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Seasonal and altitudinal variations in snow algal communities on an Alaskan glacier (Gulkana glacier in the Alaska range)

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Abstract
Snow and ice algae are cold tolerant algae growing on the surface of snow and ice, and they play an important role in the carbon cycles for glaciers and snowfields in the world. Seasonal and altitudinal variations in seven major taxa of algae (green algae and cyanobacteria) were investigated on the Gulkana glacier in Alaska at six different elevations from May to September in 2001. The snow algal communities and their biomasses changed over time and elevation. Snow algae were rarely observed on the glacier in May although air temperature had been above 0 °C since the middle of the month and surface snow had melted. In June, algae appeared in the lower areas of the glacier, where the ablation ice surface was exposed. In August, the distribution of algae was extended to the upper parts of the glacier as the snow line was elevated. In September, the glacier surface was finally covered with new winter snow, which terminated algal growth in the season. Mean algal biomass of the study sites continuously increased and reached 6.3×10 μl m^{-2} in cell volume or 13 mg carbon m^{-2} in September. The algal community was dominated by *Chlamydomonas nivalis* on the snow surface, and by *Ancylonema nordenskiöldii* and *Mesotaenium berggrenii* on the ice surface throughout the melting season. Other algae were less abundant and appeared in only a limited area of the glacier. Results in this study suggest that algae on both snow and ice surfaces significantly contribute to the net production of organic carbon on the glacier and substantially affect surface albedo of the snow and ice during the melting season.

Keywords: snow algae, glacier, Alaska, community structure

S Online supplementary data available from stacks.iop.org/ERL/8/035002/mmedia

1. Introduction

Snow and ice algae are autotrophic microbes and are commonly observed on glaciers and snowfields worldwide. They grow in cryoconite holes and on thawing snow or ice surfaces and produce a substantial amount of organic carbon. For example, *in situ* measurements revealed that the primary productivity in cryoconite holes has the potential to produce as much as 98 Gg of carbon per year on a global basis (Anesio *et al* 2009) although considerable uncertainty surrounds the validity of the global upscaling. Moreover, models of carbon fluxes on the Greenland ice sheet predicted that algae on

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glacial ice surfaces considerably fix more carbon than those in cryoconite holes, suggesting that the glacier surfaces are potentially of global importance in carbon cycling (Cook *et al* 2012). In Alaska, an estimate with a satellite image showed that 1.2 kg km^{-2} of carbon can be produced by snow algae during the summer on the Harding Icefield (Takeuchi *et al* 2006a). The algal products sustain heterotrophic organisms including cold tolerant animal and bacterial communities which live there. For example, there are midges and copepods on Himalayan glaciers, and ice worms and collembolas on North American glaciers (see e.g. Goodman 1971, Kohshima 1984, Kikuchi 1994, Hoham and Duval 2001, Aitchison 2001). These organisms can store or transform organic carbon on glaciers, and release it into a proglacial stream thus affecting carbon cycling in glacier-fed rivers (e.g. Singer *et al* 2012). Therefore, snow algae play an important role as a primary producer in such simple food webs and carbon cycles on snowfields and glaciers (e.g. Kohshima 1987, Hoham and Duval 2001, Hodson *et al* 2008, 2010).

Bloom of snow algae can visibly change the color of the snow or ice and can alter its surface albedo. Red colored snow is a typical algal bloom (usually by *Chlamydomonas nivalis)* observed on snow surfaces worldwide (e.g. Hoham and Duval 2001). Organic matter derived from such snow algae including algal cells, dead body of algae, and some other materials, can reduce the surface albedo, enhance the absorbance of solar radiation, and then accelerate the melt rate of the snow or ice surface (e.g. Thomas and Duval 1995, Takeuchi 2009). Studies on the Greenland ice sheet have recently shown that strongly pigmented ice algae have a potential impact on ice surface albedo (Yallop *et al* 2012) and that cyanobacteria also play a role in forming dark regions, such as the low-albedo ice surfaces that have appeared in the west margin of the Greenland ice sheet (Wientjes and Oerlemans 2010, Wientjes *et al* 2011). On Asian glaciers, abundant filamentous cyanobacteria form granular algal mats (cryoconite granules) and cover the entire glacier surface (Takeuchi *et al* 2001, Takeuchi and Li 2008). They significantly reduce the surface albedo of glaciers and could affect their mass balance. Thus, it is important to determine the factors affecting algal biomass and community structure for evaluation of the melt rate of snow and ice.

Snow algal communities on glaciers usually consist of several taxa including green algae and cyanobacteria and vary significantly among different altitudes of the glacier surface. Spatial variation in snow algal communities has been described on glaciers in the Himalayas, Altai, Patagonia, Alaska, and Greenland (e.g. Yoshimura *et al* 1997, Takeuchi 2001, Takeuchi and Kohshima 2004, Takeuchi *et al* 2006b, Uetake *et al* 2010). According to these studies, the algal community in the upper snow area of glaciers is usually dominated by snow environment specialists, which preferably grow on a snow surface, whereas that in the lower ice area is dominated by ice environment specialists, which preferably grow on an ice surface. Furthermore, generalist algae, which could grow on both snow and ice surfaces, can be distributed in all areas of glaciers (e.g. *Mesotaenium berggrenii* in the Himalayas, which appeared in both snow and ice areas Yoshimura *et al* 1997), and opportunist algae, which could grow in special conditions, appear in certain areas of glaciers (e.g. *Cylindrocystis brébissonii* in Alaska, which appeared in only the area near the glacier terminus, Takeuchi 2001). Total algal biomass also significantly changes with elevation; it is greater in the lower part in Himalayan glaciers (e.g. Yoshimura *et al* 1997, Takeuchi *et al* 1998) or in the middle part in an Alaskan glacier (e.g. Takeuchi 2001). However, these observations were based on a single snap-shot during the melting season and biomass and community structure can possibly change intra-seasonally.

Ice core studies revealed that algal biomass and species composition preserved in the past layers of the glacier showed significant inter-annual variation (e.g. Yoshimura *et al* 2000, Takeuchi *et al* 2009). This is probably due to variations in physical conditions, such as air temperature, precipitation, and solar radiation during the melting season and/or in chemical conditions of snow, which could affect algal growth. As physical and chemical conditions on the glacier surface also change through the melting season, the snow algal community would seasonally change in biomass or species composition. However, little is known about the intra-seasonal change of the algal community on glaciers. The seasonal changes could be valuable in understanding the ecology of glacial algae and in evaluating the net production of organic carbon on glaciers and their effect on the surface albedo of snow and ice.

In this study, the author aims to describe a seasonal change of snow algal communities on an Alaskan glacier (Gulkana glacier in central Alaska). The altitudinal distribution of the algal community was investigated four times from May to September in 2001. The seasonal variation of the community is discussed in terms of the physical and chemical conditions of the glacier surface. The effect of the algal community on surface albedo is also discussed with the spectral reflectivities that were simultaneously measured and has been published elsewhere (Takeuchi 2009).

2. Study site and methods

The investigations were carried out in 2001 on the Gulkana glacier, located in the Alaska Range, in Alaska, United States of America (figure 1, photographs of the glacier are available as supplementary information available at stacks.iop.org/ERL/8/035002/mmedia). The glacier flows west to south from Icefall Peak (about 2440 m above sea level (a.s.l.)) down to the terminus at an elevation of about 1220 m a.s.l. This glacier is easily accessible from the Richardson Highway and has been monitored for several decades by the University of Alaska and the United States Geological Survey (USGS, e.g. Josberger *et al* 2007). The glacier has been generally receding over the last 50 years and has lost 11 $\pm$ 5 m in ice equivalent thickness averaged over the whole glacier between 1954 and 1993 (Dowdeswell *et al* 1997). The length and area of the glacier are approximately 4 km and 21.8 km^2, respectively. The equilibrium line of the glacial mass balance in the year (2001) was approximately 1790 m a.s.l. by USGS measurement (http://ak.water.usgs.gov/glaciology/gulkana/index.html).

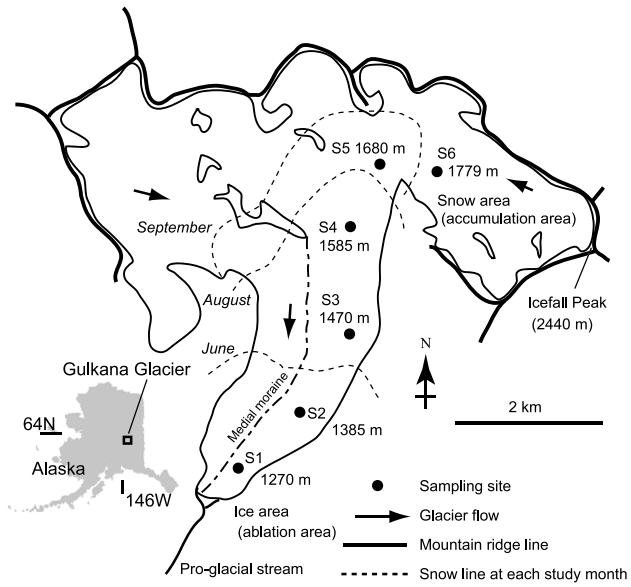

Figure 1. A map of the Gulkana glacier in the Alaska range, showing sampling sites and locations of the snow line in each study month on the glacier surface. The snow line in May was located about 3 km downstream from the glacier terminus at an elevation of 1055 m.

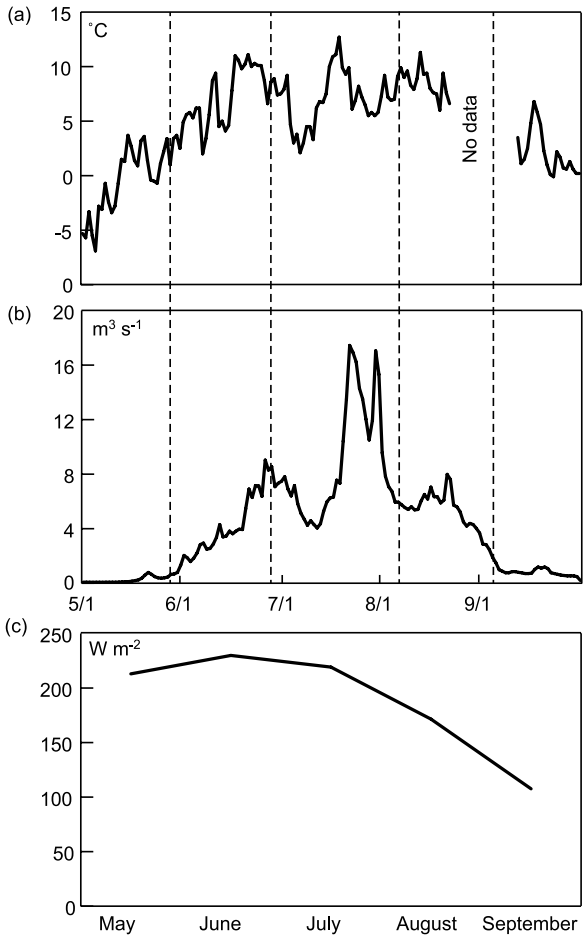

Figure 2. Air temperature (a) and glacier discharge (b) recorded at the Gulkana glacier during the study period by USGS, and the 30 year average of monthly solar radiation (1961–1990) (c) measured at the metrological station (Gulkana Station). Dashed lines indicate the dates of sample collection.

Prior to this research, sampling was conducted on the glacier in August 2000. The investigation revealed that the snow algal community on the glacier consisted of seven taxa and the biomass and community structure varied with altitude (Takeuchi 2001). The abundance of organic matter and mineral particles on the glacier surface ranged from 0.09 to 7.9 g m^{-2}, and from 0.67 to 97.8 g m^{-2}, respectively, and varied with the elevation (Takeuchi 2002). Recently, community structure and phenotypes of bacteria and yeasts on the glacier have been described by DNA analysis and culturing (Segawa *et al* 2010, Uetake *et al* 2012). While these studies were based on a single sampling in the summer melting season, this paper aims to describe seasonal variations in the community based on four sampling occasions in 2001.

Daily means of air temperature and discharge of the glacier, measured from May to September in 2001 at the automatic station of the Gulkana glacier by USGS (http://ak.water.usgs.gov/glaciology/gulkana/index.html), are shown in figure 2. The discharge is roughly indicative of melt activity on the glacier surface, although the discharge lagged from meltwater production by a few days due to water storage in the drainage system of the glacier (Kido *et al* 2007). Since solar radiation was not measured at the station, a 30 year average of monthly solar radiation, 1961–1990, measured at the meteorological station (Gulkana Station, located at approximately 123 km south from the glacier, the data can be downloaded from the National Solar Radiation Data Base, www.nrel.gov/rredc/solar_data.html) is shown in figure 2.

The sampling was carried out four times from spring to late summer of 2001. The four periods of the sampling were in May (from 28 May to 1 June), in June (from 25 to 29 June), in August (from 6 to 10 August), and in September (from 3 to 7 September). In each sampling, collections of surface ice/snow were carried out at six sites, from 1270 m to 1770 m a.s.l. (S1–S6, figure 1). The six sites were the same locations as the sites of the former study in 2000 (Takeuchi 2001) and were determined by GPS. All sites were at least 500 m away from the side margin of the glacier. The number of sites was decided by considering possible logistics of the sampling and sufficient numbers to describe seasonal changes of the algal community. The slope of the sampling surface varied from 7° to 12° between site S2 and S6, and was slightly steeper at site S1 (12°–15°). The samples in May and September in 2001 were collected only at sites 2 and 4, and at sites 1–5, respectively.

Surface ice/snow was collected with a stainless-steel scoop (1–2 cm in depth). Five samples were collected from the randomly selected surfaces at each site. The collected area on the surface was measured to calculate the amount of algal volume biomass per unit area. The collected samples were melted and preserved as a 3% formalin solution in clean 125 ml polyethylene bottles. All samples were transported to the International Arctic Research Center, University of Alaska Fairbanks (about 4 h). Electrical conductivity (EC) and pH for glacial meltwater and snow were measured *in situ* and in

the laboratory, respectively, with a portable pH–conductivity meter (Cyberscan PC300, Eutech Instruments Pte Ltd, USA).

The algal biomass of each site was represented by algal cell volume (biovolume) per unit area. Cell counts and estimations of cell volume were conducted with an optical microscope (Nikon E600). The samples were stained with 0.5% erythrosine (0.1 ml was added to 3 ml of the sample) and ultrasonicated for 5 min to loosen sedimented particles. 50–1000 μl of the sample water was filtered through a hydrophilized PTFE membrane filter (pore size 0.5 μm, Millipore FHLC01300), which became transparent with water, and the number of algae on the filter was counted (1–3 lines on the filter). The counting was conducted 3–6 times on each sample. From the mean results and filtered sample water, the cell concentration (cells ml^{-1}) of the sample was obtained. Mean cell volume was estimated by measuring the size of 50–100 cells for each species, which was identified as described in Takeuchi (2001). The total algal biomass was estimated by summing values obtained by multiplying algal concentrations by the mean cell volume. This calculation was done for each species at each site. To obtain the spatial biomass at each site, the total biomass was represented as a cell volume per unit area of glacier surface (μl m^{-2}). Community structure was represented by the mean proportion of each species in five samples to the total algal volume at each sampling point. In order to facilitate comparison with other studies, algal biomass was also expressed in carbon equivalent (mg C), using a conversion factor of 0.02 mg carbon per 1 μl cell volume (Fogg 1967).

3. Results

3.1. Snow algae on the glacier

Seven taxa of snow algae were observed on the glacier surface. The algal taxa observed in this study season were the same as those observed in the previous year in 2000 (Takeuchi 2001). The algae included five green algae (Chlorophyta) and two cyanobacteria. The green algae are *Chlamydomonas* (*Cd.*) *nivalis*, *Mesotaenium* (*M.*) *berggrenii*, *Ancylonema* (*A.*) *nordenskiöldii*, *Cylindrocystis* (*Cyl.*) *brébissonii*, *Raphidonema* sp. Both of the cyanobacteria are filamentous Oscillatoriaceae cyanobacteria.

3.2. Seasonal and spatial variations in the total biomass of snow algae

Microscopy of the snow and ice samples revealed that snow algae were not present on the glacier in May, but they appeared from late spring (June) until late summer (September, figure 3). In May, neither snow sample collected at two sites on the glacier (sites S2 and S4) contained any algal cells. The glacier surface at this time was still completely covered with winter snow. The snow depths were 39 cm at site S2 and 54 cm at site S4 when the samples were collected. The surface snow was thawing in daytime in all the study sites. The snow temperatures were constantly 0 °C from the surface to the bottom in both sites. Although there

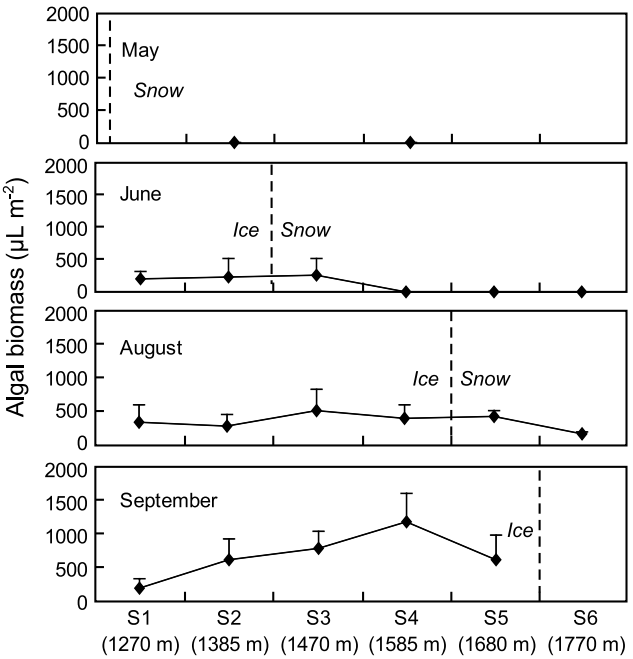

Figure 3. Seasonal change in the altitudinal distribution pattern of the total algal cell volume biomass on Gulkana glacier from May to September 2001. The dashed lines indicate the location of the snow line. Error bar = standard deviation.

were no algae on the glacier, visible red snow was observed approximately 3 km downstream from the terminus of the glacier. The winter snow was still on the ground down to about the elevation of 1055 m. The red snow was apparent just above the snow line. Microscopy revealed that the red snow contained abundant spherical red algal cells of *Cd. nivalis*. Thus, although snow alga had not appeared yet on the glacier surface in this month, snow algae bloomed on the seasonal snow cover further downstream of the glacier.

In June, snow algae were observed at the lower three sites. The mean algal biomass among the sites ranged from 213 to 262 μl m^{-2} or from 4.3 to 5.2 mg C m^{-2}. There was no significant difference in the biomass among the sites (one-way ANOVA, $F = 3.885$, $P = 0.946 > 0.05$).

In August, snow algae were observed at all of the study sites (figure 3). The mean algal biomass ranged from 166 to 521 μl m^{-2} or from 3.3 to 10.4 mg C m^{-2}. There was no significant difference in the biomass among the sites (one-way ANOVA, $F = 2.621$, $P = 0.130 > 0.05$).

In September, the algae were observed at the lower five sites on the glacier (figure 3). The sample at the highest site (site S6) could not be collected in this month due to heavy snow fall during the sampling. The snow line was located above site S5, thus all of the lower five sites are in the ice area. The mean algal biomass ranged from 190 to 1178 μl m^{-2} or from 3.8 to 23.6 mg C m^{-2}. The biomass gradually increased from the lowest site (S1, 190 μl m^{-2} or 3.8 mg C m^{-2}) to the middle site (S4, 1178 μl m^{-2} or 23.6 mg C m^{-2}), and decreased at the higher site (S5, 619 μl m^{-2} or 12.4 mg C m^{-2}). There was a significant difference in the biomass among the sites (one-way ANOVA, $F = 2.866$, $P = 0.002 < 0.01$). The algal biomass in August and September

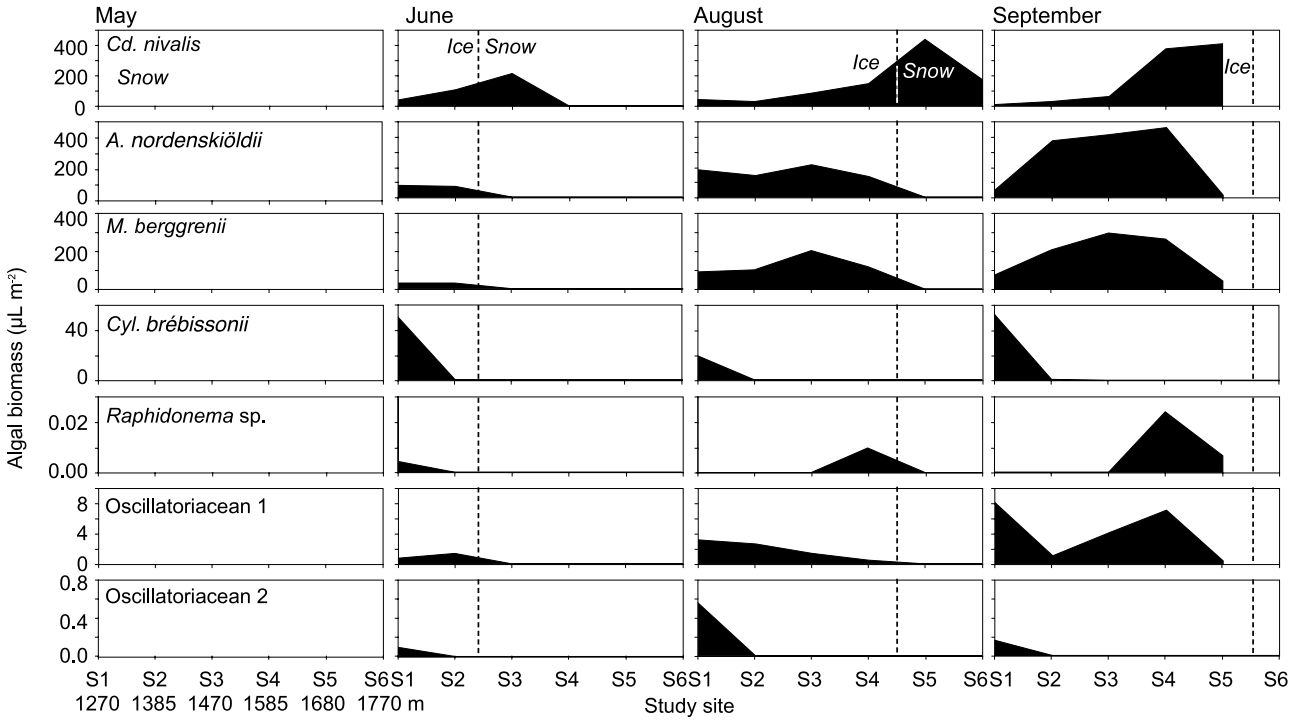

Figure 4. Seasonal change in the altitudinal distribution pattern of seven algal taxa (cell volume biomass) on the Gulkana glacier from May to September 2001. The dashed lines indicate the location of the snow line.

was comparable to those in August of the previous year, 2000, which ranged from 84 to 882 μl m^{-2} (Takeuchi 2001). The altitudinal trend of the biomass observed in September was also similar to that in 2000.

The biomass at all of the sites on the glacier generally increased from May to September (figure 3) although the appearance of algae on the surface was delayed at higher sites. The mean algal biomass of the study sites continuously increased from 0.0 μl m^{-2} in May to 628 μl m^{-2} or 13 mg C m^{-2} in September. Although the appearance of algae was late at site S4, its biomass showed significantly higher increasing rate (25.1 μl m^{-2} day^{-1} or 0.50 mg C m^{-2} day^{-1}) compared with other sites (0.21–11.6 μl m^{-2} day^{-1} or 0.004–0.23 mg C m^{-2} day^{-1}). A statistical test shows that the seasonal variations in the biomass were significant at sites S2–S6, (one-way ANOVA, S2: $F = 5.82, P = 0.006$; S3 : $F = 4.35, P = 0.037$; S4: $F = 26.1, P = 0.000$; S5: $F = 10.7, P = 0.002$; S6: $F = 60.1, P = 0.000$), while they were not significant at site S1 ($F = 1.21, P = 0.33 > 0.05$).

EC and pH were did not significantly vary among the study sites and seasons. All of the ECs measured on the glacier were less than 4.0 μS cm^{-2}. The EC for snow in May was slightly higher, but there was no significant difference among the study sites and seasons. pH ranged from 4.80 to 5.69, and showed no clear trend among the study sites, seasons, snow, or ice.

3.3. Seasonal change in the algal community

Each algal taxon showed a distinctive pattern of spatial and seasonal changes of its biomass (figure 4). *Cd. nivalis* generally distributed from the ice area to the upper snow area. Its distribution expanded gradually upward of the glacier from June to September. The maximum biomass was always located at the snow surface near the snow line. The location moved upward as the snow line rose; it was at site S3 in June and at site S5 in August and September. The maximum site was visibly recognized as red snow in the field since this alga has a red pigment. Red snow was always observed at just above the snow line throughout the study period. *M. berggrenii* and *A. nordenskiöldii* distributed in the entire ice surface and their distribution expanded to the upper part as the ice surface was exposed from June to September. The maximum biomasses of both algae were observed at the middle part (sites S3 or S4) of the glacier. Their biomass gradually increased until September. *Cyl. brébissonii* and Oscillatoriacean cyanobacterium 2 appeared at the lowest site of the ice surface throughout the seasons. *Raphidonema* sp. appeared near the snow line in the ice area. Its location moved with the rising snow line. The altitudinal distribution of community structure in August agreed well with that in August of the previous year, 2000 (Takeuchi 2001).

Seasonal change in the algal community structure at each study site showed that the structure generally changed from the dominance of *Cd. nivalis* to the dominance of *A. nordenskiöldii* and *M. berggrenii* (figure 5). In the snow area, the biomass of *Cd. nivalis* accounted for more than 99% to the total algal biomass (e.g. site S3 in June, S5 in August). After the snow disappeared and the bare ice surface was exposed, *A. nordenskiöldii* and *M. berggrenii* appeared. In the bare ice area, the two algae accounted for 44–96% to the total biomass. The proportion of *A. nordenskiöldii* was slightly

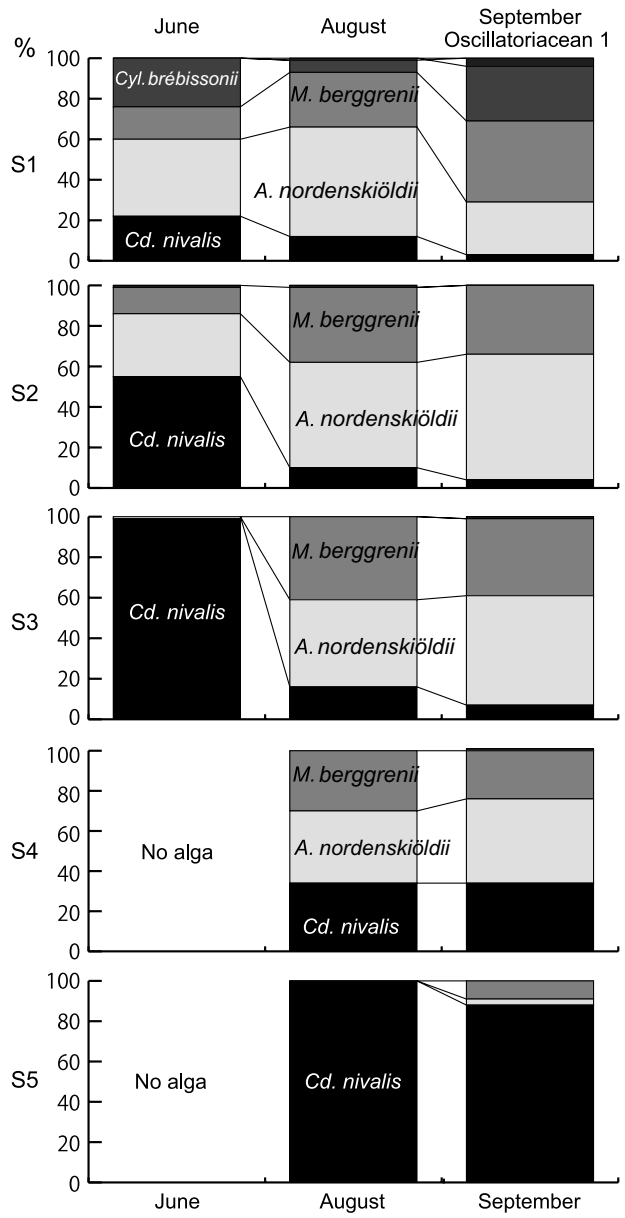

Figure 5. Seasonal change in algal community structure at study sites S1–S5 on the Gulkana glacier from June to September 2001.

larger than that of *M. berggrenii* (mean: 40% versus 28%). *Cyl. brébissonii*, which appeared only at the lowest site (S1), accounted for 6–27% of the total biomass at the site. The other algae observed on the glacier were rather minor in terms of the cell volume biomass, accounting for less than 8% of the total biomass.

4. Discussion

4.1. Appearance and seasonal change of snow algae on the glacier

The difference in timing of the algal appearance among the study sites is likely attributed to the condition of the snow. The taxon that appeared first was *Cd. nivalis* in all of the study sites, thus the conditions of the beginning of algal growth are those for *Cd. nivalis* on the snow surface. The appearance of *Cd. nivalis* started in the snow surface further downstream from the glacier terminus in May, then gradually moved up to the glacier: site S3 in June and site S5 in August. These areas were the snow surfaces just above the snow line, suggesting that the snow depth on the ice surface is one of the important conditions. As described in other studies on snowfields (e.g. Hoham 1980), snow algal blooms are initiated when air temperatures remain above freezing for several consecutive days, a meltwater develops in the snow, nutrients and dissolved gases are available to algae, and light penetrates through the snow. With a combination of the above factors, the resting zygospores germinate at the snow–previous ice surface interface releasing zoospores that swim in the liquid meltwater towards the surface of the snow, causing visible blooms only a few days after germination. When algae were rarely observed on the glacier in May, the air temperature had been above freezing since the middle of May (figure 2) and the surface snow melted in all of the study areas, indicating that snow melting is not the only condition for the initiation of algal growth on the glacier. Chemical conditions such as EC and pH seem not to associate with the algal initiation since there was no significant difference among the study sites and seasons. However, no other chemical analyses were carried out in this study and thus the influence of other chemical variables (e.g. nitrogen and phosphorus) on the growth of algae during the melt season is still unknown. The snow depths on the glacier in May were 39 cm and 54 cm at sites S2 and S4, respectively, which were almost the same as or deeper than the limit of the snow depth for algal growth (40 cm, Müller *et al* 2001). The snow depth that is shallow enough (less than 40 cm) for light penetration and migration for algae under the snow, which occurred in June, is probably an important condition on this glacier. The area in which algae were observed was also characterized by high liquid water content. Melt water of the snow surface usually percolates down in the layers and flows to the lower area along the ice surface below, and thus the water content of snow is very high at the transition zone of snow and ice. Snow algae grows in the liquid water film surrounding snow grains (e.g. Fukushima 1963), thus water contents could also play a role in the initiation of algal growth.

Once the algae appeared on the surface, the algal biomass generally kept increasing until the end of the melt season (September) in most of the sites (sites S2 to S6), but it did not significantly change in the lowest site S1. The increase of biomass throughout the melt season suggests that the algal growth rate was always larger than the rate of death and removal of algae. Although solar radiation, air temperature, and melt activity decreased from August (figure 2), the biomass kept increasing. The continuous increase suggests a lack of any physical or chemical limitation for algal growth during the melt season in this area. On the contrary, the biomass without significant change at the site S1 suggests that the algal growth rate was roughly equivalent to the rate of death or removal of algae. As described in previous papers (Takeuchi 2002, 2009), amounts of surface dust at the site S1 are significantly greater than those at the upper sites.

This is likely due to the larger supply of windblown mineral particles from the surrounding ground, and of subglacial fine sediment (till) from basal ice. The large amounts of mineral dust covering the ice surface may limit photosynthesis of the algae. Furthermore, since the slope is a major factor determining the accumulation of organic matter (Stibal *et al* 2012), the steeper slope and greater running meltwater on the surface in this lowest area possibly wash the algal cells out of the glacier.

4.2. Seasonal changes and type of snow algal taxa

According to the previous study of snow algae on the glacier (Takeuchi 2001), the snow algae can be classified into three types based on their spatial distribution. *Cd. nivalis* was classified as a snow environment specialist. *A. nordenskiöldii* and *M. berggrenii* were classified as ice environment specialists. The four other algae, *Cyl. brébissonii*, *Raphidonema* sp., and two Oscillatoriaceae cyanobacteria, were classified as opportunists. The seasonal changes in distribution patterns of each taxon were also distinct among the types. The results supported the spatial distribution of each algal taxon being determined by their preferable conditions on the glacier surface throughout the melting seasons. The seasonal change of the distribution of each taxon is likely due to changes of the physical conditions associated with the retreat of the seasonal snow line.

The snow environmental specialist, *Cd. nivalis*, was dominant on the snow area throughout the seasons. However, its distribution did not extend to all of the snow area, but to the limited areas, which were the snow surfaces just above the snow line. As mentioned above, the distribution may be due to high liquid water content in the snow and/or a snow depth that is shallow enough for the migration of algae from the bottom of the snow.

The ice environment specialists, *A. nordenskiöldii* and *M. berggrenii*, appeared on the ice surface immediately after the winter snow disappeared. They distributed widely on the bare ice area and remained dominant until the end of the melting season, suggesting that these two algae are the most adaptable taxa to the ice environment. This is consistent with the studies on ecophysiology and ultrastructure of the two taxa, which showed that they have a freezing tolerance, and are adapted to temperatures close to the freezing point and to high light conditions (Remias *et al* 2009, 2012). Their biomass kept increasing from June to September in the middle area of the glacier, suggesting that there was no limitation, such as nutrients, for their growth in this area.

The opportunist algae, *Cyl. brébissonii* and Oscillatoriacean cyanobacterium 2, were distributed only in the lowest site (S1), and did not expand their distribution to the upper part throughout the seasons. They are likely to associate with special conditions of the lowest area of the glacier. It has been reported that *Cyl. brébissonii* is a soil alga and has a higher optimum growth temperature (+10 °C, Hoham 1975). As mentioned above, large amounts of mineral dust covered the bare ice surface in this area. The abundant mineral dust may alter surface ice structure and chemical conditions on the surface. Since the mineral dust has lower reflectance than ice, it could absorb solar radiation and slightly increase meltwater temperature on the ice surface. These conditions may be preferable to the algae.

Raphidonema sp. appeared on the glacier from June to September and were observed at only the area just below the snow line. Stibal and Elster (2005) reported that *Raphidonema nivale* observed on a glacier in Svalbard is a soil species, which is well adapted to soil environment and is only occasionally brought on snow by wind. Since *Raphidonema* sp. observed on the Gulkana glacier is morphologically very similar to *Raphidonema nivale*, it may also be a soil alga. The proportion of *Raphidonema* sp. to the total algal biomass was very small (less than 0.01% to the total cell volume), suggesting that they are not specialized on snow or ice. The alga was observed on the area just below the snow line, probably because the amount of running meltwater in this area is less than in the lower area.

The two Oscillatoriacean cyanobacteria observed on the ice surface are also probably originally from soil. It has been reported that most of the cyanobacteria observed on glaciers were also be found in soil around the glacier (e.g. Stibal *et al* 2006). Their appearance is, therefore, similar to the other soil algae on the glacier.

These differences of each alga are important to evaluate the net production of organic carbon on the glacier. In particular, *Cd. nivalis* in the snow area and *A. nordenskiöldii* and *M. berggrenii* in the ice area, are likely to be the major algae to produce organic carbon on this glacier. The results indicate that algae grew on all of the exposed ice area, but on the limited part on the snow area throughout the melting season. The proportion of algal biomass between snow and ice areas did not change greatly from June to August, which were 37.3% and 62.7% in June and 36.3% and 63.7% in August. The result suggests that algae on the ice areas account for the large part of the net production of organic carbon on the glacier, but algae on the snow area also significantly contribute to it during the melting season. In order to evaluate exactly the relative importance between snow and ice algae for the net production of organic carbon, more information on algae and other organic matter is necessary, such as life span and the biomass–carbon ratio of each alga, and altitudinal distribution of the glacier area.

4.3. Effect of algal community on the spectral albedo of the glacier surface

According to a study on spectral reflectance on the glacier surface (Takeuchi 2009), it varied spatially and seasonally, and was altered substantially by impurities, such as mineral particles, organic matter, and algal cells on snow and ice of this glacier. Since each algal taxon has different secondary pigments, change in algal biomass and community structure may affect the spectral reflectance on the glacier surface. In order to evaluate the effect of algal community on the surface albedo, the spectral reflectances reported in Takeuchi (2009) were reexamined with the results of this study.

The snow surfaces showing the distinctive spectrum with two absorptions at wavelength ranges of 400–600 and

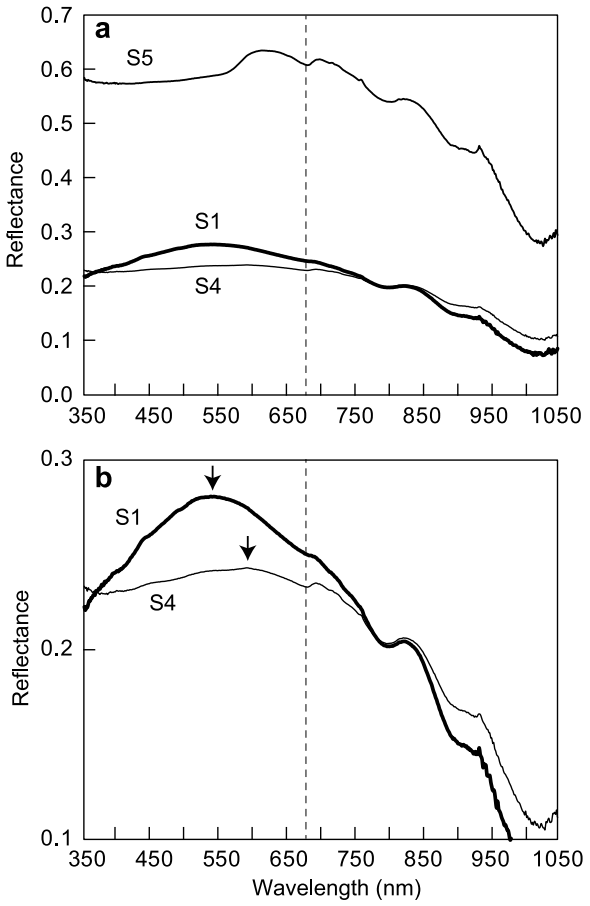

Figure 6. Spectral reflectance curves on the snow and ice surfaces at sites S1, S4, and S5, taken in August 2001 on the Gulkana glacier, sourced from Takeuchi (2009). The curves show absorption features of algal pigments (a), enlargement of the spectra in the reflectance between 0.1 and 0.3 (b). The arrows indicate the peaks of curves. The dashed line indicates 680 nm, where chlorophyll absorption is maximal.

670–680 nm (figure 6) corresponded to the surfaces where *Cd. nivalis* were abundant. The spectrum agreed with the absorptions of primary and secondary pigments of *Cd. nivalis*; the range of 400–600 nm was mainly due to carotenoids, while the range of 670–680 nm was due to chlorophylls (e.g. Bidigare *et al* 1993). This type of spectrum was observed at S3 in June and at S5 and S6 in August, where *Cd. nivalis* was dominant and its biomass was more than 150 μl m^{-2}.

The spectrum of the bare ice surface at site S4 in August, where *A. nordenskiöldii* and *M. berggrenii* were dominant, was generally low and flat in the visible range, but there was a small absorption at wavelength ranges of 670–680 nm, corresponding to chlorophylls, and a gradual decrease as wavelength decreased at ranges of 350–590 nm (figure 6). The absorption of 350–590 nm is probably due to the brownish secondary pigment of *A. nordenskiöldii* and *M. berggrenii* (Yallop *et al* 2012, Remias *et al* 2009, 2012). The spectral absorption of the pigment gradually increases as wavelength decreases in the range of 350–590 nm (Remias *et al* 2012), which agrees with the spectrum of the glacial surface. However, the feature of these algal pigments was very small on the spectrum. This is probably due to the effect of other impurities, such as dead bodies of algae, humic substance, and mineral particles, which may be more abundant and have a larger effect on the spectrum compared with the algae.

In contrast to the spectrum at site S4, that of the bare ice surface at site S1 was slightly different. The spectrum did not show absorption at wavelength ranges of 670–680 nm, but a flat peak at 540 nm (figure 6). The algal community at the site was predominantly *A. nordenskiöldii* and *M. berggrenii* and the total algal biomass was comparable to that at the other sites, but amounts of mineral particles on the surface was three- to four-fold greater than those of the ice surface of the upper sites (Takeuchi 2009). Thus, the effect of mineral particles is likely much stronger than that of algae, causing the spectrum that did not show any algal absorption features.

The results showed that the algal community does affect spectral albedo on the glacier surface, but the effect may not be apparent if other impurities, such as mineral and other organic particles, are more optically effective. To parameterize surface albedo on the glacier, it is essential to quantify the supply and optical effect of mineral particles and to understand the formation process of humic substances and other organic particles, as well as to study quantitatively the seasonal variation of snow algae on the glacier surface.

5. Conclusions

Investigations on the Gulkana glacier in Alaska in a melting season from May to September 2001 revealed that the algal community and biomass on the glacier surface varied spatially and seasonally although there is still a potential to miss other transient events due to the limited temporal resolution of sampling in this study. Algae appeared on the snow surface when the snow line was close to the area. Algal biomass continuously increased until the end of the melting season (September), except at the lowest area of the glacier, where the algal biomass did not significantly change. The algal community started with a predominance of *Cd. nivalis* (snow environment specialist), then changed to dominance of *A. nordenskiöldii* and *M. berggrenii* (ice environment specialists). In some locations, other opportunist algae, which are originally from soil surrounding the glacier, appeared, but they accounted for only a small part to the total algal biomass. This seasonal change is basically caused by the change of surface conditions, i.e. from snow to ice. The change in algal community at lower sites proceeded to that of upper parts of the glacier as the snow line rose on the glacier. Although this study is limited to a single melting season, the altitudinal distribution of algal biomass and community structure in the summer season repeated in 2000 and 2001, thus the distribution probably appears in every year. However, recent retreat and shrinkage of the glacier may affect the spatial and/or seasonal variations in algal communities on the surface.

Results in this study also showed that *Cd. nivalis* in the snow area and *A. nordenskiöldii* and *M. berggrenii* in the ice area, were the major algae to produce organic carbon and to affect surface albedo on the glacier. The

three algae were common taxa observed on other glaciers in Alaska and worldwide. The snow environment specialist, *Cd. nivalis*, is reported all over the world as a cause of the red snow phenomenon (e.g. Hoham and Duval 2001). Two ice environment specialist algae, *A. nordenskiöldii* and *M. berggrenii* are commonly observed on the bare ice surface of Alaska, Greenland, Svalbard, Altai, and the Himalayas (e.g. Kol 1942, Yallop *et al* 2012, Takeuchi *et al* 2003, 2006b, Remias *et al* 2009, 2012). A similar seasonal change in algal community may occur on such glaciers, however, community structure and total algal biomass vary geographically (e.g. Takeuchi *et al* 2006b). Since the algal community could affect the net carbon flux and surface albedo on the glacier, it is important to know what is responsible for the geographical variations not only to understand glacier ecosystems but also to evaluate glacial melting. Seasonal variation in algal community on the glacier could be useful to understand the conditions that determine the algal community in each geographical location. Although water content and surface conditions seem to be important on the studied glacier, effects of windblown dust and nutrient availabilities, and climate conditions such as precipitation and solar radiation, may also be important on other glaciers. Furthermore, we need to understand the life cycles of each alga on the glacier. Although further studies are necessary, understanding of snow and ice algal communities on glaciers is important to predict future changes of glacier ecosystems as a result of global climate change.

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