllogigas* tissue after 6 hr. pre-treatment at indicated temperatures followed by 17 hr. "recovery" at +1° C.

TABLE II. TOTAL CHLOROPHYLL CONTENT

Species	μg. Chl. cm.$^{-2}$	μg. Chl. mg.$^{-1}$	
Monostroma	9·9	4·7	
Ascoseira—sterile	29·0	2·6	
—fertile	39·8	3·5	
Phyllogigas—young	27·8	1·9	
—old	32·0	2·2	
Demarestia anceps	20·7	3·6	
Iridaea	18·5	1·4	
Leptosarca	9·6	2·7	
Myriogramme	9·9	3·5	
Porphyra umbilicalis	13·1	7·3	
Porphyra spp.	5·3	4·4	
Pseudophycodrys	14·7	4·2	
Laminaria hyperborea—new frond	21·7	1·6	(unpublished data
—old frond	30·8	1·3	of E. A. Drew)
L. digitata	29·8	1·8	(unpublished data of E. A. Drew)
Gracilaria	—	0·9	(Calabrese and Felicini, 1973)
Petroglossum	—	1·6	(Calabrese, 1972)

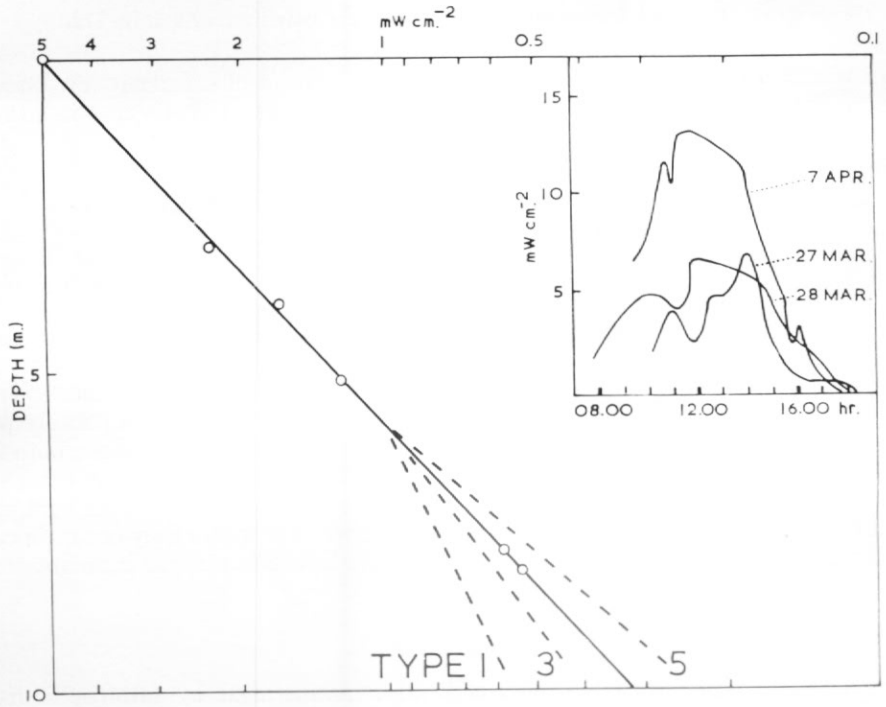

Fig. 11. Surface and under-water irradiance at Signy Island.
Under-water profile recorded at 12.30 hr. local time, 27 March 1975, at Cam Rock.
The inset shows surface irradiance throughout three different days in late summer, one of which was particularly sunny (7 April 1975).

Light compensation depths

Day lengths of approximately 12 hr. are indicated in the inset of Fig. 11 for the late summer, corresponding closely with meteorological data for lat. 60°S. shown in Fig. 12. At this latitude the periods of continuous light in summer and continuous dark in winter are relatively short,

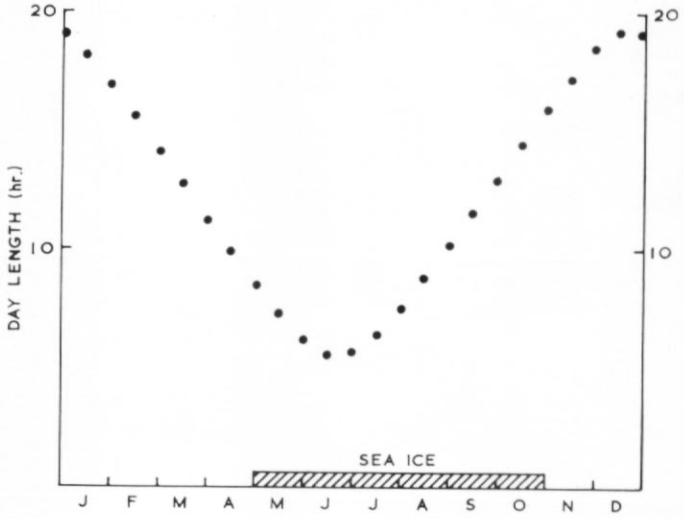

Fig. 12. Day length and ice cover expected at Signy Island throughout the year.

although winter sea ice will considerably extend the duration of extremely low under-water irradiance. There are three situations in which to consider the daily net carbon accretion of sub-littoral algae at Signy Island in relation to available light energy:

Midsummer = (net μg. C cm.$^{-2}$ hr.$^{-1} \times 24$),
Early/late summer = (net μg. C cm.$^{-2}$ hr.$^{-1} \times 12$)—(respiration $\times 12$),
Winter = (zero)—(respiration $\times 24$).

During the active growth period the situation probably averages between the first two alternatives but since an integrated average annual value for day length is only about 11 hr., close to the early/late summer situation, an optimistic estimate of the compensation depth for growth of these plants in the sea will be that depth at which average irradiance is the same as the irradiance in Figs. 5 and 6, which gives an apparent net photosynthesis rate equal to the dark respiration rate. Such an estimate is independent of the uncertainties of photorespiration, although it does not take into account the effect of ice cover nor of solar angle, both features which tend to reduce under-water irradiance further. Values for the light compensation irradiance and the depth at which this occurs under the typical conditions of the light profile in Fig. 11 are set out in Table III; increased clarity of the water in winter only occurs in conjunction with sea-ice cover and will therefore probably have little effect on the irradiance reaching the plants during that season.

Discussion

Zaneveld's suggestion of active growth of benthic marine algae by autotrophic means at depths as great as 600 m. in the Southern Ocean must be discounted in view of the very low light intensity at such depths in even the clearest ocean waters; Jerlov and Koczy (1951) found 0·0000001 per cent of surface irradiance at 600 m., representing only 4×10^{-5} mW cm.$^{-2}$ on

TABLE III. LIGHT-COMPENSATION DEPTHS

Species	*Compensation irradiance* (net P = dark R) (mW cm.$^{-2}$)	*Depth equivalent of compensation irradiance* (m.)
Monostroma	0·7	7·0
Ascoseira	2·6	2·5
Desmarestia anceps	0·3	10·2
D. ligulata	0·4	9·2
Phyllogigas	0·6	7·7
Gigartina	0·3	10·2
Iridaea	0·6	7·7
Leptosarca	0·3	10·2
Myriogramme	0·2	11·6
Plocamium	0·5	8·3
Porphyra umbilicalis	0·2	11·6
Porphyra spp.	0·6	7·7
Pseudophycodrys spp.	0·3	10·2

Calculated assuming annual average day length of 12 hr. and using the apparent photosynthesis and respiration rates shown in Figs. 5 and 6.

the sunniest possible day, whereas light compensation points of about 2×10^{-1} mW cm.$^{-2}$ are the lowest for the Antarctic algae investigated in this study. It is possible that transportation on the under surface of icebergs, mentioned by Zaneveld (1968) himself, may account for most of the deep-water material he collected by dredging, the algae actually originating in much shallower depths.

The respiration rates determined in this study are not much lower than those for similar algae in more temperate waters, as might be expected, since Newell and Pye (1968) showed that even temperate algae have low Q_{10} values for respiration in the 0–10° C range during winter in Britain. However, the compensation depths recorded in Table III account for the growth of most of the algae at Signy Island over the depth range in which they were observed to occur. The shallow values for *Ascoseira* are consistent with its restriction to the very shallow sublittoral (down to 1·5 m. according to Price and Redfearn (1968)), whilst *Phyllogigas* and *Desmarestia anceps* are usually limited to 10–15 m., although this coincides with the limit of solid substrate in the area investigated. Their penetration to 33 and 15 m., respectively, at sites a little farther offshore may be associated with increased water clarity at these sites, although Horne and others (1969), working about 2·5 km. offshore from Signy Island in 1967, reported maximum clarity only slightly greater than that indicated in Fig. 11, with the 1 per cent surface irradiance level at 17 m. in March but more usually about 10 m. in the earlier part of the year. Since all the algae used in this investigation were collected in the upper 10 m. of the sub-littoral, it is only possible to speculate on any further adaptation to low light intensity which deeper-growing material may achieve. Certainly, one possible adaptation—reduction of thallus density or increase in specific lamina area, as observed in deep-growing *Laminaria hyperborea* in Britain and which may effectively reduce the respiratory load on a given light-absorbing area—was not apparent in deep *Phyllogigas*, since these fronds were more massive than shallower material, possibly due to their considerably greater age (personal communication from R. M. Hastings).

It does not seem necessary at this point to invoke heterotrophic nutrition to account for the growth of most of the benthic marine algae at Signy Island, despite the turbid conditions found there. Nevertheless, more work is required to determine their metabolic processes overwinter, since respiration is probably not much reduced below the summer level (water temperature changes very little here) whereas, although lamina expansion in *Phyllogigas* apparently ceases

in winter (unpublished data of R. M. Hastings), the formation of reproduction structures found on the fronds early in the spring (personal communication from R. M. Hastings) suggests, as did Wilce (1967) for similar reasons, that some development continues even under thick sea ice in winter.

The rates of photosynthesis determined in this investigation are quite comparable with those found by other workers using winter material of temperate algae at low water temperatures, and appropriate data are set out in Table IV. Care was taken to use only net photo-

TABLE IV. COMPARISON OF RATES OF LIGHT-SATURATED PHOTOSYNTHESIS WITH APPROPRIATE ALGAE ELSEWHERE

Species	μg. C mg.$^{-1}$ hr.$^{-1}$	°C	*Source of data*
Monostroma nitidum	4·05	10	Yokohama (1973)
Monostroma hariotii	3·40	1	This study*
Fucus spp. (Arctic)	0·54	0	Healey (1972)
Ascoseira mirabilis	0·72	1	This study*
Laminaria hyperborea	0·34	10	Unpublished data of E. A. Drew
Phyllogigas grandifolius	0·42	1	This study*
Porphyra umbilicalis	4·78	5	Unpublished data of E. A. Drew and J. E. Forbes
Porphyra umbilicalis	4·89	1	This study*
Phycodrys rubens	2·11	5	Mathieson and Norall (1975)
Pseudophycodrys spp.	0·92	1	This study

* Calculated from area basis using data in Table I.
Algae paired for taxonomic or tissue thickness similarities.
All other workers used oxygen method and weight basis for data.

synthesis values determined with an oxygen method, since previous work and also a series of experiments at Signy Island (unpublished data of E. A. Drew) have shown that the ^{14}C method gives consistently higher results, often nearly twice those for simultaneous oxygen methods. Those authors who have measured light-saturation levels for similar sub-littoral algae (Luning, 1971; Mathieson and Norall, 1975) indicate saturation in the region of 1–2 mW cm.$^{-2}$ visible radiation, as was also found in the Antarctic algae studied, although intertidal algae usually have much higher light-saturation levels (Mathieson and Burns, 1971; unpublished data of E. A. Drew and J. E. Forbes); the low saturation level for intertidal *Porphyra* at Signy Island is possibly due to the generally low levels of irradiance even above the water so that adaptation to high intensities has not occurred.

The optimal temperatures for photosynthesis in winter material of temperate sub-littoral algae seem to be in the region of 15° C (Mathieson and Norall, 1975)—the same as the Antarctic species—although Yokohama (1973) indicated optima at or above 20° C for his low-water mark and immediate sub-littoral material even in winter; however, minimum sea temperature in his area was about 13·5° C, which is warm for a temperate region and may account for the higher temperature optima. Healey (1972) indicated that Arctic seaweeds photosynthesize best between 20° and 25° C but he considered these to be similar to temperate species also.

Except in the case of *Ascoseira*, which showed very high respiration rates at elevated temperatures, the temperature-response curves for the Antarctic algae are similar to those reported by other workers such as Newell and Pye (1968) and Yokohama (1973). Values for *Phyllogigas* are compared with winter data for several comparable brown algae in Fig. 13; they are all very similar. The respiration rates for the red algae investigated are also similar to those reported by various authors for a range of temperate red algae, whilst W. A. A. Robertson (personal

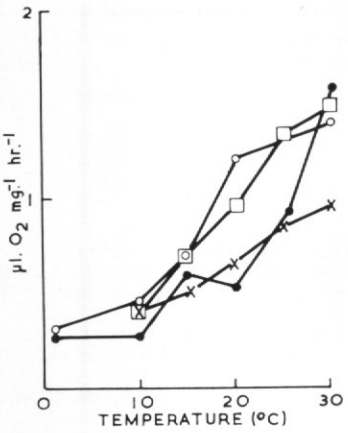

Fig. 13. The temperature response of respiration in *Phyllogigas* compared with several temperate brown algae.
——●—— *Phyllogigas*.
——○—— *Fucus* (Newell and Pye, 1968).
——□—— *Padina* (Yokohama, 1973).
——×—— *Undaria* (Yokohama, 1973).

communication), using methods very similar to those used in the Antarctic investigation, found values equivalent to about 0·4 µg. C cm.$^{-2}$ hr.$^{-1}$ for respiration in most sub-littoral red algae in Britain.

Thus, the Antarctic species investigated showed no marked physiological adaptation to their particularly harsh environment beyond that expected in winter material of temperate species. In addition to similarities of photosynthesis and respiration rates and the temperature responses of these two processes, there was very little difference in chlorophyll content between at least the massive brown Antarctic species and the temperate *Laminaria* species. Healey (1972) also concluded for Arctic species that the degree of adaptation was small. It seems likely that the benthic marine algae at Signy Island persist to 10 m. and deeper by means of autotrophic activity limited by light availability and, when the light is bright enough, by low water temperature. The relatively small number of species present, some identical with very widespread temperate species, suggests that few benthic macroscopic algae are able to maintain the correct balance between photosynthesis and respiration to give positive accretion under these conditions and have not the ability to adapt further in this direction. Concerning the species endemic to the Antarctic, the restriction of *Ascoseira* to such cold waters is clearly a function of its exceptionally high respiration rate, which restricts it to the very shallow sub-littoral there and makes its growth at higher water temperatures impossible. However, there appears to be no reason why the other important endemic species *Phyllogigas* should be restricted to the Antarctic by physiological factors alone, although it may suffer considerably from competition with the prolific growth of the dense surface-canopy forming *Macrocystis pyrifera* which is encountered on all sub-Antarctic islands and continental shores farther north.

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