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In situ primary production in young Antarctic sea ice

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Abstract

An *in situ* incubation technique used successfully to measure the photosynthetic carbon assimilation of internal algal assemblages within thick multiyear Arctic ice was developed and improved to measure the photosynthetic carbon assimilation within young sea ice only 50 cm thick (Eastern Weddell Sea, Antarctica). The light transmission was improved by the construction of a cylindrical frame instead of using a transparent acrylic-glass barrel. The new device enabled some of the first precise measurements of *in situ* photosynthetic carbon assimilation in newly formed Antarctic sea ice, which is an important component in the sea ice ecosystem of the Antarctic Ocean. The rates of carbon assimilation of the interior algal assemblage (top to 5 cm from bottom) was 0.25 mg C m^{-2} d^{-1} whereas the bottom algal community (lowest 5 cm) attained only 0.02 mg C m^{-2} d^{-1}. Chl *a* specific production rates (P^{Chl}) for bottom algae (0.020 – 0.056 μg C μg chl a^{-1} h^{-1}) revealed strong light limitation, whereas the interior algae (P^{Chl} = 0.7 – 1.2 μg C μg chl a^{-1} h^{-1}) were probably more limited by low temperatures (< –5 °C) and high brine salinities.

Introduction

The *in situ* incubation technique developed by Mock & Gradinger (1999) provided the first precise measurements of an actively growing and photosynthesising algal community within the interior of first and multi year sea ice in the Arctic Ocean. The method permits carbon assimilation to be measured at a fine-scale of 1 cm thick vertical sections throughout the ice column, without severe disruption of ice morphology, geochemistry and light field. These results led to revised estimates of Arctic sea ice algal production, because until these measurements had been made, primary production within the interior of sea ice had been mostly neglected (e.g. Clasby et al., 1973; Smith & Herman, 1991, Gosselin et al., 1997). This is also true for Antarctic sea ice, where rich infiltration / freeboard, bottom and platelet algal communities are well studied, but not integrated production estimates that take into account ice interior carbon assimilation (e.g. Sullivan et al., 1985; Arrigo et al., 1997; Trenerry et al., 2002). Consequently, new methodologies for determining *in situ* profiles of photosynthesis and respiration within Antarctic sea ice are highly pertinent. Therefore, I improved the method described by Mock & Gradinger (1999) and adjusted the device for measurements in young sea ice stages (<1 m thick), which are more representative for the seasonal Antarctic pack ice, than for the Arctic which is mostly covered by thick multi-year ice (Melnikov, 1997).

Material and methods

Site and sampling

Sea ice algae were collected in the Weddell Sea (Antarctica) during the RV Polarstern expedition ANT XVI / 3 from 18 March 1999 to 10 May 1999. The continuous decrease of sea water temperature in autumn 1999 caused sea ice formation from the middle of February close to the continental ice shelf at ca. 70°

S, 06° W. Thus, the sampled ice floe was estimated to be 2 months old on 17 April 1999. All samples were taken from one young ice floe of 50 cm thickness with a 5 cm snow cover (station PS 53 177, day of the year 107) at 70° 02′ 04″ S, 06° 00′ 06″ W using a 12 cm ice auger. Sampling of ice cores as well as light and photosynthesis measurements were done at this one station. Three ice cores were drilled for the *in situ* determinations: one for temperature profile measurements and pigment concentrations and two for determination of carbon assimilation parameters. All ice cores were taken in proximity to each other, about 100 m away from the research vessel. Care was taken to avoid disturbance of the site.

Irradiance

Total photosynthetically active radiation (PAR) was measured with a 2π sensor (LICOR 193) on the sea ice surface and a 4π sensor (LICOR 193 SB) positioned directly underneath the ice floe and recorded with a data logger (LICOR LI 1000) from 07:00 am to 16:00 pm (UTC). The ice core was returned into the original core hole and covered with snow to the original snow depth after installation of the sensors. The 2π sensor was placed approximately 10 m away from this hole. In order to calculate PAR in sea ice, we used the 4π data and Beer's law. The PAR flux on the top of each algal layer was calculated upward back to the surface using the equation:

$$E_o\ (z + \mathrm{d}z) = E_\mathrm{o}\ (\mathrm{z})\ \mathrm{e}^{[-(k_i \cdot \mathrm{d}z + kchl \cdot\ chl(z))]} \qquad (1)$$

where E_o (z) is the PAR on the top of the algal layer (μmol m^{-2} s^{-1}); E_o (z + dz) is the PAR penetrating through the algal layer (μmol m^{-2}s^{-1}); k_i is the diffuse attenuation coefficient for ice (1.5 m^{-1}) (Maykut, 1985); dz is the ice layer thickness (m); $k$chl is the mean spectral attenuation coefficient for chlorophyll *a* (0.035 m^{2}mg^{-1}) (Smith et al., 1988); Chl (z) = chlorophyll *a* (chl *a*) concentration in each ice slice (mg m^{-2}).

Physico-chemical parameters and pigments

Snow depth was measured prior to coring. Ice core temperature (Testotherm 700 thermometer) was recorded on core 1, which immediately after coring was placed in an insulated tube to avoid rapid cooling. Temperature was measured at 1–10 cm intervals by inserting the thermometer through the walls of the insulating tube into holes drilled into the interior of the ice core. The core was then sawed into 1–10 cm long sections using a stainless steel saw. These were transferred into clean polyethylene cans and transported to the ship, and thawed (4 °C over night) for the determination of algal pigment concentration (chl a and phaeopigments). Thawed core sections were filtered onto Whatman GF/F filters and the pigments retained on the filters analysed, following extraction in acetone, with a Turner Designs Model 10-AU digital fluorometer according to Arar & Collins (1992).

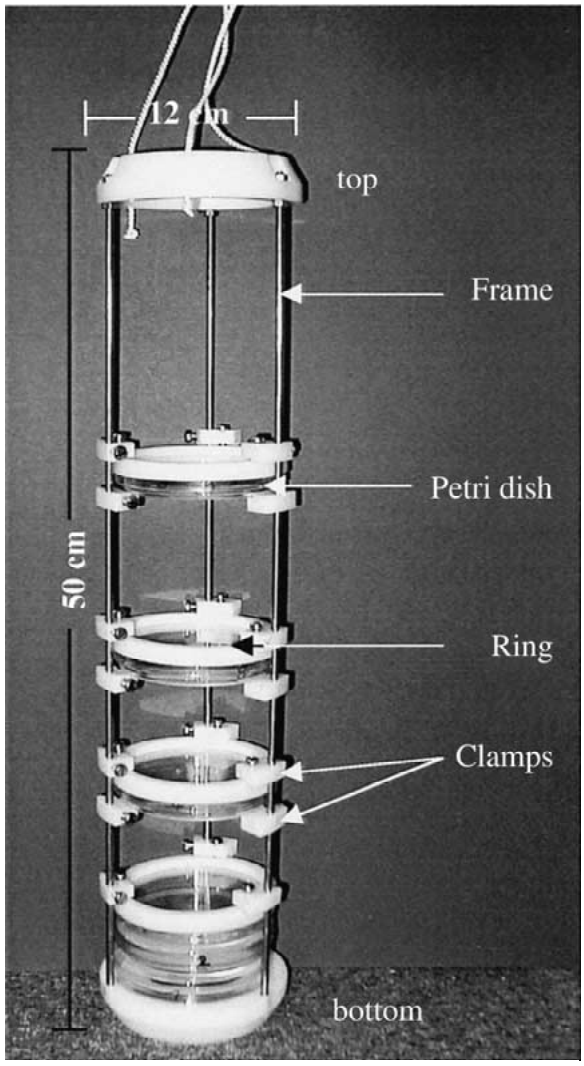

Figure 1. Photo of the new incubation system. Each petri dish serves as one incubation chamber.

Algal carbon production and growth rates

The second core was carefully extracted to avoid loss of the bottom portion. To minimise exposure of the shade-acclimated cells to the higher irradiances above

the ice, all ice core-handling processes took place under dark foil. Using a stainless steel saw, 6 slices of 1 cm thickness were cut from the following ice depths, beginning from the bottom of the core: (1) 0–1 cm, (2) 1–2 cm, (3) 2–3 cm, (4) 11–12 cm, (5) 20–21 cm, (6) 30–31 cm. Each of these 1 cm thick 6 slices was put into a glass petri dish, inoculated with 15 ml pre-filtered (0.2 μm) brine (obtained by sack hole drilling) at *in situ* temperature and 50 μl (15 μCi) $NaH^{14}CO_3$ (Amersham International plc, Little Chalfont, UK). The petri dish was sealed with a small transparent non-toxic silicon ring and clamps. The remaining core sections together with the 6 petri dishes were placed in a cylindical frame (Figure 1), in their original positions. These new developments increased light transmission when compared with the acrylic-glass barrel used by Mock & Gradinger (1999). The frame was then returned into the original core hole and secured with ropes. The core hole was then covered with snow to the original snow depth. In order to determine the dark carbon fixation, the bottom segment (0–1 cm) of a parallel core was incubated in a black petri dish whithin a sack hole of 20 cm depth. The sack hole was closed with the drilled ice core and covered with snow. After 8 h incubation, the black petri dish and the frame was removed from the floe and immediately covered with black plastic foil and transported to the laboratory on RV 'Polarstern'. Each incubation was terminated by adding 500 μl DCMU, final concentration ca. 2 mg l^{-1}, after the contents of the dish had melted (ca. 30 min) in the dark at room temperature. Three 15 ml aliquots of each sample were acidified with 150 μl 1 N HCl (pH <2). Non-fixed ^{14}C was removed by bubbling with air for 20 min. Ten ml of each aliquot were dispensed into 20 ml plastic vials and mixed with 10 ml scintilation cocktail (Packard). The samples were radio-assayed in a Packard TriCarb liquid scintillation counter. Quench correction was performed by automatic external standardisation. Dark carbon fixation was between 5 and 15% of light carbon fixation. Carbon production was calculated according to Strickland & Parsons (1972). The chl *a* specific photosynthetic rate P^{chl} was calculated by dividing the primary production (μg C l^{-1} h^{-1}) with the chl *a* concentration (μg chl *a* l^{-1}). Gross algal growth rates (μ+r), which are the sum of the specific growth rate of dark respiration (d^{-1}), were estimated from the $P^{Chl\,a}$ data (Sakshaug et al., 1989). A factor of 0.03 was used for chl *a* C^{-1} ratio (Mock & Gradinger, 2000).

Results and discussion

In situ photosynthetic rates of ice algae throughout ice floes was determined successfully using a new incubation method that can be deployed in first and multi year sea ice in the Arctic ocean. However, significant modifications were necessary before this technique could be deployed for measurements in young ice with a thickness below 1 m. This was mostly achieved by designing a new supporting frame (Fig. 1) which increased the light transmission incident on the radiolabelled incubations avoiding an underestimation by light absorption of the acrylic-glass barrel. The rods and all other holders that make up the frame frame were as thin as possible to avoid shading of the petridishes with the samples inside, at the same time being strong enough for deployment within the ice core hole. These improvements are vital for measurements at low incident light conditions such as during autumn or under thick snow cover. Frames of different length (25, 50, 100 cm) enabled measurements in young ice, which would have been too complicated with the previously used acrylic-glass barrels. The black petri dish for determination of dark carbon assimilation was not included in the new device, but was incubated elsewhere. This avoided the problems of the dark petri dish shading incubations beneath it in the incubation array.

The absolute measured range of surface irradiance at Stn. 107 was 28–194 μmol photons m^{-2} s^{-1}, and the mean under-ice irradiance was below 1.2% of the incident surface irradiance (Table 1). The modeled PAR values inside the ice floe over the entire incubation period decreased with depth (Table 1), which depends on attenuation and absorption of light by ice crystals, gas bubbles, brine, particles and micro-algae (e.g. Perovich & Grenfell, 1981; Mobley et al., 1998). The temperatures of new ice ranged between –2.4 and –11.3 °C and decreased with the distance from the ice–water interface. Ice salinity ranged from 7.9 to 10.8 in characteristic C-profile with increasing salinity to the top and the bottom of sea ice and minimum salinities in the middle. This pattern is probably the result of rapid freezing near the surface trapping larger amounts of salt (Martin, 1974). When the cold, dense brine from the upper layer of the ice fills the brine channels, the equilibrium brine level is lower than when warmer, and less saline seawater fills the channels. This small mass perturbation results in a large pressure imbalance within the brine drainage tube, which accelerates seawater up the tube until the second higher equilibrium level is reached (Martin, 1974).

Table 1. In situ variables of station 107; Light intensities are given as means ± standard deviations of 360 measurements over a time of 8 h

Distance to ice water interface [cm]	Light [μmol photons m^{-2} s^{-1}]	Temperature [°C]	Salinity [PSU]	Chl *a* [μg l^{-1}]	Phaeo / Chl *a* [μg l^{-1}]
40–50	2.9 ± 0.9	–11.3	10.8	0.01	0.23
30–40	2.5 ± 0.8	–8.3	9.5	0.05	0.02
20–30	2.2 ± 0.7	–6.1	7.8	0.03	0.03
10–20	1.9 ± 0.6	–4.6	6.4	0.10	0.06
5–10	1.6 ± 0.5	–4.0	7.4	0.14	0.10
3–5	1.5 ± 0.5	–3.7	6.9	1.18	0.06
2–3	1.4 ± 0.5	–3.7	6.6	4.09	0.07
1–2	1.4 ± 0.4	–3.1	6.5	6.32	0.02
0–1	1.4 ± 0.4	–2.4	7.9	1.13	0.02

Table 2. In situ variables of station 107: ice and snow thickness (cm), under ice iradiance (% of surface), incubation period ($T_{incubation}$; UTC), carbon assimilation (mg C m^{-2} d^{-1}), chl *a* specific photosynthetic rate ($P^{chl a}$) (μg C μg chl a^{-1} h^{-1}), growth rate ($\mu + r$), which is the sum of the specific growth rate of dark respiration (d^{-1}) and chl *a* (mg m^{-2}); values represent means or ranges

Parameter	Ice habitat	Data
Ice type		Young ice
Ice thickness		50
Snow thickness		5
Under-ice irradiance		1.2
$T_{incubation}$		07: 42 – 15: 45
Carbon assimilation	Interior (>5–50 cm)	0.25
	Bottom (0–5 cm)	0.03
P^{Chla}	Interior (>5–50 cm)	0.700 – 1.170
	Bottom (0–5 cm)	0.020 – 0.056
Growth rate	Interior (>5–50 cm)	0.140 – 0.230
	Bottom (0–5 cm)	0.004 – 0.013
Chl *a*	Interior (>5–50 cm)	0.03
	Bottom (0–5 cm)	0.14

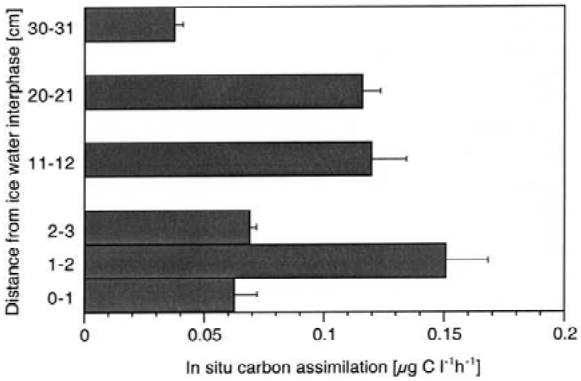

Figure 2. Vertical profiles of *in situ* carbon assimilation. *n*=3; error bars denote standard deviations; depth intervals are given relative to the bottom of the ice floe.

High brine salinities, extremly cold temperatures and reduced light supply limits primary production of ice algae (Kottmeier & Sullivan, 1988; Gleitz & Thomas, 1993; Arrigo et al., 1993; Kirst & Wiencke, 1995), but each factor probably has a different significance relative to the others and depending on depth in sea ice (Arrigo et al., 1993). *In situ* carbon assimilation in general was relatively low, ranging between 0.04 and 0.15 μg C l^{-1} h^{-1} (Fig. 2). High rates were recorded in the bottom 1–2 cm at the chl *a* maximum (6.32 μg l^{-1}) and in the middle of the ice core. Integrated production rates of interior sea ice algae (<5–50 cm) exceeded the production of the bottom algal communities (Table 2). The same pattern was observed for chl *a* specific primary production ($P^{Chl a}$, Table 2). The opposite was observed for integrated chl *a* concentration of 0.03 mg m^{-2} in the interior (>5–50 cm), whereas the bottom layers (0–5 cm) contributed 0.14 mg m^{-2} (Table 2). Maximum growth rates of the algae (0.23 d^{-1}) occurred in the interior parts of sea ice, whereas the growth of bottom ice algae was negligible (Table 2). Low chl *a* specific production rates of ice algae in the bottom few centimetres, which was responsible for low growth rates, indicate a strong light limitation of primary production, whereas P^{Chla} rates in the middle and top of the ice flow were more than 10 fold higher despite temperatures down to –7 °C (Table 2). Light seems to be the most limiting factor in the bottom of sea ice, whereas

temperature in conjunction with increasing salinities limit algal productivity in the middle and especially in the top of sea ice (Arrigo et al., 1993). Low downwelling irradiance in autumn and 5 cm snow cover were responsible for relatively low light intensities within young sea ice, whereby the largest uncertainty is probably the snow cover. Nevertheless, Hoshiai (1985) found an unstable snow cover ranging between 5 and 20 cm on the top of autumn Antarctic sea ice. However, the actual growth rate of 0.004–0.013 d^{-1} is far too low in order to build up 6.32 μg chl *a* l^{-1} in 2 months with an assumed initial chl *a* concentration of 0.2 μg l^{-1} (Hoshiai, 1985). Nonetheless, algae in the upper parts received irradiances about twice as high as in the bottom of sea ice.

The ice algae are still active in autumn sea ice and low temperatures, irradiance and high brine salinities are most limiting algal photosynthesis and growth (e.g. Palmisano et al., 1985a, b, 1987; Sullivan et al., 1985; Grossi et al., 1987). Consequently autumn ice algae only remain photosynthetically active if they are able to continuously adapt to increasing brine salinities and decreasing light intensity until the light decreases below the threshold value for positive net photosynthesis. And this adaptation has to be even stronger in bottom of sea ice, where self-shading is also important for the reduction of light intensity (Palmisano et al., 1987).

With this improved *in situ* method, it is now able to make measurements even in young Antarctic sea ice. Nevertheless, this investigation is only another small step towards obtaining a realistic, precise and logistically cost effective estimates of sea ice primary production. Despite these improvements, such measurements remain unsatisfactory and creative methodologies need to be designed that enable photosynthetic and respiration measurements to be made in undisturbed *in situ* conditions (Mock & Gradinger, 1999). There is much promise in the adaptation of microelectrode techniques (McMinn & Ashworth, 1998; McMinn et al., 2000), although due to fragility, the methodologies for deploying these within the interior of the ice remains elusive. *In situ* incubations with radio-labelled tracers will remain a key tool in the study of ice productivity for the foreseeable future, and will generate key information, especially if they can be combined with parallel incubations to determine *in situ* heterotrophic activity.

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