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Algal communities attached to free-drifting, Antarctic icebergs

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ABSTRACT

Disintegration of the Antarctic Peninsula's eastern ice shelves has increased the population of icebergs traversing the Weddell Sea, but until recently little was known about their ecological impact on the pelagic environment. Here we describe a class of algal communities that occur on the submerged flanks of large, free-drifting, glacially-derived tabular icebergs. We used remotely operated vehicles to examine these icebergs directly for the first time, to survey the algal communities and collect material for shipboard laboratory studies. The communities, principally diatoms, were associated with a characteristic cupped configuration of the ice surface, and they served as feeding sites for aggregations of Antarctic krill. Production rate measurements indicate that these communities are providing a substantial contribution to regional primary production in summer. As the number of icebergs grows, the number of algae communities may also be increasing, along with their cumulative contribution to organic carbon flux.

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1. Introduction

South of 60°S, algae have been found to associate with ice in several ways, including: phytoplankton at the edge of shelf and pack ice, microalgae within the brine channels of pack ice, algal turf on the underside of annual sea ice, and patches beneath grounded icebergs (Brierley and Thomas, 2002; Garrison et al., 2005; Thrush et al., 2006). Here we describe another ecological association between algae and ice – extensive communities of diatoms growing along the submerged flanks of free-drifting icebergs.

Rising temperatures in the region of the Antarctic Peninsula have been linked to an increase in the numbers of large tabular icebergs that have broken away from the Larsen Ice Shelf (Scambos et al., 2000). In the Weddell Sea, on the eastern side of the Peninsula, icebergs that are not grounded or constrained by seasonal pack ice typically follow northerly currents through "Iceberg Alley" and eventually into the circumpolar flow of the Southern Ocean (Schodlok et al., 2006). Tabular icebergs derived from the glacier-fed ice shelves are flat and typically hundreds of meters thick (Gladstone et al., 2001). Because their ice is formed in terrestrial glaciers, these icebergs do not carry the marine algae that are commonly incorporated annually into the relatively thin, seasonal pack ice that forms from freezing seawater. While much has been learned in recent years about the influence of seasonal pack ice on the pelagic ecosystem (Brierley and Thomas, 2002), the ecological impact of large, free-drifting icebergs has only recently been examined (Smith et al., 2007).

In Smith et al., (2007) we briefly reported the discovery of diatom communities occupying the submerged flanks of free-drifting icebergs during a cruise aboard the ARSV L. M. Gould in the Weddell Sea in 2005. In the present paper we address this discovery in greater detail with additional data collected during a cruise of the RVIB Nathaniel B. Palmer, again in the Weddell Sea, during 2009.

2. Methods

2.1. Field surveys and sampling

Danger from falling ice precludes a close approach to large, tabular icebergs at the sea surface. We used small, remotely operated vehicles (ROVs) to investigate the subsurface portions of two tabular icebergs in the Weddell Sea during the late austral spring of 2005 (Smith et al., 2007); and of one large tabular, and four smaller icebergs during the late austral summer of 2009 (Smith, this issue). Color video images, transmitted up the vehicles' tethers, gave us the ability to directly examine these icebergs in real time. To our knowledge, these are the first such direct observations of free-drifting icebergs.

We used a small, Phantom DS-2 ROV to examine and survey the submerged flanks of icebergs W-86 and A-52 in December of 2005. During each dive, the ship stood off at a safe distance while the ROV was flown to the side of the iceberg to conduct its surveys and sampling. Color video feed with graphic overlays of heading and depth, were monitored and recorded at a shipboard control station.

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The ROV was fitted with an oval, 25-μm-mesh, 0.5-m plankton net that was scraped along the ice to collect samples from its surface. While the ROV tether length (600 m) and the required stand-off distance (300 m) did not permit inspection of the undersides of the icebergs, we were able to examine their vertical faces down to 150 m depth and the corners leading beneath, down to about 200 m. A total of six such dives were made in 2005, averaging 2.5 hours in duration.

In March and April of 2009 we used a much improved ROV (Hobson et al., this issue) to survey and sample iceberg C-18a in the Weddell Sea and for comparison, some smaller icebergs in Iceberg Alley. The upgraded ROV had high-definition video, a CTD unit and a suction sampler. In this configuration we used the nozzle of the suction sampler to separate algae from the ice face, and its pump to collect the dislodged samples. Vertical transects up and/or down the ice face were conducted to document the depth range of the algal distribution; nine biology dives, averaging 2.7 hours duration were made (Sherlock et al., this issue).

2.2. Laboratory and in situ measurements

For production rate measurements in 2005, biomass was estimated by the determination of chlorophyll *a*. Diatom samples collected from iceberg A-52 were kept in running, filtered seawater in 250-ml polycarbonate bottles aboard ship for 3 days under 25% sunlight. This illumination level is the average Photosynthetic Available Radiation (PAR) to which phytoplankton is exposed in the summer mixed layer (Vernet et al., 2008). Samples were divided into aliquots, filtered onto Whatman GF/F filters to extract the water, and placed in 90% acetone:water for 24 hours (Lorenzen, 1967). Chlorophyll concentration in the extract was measured in a Turner Designs AU-10, calibrated with pure chlorophyll *a* from Sigma Co.

Primary production was measured in 24-hour incubations at Palmer Station by the Carbon radioactive method (Parsons et al., 1984). Samples were prepared as for the biomass determination, and for 3 days prior to the incubations the material was kept at 25% PAR. Equal amounts of algal material were divided into 25-ml bottles. Six light bottles were incubated at different light intensities using neutral density filters (100%, 50%, 25%, 10%, 5% and 0.5% of incident radiation at the surface). One additional bottle was used as a dark reference and an eighth bottle was used to determine carbon uptake at time zero. Each bottle was inoculated with 8 μCuries of ^{14}C and incubated for 24 h to determine daily rates. Specific activity was measured for each incubation. Average daily in-water irradiance was estimated for surface flux measured with a radiometer, GUV-511 from Biospherical Instruments Inc., placed close to the incubation and corrected for percent light transmission at each bottle assuming an 82% transmission at the air-water interface (Mitchell and Holm-Hansen 1991).

In 2009 we measured PAR with a Biospherical Instruments model #QSP-200L4S sensor. The instrument was mounted on the ROV such that there was no shading, and the vehicle's lights were turned off during the measurements. We collected samples of the diatoms growing on the flanks of icebergs C-18a and IA-4 (Smith, this issue) with the suction sampler. Experiments were carried out with algae from 47 and 26 m depths, respectively. Chlorophyll *a* concentration was measured to provide an estimate of diatom biomass (Lorenzen, 1965, 1967). For cell counts, a tuft of diatoms was divided into five sections; the number of strands in each section and the number of cells in each strand were counted with a Zeiss Axioscope 50 using phase contrast at 100 X magnification. Photosynthesis potential was measured with Photosynthesis versus Irradiance (P vs E) curves (Vernet and Smith, 2007) with algae exposed for 2 hours to 22 different irradiances, from 0 to 732 $\mu E\ m^{-2}\ s^{-1}$. Diatom tufts were broken up into equal amounts of cells in 30 aliquots; 27 for the photosynthesis experiments and 3 for chlorophyll *a* determination. Data were fit to a model that included photoinhibition (Harrison and Platt, 1980).

3. Results

3.1. Icebergs W-86 and A-52 in 2005

One of the icebergs we examined in 2005, W-86, was roughly triangular in shape with a maximum dimension of <2 km. Its height above the sea surface averaged 41 m and its submerged depth was about 300 m. The second iceberg, A-52, had an oblong shape 21 km in length with a maximum width of 5 km. Its aerial height averaged 28.5 m and its submerged depth was about 230 m. These icebergs were located approximately 130 km apart (Smith, this issue).

Unlike the rugged, windswept and fractured aerial portions of the iceberg perimeter, the submerged faces were most often smooth and glassy. A common configuration of the underwater face of the ice comprised a network of shallow, circular depressions, each about 6-8 cm in diameter and 1-2 cm deep (Fig. 1). Between the depressions were distinct, raised ridges. Broad expanses of the ice face were covered by these shallow, reticulated pockets, frequently for tens of meters in all directions (Sherlock et al., this issue). This configuration is similar in appearance to the ablation hollows or "suncups" that can form when dirty snow melts (Betterton, 2001). Anecdotal observations of similar, "golf ball-like" ice dimples have been reported on grounded icebergs (Stone, 2003) and on the underside of ice shelves (Gutt, 2002) albeit without associated algal communities.

Roughly half of the submerged areas we examined on both icebergs had tufts of dark, brown-colored algae attached to the raised ridges between these depressions (Fig. 2). The tufts were short, from <1 cm to about 3 cm in length, thick and floccose. In areas where the growth was sparse there were gaps between individual tufts, while in areas where the algae was dense, the tufts were crowded together in thick, matted rings that outlined the ice hollows. The algae first appeared at depths well below the zone of wave surge, from 6–8 m beneath the surface, and their vertical range extended downward to about 60 m, where

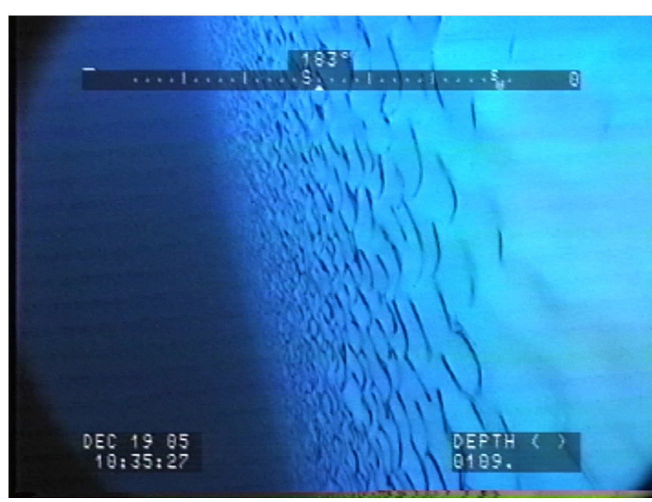

Fig. 1. ROV video frame grab of the submerged vertical flank of iceberg A-52 at a depth of 33 m, showing the ablation pockets that in many other areas were populated with algal communities. The hollows in this region are highly eroded, which may explain the absence of algae. The video overlay contains information on time, heading, and depth from the ROV (displayed depth values are uncorrected).

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Fig. 2. Algal tufts attached to the circular ridges separating ablation pockets at 10 m depth on a gently sloping terrace that projected horizontally from iceberg A-52. The width of the close-up video frame grab on the left is about 30 cm. The frame grab on the right encompasses an area of about 1 m^2. All of the dark material on the ice in these images is algae.

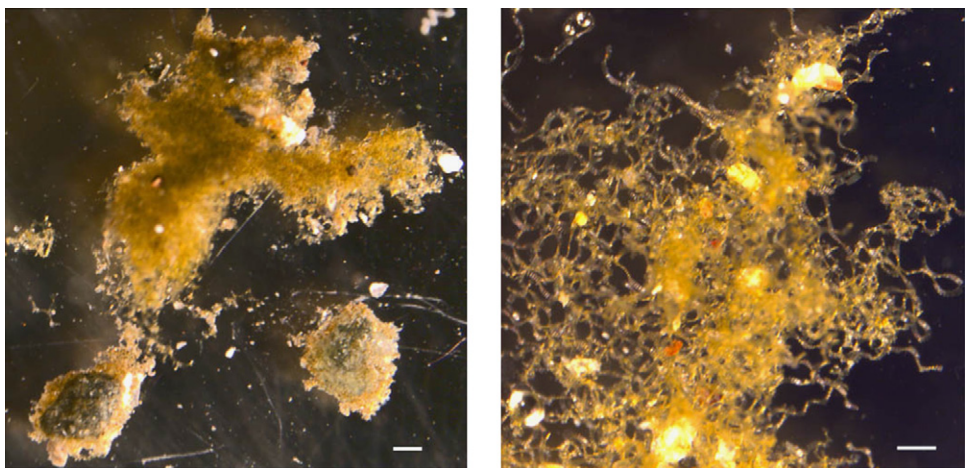

Fig. 3. Micrographs of fragments from algal tufts (*Thalassioneis signyensis*) removed from iceberg A-52. Examination under the microscope showed masses of diatom strands, some of which were attached to very small rocks. Scale bars are 100 μm.

downwelling light levels were 22% (at W-86) and 8% (at A-52) of that at the surface. At the lower extent of the algal communities' vertical range, the tufts thinned out and became sparse.

The attached algae were most abundant at depths between about 15 and 45 m, where individual tufts combined to form mats. The algae were most luxuriant and most abundant on a gently sloping, horizontal terrace that jutted out from A-52 at depths from 10 to 28 m (Fig. 2). Whereas most of the algae we observed were on vertical faces, this wide shoulder had a broad, horizontal exposure to sunlight. While krill were numerous in the water near both icebergs (Smith et al., 2007), they were particularly abundant near the algal communities. Krill were especially populous in the well-illuminated terrace region and as the ROV flew above it, grazing krill were startled upward and away from the algae.

Under a light microscope, the collected tufts were revealed to be clusters of elongate diatom strings attached to small, sand-grain-sized rocks that were too small to be evident in the video images. The diatoms were arranged in filaments, with multiple strands attached to each tiny rock (Fig. 3). Branches and helical twisting gave the combined strands their tufted appearance. Individual cells were contained in the strands by mucilaginous sheaths. The diatoms were highly pigmented with a dark yellow or golden color. Because of the incorporated small rocks, individual tufts were most often negatively buoyant, and when dislodged from the ice they sank slowly.

The diatom *Thalassioneis signyensis* was the dominant species in the algal communities we sampled on both icebergs. This species had been previously known only as solitary cells (Round et al., 1990). Along with two additional diatoms found on the icebergs (*Odontella* sp. and *Pseudonitzschia* sp.), *T. signyensis* has also been reported from collections within Antarctic pack ice (Medlin and Priddle, 1990). Epiphytes were present on the diatom strands, including diatoms of the genera *Nitzschia* and *Synedropsis*. Also present within the tufts were ciliates, foraminiferans, and mineral particles, as well as zooplankton fecal pellets, and eggs. These biological inclusions indicate an active food web within the algal communities. On the ice surface itself, we observed juvenile nototheniid icefish and polynoid polychaete worms (Smith et al., 2007: Sherlock et al., this issue). Diatom mats have been reported growing on the underside of seasonal pack ice (McConville and Wetherbee, 1983), and on the sides of grounded icebergs (Whitaker, 1977: Arrigo et al., 2010).

From samples that we collected at iceberg A-52, the chlorophyll *a* biomass of a small algal tuft was 7.91 ± 1.055 μg. A low concentration of phaeopigments (<1.3% of chlorophyll concentration) suggests that the diatoms were healthy and actively growing. Measured rates of production from incubations with radioactive carbon were relatively low per unit of biomass, which indicates an adaptation to lower light levels (Fig. 4). The maximum production rates we measured were 1.37 μg C μg chla^{-1} d^{-1} at an average daily irradiance of 34 μE m^{-2} s^{-1}. With an estimated 1372 algal tufts per m^2, we calculated a minimum potential daily production of 7.08 mg C m^{-2} d^{-1} and a depth-integrated production from 8 to 83 m depth (1% irradiance) of 655 mg C m^{-1} d^{-1} at iceberg A-52 (Smith et al., 2007). Algal attachment was restricted to the rims of the

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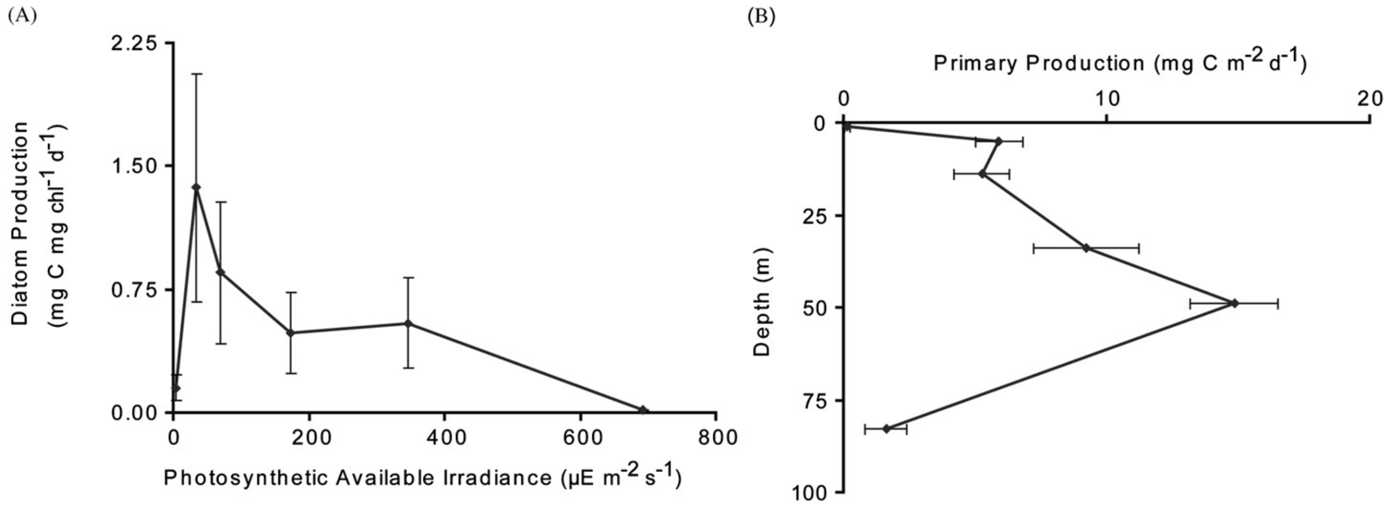

Fig. 4. Production rate measurements of *Thalassioneis signyensis* removed from iceberg A-52. A) Biomass-specific carbon uptake rates (μg C μg chla^{-1} h^{-1}) incubated for 24 h at 100, 50, 25, 10, 5 and 0.5% of incident surface radiation. Brackets depict standard error of the measurement. Maximum production rate at irradiance equivalent to 5% is comparable to phytoplankton maximum photosynthetic rate in Antarctic coastal waters. B) Estimated daily production (μg C m^{-2} d^{-1}) at different depths on the iceberg's flank based on *in situ* irradiance levels determined from Conductivity-Temperature-Depth casts in the vicinity of the iceberg.

circular ablation pockets, reducing the potential growth area to <10% of the total surface. This rate of production is comparable to that of benthic algal mats measured in McMurdo Sound, with an estimated 945 mg C m^{-2} d^{-1} based on 18 hours of daylight (Dayton et al., 1986).

3.2. Icebergs C-18a and IA-4 in 2009

Tabular iceberg C-18a, examined in 2009, had the shape of an elongate rectangle approximately 35 km in length and 6 km in width. Its height above the sea surface was 28 m and its depth below sea level was about 215 m. Iceberg IA-4 was one of several small, irregular icebergs that we investigated in Iceberg Alley (Smith, this issue). Its maximum dimension was <2 km, its height was <25 m and its depth was 167 m. As we observed in 2005, much of the subsurface face of these icebergs showed broad expanses of ablation pockets. While their origin is still uncertain, these features may be the result of convection currents, with recently melted fresh water rising toward the surface, where it mixes with more saline water then descends along the ice face in vortices that carve out the pockets (Huppert and Josberger, 1980; Sherlock et al., this issue). As before, the elevated rims of these pockets were the attachment sites of the diatoms.

Diatom tufts and mats were observed on C-18a at depths between 36 and 100 m, with highest densities between 38 and 55 m. On IA-4 the range was 20 to 145 m with the greatest density from 20 to 25 m. In general, the density of algal mats observed in the late summer of 2009 appeared to be lower than those we studied in the late Spring of 2005 (Sherlock et al., this issue).

The same diatom species found in December 2005, *Thalassioneis signyensis*, was also dominant in March/April 2009. The algae samples collected in 2009 had the same aspect as the 2005 samples: an arborescent growth pattern with a deep golden brown color, attached to small minerals, located at the edge of the ablation pockets on the submerged face of the iceberg, with multiple helicoidal strands and abundant cells per strand. The new material we collected allowed a better description of diatom biomass and photosynthesis. A small tuft, representative of those observed at C-18a, had 27 helicoidal strands with 31±19 cells per strand, or 2015 cells in the tuft; larger examples were up to ten times that size, with more numerous strands (Fig. 3). Abundance of cells in doublets indicated healthy diatoms, in active division, with golden brown chloroplasts. Chlorophyll *a* cell content was 10.66 pg/cell, or 24.25 ng chl*a* in a tuft. Fresh material observed under 40 X magnification revealed epiphytes, naviculoid diatoms, and *Chaetoceros* sp. as additional components of the algae-based community.

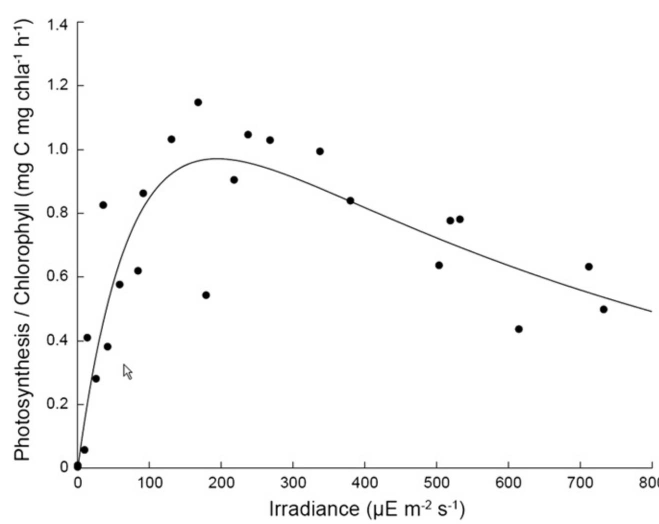

Fig. 5. Photosynthesis vs Irradiance (P vs E) curve describing carbon incorporation as a function of available irradiance for samples of *Thalassioneis signyensis* collected from iceberg IA-4 in Iceberg Alley.

Estimation of photosynthetic parameters with algae collected from IA-4, showed a carbon incorporation of ~1 μg C μg chl*a*$^{-1}$ h^{-1}, similar to planktonic diatoms in this area (Vernet et al., this issue). Cells showed acclimation to low light, with high α or light-limited response and strong photoinhibition (β): Pmax=0.97107 μg C (μg chl*a*)$^{-1}$ h^{-1}, α=0.01657 mg C (mg chl*a*)$^{-1}$ h^{-1} (μE m^{-2} s^{-1})$^{-1}$, I_k=586 μE m^{-2} s^{-1} and β=0.001788 mg C (mg chl*a*)$^{-1}$ h^{-1} (μE m^{-2} s^{-1})$^{-1}$, r^2=0.755 (Fig. 5).

Photosynthesis in situ was estimated from measured irradiance at depth, the response of photosynthesis at different light intensities, and the density of diatoms as chlorophyll concentration per unit area. Primary Production=Ps* (1-EXP$^{-(\alpha^*E/Ps)}$)*EXP$^{-(\beta^*E/Ps)}$ where E is the irradiance in situ (Fig. 6). Average daily surface irradiance between 4/2/09 and 4/8/09 was 184.64±80.99 μE m^{-2} s^{-1}. Tufts

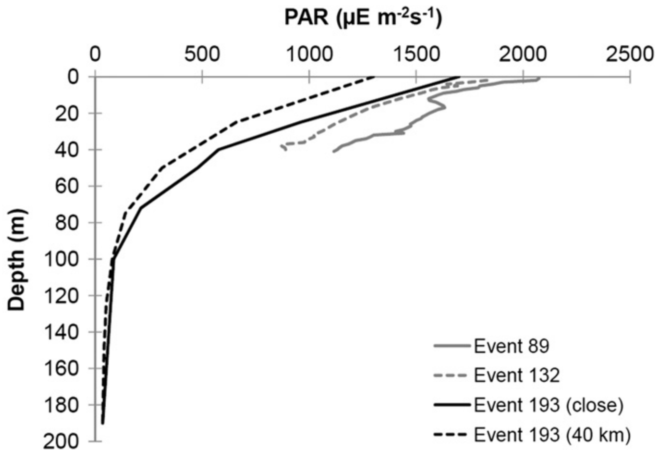

Fig. 6. Underwater Photosynthetic Available Radiation (PAR) near (within a few meters) and far (40 m away) from the submerged iceberg flank. Events (stations) 89 and 132 were at iceberg C-18a; events 193-40 were in Iceberg Alley. Algal tufts found between 25 and 75 m were exposed to an average daily irradiance of 22-60 $\mu E\ m^{-2}\ s^{-1}$.

growing between 66 and 44 m depth were exposed to 12% to 33% of surface irradiance (Fig. 6), or $22.16 \pm 9.91\ \mu E\ m^{-2}\ s^{-1}$ and $60.93 \pm 26.72\ \mu E\ m^{-2}\ s^{-1}$, respectively. For the week of sampling, with 10.33 hours of daily sunlight, a tuft had a maximum incorporation of from 0.23 to 21.83 $\mu g\ C\ day^{-1}$. At depth, production decreased to ranges of 0.076 to 5.85, and 0.16 to 13.06 $\mu g\ C\ tuft^{-1}\ day^{-1}$. With 100 tufts m^{-2}, primary production was between 7.7 and 1306 $\mu g\ C\ m^{-2}\ day^{-1}$. Overall photosynthesis during late summer was low due to the depth at which the tufts and mats were found, the relative scarcity of extensive mats on the iceberg's submerged face and the short day length.

3.3. Relative importance of iceberg algae production

If W-86 and A-52 are typical of tabular icebergs in this region (Smith et al., 2007), then we can make a rough estimate of the contribution of attached iceberg-algae communities to overall summer productivity in the Weddell Sea. Satellite imagery from an area adjacent to our 2005 study sites revealed a total of 89 icebergs about the size of W-86 ($>0.1\ km^2$) or larger, within a scanned area of 11,265 km^2 (Smith et al., 2007). We treated these icebergs as cylinders with a submerged height of 30 m (the vertical distance over which algal growth was most abundant) to obtain the total surface area available for algal attachment. We reduced the potential attachment area to one-eighth, to account for our observations that only a portion of the total submerged surface area had ablation pockets, and not all of those areas had algae. We estimate that the 89 icebergs had a total area of 0.575 km^2 that would support attached algae. Factoring in the production rates we measured in the lab yields a total potential production rate for the scanned area of 203.5 $g\ C\ d^{-1}$. The production rate of attached iceberg algae (163.5 $mg\ C\ m^{-2}\ d^{-1}$) is the same order of magnitude as the daily average of phytoplankton production in the area (518 $mg\ C\ m^{-2}\ d^{-1}$), modeled from chlorophyll *a* biomass, day length, depth of the euphotic zone, and a photosynthetic efficiency of 1.1 $\mu g\ C\ \mu g\ chl a^{-1}\ h^{-1}$ (Dierssen et al., 2002).

4. Discussion

The consistency with which the diatom *Thalassioneis signyensis* formed the basis of the algal communities we sampled implies that this species is particularly successful in exploiting this ecological niche. A planktonic source cannot be ruled out although the species was not found in our synoptic phytoplankton samples (Cefarelli et al., this issue). *Thalassioneis signyensis* was frequently found in sea ice samples from Signy Island, in the Atlantic sector of the Southern Ocean, north of our study area (Round et al., 1990). Although not previously recorded in the Weddell Sea, the proximity of Signy Island to our area of study suggests the presence of this species in the region. If *T. signyensis* occurs in sea ice within the Weddell Sea gyre at a time when pack ice surrounds icebergs, or occurs in or on ice shelves where icebergs originate, a mechanism would be provided for seeding the iceberg flanks. Colonization of the icebergs could occur during contact and attached strands could grow to higher densities once exposed to higher irradiance in the open waters of the northwestern Weddell Sea.

Apparent changes in the relative abundance of algal mats from late spring to late summer could result from grazing, especially during periods of lower phytoplankton abundance in the water column. Krill were abundant around the icebergs we studied (Kaufmann et al., this issue; Sherlock et al., this issue), particularly in the areas populated with algal mats. As light decreases during fall due to shorter days and lower sun angles, in situ algal growth would likely decline further, with the diatom populations unable to fully compensate for losses to grazing.

The fate of the attached algal communities beyond any seasonal cycles is coupled to the fate of the icebergs themselves. Large tabular icebergs in the Southern Ocean will eventually ablate and disperse their attached communities into the pelagic zone. Those diatoms attached to mineral grains will likely sink to the benthos. Smaller icebergs that fragment or melt before reaching the Circumpolar Current will distribute their biomass into the Weddell and Scotia Seas. Throughout these passages the attached diatoms will be grazed by krill and other consumers. Bathed in the nutrients released from the melting ice (Lin et al., this issue), these algae are not constrained by the growth limitations imposed on algae that live within the brine channels of pack ice. Likewise, iceberg algae are far more accessible to krill and other grazers, than are algae bound up within pack ice. With a productivity rate comparable to that of benthic algae, attached iceberg algae may be regarded as "Lagrangian benthic algae" in a pelagic habitat.

The discovery of algal communities attached to free-drifting icebergs adds a third tier to the system of offshore primary production in the Weddell Sea. Production by phytoplankton in open water is widespread and is clearly the predominant source of organic carbon on an annual basis. Production by algae associated with seasonal pack ice is another important food source for higher trophic levels, particularly where phytoplankton production is low (Lizotte, 2001). Algal communities attached to drifting icebergs contribute to production in several ways. They provide accessible forage for krill and are a likely source of seed stock for phytoplankton blooms. They add to the productivity of the recently described hot spots around individual icebergs (Smith et al., 2007) as well as to the overall primary production of the region.

5. Conclusions

1. Communities of filamentous diatoms occur commonly on the submerged flanks of free-drifting, tabular icebergs in the Weddell Sea.
2. Typically, the diatoms grow in tufts and mats along the rims of characteristic, circular ablation pockets in the ice face.
3. The principal constituent species is *Thalassioneis signyensis*.
4. The algal communities serve as aggregation sites for grazing krill.

5. The productivity of the iceberg algae communities provides a substantial contribution to summer primary production in the Weddell Sea, and probably elsewhere in the Southern Ocean.

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