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Inter-annual sea-ice dynamics and micro-algal biomass in winter pack ice of Marguerite Bay, Antarctica

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ABSTRACT

The geographic remoteness, the lack of remote sensing capabilities, and the lack of appropriate environmental sensors make the detection of seasonal trends or inter-annual variations in sea-ice microbial biomass or production processes within the pack ice of the Antarctic extremely rare. The evaluation of their inter-annual variability in the context of ice dynamics and trends in regional climate has not been possible. During the late winters of 2001 (July–August) and 2002 (August–September) we assessed sea-ice dynamics, sea-ice characteristics, and biomass of sea-ice microbiota along the Western Antarctic Peninsula. These two winters were marked by large contrasts in the dates of initial ice formation (late June in 2001 and April in 2002), which resulted in differences in the physical pack-ice characteristics. Chlorophyll *a* (chl *a*) content in ice cores differed between the study years, with 2002 having 10-fold higher chl *a* content. The difference in ice-core chl *a* content is best explained by the timing of ice formation that leads to less phytoplankton scavenging from the water column and a lack of transfer of solar energy into the pack-ice ecosystem. Such a tractable atmosphere ocean–ice–biota coupling may help in evaluating underlying processes responsible for long-term trends in recruitment cycles of upper trophic levels as well as future projections on the response of the Antarctic marine ecosystems to variability in local climate.

1. Introduction

The annual advance and retreat of sea ice from a summer minimum of 4 million km^2 to a winter maximum of approximately 20 million km^2 play a dominant role in the Southern Ocean ecosystem, and has been called the largest seasonal process on Earth (Laws, 1985). West of the Antarctic Peninsula, the seasonal coverage of sea ice and the advance and retreat of the sea ice appear to be changing in response to changes in climate which are pronounced in this region (Stammerjohn et al., 2003; Stammerjohn and Smith, 1996). Changes in mesoscale ice dynamics are often cited as a factor perhaps controlling changes in phytoplankton (Moline et al., 2004), zooplankton (Atkinson et al., 2004; Loeb et al., 1997), as well as marine mammals and birds (Ainley et al., 2005; Croxall et al., 2002; Fraser and Hofmann, 2003).

The Antarctic peninsula region is an area where Antarctic krill (*Euphausia superba*) populations have traditionally been abundant (Everson, 2000; Hofmann and Murphy, 2004; Quetin and Ross, 2003). Their abundance in this region is believed to be linked to a combination of factors leading to high recruitment. These factors include an on-shelf circulation pattern in the southwestern peninsula area (Marguerite Bay), which retains spawned eggs in areas with relatively warm bottom waters at depths shallow enough for nauplia, metanauplia, and furcilia stages to migrate to surface waters during winter (Hofmann et al., 2002; Hofmann and Murphy, 2004; Lascara et al., 1999; Quetin and Ross, 2003). Critical to the energetics and survival (and hence recruitment) of furcilia and larval krill is their ability to then feed during winter months (Atkinson et al., 2002; Daly, 1990; Quetin and Ross, 2003)—ironically at a time when the pronounced seasonal cycle of solar radiation coupled with the seasonally low temperatures and maximum ice coverage imposes overarching constraints on ecosystem primary production.

In addition to being a physical barrier and floating platform—sea ice is a habitat for the colonization and growth of micro-algal communities (e.g. Garrison et al., 1986; Horner et al., 1992; Thomas, 2004; Thomas and Dieckmann, 2003). Sea-ice microbial communities are recognized as having the potential for being extremely productive during spring, summer, and autumn periods (Arrigo et al., 1993; Fritsen et al., 1994; Grossi et al., 1987; Hoshiai,

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1985; Thomas et al., 1998). Perhaps because of the winter darkness and simple logistical constraints of polar marine operations in winter, the winter productivity and ecology of sea-ice microbial communities have been studied less. Kottmeier and Sullivan (1987) sampled eight ice cores along the western Antarctic peninsula during late August and September of 1985, and based on findings of 2–23 mg chl $a\,m^{-2}$ in ice cores and measured rates of photosynthesis of 24.7–60 mg C $m^{-2}\,d^{-1}$ they suggested that sea-ice-based primary production can occur during winter.

A growing number of studies are starting to reveal the presence of mesoscale (10–100 km) variations in Antarctic pack-ice micro-algal communities (Arrigo et al., 2003; Garrison et al., 2005, 2003). However, there remains little information regarding the seasonal and inter-annual variability in seasonal biomass in pack ice of the Southern Ocean, the factors that may control these variations (if present), and what impacts (if any) variations in sea-ice biota might have on the ice-associated ecosystems of the Southern Ocean.

During successive austral winters of 2001 and 2002 the US Southern Ocean GLOBEC program (Hofmann et al., 2002) visited the pack ice along the shelf near Marguerite Bay, at the southern end of the Antarctic Peninsula. Water-column surveys, ice characterization programs, and ice sampling occurred during these cruises in an effort to document the stocks of sea-ice biota available for overwintering *E. superba* juveniles. Herein, we report on the ice dynamics, pack-ice-cover characteristics, and the inter-annual variability in sea-ice micro-algal biomass documented during these studies.

2. Methods

2.1. Study area

A series of cruises onboard the ARSV Lawrence M. Gould (LMG) and RVIB Nathanial B. Palmer (NBP) were utilized during 2001 and 2002 for the studies of sea-ice properties, microscale sea-ice microbial community distributions, and mesoscale sea-ice microbial biomass characterizations. Sampling on these cruises occurred from July 27 to August 24, 2001 and August 5 to September 10, 2002. Studies and sampling on board the LMG were primarily limited to longer duration (several days) stations (Figs. 1B and C), where ice coring occurred on individual ice floes within a more spatially limited area. The locations of the LMG stations were embedded within the much broader sampling and observational areas of the NBP (Figs. 1A and B), which conducted a spatial survey of the region that allowed more spatially extensive physical oceanography measures, ice observations, and ice coring to occur within and adjacent to Marguerite Bay. This approach was aimed at providing a synoptic view of the region and allowed placing measurements collected on the LMG in a larger spatial context (Hofmann et al., 2002).

2.2. Ice observations

Standard visual observations of the ocean's sea-ice coverage were conducted from the vessel's bridges when the ships were moving. The observations followed ASPeCT sea-ice observing protocols (Worby et al., 1999). Briefly, these observations recorded the primary types and thickness of ice present, coverage statistics, snow thickness observations, ridging, and ice floe thickness statistics. Thickness observations were aided by the use of reference buoys that were lowered near the water–ice line, where they could be used as a size reference for floes turned on their sides due to the passing of the ice along the ship's hull.

2.3. Sample collection, processing, and analysis

Water-column samples were obtained 10–20 m intervals spanning the upper 100 m of the water column using Niskin bottles deployed on rosettes. Water was immediately transferred from Niskin bottles to dark HDPE bottles, and samples were processed immediately for the determination of chlorophyll *a* (chl *a*) concentrations. Samples of newly forming frazil were collected using nets and buckets lowered from the sides of a zodiac and newly formed nilas were collected using a hand saw. Ice cores were nominally collected along thickness transects (described in Perovich et al., 2004) that targeted the predominant ice floes at the ice stations. An additional goal was to collect a large number of cores in as random a process as possible from each ice station. Therefore, in addition to collections occurring along ice-thickness transects, we obtained a large number of cores from locations that were determined by walking into an area that appeared to represent the predominant type of ice in the region (determined by ice observations) and haphazardly tossing a glove into the air and collecting cores where the glove landed. This sampling did not intentionally bias sampling of either the level or deformed ice. Seven-centimeter-diameter core barrels (Kovacs Enterprises) were used for all ice-core collections. When ice cores were sectioned in order to assess the vertical distributions of biomass the ice-core sections were placed into 4-L HDPE wide mouth jars and placed in darkened coolers for transport to the ship's environmental rooms for melting. When cores were obtained in order to simply determine the integrated biomass measures, entire ice cores were placed in large opaque buckets for melting. Core samples were melted with and without the addition of 0.2-μm filtered seawater (FSW) in the dark and in incubators and environmental rooms to maintain low temperatures (−2 to 0 °C). Routine procedures and care were taken to ensure that the FSW remained free of bacteria and chl *a* through the standard use of sequential filtrations through in-line 0.2-μm filters and storage in 0 °C environmental rooms. Blanks were routinely prepared from the FSW for monitoring potential chl *a* and bacterial contamination of samples.

Additions of seawater are routinely used when processing ice for biomass determinations in order to buffer the ice-bound organisms from osmotic shock or cell expansion and breakage—which is especially needed when identifications of protists or physiological measures are desired. Melting ice cores without the addition of FSW risk the cellular integrity of protists and cellular osmotic shock, yet its affects on measures of chl *a* have not been reported. Because the preparation and maintenance of large volumes of FSW consume a large amount of time and resources during cruises we evaluated melting ice cores without the addition of FSW for obtaining chl *a* measurements early in the SO GLOBEC cruises. This evaluation was conducted on ice cores collected during the July 2001 LMG cruise, where 10 pairs of cores were collected side by side (within 5 cm of each other). A paired comparison *t*-test showed that chl *a* measured on cores melted without the addition of FSW did not significantly differ from that obtained from the melting in FSW ($p = 0.3511$, critical two-tailed statistic). Microscopic examinations did confirm that soft-bodied protists were hard to identity in ice meltwater without the addition of FSW and that nondescript particulate matter (e.g., detritus, lipid droplets) did appear to be more prevalent in these sample, which is consistent with prior reports (Garrison and Buck, 1986). We also noted that the particulate matter was especially sticky on the sidewalls of the jars and buckets in the samples that were not melted with FSW (rubber policemen and spatulas were

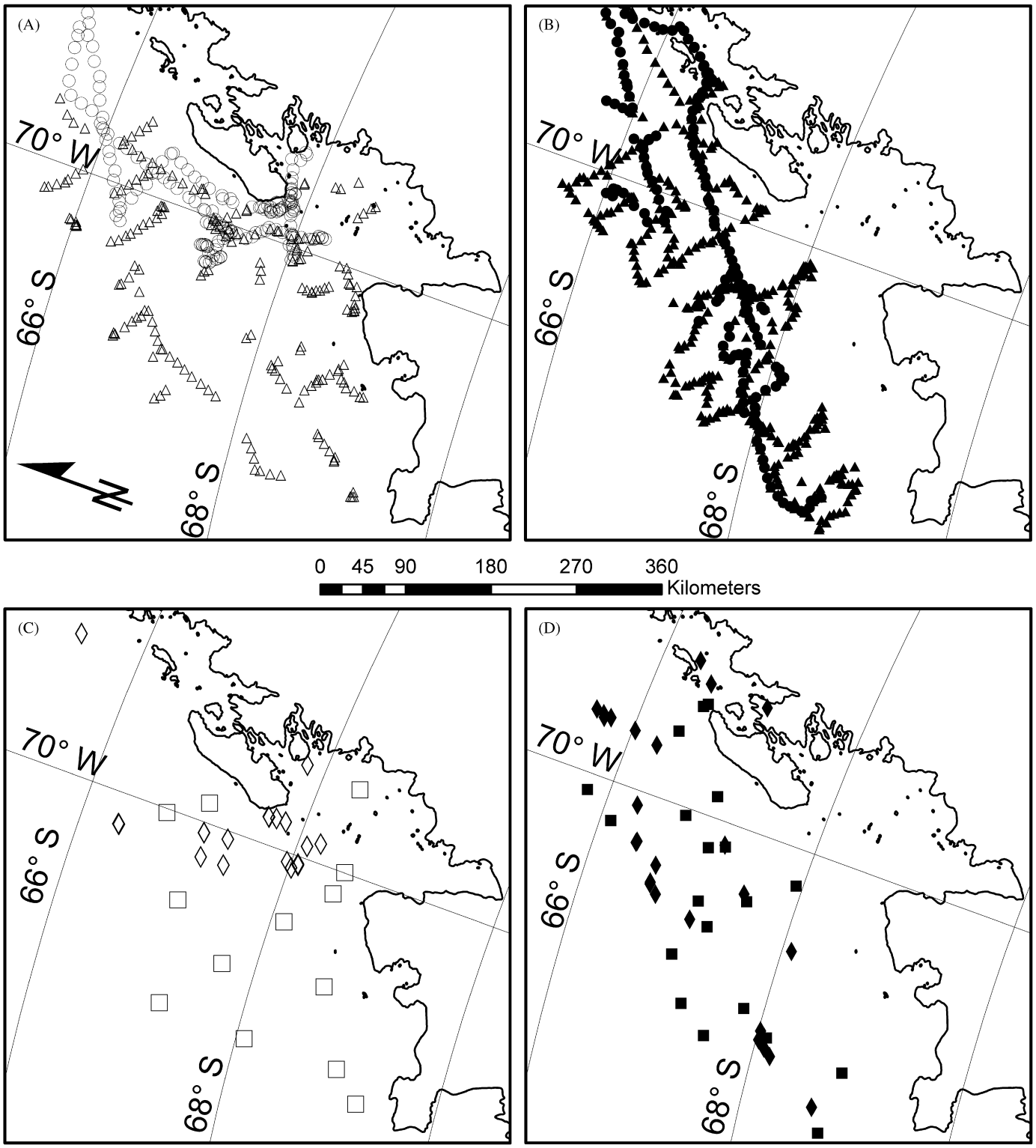

Fig. 1. Locations of ice observations (A and B) made during cruises on board the ARSV Lawrence M. Gould (circles) and RVIB Nathanial B. Palmer (triangles) during 2001 (A) and 2002 (B). Locations where ice cores were taken are also shown (2001 = C, 2002 = D; NBP cores in squares and LMG cores in diamonds). For more information on cruises see http://www.ccpo.odu.edu/Research/globec_menu.html and Hofmann et al. (2002).

routinely used to wash the sides of the containers just prior to samples for constituent analysis of samples melted with and without FSW additions).

Ice-core meltwater and sea water were filtered through GF/F filters and filters were retained for analysis of chl *a*. Filters were frozen (−80 °C) until extraction in 90% acetone and analysis of chl *a* content via fluorometry (Parson et al., 1984). Chl *a* in ice-core meltwater was corrected for dilutions by FSW (when FSW was used for ice-core melting). All values are presented herein as chl *a* concentrations in ice meltwater.

3. Results

3.1. Air temperatures and snowfall

Average monthly air temperatures measured at Rothera station dropped below freezing beginning in March of both 2001 and 2002 (Fig. 2). Air temperatures during March and April were similar between these years, yet from May until June of 2002 average monthly air temperatures were ca. 10 °C lower than during 2001. Average temperatures in July were similar (within 0.2 °C), yet from August to November of 2002 average monthly air temperatures were 1.1–6.9 °C lower than in 2001.

Snow fall and snow accumulation on the pack ice could not be measured prior to the study period due to the lack of *in situ* time series platforms on the ice (e.g., buoys) or adequate satellite sensors. However, snow accumulation (routinely measured manually at Rothera station) showed marked differences between 2001 and 2002 (Fig. 3), with 2001 having almost double the seasonal accumulation than that of 2002. The actual rates of snow accumulation were similar between the years from May to July and from September to November. However, rates in April and August were extremely different, which led to ca. 10-cm difference in snow accumulation in the early winter season and over 50-cm difference in accumulated snow during September, October, and November. These differences generally agree with measures of snow accumulation by Argos mass-balance buoys deployed in August–November 2001 and September–December of 2002, which recorded roughly 1 m of snow accumulation in 2001 and only 50 cm in 2002 (Perovich et al., 2004).

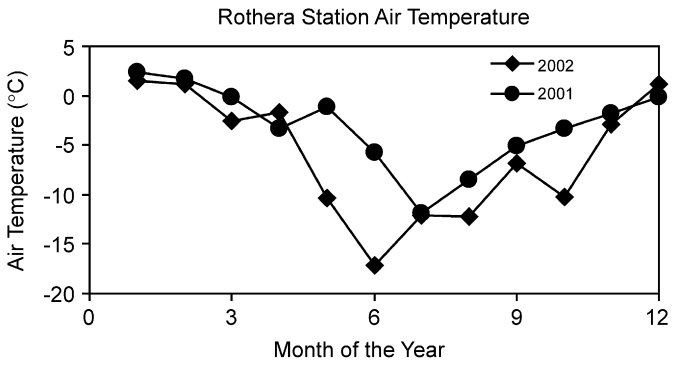

Fig. 2. Monthly averaged air temperatures at Rothera Station (British Antarctic Survey) during 2001 and 2002.

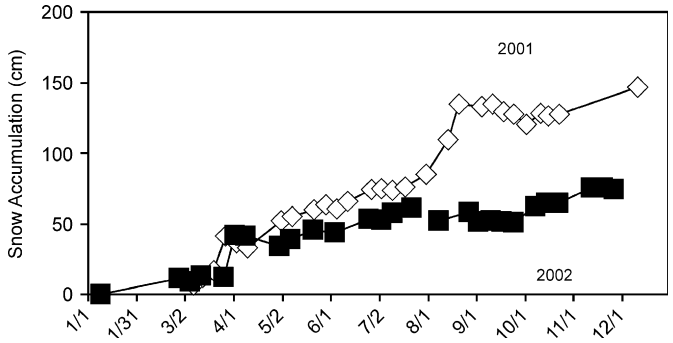

Fig. 3. Snow accumulation at Rothera Station measured during 2001 and 2002. (data courtesy of the meteorological monitoring team of the Rothera Station—British Antarctic Survey).

3.2. Ice dynamics

The annual advance of the pack-ice cover in the area of Marguerite Bay differed between the study years. The pack ice was present and covering Marguerite Bay and adjacent regions by mid-May in 2002 (Fig. 4). In contrast, Marguerite Bay was open water in May of 2001 (Fig. 4) and only in the latter part of May was ice forming in the southern reaches of Marguerite Bay and to the west of Alexander Island (also see (Perovich et al., 2004). The major expansion of ice coverage in the study area during 2001 occurred by mid-June. The study region was covered by pack ice having greater than 90% coverage throughout July to September in both years of the study.

3.3. Pack-ice statistics

When ice observations are broken into the ice types according to ASPeCt ice observation protocols a few substantial distinguishing characteristics of the ice covers are apparent between the two study years. Most notable are the differences in the coverage of 0.3–0.7 and 0.7–1.2 m thick first-year (FY) ice. FY ice 0.3–0.7 m thick comprised 58% of the areal coverage of the observations in 2001 and decreased to 43% in 2002. In contrast, the 0.7–1.2 m FY ice increased from 13% in 2001 to 26% in 2002. Also notable was the increase in the fraction of the ice surface area that was ridged, which increased from 12% in 2001 to 23% in 2002.

The observations in the NBP occurred over the more extensive survey grid while the LMG-based observations were limited to the areas more central to the study grid. Because of these differences in the ship's operational ranges it is not too surprising that the observations on the NBP yielded slightly larger values of the mean ice thicknesses (due to observing more ice floes between 60 and 90 cm thick) compared to those observations obtained from the LMG in both 2001 and 2002 (Fig. 5). Observations on the LMG recorded pack ice with mean thicknesses that were thicker in 2002 (mean = 48.8 ± 21.8 cm) than in 2001 (mean = 37.8 ± 15.3 cm). Observations from the NBP in 2001 and 2002 yielded ice-cover statistics for ice-thickness distributions that were more similar than those on the LMG, with ice thicknesses being 53.1 ± 16.0 cm in 2001 and 53.5 ± 21.2 in 2002 (Fig. 5). Snow cover thicknesses were also similar at 18.3 cm in 2001 and 17.6 cm 2002. The operational range of the NBP was different between years,

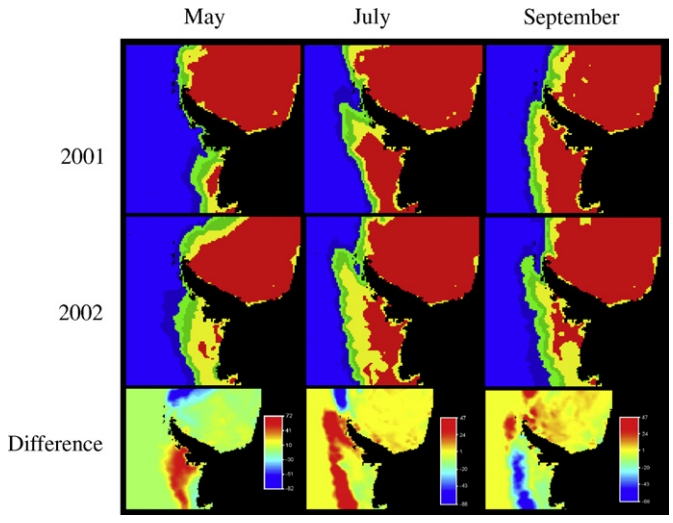

Fig. 4. Ice concentrations during May, July, and September of 2001 and 2002 (Comiso, 1990). Red, 80–100%; yellow, 50–80%; green, 30–50%; blue, 0–15%. Differences in images (lower panels) illustrate the difference in ice coverage in the region of Marguerite Bay occurring between the different months of each year.

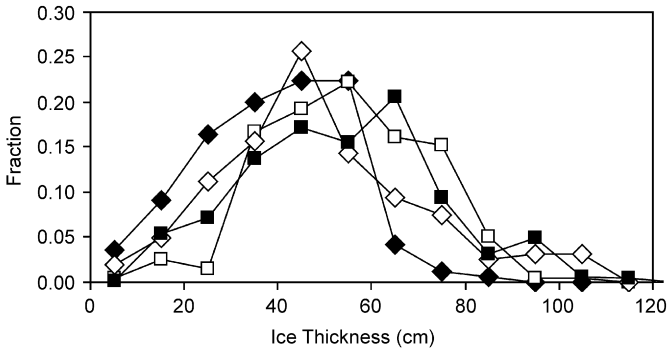

Fig. 5. Thickness distributions for ice observed from the LMG (diamonds) and NBP (squares) during GLOBEC cruises of 2001 (open symbols) and 2002 (closed symbols).

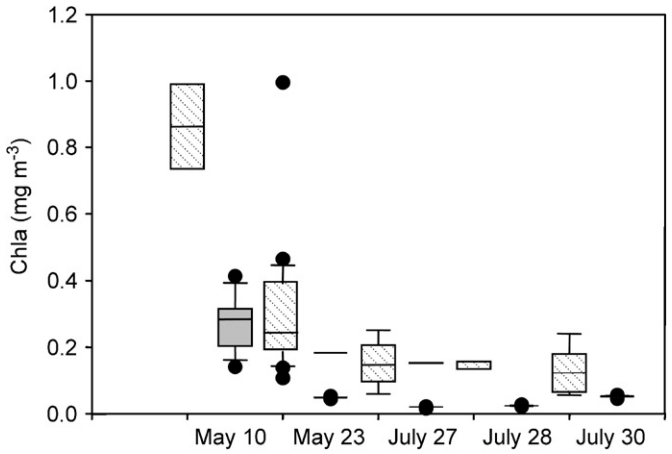

Fig. 6. Chlorophyll *a* concentrations in water collected in the upper 50 m of water column (gray boxes) and in newly formed ice (hatched boxes) collected at different times during the 2001 SO-GLOBEC cruises. Boxes show 65% confidence intervals while error bars denote 95% confidence intervals.

with the NBP ranging into Marguerite Bay region in 2001 and during 2002 the NBP was limited to regions adjacent to Marguerite Bay. Hence, the NBP statistics as well as those on the LMG are prone to biases caused by operational differences between the study years.

3.4. Water column and new ice biomass (2001 and 2002)

Chl *a* concentrations in the upper 100 m of the water column ranged from 0.20 to 0.51 $\mu g\,l^{-1}$ during the early May cruises and decreased by an order of magnitude to 0.019–0.050 $\mu g\,l^{-1}$ in the July–September time period. Collections of actively forming new ice in areas of frazil formation in leads and open water occurred primarily in 2001 as this was more of an ongoing process within the SO-GLOBEC grid during that year. The largest values for chl *a* in newly forming ice were encountered in Laboef Fjord in May of 2001, where newly forming ice had concentrations of up to 0.9 μg chl $a\,l^{-1}$ and the underlying water column (0–50 m depth) had concentrations of 0.29 $\mu g\,l^{-1}$. New ice and frazil ice had concentrations that were 2.5–7.8 times those in the water column (Fig. 6, Table 1) even during the mid-winter periods (July).

3.5. Ice floe's biomass

The necessity of obtaining a large number of ice cores for determining significant differences in micro-algal biomass led to the collection of over 100 ice cores in both 2001 and 2002. Ice coring was restricted to the ice floes that were generally thicker than 30 cm. Sampling of pancake, young gray white ice, shuga, and brash was more limited or did not happen due to the time and safety constraints. Despite this limitation, the routine ship-based observations indicate that we collected a large number of samples from the types of ice floes that covered over 70% of the ocean surface during the study periods.

Cores collected from FY ice of 0.3–1.2 m had chl *a* concentrations averaging approximately 1 μg chl $a\,l^{-1}$ of ice meltwater (Table 1) during 2001. The maximum concentrations of chl *a* reached 18.6 and 28.0 $\mu g\,l^{-1}$ in two separate ice cores that were collected at different stations, yet both were collected from the NBP well within Marguerite Bay (67.22°S, 74.47°W and 67.1°S, 69.53°W) in two of the more coastal stations of the study. The ice cores in general revealed no apparent trend in the vertical distributions of algal biomass, with maxima occurring within ice-core sections from the top, interior, and bottom of the ice cores

Table 1
Summary statistics of the pack-ice coverage, ice (H_i) and snow (h_s) thicknesses derived from observations and depth-averaged chla content (mg chla m^{-3}) of ice cores (lengths = C_l) collected during 2001 and 2002

Ice type	Observation statistics			Ice sample and core statistics	
	Coverage (%)	H_i	h_s	Chl *a*	C_l
Frazil					
2001	0.25	0.03±0.02 (6)	0±0	3.64±1.66 (2)	0.05±0
2002	0.13	0.06±0.04 (5)	0±0	NS[a]	NS
Shuga					
2001	0	NO[b]	NO	NS	NS
2002	0.85	0.08±0.02 (33)	0±0	NS	NS
Grease					
2001	0.36	0.03±0.03 (11)	0±0	NS	NS
2002	0.28	0.06±0.03 (13)	0±0	NS	NS
Nilas					
2001	3.44	0.06±0.02 (68)	0.2±0.5	0.14±0.1 (3)	0.04±0.01
2002	2.54	0.07±0.03 (50)	0.2±0.6	NS	NS
Pancakes					
2001	2.51	0.13±0.05 (28)	2.8±4.7	NS	NS
2002	2.18	0.16±0.04 (36)	5.9±4	NS	NS
Young gray ice, 0.10–0.15 m					
2001	3.83	0.12±0.02 (53)	1±1.6	1.42±0.22 (2)	0.1±0
2002	4.75	0.11±0.02 (123)	2.5±3.5	NS	NS
Young gray-white ice, 0.15–0.30 m					
2001	3.53	0.19±0.05 (53)	2.5±2.7	NS	NS
2002	8.28	0.21±0.06 (153)	5.2±4.5	NS	NS
First year, 0.30–0.70 m					
2001	58.84	0.5±0.1 (390)	17.2±8.4	1.55±2.22 (72)	0.49±0.2
2002	43.41	0.52±0.1 (519)	19.6±6.8	9.34±14.25 (179)	1.01±0.66
First year, 0.70–1.20 m					
2001	13.33	0.76±0.09 (60)	27.1±7.6	0.92±0.8 (20)	1.01±0.38
2002	26.05	0.84±0.11 (295)	25.1±9.4	5.36±6.47 (31)	0.97±0.29
First year, >1.20 m					
2001	0	NO	NO	1.79±1.6 (2)	1.59±0.2
2002	0.3	1.59±0.3 (5)	45±38.7	1.27±NA (1)	4±NA
Multiyear floes					
2001	0	NO	NO	NS	NS
2002	0.03	2±0 (2)	80±0	6.02±4.52 (7)	3.31±0.48
Brash					
2001	5.59	0.26±0.13 (110)	0±0	0.21±0.03 (2)	0.15±0.03
2002	2.26	0.17±0.1 (94)	0±0.3	NS	NS

[a] NS indicates none of this ice type was sampled.
[b] NO indicates none of this ice type was observed.

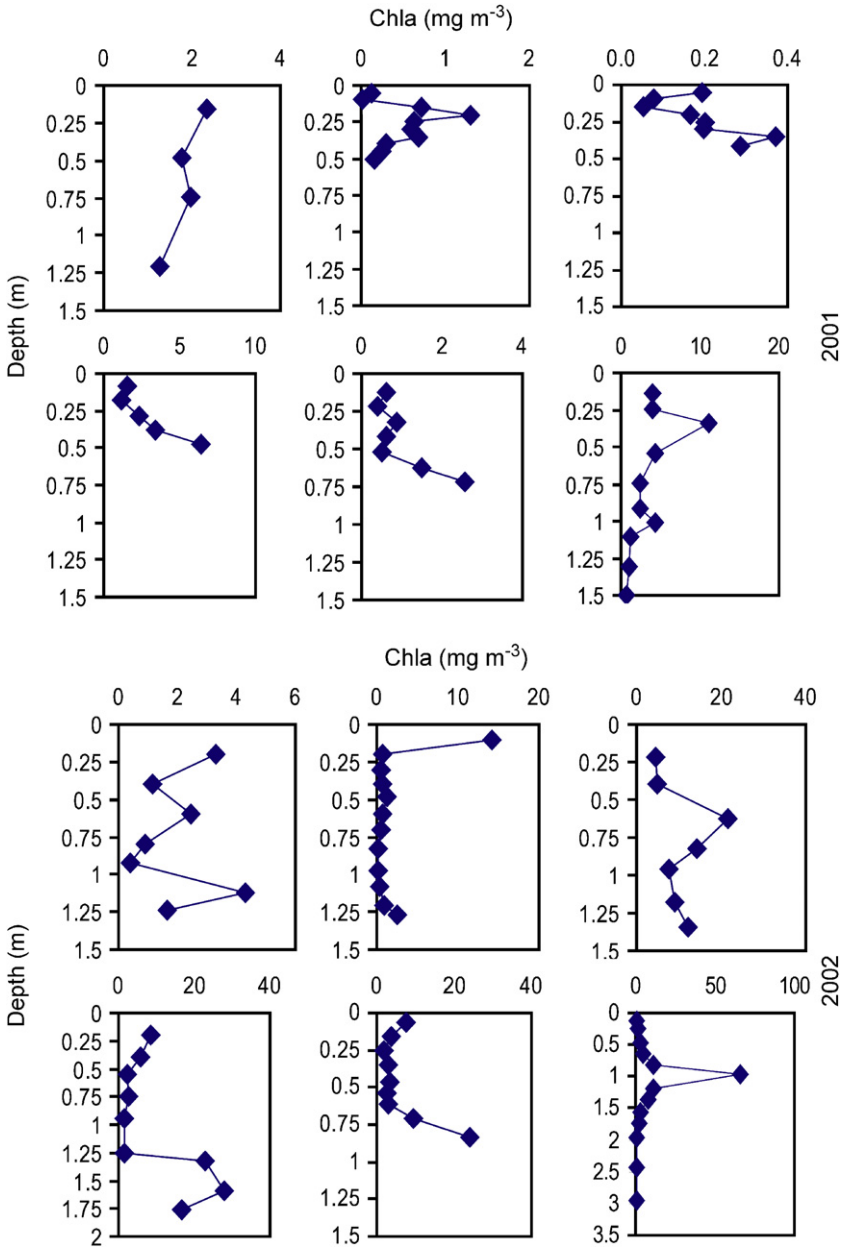

Fig. 7. Examples of the vertical profiles of chlorophyll *a* in ice cores from both 2001 and 2002 studies illustrating maxima occurring in bottom, middle, and surface sections of the ice floes. Note the differences in the scales for chl *a* concentrations among the ice cores.

(Fig. 7). It should be noted that there were only two to three anecdotal observations of visible colorations of sea ice throughout the GLOBEC study grid and throughout the duration of the 2001 cruises.

In direct contrast to 2001, the ice cover of 2002 contained floes that were visibly colored by algal pigments throughout the study area and throughout the duration of the winter (July–September) cruises. Routine observations of ice blocks during times when the ships were moving showed that ca. 40% of the ice floes contained visible pigmentation/coloration. In keeping with what was readily apparent from visual observations the ice cores contained ~10-fold higher chl *a* content during the 2002 winter cruises (FY ice of 0.3–0.7 m averaged 9.4 μg chl $a\,l^{-1}$ and FY 0.7–1.2 m ice averaged 5.36 μg chl $a\,l^{-1}$; Table 1). Several floes in 2002 were classified as multiyear floes and the chl *a* content of these cores averaged 6.02 $\mu g\,l^{-1}$. Similar to the findings in 2001, the maximum biomass in a core's vertical chl *a* profile occurred at different depths from different locations (Fig. 7).

Note that the summary statistics reveal a large variance in the chl *a* content in the ice cores. The large variance is due to the large spatial variability that is typical of sea ice (Fiala et al., 2006) and especially pack-ice systems (Dieckmann et al., 1998; Eicken et al., 1991). This variability led to a log-normal distribution of ice-core biomass in each year (Fig. 8). Comparison of the chl *a* content of the ice cores collected during the 2001 and 2002 season readily reveals that the 2002 studies yielded a significant ~10-fold higher biomass than in 2001.

During both years there was an apparent correspondence between the time of the ice core's collection and the natural-log-transformed chl *a* content within the ice cores (Fig. 9). These apparent increases yield estimates of chl *a*-specific micro-algal population growth rates of 0.04–0.09 d^{-1} during the studies.

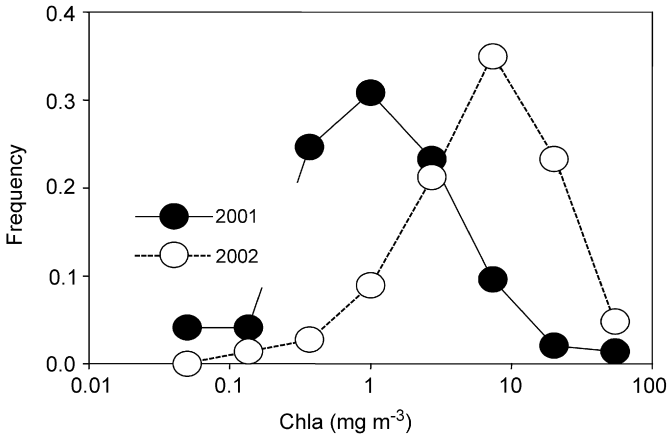

Fig. 8. Histogram of chlorophyll *a* content of ice cores that were collected at overlapping times of the year during 2001 and 2002 cruises.

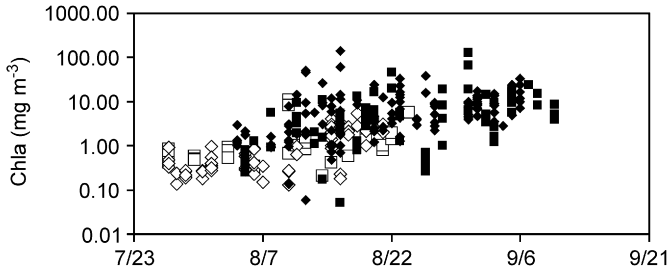

Fig. 9. Depth-averaged chlorophyll *a* content of ice cores collected during 2001 and 2002 shown in relation to the time (month/day) of the core collections. Open symbols denote 2001 samples and closed symbols represent those in 2002.

Limiting the statistical comparison of biomass in the ice cores that were collected only during the same days of the year between years (i.e. August) yields the same significant result that the ice cores in 2002 had significantly higher chl *a* content ($p<0.001$, Mann–Whitney Rank Sum test).

4. Discussion

Algal cells have been reported to be selectively scavenged and concentrated into the sea-ice matrix during the ice formation process (Ackley and Sullivan, 1994; Garrison et al., 1983; Grossmann and Gleitz, 1993). Consistent with these reports, chl *a* scavenging factors were measured to be fivefold during the initial frazil and grease ice formation processes. With ice formation occurring in May of 2002 (when water-column concentrations were 0.2–0.6 μg chl $a\,l^{-1}$) the scavenging of phytoplankton biomass could have accounted for 3 up to 6 μg chl $a\,l^{-1}$in the ice (making the conservative assumptions of scavenging factors of 5 up to 10 fold). During 2001 when the ice cover was forming in June and the water-column concentrations were below 0.2 μg chl $a\,l^{-1}$ the scavenging affects could have only accounted for 1–2 μg chl $a\,l^{-1}$ in the ice. These values are on the order of those routinely measured in the ice during 2001. Only on a few occasions was ice sampled with chl *a* higher than 1–2 μg l^{-1} and these samples were collected in small areas where the ice may have been formed in May.

In situ growth of sea-ice biota during the late autumn and late winter periods is likely to account for some of the biomass measured in the ice floes during 2002 (and possibly in some of the ice that was collected during 2001). Unfortunately we did not occupy ice floes during the late autumn period to document ice-algal dynamics. However, based on the timing of ice formation in the region as determined by earlier ship operations and from the satellite images it is likely that *in situ* production and algal biomass accumulation occurred to a much larger degree in 2002 than in 2001.

The differences in the air temperature at Rothera Station suggest that early season cold temperatures governed the timing of the onset of sea-ice formation. However, additional factors (such as condition of the region's water-column heat content and the circulation) are likely to have reciprocal interactions with the atmosphere (Stammerjohn et al., 2003) such that the ice conditions may have been the factor controlling the lower temperatures at Rothera Station in April and May.

The processes governing ice formation in the Marguerite Bay and adjacent shelf region create pack ice that has formed primarily through the pancake ice cycle (Eicken, 1992; Thomas and Dieckmann, 2002) with subsequent deformation and snow-ice formation (through flooding and freezing; Perovich et al., 2004). The result of these processes and the region's relatively warm setting and high snowfall (e.g., Fig. 3 and Perovich et al., 2004) creates a relatively warm and porous ice pack, which contains a number of different types of sea-ice microhabitats, where microbiota can colonize and proliferate. Hence, the pack ice in this region is expected to have production and accumulation of microbial biomass in surface, near-surface, and internal layers within the sea ice, which was evident in many of the ice-core profiles. Maxima of algal biomass at the bottom of the ice were documented. However, these accumulations were not observed to the extent that biomass has been found in land fast-ice systems (Grossi and Sullivan, 1985; Gunther and Dieckman, 2001) or in pack ice where cold temperatures and thin snow cover (Arrigo et al., 2003) have created relatively cold and saline conditions within the sea-ice interior.

Higher snow fall in 2001 (Fig. 3) may have contributed to the lower ice-algal biomass during that year. However, the statistics on snow thicknesses did not show that the ice had a substantially deeper snow cover in 2001. High snow fall on sea ice does not necessarily translate into more snow cover on the ice and reduced primary productivity. Rather, high snow fall when coupled with a high ocean heat flux can translate into snow flooding and freezing. The flooding and freezing also acts to thin the snow cover and thicken the sea-ice column through snow-ice formation (Jeffries et al., 1998). Through this process, near-surface habitats can be created, which increases the potential for sea-ice productivity and biomass accumulation (due to the creation of surface habitats near higher light and by warming the inner portions of the ice cover; Fritsen et al., 1998). Although less snowfall in 2002 may have helped in the enhancement of production and biomass accumulation in that year, the visual snow cover statistics on the sea ice as well as the statistics on snow depth along thickness transects (Perovich et al., 2004) show only a marginal difference in snow cover on the ice in the region. Therefore, the seasonal decline of phytoplankton biomass (available for incorporation into the new ice) and the seasonally declining radiation (available for growth of algae once in the ice habitats) when coupled with the differences in the timing of ice formation (late in 2001 and earlier in 2002) remain the most parsimonious explanation for the inter-annual variation in sea-ice-algal biomass observed.

The documentation of inter-annual variability in ice-algal biomass is one of the first results showing inter-annual variation in winter sea-ice biota in the pack-ice regime. This result readily leads to the speculation that the timing of ice formation may be a significant determining factor governing the amount of energy available to biota and ecosystems that rely on this energy during the winter months. Most notably, the juvenile krill and ice-associated life stages of other zooplankton that are known to rely

on ice-algal biomass in the winter (Atkinson et al., 2002; Bathmann et al., 1993; Daly, 1990) may be susceptible to this level of variation in food availability. Much work needs to be done to investigate whether or not the low levels of ice biomass similar to those documented during 2001 are perhaps limiting for grazing and zooplankton growth. However, the correspondence between low ice-algal biomass in 2001 and low growth rates of juvenile krill in 2001 (Quetin et al., 2007) suggests that that this may be the case. It is worthwhile to consider that as the plausible links between the autumnal phytoplankton biomass decline, the timing of ice formation and winter ice-algal biomass to the overwintering success of young krill may help provide additional mechanistic explanations for the associations between observed changes in the region's climate and changes in the local marine ecosystem (Fraser and Hofmann, 2003; Hofmann et al., 2002; Moline et al., 2004; Ducklow et al., 2006).

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