

Algal Biomass in the East Antarctic Pack Ice



Michael Grose

Being a dissertation submitted in fulfillment of the requirements for the degree of

Masters of Science by Research (Msc)

Institute of Antarctic & Southern Ocean Studies (IASOS)

University of Tasmania, 2004

Declaration

I hereby declare that this thesis contains no material which has been accepted for the award of any degree or diploma in any university, and that, to the best of my knowledge and belief, this thesis contains no copy or paraphrase of material previously published or written by any other person, except where due reference is made in the text.

A handwritten signature in black ink, appearing to read 'Michael Grose', written in a cursive style.

Michael Grose
IASOS
University of Tasmania
2004

Authority of Access

This thesis may be made available for loan and limited copying in accordance with the *Copyright Act 1968*.

A handwritten signature in black ink, reading "Michael Grose". The signature is written in a cursive style with a large, stylized 'M' and 'G'.

Michael Grose

2004

Acknowledgments

I would like to thank a number of people for their support, ideas and help during this research.

My supervisor Assoc Prof Andrew McMinn, and my advisors Dr Rob Massom, Chris Walisham and Dr Steven Nicol.

The crew and expeditioners of Polar Bird Voyage 3 2001. Especially Dr Collin Roesler, Heidi Franklin, Louise Trennery, Mel Fitzpatrick, Dr Donna Roberts.

All the other IASOS students for advice and support, especially Matt Paget for computer advice and sea ice help.

My family, friends and housemates for their help, support and good times.

Petya Fitzpatrick, least of all for her support, guidance and editing skills. Most of all for being Petya Fitzpatrick.

Publications

Papers in Refereed Journals

1. Grose, M; McMinn, A (2002) Algal biomass in east Antarctic pack ice: how much is in the east? In: Huiskes, A.H.L; Gieskes, W.W.C; Rozema, J; Schorno R.M.L; van der Vies, S.M; Wolff, W.J. (eds) **Antarctic Biology in a global context**. Backhuys Publishers, Leiden, pp 21-25.

Presentations

1. Grose, M; McMinn, A (2001) **Algal biomass in east Antarctic pack ice: how much is in the east?** Poster Presentation, Scientific Committee on Antarctic Research (SCAR) VIII Biology Symposium: Antarctic Biology in A Global Context, Amsterdam the Netherlands.
2. Grose, M; McMinn, A (2001) **Algal biomass in east Antarctic pack ice: how much is in the east?** Poster and Oral Presentation, Australasian Society of Phycology and Aquatic Botany (ASPAB) National Annual Congress, Heron Island 2001.
3. Grose, M; McMinn, A (2001) **Algal biomass in east Antarctic pack ice: how much is in the east?** Poster Presentation, Australian Academy of Technological Science and Engineering (AATSE), National meeting, Hobart 2001.

Abstract

Sea ice algal biomass in the eastern Antarctic zone was assessed using measurements and observations. This assessment was entered into a simple model, using remote sensing data to estimate habitat extent, to make an estimate of total sea ice algal biomass in the region.

The late spring (2000) algal biomass and species composition in the bottom and surface communities in pack ice floes in East Antarctica (105-115°E) is described. Ice cores and surface ice samples were taken, and a simple ship based observation technique to estimate algal biomass is evaluated and assessed. Measured values of biomass compared well with observed values. The bottom algal biomass was between 0.66 to 28.05 mg Chl *a* m⁻², and highly variable across the bottom of ice floes. Surface ice algal biomass was less than the bottom and was heavily influenced by floe edge effects.

Remote sensing data, viewed in GIS software, was used to calculate the ice thickness distribution and the habitat extent of each ice type across the entire study area (30-150°E). This information was used, together with measurements of the distribution of algal biomass within the ice column, to estimate total algal biomass. The total sea ice algal biomass in this region was estimated to be 7.81 Tg C on 20 November 2000, 80% of which was in the bottom community. Extrapolating this result to December based on a conservative ice algal growth rate resulted in a maximum standing algal crop of 8.51 Tg C, 95% of which was in pack ice, and 80% was in the pack ice bottom community. This is ~14% of the Antarctic ice algal biomass. These results suggest that bottom communities are far more important in the East Antarctic region than they have previously been assessed to be.

Table of Contents

<i>Chapter 1.1 Physical Properties of Sea Ice</i>	<i>1</i>
1.1.1 Introduction	1
1.1.2 Sea Ice Formation	1
1.1.3 Ice Growth	2
1.1.4 Melting	2
1.1.5 The Eastern Region	3
<i>Chapter 1.2. Ecology in the Sea Ice Zone</i>	<i>4</i>
1.2.1 Sea Ice and the Food Web	4
1.2.2 Ice Algae as a Food Source	6
1.2.2.a Krill	7
1.2.3 Ice Algae in the Carbon cycle	8
<i>Chapter 1.3. Sea Ice Algal Ecology</i>	<i>10</i>
1.3.1 Introduction	10
1.3.2 Algal Community Ecology	10
1.3.3 Controlling Factors of Algal Biomass	12
1.3.3 Establishment of communities	13
1.3.4 Demise of Communities	14
<i>Chapter 1.4. Estimating Total Algal Biomass</i>	<i>15</i>
1.4.1 Previous Estimates	15
Technique	15
1.4.1a Extrapolation	16
1.4.1b Models	16
1.4.2 Other Useful Techniques and Ideas for making an estimate	17
1.4.3 Sea Ice Data Sources	18
1.4.3a Remote Sensing	18
<i>Chapter 2. Distribution and Composition of Algal Biomass in East Antarctic Pack Ice During Late Spring 2000</i>	<i>19</i>
2.1 Abstract	19
2.2 Introduction	19
2.3 Materials & Methods	20
2.4 Results	24
2.5 Discussion	27
<i>Chapter 3 The Estimate of Algal Biomass in East Antarctic Pack Ice</i>	<i>28</i>
3.1 Abstract	28
3.2 Introduction	28
3.3 Methods	29
3.4 Results	30

3.5 Discussion	33
Chapter 4 Discussion and Conclusions	35
4.1 Overview	35
4.2 Main conclusion	35
4.3 Other conclusions, other points	36
4.4 Limitations, sources of error	36
4.5 Future research	37
References	38

Tables

Table 1.1.1. Mechanisms of New Ice Formation	1
Table 1.3.1 Sea Ice Algae Communities found in Antarctic Sea Ice	11
Table 1.4.1. Estimates of total Algal Production in the sea ice zone, Antarctica	15
Table 2.1. Chlorophyll a Concentration of the Bottom Algae Community of East Antarctic Pack Ice Floes in Late Spring 2000	25
Table 2.2. Diatom biodiversity in surface ice and snow across pack ice floes	26
Table 3.1 Total sea ice area and sea ice algal biomass parameters from east Antarctica (30-150°E) in spring 2000/2001. Data was measured in November and extrapolated forward into December and backwards to August. No values are given beyond December because the rapidly melting ice changed the natural algal habitats	31

Figures

Figure 1.2.1 The Southern Ocean ecosystem (energy flow) associated with intact sea ice – Winter / early Spring	5
Figure 1.2.2. The Southern Ocean food web (energy flow) in the marginal ice edge ecosystem during a phytoplankton bloom. Dashed lines represent vertical migration	5
Figure 1.2.3. Feeding relationships of the communities associated with Antarctic sea ice, including the “microbial loop” associated with this community	6
Figure 2.1. Ice Chart of the Casey Region (NSIDC Colorado University) showing Ship’s Track (RV Polar Bird) and Sampling Sites	20
Figure 2.2 Ship track of the RV Aurora Australis, V3 2000	21
Figure 2.3. Colour Chart for Observation of "Brown" Sea Ice Colour (colours initially assigned visually, then calibrated against in situ ice chlorophyll a)	22
Figure 2.4. Relationship between observed and measured Chl a biomass	22
Figure 2.5 Calibration of observed colour with measured algal biomass from sea ice cores Antarctica Spring 2000 - linear regression including equation of line.	23
Figure 2.6. Integrated surface ice biomass across pack ice floes - East Antarctica (30°-150°E), spring 2000. Each line represents a transect on a different floe in the same area	25
Figure 3.1 Biomass distribution in eastern Antarctica (30-150E), Spring 2000. Biomass is an integration of surface and bottom communities estimated from ice core values and extrapolated using NOAA ice charts derived from passive microwave satellite data	32
Figure 3.2 Ice extent and total sea ice algal biomass in East Antarctica (30-150°E), Spring 2000.	34

Chapter 1.1 Physical Properties of Sea Ice

1.1.1 Introduction

Sea ice is a globally significant habitat for biology. As an ecosystem type, seasonally ice covered seas cover $35 \times 10^6 \text{ km}^2$, or 13% of the world surface (Parkinson and Gloersen 1993). This is larger than most terrestrial biomes such as grasslands, tundra or deserts (Lizotte 2001). Each year a ring of unbounded sea ice forms around the Antarctic continent and a land-bounded basin of sea ice forms in the Arctic. Sea ice provides a vast physical habitat for sea ice algae communities to grow in. A strong interaction exists between the physical processes that form, evolve and deteriorate sea ice, and the biological communities located within sea ice (Ackley & Sullivan 1994).

Apart from where specifically noted, this study is concerned with Antarctic sea ice, not Arctic, and may have differences to Arctic structures of processes. The Antarctic sea ice cover ranges from $20 \times 10^6 \text{ km}^2$ in late winter (September & October) to about $4 \times 10^6 \text{ km}^2$ in late summer (February & March) (Zwally *et al.* 1983, Comiso & Zwally 1984). The ice edge advances most rapidly in May and June, moving north at a rate of 4.2 million km^2 per month. November and December are the months of most rapid retreat, when the ice edge recedes at a rate of 6.9 million km^2 per month (Squire 1987). The average rate of advance is 2.4 million km^2 per month and average rate of retreat is 3.3 million km^2 per month. Sea ice can be divided into two different types; fast ice which is a continuous sheet of sea ice attached to land; and pack ice, which is non-attached, drifting sea ice. The distribution of pack ice is highly variable as the ice cover is frequently broken up by storms and the resulting floes drift large distances driven by surface currents and winds.

1.1.2 Sea Ice Formation

Sea ice can form rapidly in Antarctic waters in a matter of hours. The seawater surrounding Antarctica freezes at a temperature between -1.84°C and -1.87°C , depending on the salinity (Knox 1994). Once the freezing point has been reached, minute spherical crystals of pure ice form – which then grow into thin discs or needles (Nicol & Allison 1997). New, unattached ice forms floating crystals called frazil. Water containing frazil can sometimes appear greasy; and is called grease ice. The subsequent ice formation process is then dependant on the turbulence of the water. The four general formation processes are summarised in table 1.1.1.

Table 1.1.1. Mechanisms of New Ice Formation

Undisturbed	With Turbulence	Under Ice	Freeboard
1. Discoids grow into hexagonal dendritic stars called 'frazil' crystals.	1. Frazil forms a layer of 'grease' ice several metres thick.	1. Heat is removed from the ice-water interface into the ice	1. The weight of snow cover depresses the surface of the ice below sea level.
2. Frazil consolidates into a new flexible sheet called 'nilas' – 0.1 to 0.2 m thick.	2. Frazil consolidates in plumes then into circular pieces with upturned edges called 'pancakes'.	2. Long columnar crystals form under ice	2. Seawater infiltrates into the snow layer.
3. Nilas sheets raft and consolidate.	3. Pancakes grow, raft and fuse together.	3. Crystals consolidate into 'congelation' ice	3. Seawater freezes to form 'snow-ice'.

Adapted from Nicol & Allison (1997)

In undisturbed conditions, frazil crystals accumulate to form a flat consolidated layer called a nilas sheet. In turbulent conditions, frazil crystals aggregate into small discs called pancakes. Pancakes may develop upturned edges from buffeting into each other.

New ice also forms in association with existing sea ice, at the under ice surface or the surface snow layer flooded with seawater (the freeboard layer). Long ice crystals grow under the ice, called congelation ice. This process is slow since the covering ice sheet is an effective insulator, limiting heat loss. Seawater infiltrating the snow at the freeboard layer freezes quickly to form 'snow-ice', as it is exposed directly to the much colder atmospheric temperature.

A biologically important result of sea ice formation is the incorporation of phytoplankton and other biological material from the seawater directly into the ice. Cells can provide a nucleation site for ice crystal formation or can be scavenged by existing ice crystals (Garrison *et al.* 1983). Algal cells also become incorporated into sea ice through subsequent ice formation by flooding of snow by seawater, and into congelation crystals. Ice algae in ice affects the porosity of the ice, which in turn affects its mechanical strength and the break up of floes during melting (Eicken *et al.* 1991).

1.1.3 Ice Growth

Once new ice has formed, dynamic, mechanical processes are very important. Since sea ice is highly mobile, it is often in compression or in divergence. Compression causes ice sheets to slide on top of each other (raft) and join together (fuse). As well as ice rafting, ice grows through new ice freezing onto the under-surface of a sea ice sheet to form congelation ice (accretion). In periods of higher water temperature, ice can also melt off the bottom of the sheet (ablation). A typical pack ice floe of 40 cm thickness is usually made up of several layers of frazil, congelation and snow-ice, indicating repeated rafting and ridging, as well as periods of new ice growth on the under surface. Typically, textural analysis of east Antarctic pack ice shows 39% congelation ice, 47% frazil ice, 13% snow-ice and 1% other types (Worby *et al.* 1998).

Ice grows continuously throughout autumn and winter. The mean ice thickness changes from 0.31 m in December to 0.52 m in August (undeformed and including open-water areas) and the mean snow thickness changes from 0.02 m in March to 0.12 m in September – including open water and snow-free areas (Worby *et al.* 1998). The peak in sea ice cover occurs in September or October, after this there is no net ice growth of ice (Comiso & Zwally 1984). Localised formation of new ice types can occur, but no net gain of ice mass is made.

The maximum ice cover varies from year to year, in both extent and timing. The maximum extent of sea ice cover has been influenced by changes in climate, indicated from various sources such as sediments (e.g. Murphy *et al.* 1995), fast ice records (Murphy *et al.* 1995) and whaling records of ice edge (de la Mare 1997). An asymmetry has been observed in the changes in sea ice extent in the Arctic and Antarctic (Cavalieri *et al.* 1997).

1.1.4 Melting

New ice formation occurs in the autumn and winter months, creating a heterogenous cover of different ice types and open water (Worby & Massom 1995). Pack ice completely disintegrates and melts in spring and summer, fast ice may partially do so. Due to the dynamic mechanical processes, and the heterogenous cover, melting is not an even process. Winds are a dominant factor not only in the climatology of Antarctica, but also the sea ice melt and the associated formation of phytoplankton blooms (Goodrick 1997). Katabatic winds blowing offshore are important to the ice melt near the coast, other winds are important throughout the entire sea ice zone. Wind causes ice movement, including the break up of patches of ice and blowing ice off shore into warmer waters, and this causes a more rapid decline in ice cover. By mid-summer, remnant multi-year ice is the

only ice remaining and there are generally no thin or forming ice types. The remnant ice is generally composed of uniform floes greater than 0.6 m thick. Specific localised events and conditions affect the pattern of ice break out and melting.

Sea ice models of dynamics and thermodynamics have been relatively successful in describing the sea ice movement, formation and demise (Lu 1998, Lu *et al.* 1988, Walsh *et al.* 1993, Pollard & Thompson 1994).

1.1.5 The Eastern Region

The sea ice region studied here is that between 30 and 150°E, which is within the “south-west Pacific” region of some studies (Arrigo *et al.* 1997, Lizotte 2001), or the “Indian Ocean” sector of some others (Quetin *et al.* 1994). The sea ice of this region is in a band that extends from as little as 300 km from the coast and retreats close to the coast in summer (Worby *et al.* 1998). The latitude of the sea ice zone dictates the solar radiation, day length and growing season available for algal communities in the ice. The open coastline of East Antarctica makes it highly vulnerable to storms and the effects of wave and swell penetration (Massom *et al.* 1999). Other regions such as the Weddell and Ross Seas are less exposed and bound by landforms and so the ice persists for longer.

East Antarctic pack ice is highly mobile, with a mean drift rate calculated to be 0.22 m s^{-1} (Worby *et al.* 1998). Movement of ice in the region is in net divergence, but there are frequent periods of convergence which cause rafting, ridging and deformation of the ice. There is considerable variability in sea ice structure and thickness within this area, with the influence of polynyas, glacier tongues and iceberg activity. For example, the Mertz Glacier Tongue and the associated Mertz Polynya occur in the region 140-150°E. These features create a semi-constant “stream” of thick broken-out fast ice floes and other large floes extending westwards from the north end of the glacier terminus (Massom *et al.* 2000). A cycle of “back-filling” and “flushing out” of ice in the polynya varies inter-annually (Massom *et al.*, 2000). Two separate zones at 90-120°E and 120-150°E are used to separate areas of different ice thickness distribution and characteristics (Allison & Worby 1994). A more detailed description of the structure, properties and drift of east Antarctic pack ice region is available in Worby *et al.* (1998), Allison & Worby (1994), and Worby & Massom (1995).

Chapter 1.2. Ecology in the Sea Ice Zone

1.2.1 Sea Ice and the Food Web

The Antarctic marine ecosystem – the assemblage of plants, animals, microbes, biogeochemical cycles, ocean, sea ice and island components south of the Antarctic Convergence – is among the largest readily defined biomes on Earth (36 x 106 km²; Hedgpeth 1977). The Antarctic marine ecosystem was once thought to comprise mainly a simple chain from diatoms to krill to whales (Nicol & Allison 1997). It is now known that the ecosystem is not so simple and that this pathway is not the only energy path through the ecosystem and there are many other important components. The present view is that the ecosystem is composed of a series of communities that vary in space and time in the waters between the Antarctic convergence and the continent, rather than a single ecosystem (Nicol & Allison 1997). However, the links between primary producers, grazers and apex predators (seabirds, seals and whales) are often short and may involve fewer than three or four key species. Predators tend to concentrate on a core group of prey species, for example, the abundant euphausiids and fish close to the base of the food web. Prey/predator interactions (i.e. krill/Adelie penguins) are strongly mediated by critical periods during reproduction of both prey and predator.

The dynamics of these different communities vary greatly, and are affected by local conditions. Ocean circulation greatly affects not only the sea ice extent, but also the ecosystem structure in the east Antarctic region (Nicol *et al.* 2000a). Near Antarctica, the sea ice cover not only determines the ecology of ice biota, but it also influences the pelagic systems under the ice and at the ice edge (Legendre *et al.* 1992). Within the sea ice zone there are four distinct zones and four corresponding regional ecosystem structures; seasonal pack ice, coastal zone, perennial pack ice, and marginal ice zone (Eicken 1992). The annual pack ice is heavily affected by ocean swell at the outer edge. The physical action of ocean swell imparts a distinctive structure to Antarctic sea ice (Ackley *et al.* 1979) and creates a range of ice-related habitats which support the development of diverse biological sea ice communities (Legendre *et al.* 1992; Ackley and Sullivan 1994; Arrigo *et al.* 1997). The sea ice algal communities are discussed in detail in the next chapter.

Primary producers are grazed by a complex web of consumers, comprising fish, squid, crustaceans and heterotrophic microorganisms, of which krill are the most abundant. The sea ice extent also affects the population structure of the consumers. There is a possible relationship between sea ice extent and krill or salp dominance in the ecosystem. Greater ice extent has been observed to yield high krill abundance while a decrease in sea ice extent is followed by an increase in salp dominance (Loeb *et al.* 1997; Nicol *et al.* 2000a, b). This relationship appears to be due to the role of sea ice as a habitat and a food source for the consumers.

The consumers in turn are utilized by the predators of the sea ice zone; mainly penguins, seabirds, seals and whales. The sea ice cover represents both a barrier preventing surfacing by diving animals and a haul out platform for resting and breeding. Within the different Antarctic regions, the numbers of top predators can reflect the general richness or productivity of the area (van Franeker 1992).

The present view of the food web in Antarctic sea ice is outlined in Figures 1.2.1 and 1.2.2, showing the numerous consumer level interactions. Figure 1.2.1 shows the food web with intact ice and Figure 1.2.2 shows the food web during the spring ice edge phytoplankton bloom.

Figure 1.2.1 The Southern Ocean ecosystem (energy flow) associated with intact sea ice – Winter / early Spring

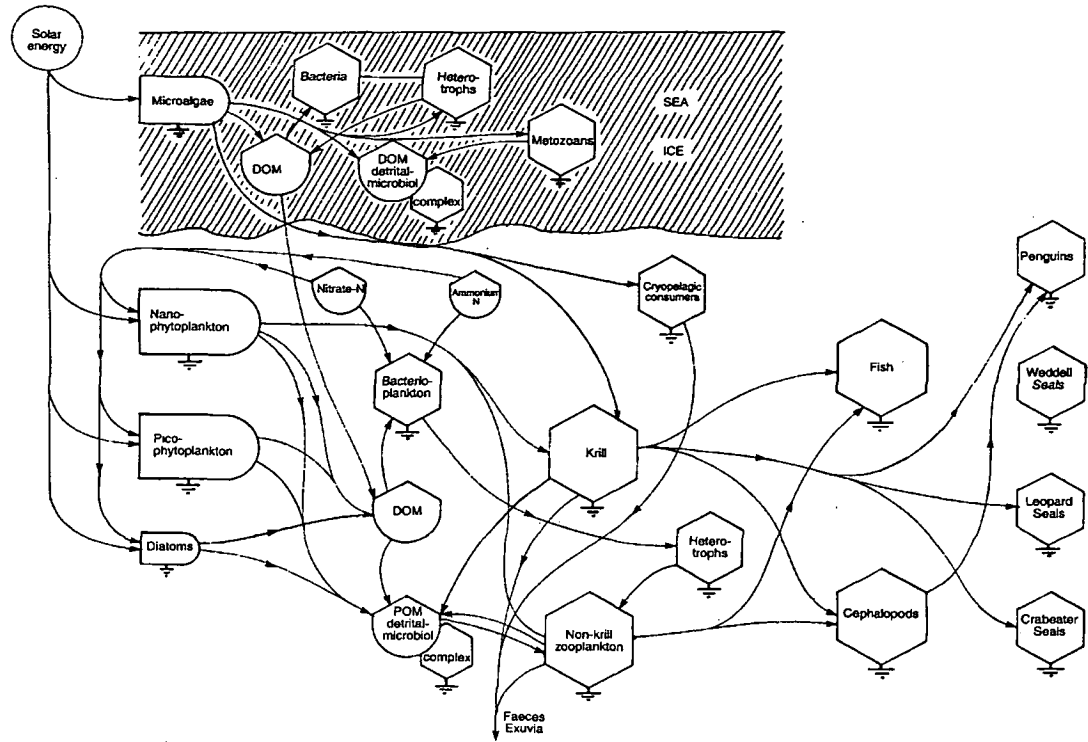
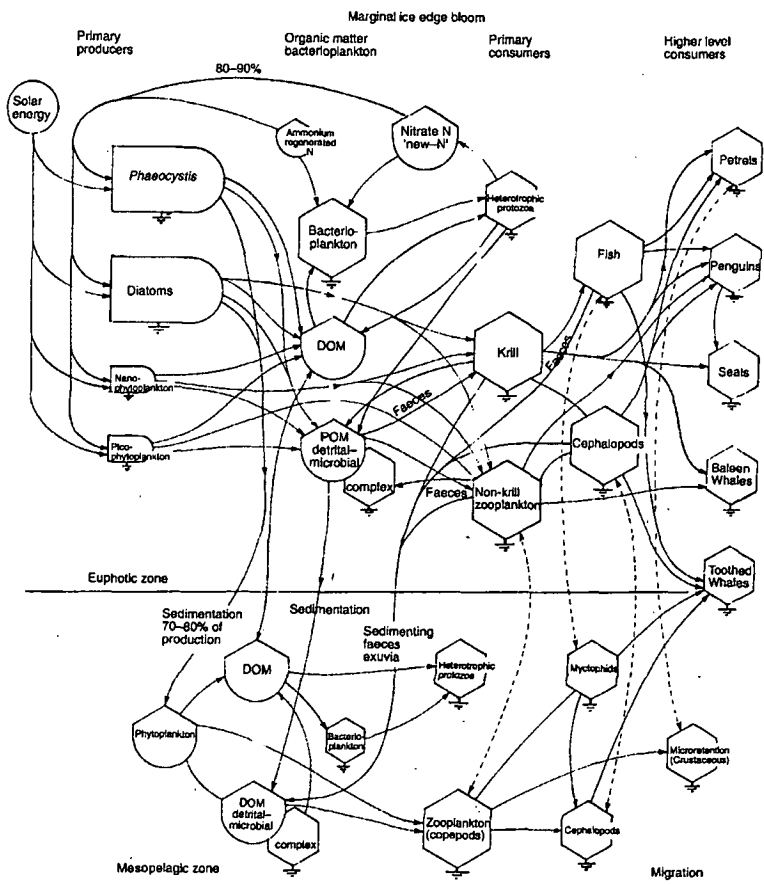


Figure 1.2.2. The Southern Ocean food web (energy flow) in the marginal ice edge ecosystem during a phytoplankton bloom. Dashed lines represent vertical migration

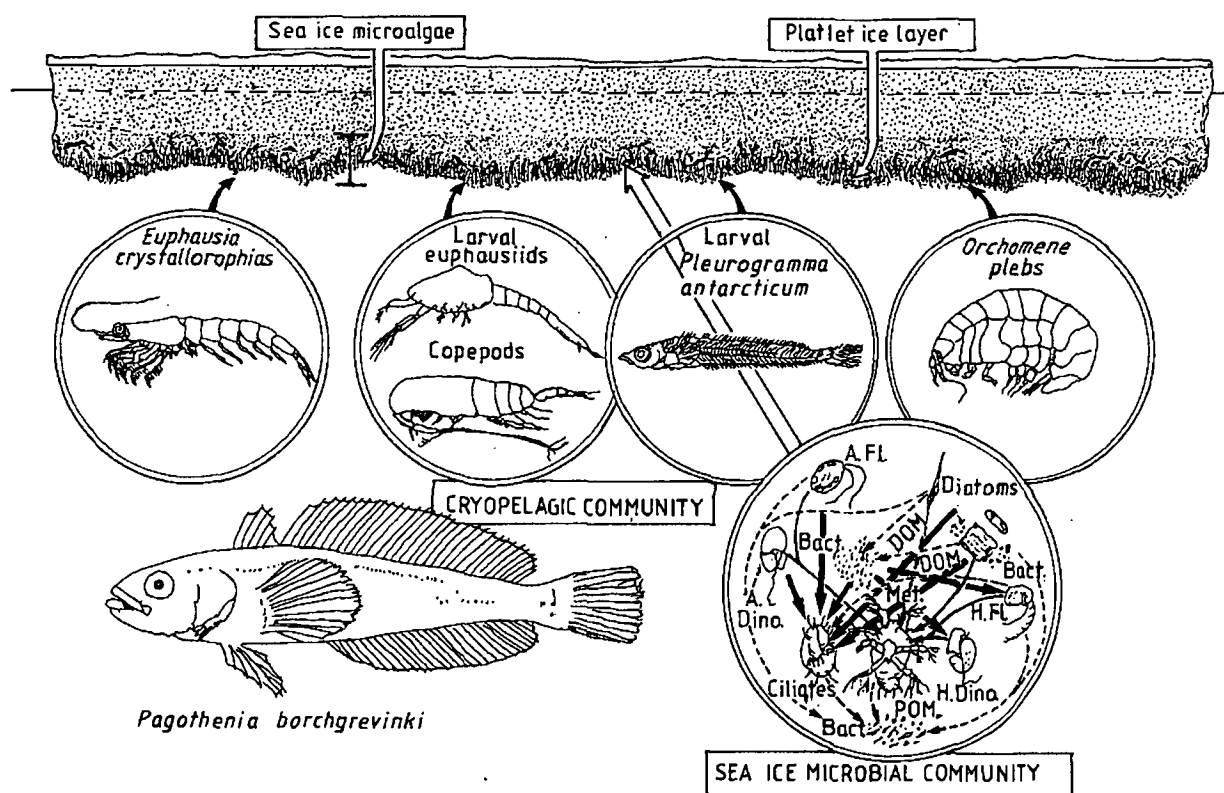


(source: Knox 1994)

The consumers in the sea ice zone graze on several communities of autotrophic organisms. The major communities of primary producers, or sources of organic carbon, are within 4 divisions; the non-ice edge phytoplankton, the pack ice algae, the fast ice algae and the phytoplankton associated with the spring ice edge bloom. All these communities form part of a complex microbial loop, comprised of large diatoms, flagellates, heterotrophic microorganisms, and bacteria (Figure 1.2.3). This study is concerned with the sea ice microbial community (SIMCO) associated with pack ice as a source of primary production to consumers. The community ecology of the pack ice algae is discussed in the following chapter.

Figure 1.2.3. Feeding relationships of the communities associated with Antarctic sea ice, including the “microbial loop” associated with this community

A.FI = Autotrophic flagellate; H.FI = Heterotrophic flagellate; Dino. = Dinoflagellate; H.Dino = Heterotrophic dinoflagellate; Bact. = Bacteria; DOM = Dissolved organic matter; POM = Particulate organic matter



Source: Knox (1994)

1.2.2 Ice Algae as a Food Source

Various metazoans live in the ice and use autotrophs as a food source (Hamner *et al.* 1983, Hoshiai & Tanimura 1986, Hoshiai *et al.* 1987, Kottmeier & Sullivan 1987, Daly & Macaulay 1988, Garrison & Buck 1989a). Ice algae represents a major potential food source to grazers, especially in winter when the ice algal concentration in the sea ice bottom is high but the phytoplankton standing crop is low (Fukuchi *et al.* 1985). It therefore appears likely that the grazers opportunistically use ice algae as a major food source. There are a variety of

strategies employed by zooplankton to survive over-winter, including starvation (Virtue *et al.* 1994), dormancy, a reduction in metabolic rate, and opportunistic feeding – including feeding on sea ice algae (Torres *et al.* 1994).

Some species of copepods appear to reproduce and breed within the ice matrix, and have connections to the ice throughout their entire life cycle (Schnack-Schiel *et al.* 1998, Swadling *et al.* 1997a). Gut contents have indicated that the copepod *Paralabidocera antarctica* utilises ice biota, consisting mainly of diatoms, as the main food source near Syowa station (Hoshiai *et al.* 1987). Amphipods graze on Arctic bottom ice algae, to varying degrees (Werner 1997). The degree to which grazers utilise ice algae as a food source is still unclear. It is possible that there is a significant transfer of carbon by this pathway. However, the lack of data and difficulty of study has meant that the pathway remains unquantified.

1.2.2.a Krill

The most abundant zooplankton in the Antarctic sea ice region is the Antarctic krill (*Euphausia superba*). The distribution of Antarctic krill, especially juveniles, is strongly influenced by the sea ice cover throughout their lives. A heavy ice cover in winter appears to lead to relatively high abundance of small krill in the population (Kawaguchi & Satake 1994), possibly because sea ice provides a safe habitat for juvenile krill (Daly 1990). The sea ice substrate may also be useful to krill as refugia from large predators (Marschall 1988).

At least part of the link between krill and sea ice is the use of sea ice biota as a food source. Antarctic krill use a variety of food sources; plankton ranging from nano-phytoplankton to macro zooplankton (Boyd *et al.* 1984), protozoans, copepods, non-crustacean metazoan food (Hopkins & Torres 1989) and cannibalism of other krill (Boyd *et al.* 1984). Antarctic krill have been observed to feed on the under surfaces of ice containing microalgae both *in situ* and in the laboratory (Stretch *et al.* 1988, Hamner *et al.* 1983, Carey 1985, Daly & Macaulay 1988, Marschall 1988, Runge & Ingram 1988, 1991, Daly 1990). Analysis of stomach contents of the crystal krill (*Euphausia crystallorophias*) has shown they feed upon some benthic algae as well as planktonic algae (Kittel & Ligowski 1980). The under ice habitat, especially in layers between over-raftered ice floes is an essential feeding ground for the first year juveniles (Frazer *et al.* 1997). Juvenile krill may use sea ice biota as their primary source of carbon and energy during spring, in the area of the Antarctic Peninsula (Daly 1998). It is hypothesised that juvenile survival, growth and recruitment are enhanced by the presence and duration of over-raftered winter ice (Quetin *et al.* 1996). Sea ice has an important effect on zooplankton after the ice melt as well. Ice-associated food (release of ice algae from melting ice and ice-edge blooms) is essential for krill ovarian development and for high reproductive output in summer (Quetin *et al.* 1994; Quetin and Ross, 2001).

The over-winter behaviour of adult krill is still uncertain. It is known that the distribution, aggregation and behaviour of krill changes dramatically in winter (Lascara *et al.* 1999). Krill have a reduced food requirement in winter, probably due to a reduction in metabolic rate caused by lower temperatures (Frazer *et al.* 1997). To meet their food requirements, krill probably employ several strategies to survive over winter including diet switching to the most abundant food source. Some research has suggested that all krill, especially juveniles, use ice algae as a food source extensively during winter (Quetin & Ross 1991). Krill have been observed to feed carnivorously in winter and it has been suggested that carnivory sustains growth until ice algae become available in late winter (Huntley *et al.* 1994). It has also been suggested that krill mainly feed on detritus over winter (Everson 1977), or organic material on the sediment surface (Kawaguchi *et al.* 1986), or cannibalism (Maihara *et al.* 1986). Krill can starve and shrink when there is no food present, and so may not eat at all over winter (Ikeda & Dixon 1982). There are a variety of possible survival strategies and it is likely that krill use more than one. The relative importance of ice algae as a food source is still unclear. Holm-Hansen & Huntley (1984) assessed the contribution to be

modest due to the low light levels available to ice algae, whilst Marschall (1988) assessed it as large since algae are a major and very available winter food source for krill. More research is needed to arrive at a conclusive answer.

The use of sea ice algae as a food source appears to be regionally variable. The extent, predictability and complexity of the under surface of the sea ice habitat affects its use as a food source (Langdon & Quetin 1991). Juvenile krill have often been observed feeding on the predictable, extensive and physically complex multi-year pack ice of Weddell Sea, but not on the unpredictable, smooth-surfaced ice cover west of the Antarctic Peninsula (Langdon & Quetin 1991). The regional oceanography and currents also appear to affect the incidence of zooplankton feeding on ice algae in winter. For example, the Weddell Sea gyre is a locally important current in terms of particle flux and an actively feeding zooplankton population has been observed feeding there (Bathmann *et al.* 1993).

The use of the under surface of pack ice as a habitat and a food source for krill is relatively unstudied in east Antarctica. The extent, predictability, physical complexity and dynamics of the east Antarctic pack ice is different to that of the Weddell Sea and other regions. Here, copepods may play a more important role, since they can account for up to 65% of the zooplankton biomass in the water column of the East Antarctic region in some areas (Swadling *et al.* 1997b). These factors, along with the specific distribution of zooplankton, the biomass of bottom algae available and the ecological processes in the East Antarctic pack ice need to be examined to assess the importance of ice algae as a food source in winter. An examination of the distribution and abundance of algal bottom communities in pack ice that are available for krill grazing (bio-available) is a useful starting point.

1.2.3 Ice Algae in the Carbon cycle

An estimate of total sea ice algal biomass is also important in the study of oceanic carbon cycles. Production by algae growing in the ice is transferred out of the production zone via mechanisms including particulate material sinking out of the euphotic zone and material passed onto the food web (Legendre *et al.* 1992). Biological production that moves to the deep ocean contributes the biological pump component of the Southern Ocean carbon “sink”.

When the pack ice melts, the accumulated algal biomass will fall into the underlying water column. High concentrations of carbon in the ice, and low concentrations in the underlying water column indicate ice algae are a significant carbon source at this time. Carbon export from the sea ice to the deep ocean can be through the direct sedimentation of algal cells. However, cell grazing is usually high, reducing or eliminating this type of export. This export varies with latitude, year and season and the bulk of the export from the ice biota may be in one pulse or a few short pulses during ice melt (Moloney 1992). The carbon produced by sea ice algae that then passes into the water column can pass directly to the deep ocean, or it can also pass through a complex “microbial loop” of microorganisms first. The characteristics of the flow of carbon through the microbial loop for Arctic sea ice changes with the stage of development of the microbial community (Vezina *et al.* 1997).

Some of the accumulated pack ice algae biomass is available for zooplankton grazing while the ice is intact; mainly the bottom communities. Grazing of ice algae may lead to carbon export to the deep ocean through several mechanisms. It is thought that the major export is through the production of rapidly sinking faecal pellets (Schnack-Schiel *et al.* 1998). Deil migrant biota could also assist in the downward transport of biogenic carbon, including faeces (Longhurst *et al.* 1990). There is also a carbon export link through grazers and higher predators, resulting in faeces and dead bodies. This important link is hard to quantify, and has been variously described as very small (0.3-0.6%; van Franeker *et al.* 1997), moderate (5%; Moloney 1992) or significant (5-22%; Huntley *et al.* 1991). Banse (1995) rebuts the finding

of Huntley *et al.* (1991), measuring seabirds, seals and whales to exhale $\leq 3\%$ of net primary production as CO₂ to the atmosphere using a box model of antarctic food webs with improved growth efficiency values.

All these mechanisms vary in space and time, and are influenced by various ecosystem properties of the food web (Legendre & Le Fèvre 1991). The interaction between primary producers, grazers and predators affects the characteristics of carbon export.

The relative importance of direct sedimentation of cells, and export through grazing is still unclear. Direct export of algal cells can be low, with only 1-10% of algal cells reaching the bottom intact (Carey 1987) and no increase in carbon export as algal cells during the ice melt (Carey 1987). Carbon export through the grazing link has been observed to be high, with up to one third of the sinking material resulting from grazing (Tremblay *et al.* 1989). It appears that the proportion of algae that is exported to deep water directly through grazing and through other pathways varies greatly and is influenced by local conditions.

Whichever pathway carbon export takes, the movement of carbon through sea ice to the deep ocean represents an important link in the carbon cycle. Since sea ice algae represents up to 25% of the carbon biomass in the ice covered Antarctic seas (Arrigo *et al.* 1997) and is an important source of primary productivity, it is a significant component of the Southern Ocean system.

Chapter 1.3. Sea Ice Algal Ecology

1.3.1 Introduction

Brown layers in sea ice have been observed since early voyages into Antarctic sea ice. Hooker (1847) first described microbial communities in the surface and bottom of ice floes. The community composition, physiology and primary productivity of sea ice micro-algae was described in detail in the 1960's at McMurdo Sound in the Ross Sea (Bunt & Wood 1963; Bunt 1963, 1964a, 1964b, 1967, 1968a 1968b; Bunt & Lee 1970). Since then, algal ecology and physiology has been investigated in detail mainly in the Weddell & Ross Seas, and also to a lesser extent in the East Antarctic region.

Most of the major taxonomic components of Antarctic microbial ecology are circumpolar in distribution (Knox 1994), including sea ice algae. The primary reason for this distribution of sea ice algae is that they are closely coupled to the planktonic system. There is an annual cycle of entrapment of marine cells into ice, and release of cells back into water as the ice melts. The assemblages in the ice are initially identical to those in the water, just more concentrated (Garrison & Buck 1985). Once entrapped, there is selective survival of algae, causing a reduction in the species number. After several months entrapped, sea ice algal communities are very different to water communities.

Diatoms are nearly always the dominant group in ice algae assemblages, usually pennate forms. However centric diatoms (Watanabe 1982; Horner 1985, 1990; Garrison *et al.* 1987), nano and micro autotrophic flagellates (Garrison & Buck 1985, 1989a; Garrison 1991), colonies of *Phaeocystis* sp., and dinoflagellates (Garrison 1991) are sometimes very abundant.

Once entrapped in ice, cells form horizontal layers due to the variation in the physical controls over cell growth down the ice column. A gradient of irradiance, brine salinity and temperature may cause active migration of motile species and differential growth rates. In general, algal abundance in the ice decreases with increasing distance from the ice - water interface and with depth of snow cover (Grossi & Sullivan 1985, McMinin *et al.* 1999b). This causes the formation of distinct communities of sea ice algae.

1.3.2 Algal Community Ecology

Algal communities vary greatly between fast ice and pack ice (chapter 1). Algae, bacteria, protozoa and small metazoans in the pack ice are found in three main community types and six assemblages (table 1.3.1).

Table 1.3.1 Sea Ice Algae Communities found in Antarctic Sea Ice

Community	Assemblage	Location	Origin
A. Surface	1 Infiltration	Snow-ice interface	Snow flooded with seawater
	2 Melt-pool	Pools on surface	Melting of ice
B. Interior	3 Brine channel	Cavities, cracks and channels in ice	Formed during freezing
	4 Band	In ice matrix	Accretion of new ice onto bottom / incorporated at time of freezing.
C. Bottom	5 Sub-ice mat strand/ sub-ice platelet ice	Loosely attached to underside	Cells from water attach to platelets or under surface & form chains
	6 Interstitial bottom	Bottom layer	Solid, hard layer of congelation ice or frozen platelets

Adapted from: (Horner 1985, Horner *et al.* 1988, Knox 1994)

Bottom communities are important and often dominate in the East Antarctic region (Grose & McMinn 2003). Sub-ice mat strand assemblages form strands of mainly chain-forming pennate diatoms trailing into the water and are found in fast ice in east Antarctica. Strands have been found to be 0 cm long in mid July, 10-15 cm in November and up to 50-60 cm in December in the Syowa area (Watanabe 1988). Assemblages have also been described in the fast ice from near Casey station (McConville & Wetherbee 1983) & McMurdo station (Grossi *et al.* 1987).

Sub-ice platelet ice assemblages are formed in loose aggregations of platelets or frazil crystals on the under surface of the sea ice. Cells aggregate in the interstices of the platelets, forming algal communities. Sub-ice platelet communities occur near ice shelves, and are most well known from McMurdo Sound (Kottmeier *et al.* 1985). They have also been seen at Syowa station in East Antarctica (Watanabe 1988).

The most important and widely distributed of the bottom assemblages in the east Antarctic pack ice is the interstitial bottom assemblage (Grose & McMinn 2003). Interstitial bottom assemblages are formed on a solid, hard layer of bottom congelation ice (Palmisano & Sullivan 1983a; Grossi *et al.* 1987; McMinn & Ashworth 1998; McMinn *et al.* 1999a,b), or in a platelet layer frozen to the underside of the ice (Bunt 1963; Bunt & Lee 1970; Palmisano & Sullivan 1985; Grossi *et al.* 1987). Platelets occur mainly where there is little disturbance, and so frozen platelet layers commonly occur in fast ice or in undisturbed thick pack ice (Grossi *et al.* 1987). Bottom assemblages on a hard layer of congelation ice have a wide distribution.

Where congelation ice is the major ice type, interstitial bottom communities generally dominate over other types, such as in the Ross Sea pack ice (Lizotte 2001). Such congelation ice with associated bottom communities have also been found in the Arctic (Smith *et al.* 1987, Michel *et al.* 1996), other areas of the Antarctic (Palmisano & Sullivan 1983a, Arrigo *et al.* 1993, Robinson *et al.* 1995, Archer *et al.* 1996, Stoecker *et al.* 1997, 1998) and Saroma Lagoon, Japan (Robineau *et al.* 1997, Kudoh *et al.* 1997, Suzuki *et al.* 1997). The dominance of congelation ice in East Antarctica could cause a dominance of interstitial bottom communities, as observed in this study (Grose & McMinn 2003). This is in contrast to Weddell Sea pack ice. In studies of total biomass, sea ice in the Weddell Sea region is thought to be dominated by surface communities (Arrigo *et al.* 1997; Legendre *et al.* 1992). Surface communities are also common in

other regions of the Antarctic and are often associated with sea ice with a heavy snow cover or in rafted sea ice conditions, which force the ice surface below the freeboard layer (Wadhams *et al.* 1987). Melt-pool assemblages occur in spring and summer when air temperatures are above zero causing pools to form on the surface of the ice (McConville & Wetherbee 1983, Stoecker *et al.* 1998, Thompson 2000). Significant bottom algal communities have also been reported from within the Weddell Sea region. Pigment profiles of Weddell Sea pack ice cores (Lizotte *et al.* 1998), mainly showed peaks in the bottom of ice profiles (Lizotte *pers. comm.* 2001).

Interior communities can be present in most areas of Antarctic pack ice. Interior communities generally dominate in sea ice that is composed of a sizable fraction of frazil ice (Lizotte 2001). Interior assemblages are of varying widths and of varying importance in different regions. They are described by Hoshiai (1977), Ackley *et al.* (1979) and Watanabe & Satoh (1987). Complex systems of brine channels are common throughout Antarctic pack ice. They contain species common to both water and bottom communities (Fritsen *et al.* 1998). Brine channel communities around Davis station have been described by McConville & Wetherbee (1983).

In East Antarctic pack ice there is a dominance of congelation ice and associated bottom communities, with less abundant surface and interior communities (e.g. Watanabe & Satoh 1987, McConville & Wetherbee 1983, Grose & McMinn 2003).

1.3.3 Controlling Factors of Algal Biomass

Vertical and horizontal distribution of Chlorophyll *a* (Chl *a*) in sea ice reflects a dynamic balance between rates of (1) sea ice formation, accretion, and degradation (2) snow accumulation (3) ice algal growth and (4) heterotrophic activity (Arrigo *et al.* 2001). These factors control the development time of the community as well as the down-welling irradiance, nutrients, temperature, salinity and grazing pressure present in the algal habitat. Irradiance and temperature are generally accepted as the most important controlling factors of algal growth, both of which are dependant on latitude, ice thickness, and the nature of the ice and snow cover (Knox 1994). Nutrient levels are also a crucial controlling factor of algal growth.

The development time of the algal community can be the determining factor of the algal biomass in pack ice. The pack ice is present for at most 9 or 10 months each year, and often for a shorter period. For this reason algal communities rarely reach the maximum theoretical biomass that can be sustained in the ice simply because there has been insufficient time for the algae to accumulate to the maximum level. The fieldwork for this study was performed during November and December. Measurements in the Ross Sea taken at this time of year showed that sea ice algal accumulation was limited mainly by the age of the ice (Arrigo *et al.* 2001). It is expected that there will be similarities between these findings and measurements in the east Antarctic pack ice.

Light is an important limiting factor of algal growth rates. Light changes in both quantity and quality through the sea ice column (SooHoo *et al.* 1987). Ice and snow cause a reduction in light; light transmission through two metres of congelation ice shows a reduction of PAR by 90% (Palmisano *et al.* 1987). Layers of ice algae further reduce the transmission of light; ice and algae together can cause a reduction in light levels to <0.5% of surface levels (Palmisano *et al.* 1987). Thick snow causes a dramatic reduction in under-ice light; PAR under 70 cm of snow is less than 3% of that beneath 7 cm of snow (Palmisano *et al.* 1985).

Strong attenuation of the longer wavelengths (i.e. >700 nm) causes the spectral composition of the light to undergo rapid changes as it passes through the ice (SooHoo *et al.* 1987, McMinn *et al.* 1999b). Red light is quickly absorbed, causing an energy maximum in the 470–480 nm wavelength in light under first year ice (Maykut & Grenfell 1975). Also, layers of ice algae shift the transmission peak by selectively absorbing blue and red wavelengths (Palmisano *et al.* 1987).

Temperature affects the growth rates of algae by limiting the speed at which enzymatic reactions and physiological processes occur. Seawater freezes to form sea ice at approximately -1.8°C . The water surrounding sea ice is at freezing point and the air temperature varies from above zero to well below freezing. In winter this causes a temperature gradient down through the ice column from approximately -20°C at the surface of the ice to -1.8°C at the ice-water interface (SooHoo *et al.* 1987).

A dynamic balance between community development time, light, temperature, nutrients and salinity gradients determines the total accumulated biomass of each algal community. The Ross Sea pack ice in November (Arrigo *et al.* 2003) was limited mainly by the development time of the community. The biomass averaged $2.53 \text{ mg Chl } a \text{ m}^{-2}$, with a high spatial variability. Patches of high chlorophyll ($11.2 \text{ mg Chl } a \text{ m}^{-2}$) and low chlorophyll ($0.24 \text{ mg Chl } a \text{ m}^{-2}$) were a function of sea ice thickness and age and to a lesser extent snow thickness. These biomass values are lower than the maximum biomass observed in areas such as the Weddell Sea and the Canadian Arctic that is mainly attributable to the early time of sampling and much higher biomasses were attained later in the year (Arrigo *et al.* 2003). In many sea ice habitats, micro algae continue to increase in abundance until early December, when elevated temperatures cause the sea ice habitat to degrade to the point where it can no longer sustain a viable microbial community (Grossi *et al.* 1987, Arrigo *et al.* 1995, Gleitz *et al.* 1996; McMinn & Ashworth 1998).

1.3.3 Establishment of communities

Algal cells are incorporated into ice as frazil crystals accumulate into grease ice (Hoshiai 1977; Watanabe & Satoh 1987), by a process of scavenging and nucleation (Ackley 1982, Garrison *et al.* 1983). Scavenging is where ice crystals move up through the water column and collect algal cells. Nucleation is where a frazil ice crystal nucleates on an algal cell when water reaches freezing point.

Bottom communities may form in several ways. Unconsolidated platelet communities form from cells scavenged as the platelets float up or from cells trapped within the platelet layer as currents move through them (Ackley *et al.* 1979). Sub ice mat strand assemblages form from the growth of cells originally incorporated in the bottom ice. Bottom congelation communities, common in the east Antarctic pack ice, form through the rapid growth of initially scavenged cells in the ice with the addition of any newly scavenged cells during ice accretion. The establishment time and the position of the chlorophyll maxima of these communities vary with local conditions (Grossi & Sullivan 1985).

Surface assemblages form through a different mechanism. Cells originate from seawater that floods the snow-ice interface (Meguro 1962) or are transported upwards through brine channels into surface melt-pools (McConville & Wetherbee 1983). Freshwater species can also be blown from the land or transported in summer melt-water from glaciers and ice shelves (Garrison & Buck 1991). Since most surface communities form from seawater flooding, the proximity of floe edges and the degree of water turbulence are important variables. A typical pattern was described by Hoshiai

(1977). Freezing was observed to commence in mid February and the development of an algal layer in brine pockets was observed by the end of March when the ice was 30 cm thick. Continued freezing created an interior assemblage during winter and a second brown layer appeared on the bottom of the ice in spring. Others have observed a similar cycle, sometimes with the addition of a melt pool assemblage (Watanabe & Satoh 1987, McConville & Wetherbee 1983).

However, the seasonal cycle of ice algal community establishment in pack ice is regionally variable. There is a dominance of interior assemblages in Weddell Sea pack ice, but not in other regions. Ackley *et al.* (1979) proposed a model to account for the differential establishment of assemblages that was dependant on physical factors. The model states that the establishment of bottom assemblages requires air temperatures high enough to promote complete brine migration to the bottom layers. Surface assemblages require heavy snowfall to push the ice below sea level and temperatures high enough to induce melting. Interior communities depend on air temperatures at or slightly below freezing point to initiate – but not to complete – the brine drainage process. It also describes a species succession of flagellate and diatom species over the year.

The maximum biomass in ice varies between regions of Antarctica. Fast ice bottom communities can reach a very high biomass indeed; up to 302 mg Chl *a* m⁻² in the McMurdo Sea (Palmisano & Sullivan 1983a) and 380 mg Chl *a* m⁻² near Cape Evans (McMinn *et al.* 2003). Pack ice bottom infiltration assemblages can experience two biomass maxima in a year, in April-June, and October-November (Watanabe & Satoh 1987).

1.3.4 Demise of Communities

Most pack ice entirely melts each summer and then reforms the next autumn. The ice edge recedes in an irregular pattern during spring, with different patches affected by different local weather and wind.

As the ice melts, the ice biota is released into the water column. The spring bloom of phytoplankton in the water column at the ice edge was thought to be due to the release of spores and vegetative cells from the ice as an inoculum for the bloom (Hasle 1969, Krebs *et al.* 1987, Smith & Nelson 1986). It is now known that the process is more complex than this. The bloom of phytoplankton is largely controlled by the physical processes of melting (increased light, formation of a stable water column, meteorological forcing), with moderate influences from grazing pressure from protozoa, deep mixing and possibly the input of iron (Lancelot *et al.* 1993). Low salinity melt-water provides vertical stability in the water column and allows phytoplankton to grow in a high light, high nutrient environment, a major factor in phytoplankton blooms (Smith & Nelson 1986, Smith 1987, Comiso *et al.* 1990). The micronutrient iron is probably a primary limiting factor of phytoplankton growth and the release of atmospheric dust that has landed on the ice over winter may provide a critical input of iron (Lancelot *et al.* 1993).

Chapter 1.4. Estimating Total Algal Biomass

In estimating the total contribution of sea ice algae to the marine environment, there are two main approaches: the estimation of total primary production and the estimation of total accumulated biomass as a proxy of primary production. The model of algal primary production rates over the growing season made by Arrigo *et al.* (1997) is an attempt at estimating total primary production from physical parameters. All the other studies are essentially chlorophyll accounting exercises and make an estimate of accumulated algal biomass or standing stock (Bunt 1968a; Heywood & Whitaker 1984; Legendre *et al.* 1992). This study also falls into this category. However, sea ice biomass, with some assumptions about whether it is at its maximum, provides a reasonable estimate of the total annual net production within the ice for that particular community (Legendre *et al.* 1992).

1.4.1 Previous Estimates

Very few attempts have been made to estimate the total biomass of pack ice algae in Antarctica. It is clear that early estimates were too low. An early study by Bunt (1968a) resulted in an estimate of 0.03 Tg C yr⁻¹, assuming that production was restricted to near shore environments. Subsequent studies have used more reliable data and utilised a more complete understanding of ice algae habitat extent and community ecology. The two most commonly referenced estimates of total pack ice algal biomass are from Arrigo *et al.* (1997) and Legendre *et al.* (1992). Arrigo *et al.* (1997) uses a modelling technique, and Legendre *et al.* (1992) uses an extrapolation technique. The estimates of total algal production are summarised in table 1.4.1.

Table 1.4.1. Estimates of total Algal Production in the sea ice zone, Antarctica

Author	Year	Technique	Estimate (Tg C yr ⁻¹)
Bunt	1968a	Extrapolation of measured rate to near-shore area only.	<0.03
Heywood & Whitaker	1984	Extrapolation of a measured rate* to the entire sea ice area.	50
Legendre <i>et al.</i>	1992	Extrapolation *.	63-70
Mathot <i>et al.</i>	1996	Extrapolation using satellite data to assess habitat extent.	30
Arrigo <i>et al.</i>	1997	Sea Ice model.	40 (Surface only)

* - From Burkholder & Mandelli (1965)

1.4.1a Extrapolation

The main technique for estimating sea ice algal biomass is through the extrapolation of average observed values of biomass to the total area of sea ice suitable for algae (the “habitat extent”). The earliest study using this technique was done by Bunt (1968a), which resulted in a low estimate of total biomass. Heywood & Whitaker (1984) extrapolated the measured production rate of Burkholder & Mandelli (1965) over the maximum sea ice extent ($20 \times 10^8 \text{ km}^2$). The most often cited estimate using this technique is by Legendre *et al.* (1992). This study extrapolated the scarce data sets of the standing crop and production rates of Antarctic sea ice algae to the estimated areal extent of the different algal communities for the entire Antarctic sea ice zone. Measured standing crop and production rates were from relatively restricted geographic locations such as the Weddell or Ross Sea, with no measurements made in the East Antarctic region. Extrapolating limited data points to large areas of sea ice can not give a precise estimate that allows for fine-scale spatial heterogeneity, only a broad-scale estimate.

Legendre *et al.* (1992) calculated the total algal biomass using previously measured values of algal biomass stock and habitat extent. Surface community standing stock ($4 \text{ mg Chl } a \text{ m}^{-2}$, after Burkholder & Mandelli 1965), and freeboard standing stock ($11 - 80 \text{ mg Chl } a \text{ m}^{-2}$, after Kottmeier & Sullivan 1990, Garrison & Buck 1991) were multiplied by 50% of the area of maximum sea ice extent ($10 \times 10^6 \text{ km}^2$, after Ackley *et al.* 1990). This results in an estimate of $4000 \text{ mg C m}^{-2} \text{ yr}^{-1}$ in the surface and $8000 \text{ mg C m}^{-2} \text{ yr}^{-1}$ in the freeboard. Fast ice standing stock ($770 \text{ mg Chl } a \text{ m}^{-2}$, after Palmisano & Sullivan 1983a) was multiplied over a 10 km thick coastal band ($0.265 \times 10^6 \text{ km}^2$), resulting in $6000-32000 \text{ mg C m}^{-2} \text{ yr}$. Assuming the yearly stock represents net annual accumulated production, this results in $63-70 \text{ Tg C year}^{-1}$ annual carbon production for all sea ice communities.

Pack ice bottom communities were ignored in the total production estimate as they were assumed to be of low importance. However, the pack ice bottom interstitial community is acknowledged to be a source of algal concentration in bloom conditions, with a biomass of $2-9 \text{ mg Chl } a \text{ m}^{-2}$ (after Dieckmann *et al.* 1990).

Mathot *et al.* (1996) used satellite images to more accurately estimate the habitat extent of sea ice algae communities. A calculation of the seasonal budget of primary production for each sea ice habitat within the Southern Ocean was made. Using monthly ice concentration contour charts from satellite data, the habitat extents of the different sea ice algae communities were more accurately calculated. Total algal biomass was estimated to be 30 Tg C , with 97% of this in the pack ice (29 Tg C).

1.4.1b Models

Modelling of primary productivity has been undertaken extensively in the aquatic environment, including Antarctic waters. A modified standard depth-integrated productivity model has been developed to account for 72-73% of the variability in primary productivity of Antarctic waters (Dierssen *et al.* 2000). Variability in productivity is determined mainly by the surface chlorophyll *a* concentrations and a minor influence of the photo adaptive variable (P^B_{opt}) (Dierssen *et al.* 2000)

There are major differences between sea ice and aquatic production. Sea ice algae are present in an approximately 2D layer within ice, rather than suspended throughout the water column. Sea ice habitat is very heterogeneous, which heavily affects ice algal biomass and algal production. Algal growth in fast ice can be simulated in a simple two-dimensional model of sea ice structure and dynamics coupled to a high resolution, time-dependent model of micro algal growth in which simulated physiological responses are determined by ambient temperature, spectral irradiance, nutrient concentration and salinity (Arrigo *et al.* 1993).

Arrigo *et al.* (1997) used an expanded version of this one-dimensional numerical model to simulate the growth and production of sea ice algae in the pack ice region. The model used inputs of microwave remote sensing data and *in situ* cloud cover and air temperature data in a grid matrix. At each vertical grid-point a calculation was made based on the proportion of first year ice, temperature, brine salinity, photosynthetically available radiation (PAR), nutrients (as a function of surface flooding and sea ice porosity) and a loss factor for death, zooplankton grazing and sinking. The seasonal changes of light and nutrient limitations were accounted for. In this model, spatial variation in production in the freeboard and surface communities was determined by snow loading (surface flooding), sea ice porosity (dependent on temperature) and the proportion of first year ice. The bottom community in pack ice was not included in the model as it was assumed that it was of negligible importance.

The total estimate of production in the sea ice using this model was $\sim 35.7 \text{ TG C yr}^{-1}$, which represents 9-25% of the total production in the ice-covered Southern Ocean. Of this, 75% was associated with first-year ice and 60% was produced in November and December. In spatial terms, nearly 50% was produced in the Weddell Sea alone, 85% in the Weddell Sea, Ross Sea and Southern Indian Ocean regions combined. The East Antarctic region was assigned a low productivity value.

Using the most recent and sophisticated estimates, total algal production appears to be between 30 and 70 Tg C yr^{-1} (Arrigo *et al.* 1997, Legendre *et al.* 1992, Mathot *et al.* 1996). This represents only 1 - 6 % of the total biogenic carbon production in the Southern Ocean, which has been estimated to be 980 to 3620 Tg C yr^{-1} (Mathot *et al.* 1996, Smith & Nelson 1986). However, sea ice algae represent a greater ecological impact than this percentage suggests because they provide food resources for higher trophic level organisms in seasons and regions where water column biological production is low or negligible (Lizotte 2001). During some periods, especially winter, the sea ice algae are likely to contribute a highly significant proportion of the total production within the ice-covered areas. Regional variations in this proportion may also exist, with the ice algae contributing a relatively higher amount of production in some areas.

1.4.2 Other Useful Techniques and Ideas for making an estimate

Ackley *et al.* (1979) proposed a model for explaining the differences between the Weddell Sea and other regions, based on physical factors. The model stated that: 1. For the development of bottom assemblages the air temperature must be high enough to promote complete brine migration to the bottom layers. 2. Surface communities depend on heavy snowfall and temperatures high enough to induce melting. 3. Interior communities (such as in Weddell Sea) depend on air temperatures at, or slightly below, freezing point to initiate, but not to complete the brine drainage process. No estimates of total algal biomass incorporate these principles.

Welch & Bergmann (1989) described the prediction of development of Arctic sea ice algae communities from environmental variables. Of the four possible controlling factors: substrate, grazers, nutrients and light, the only major limiting factor was found to be light. Algal biomass was found to be predictable from snow cover and date in the year (both of which control light levels in the ice). Substrate was only limiting when ice is undergoing melt and algae can slough off. No correlation was found between nutrients and tidal cycle, however there was a correlation between reduced algal biomass with numbers of ice-associated amphipods where they were present. Consistently high correlations between chlorophyll and snow depths as well as chlorophyll and day of the year (DOY) indicates that the Arctic algae can be predicted from either date & snow depth or light & snow depth with a similar accuracy for March - early June.

1.4.3 Sea Ice Data Sources

1.4.3a Remote Sensing

Remote sensing is a very useful tool for gathering data about large geographic areas. Monitoring of sea ice freezing and break up from satellite imagery has been done for quite some time (Dey *et al.* 1979). There is now complete geographic coverage of the Antarctic region by satellite and the resolution of satellite images has continued to improve. There are several types of sensors that are fitted to satellites for sensing the earth's surface. Sensors are either optical (visible/near infra-red or thermal infra-red), or else microwave (active or passive). The Special Sensor Microwave / Imager (SSM/I) system is the standard input used to create operational ice charts, as used here (Partington & Bertoia 2002). It is possible to obtain data on the physical parameters of sea ice are possible from satellite, but the observation of Chlorophyll concentration is not possible. Sea ice algae are contained within the ice matrix or below the ice, making remote observation of the algae impossible.

Providers of satellite images often perform some interpretation of the remotely sensed data to aid in its application. The National Ice Centre, USA provides interpreted sea ice charts that have discrete sea ice zones identified and described by the "egg" ice code system. Further detail regarding the egg code and about this remote sensing product is available at the internet site www.natice.noaa.gov (NOAA 2001). These are the primary remote sensing products used in this study.

Remote sensing data requires supplementation from other sources. Ship-based ice observations and field studies are required to "ground-truth" physical parameters such as thickness, snow and ridging. Information obtained from drill-hole thickness profiles may be important in linking ground-truthed data and remote sensing techniques (Eicken *et al.* 1991). All studies of algal biomass need to combine other data sources with satellite data.

Chapter 2. Distribution and Composition of Algal Biomass in East Antarctic Pack Ice During Late Spring 2000

2.1 Abstract

This chapter presents the field observation methods and results carried out to lay the groundwork for a production model and the creation of an estimate of ice algal biomass (Ch 3). The late spring (2000) algal biomass and species composition in the bottom and surface communities in pack ice floes in East Antarctica (105-115°E) are described. A ship based observation technique to estimate algal biomass is evaluated and assessed. Measured values of biomass compared well with observed values. The bottom algal biomass was between 0.66 to 28.05 mg Chl *a* m⁻², and highly variable across the bottom of ice floes. Surface ice algal biomass was less than the bottom and was heavily influenced by floe edge effects.

2.2 Introduction

This chapter describes in detail the measurements of algal composition and distribution made in east Antarctic sea ice to be used as the basis for an estimate of total algal biomass (Chapter 3). The distribution and composition of algal biomass in the East Antarctic pack ice (90-120° longitude) is relatively unknown. While fast ice bottom communities have been widely studied (Hoshiai 1977, 1981, McConville & Wetherbee 1983, Watanabe 1988, Watanabe & Satoh 1987), pack ice communities are less well known. Pack ice algal communities can be split into three broad categories: the bottom, interior and at the snow-ice boundary or surface (Horner 1985). Generally, either the bottom or surface communities are the most abundant.

There is no rigorous estimation of pack ice algal biomass or model of algal primary production in East Antarctic pack ice based on the specific conditions found there. The major estimates of total sea ice algae biomass are made using ecological rules derived from other areas (Arrigo *et al.* 1997, Legendre *et al.* 1992), including the assumption that the only significant biomass in the bottom is in the fast ice. However, it is known that there are significant bottom communities in other areas of the Antarctic, the Arctic and even ice cores from the Weddell Sea can show peaks in chlorophyll *a* in the bottom (Lizotte *et al.* 1998). Surface communities in pack ice are formed primarily through surface flooding of seawater, and so can display a large floe edge effect (Meguro 1962).

A better understanding of algal biomass distribution in the east Antarctic pack ice can be used to make a more specialised East Antarctic model and produce a better estimate of algal biomass for the region. This paper describes the distribution and composition of algal biomass in East Antarctic pack ice in late spring. It focuses on the bottom and surface communities, as these are the most abundant, and describes the average biomass, composition and variability of algae in these communities.

2.3 Materials & Methods

Pack ice algae was observed and sampled in the Casey region (105-115° E) from the RV Polar Bird (ANARE V3 2000-01 season). An ice chart of the region for the period showing the ships track and sampling sites is shown in Fig 2.1 and a detail of the ships track is found in Fig 2.2.

Figure 2.1. Ice Chart of the Casey Region (NSIDC Colorado University) showing Ship's Track (RV Polar Bird) and Sampling Sites

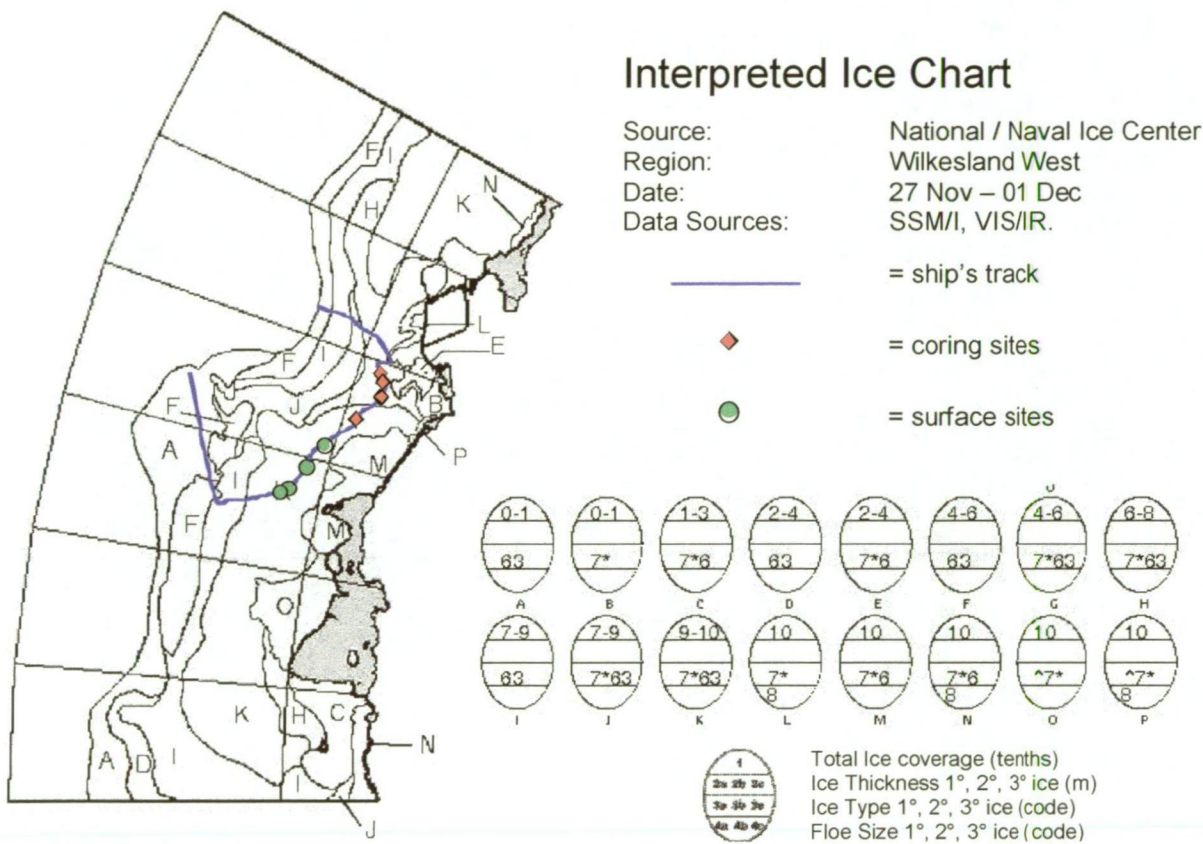
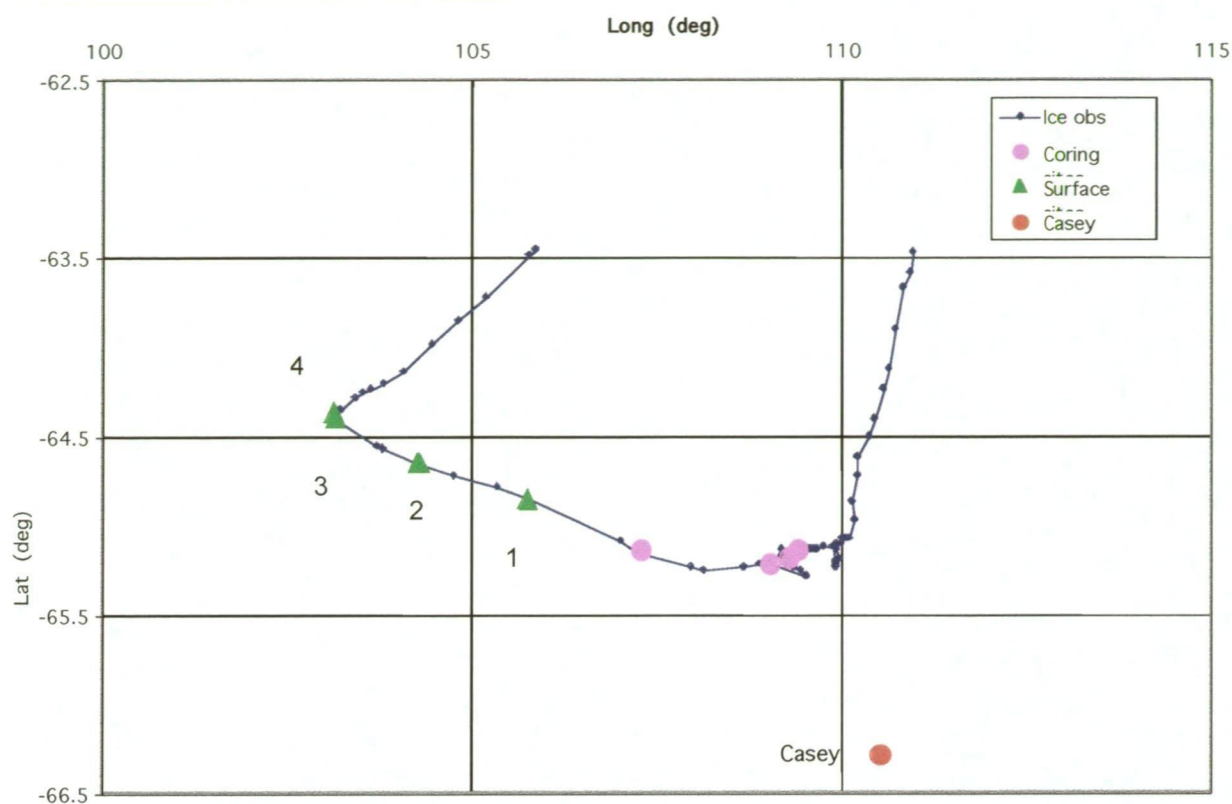


Figure 2.2 Ship track of the RV *Aurora Australis*, V3 2000



Hourly visual observations were made of ice concentration, ice type, ice thickness, floe size, ridging, snow type and snow thickness on primary, secondary and tertiary ice types in the region (Worby & Alison 1999). An additional observation of algal colour in the bottom, interior and surface of the ice surrounding the ship was made. The darkest observable colour (maximum) was compared to a colour chart calibrated with *in situ* chlorophyll concentration (Figure 2.3) with the uncovered unassisted eye under natural light and recorded. These brown hues were initially created using an estimation of the categories of observable colour then calibrated against *in situ* chlorophyll during the voyage. The relationship between observed colour and *in situ* biomass is shown in Table 2.1 and shown visually in Figure 2.4. A regression analysis of the calibration between observed colour and measured biomass is shown in Figure 2.5, displaying an intercept of -1 and a slope of 6.6 .

For each observation, the colour observed was first converted to equivalent chlorophyll using the calibration chart. The mean bottom colour was calculated as a proportion of this maximum value (see discussion), then the biomass value was corrected for the concentration of ice.

Floe edges have a significant influence on algal biomass (Meguro 1962), and an approximate 5 m edge zone of higher biomass was found in the floes measured here (see discussion). Each observation of maximum surface colour was converted to mean values by correcting for the proportion of edge and interior regions. An observed floe size of 0-20m has 75% edge zone, 25% interior, and an observed floe size 20-100m has 15% edge zone and 85% interior.

Figure 2.3. Colour Chart for Observation of "Brown" Sea Ice Colour
(colours initially assigned visually, then calibrated against *in situ* ice chlorophyll *a*)

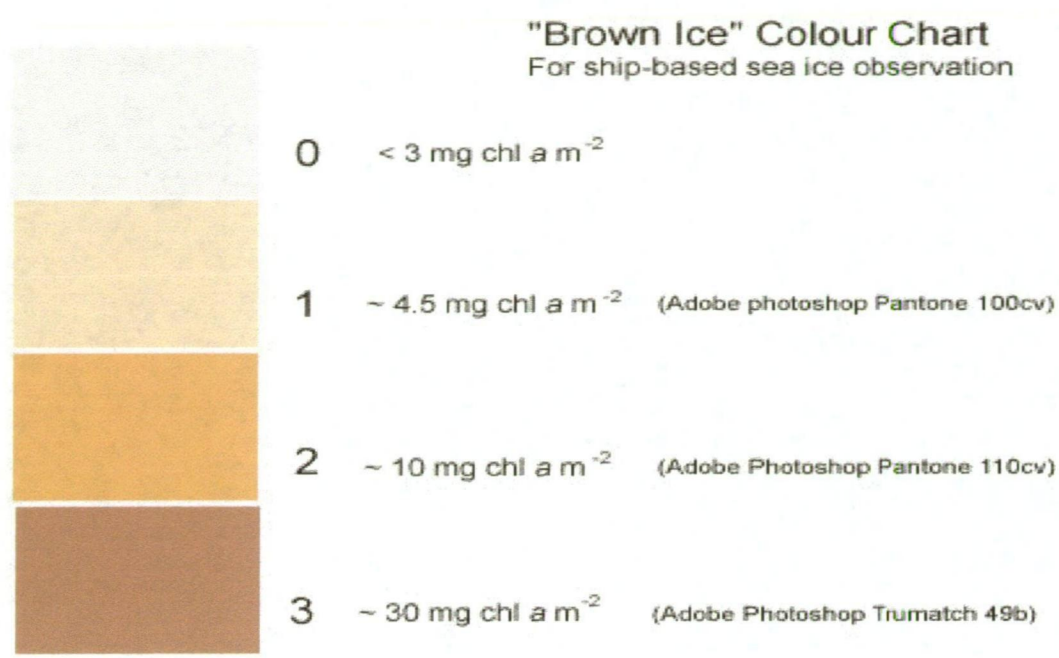


Figure 2.4. Relationship between observed and measured Chl *a* biomass

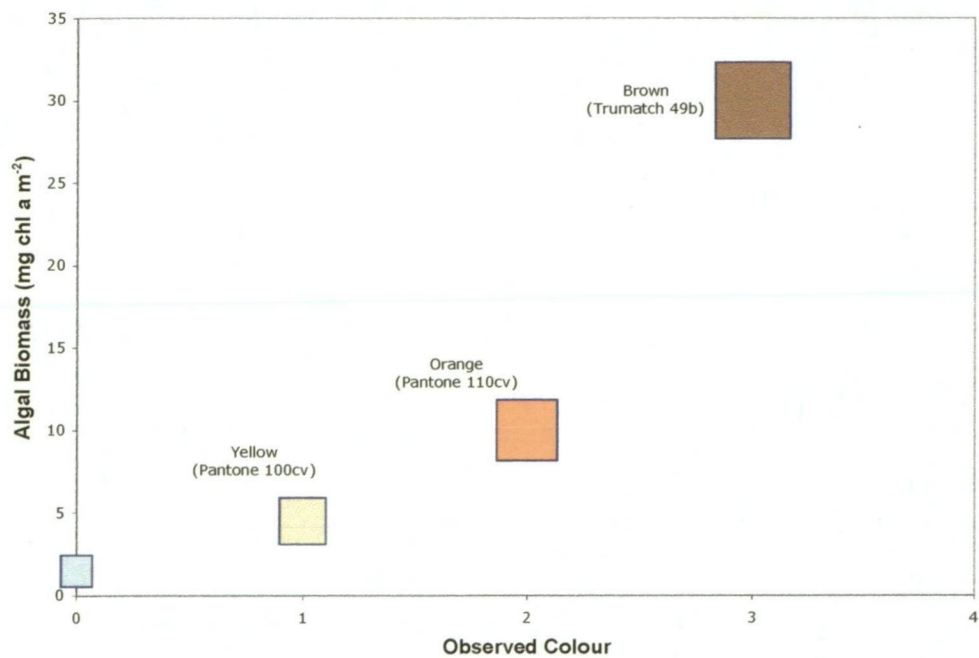
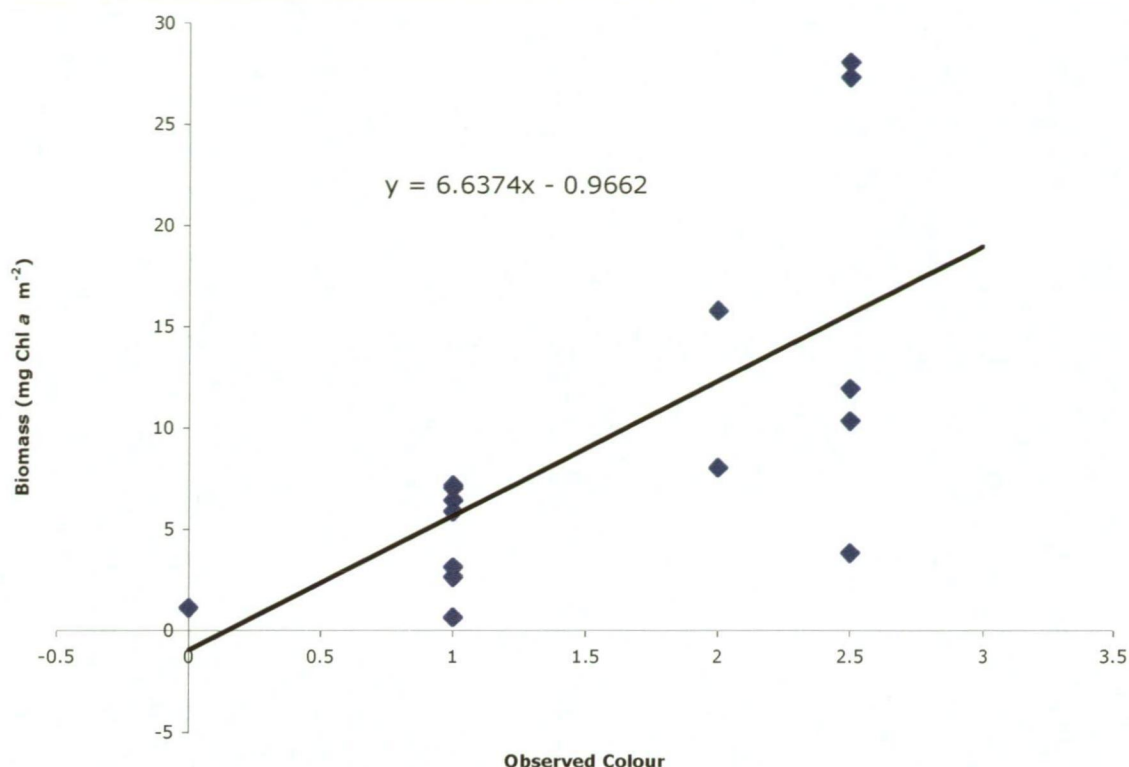


Figure 2.5 Calibration of observed colour with measured algal biomass from sea ice cores Antarctica Spring 2000 - linear regression including equation of line.



Ice was sampled opportunistically on the ships track. Ice cores were taken on several floes using a 10 cm diameter SIPRE corer. The ice and snow thickness were recorded and snow and ice samples were transported to the ship in the dark to avoid light degradation of pigments. Once on board, the cores were scraped to remove any extraneous snow or ice, and sectioned. The bottom 20 cm was sectioned as such; 1 cm, 1-5 cm, 5-10 cm, 10-20 cm. Each section was then melted in 250 ml filtered seawater at room temperature in darkness. The biomass of each sample was assessed using a Turner Fluorometer model 10-AU-005-CE (Mantoura *et al.* 1996). The chlorophyll concentration ($\mu\text{g Chl } a/\text{l}$) was adjusted for core area to gain an areal measure ($\text{mg Chl } a \text{ m}^2$). The sections were summed to gain an integrated value for the bottom community.

Samples of surface ice, slush and snow were taken along a transect line at 0, 1, 2, 3, 4, 5, 10 and 15 meters from a floe edge through the centre of the floe. Surface ice was sampled as a short core and snow was collected in a 50 ml jar. Each sample was then melted in 250 ml filtered seawater at room temperature in darkness. The chlorophyll biomass was determined as above.

50 ml sub-samples from each station of two transects were examined in order to determine the biodiversity of sea ice diatoms and relative contributions of key sea ice species to the surface community biomass. Samples were fixed with 3 drops of Lugol's iodine and maintained at 4°C until processing. Each sample was then washed in distilled water to remove the bulk of the Lugol's iodine and treated with 10% H₂O₂ for 3 days to remove the organic fraction of the sediment. Following 3 centrifuge treatments (2000 RPM for 5 minutes), samples were washed in distilled water. Prepared residues were mounted in Naphrax. Diatoms were then identified using a Zeiss Standard 20 light microscope with 100x oil immersion objective and phase contrast illumination. In most cases a count of 100 frustules per sample was made. Diatom species were then expressed as relative abundances (% total diatoms) of the 100 frustules counted per sample. In some cases 100 frustules were not encountered in a sample – species identified from those samples were included in the biodiversity analyses but not in further relative abundance analyses. Identification and taxonomy of the diatom species enumerated were based principally on Priddle & Fryxell (1985).

and Medlin & Priddle (1990). Each surface ice sub-component counts (i.e. snow, slush and ice) were then added together to determine overall surface community changes from the ice edge toward the floe centre.

2.4 Results

The pack ice sampled consisted of first or multi-year ice floes of small diameter (0-20, or 20-100 m), with abundant brash ice. From ice observations the average thickness of ice was 96 cm and snow was 47 cm (mean of observations). Frazil and grease ice often formed overnight but usually disappeared quickly in the morning.

Surface ice biomass transects are shown in Figure 2.6. Each transect shows a similar pattern, with increased magnitude and variability of chlorophyll *a* near the edge, and a lower algal biomass away from the edge. Taxa identified from the snow, slush (where applicable) and ice samples have been categorised into edge zone and interior zone groups (Table 2.2).

Bottom ice algal biomass measurements for each floe are documented in Table 2.1. Algal biomass on the bottom was measured as 0.6 to 28.05 mg Chl *a* m⁻², with an average of 8.6 mg Chl *a* m⁻², and visually observed as 1 to 25 mg Chl *a* m⁻². This is comparable to a series of cores measured to be 3.942-39.564 mg Chl *a* m⁻² (av. 14.049 mg Chl *a* m⁻²) in East Antarctic pack ice in October 1998 (McMinn & Hegseth 2003). Bottom biomass in Arctic pack ice has been measured as 0.1 to 14 mg Chl *a* m⁻² (Gosselin *et al.* 1997), and in Weddell Sea pack ice as 1.6 to 8.6 mg Chl *a* m⁻² (Dieckmann *et al.* 1990). Total depth integrated biomass was 0.24-11.2 mg Chl *a* m⁻² (average 2.53) in the Ross Sea (Arrigo *et al.* 2001), with 77% of floes having a maximum chlorophyll biomass in the bottom 0-0.1 m.

The algal biomass of the surface community was measured as 0.1 to 0.5 mg Chl *a* m⁻² and observed to be between 0 to 10mg Chl *a* m⁻². These values also compare well with measurements in October 1998 from the same area: 0.167 - 5.428 (av. 1.829) mg Chl *a* m⁻² (McMinn & Hegseth 2003). The sampled floes all had an observed surface colour of 0 (<3 mg Chl *a* m⁻²), reflected in the low measured values. The observed chlorophyll values are of the same order of magnitude as in previous estimates; 4 mg Chl *a* m⁻² (Legendre *et al.* 1992), 8 mg Chl *a* m⁻² in (in November; Arrigo *et al.* 1997).

Table 2.1. Chlorophyll a Concentration of the Bottom Algae Community of East Antarctic Pack Ice Floes in Late Spring 2000

Site no.	Lat. (deg)	Long. (deg)	Ice thick. (cm)	Obs. Colour	Biomass (mg Chl a m ⁻²)	St. Dev	% in bottom 1cm
1a	-65.08.2	109.25.3	100	1	6.44	0.5	36.2
1b			140		7.17		
Av.			120		6.8		
2a			117		3.83		
2b			160		11.94		
2c	-65.13.1	109.01.7	112	2.5	10.34	10.8	45.4
2d			166		28.05		
2e			80		27.31		
Av.			127		16.3		
3a			168		1.12		
3b	-65.13.1	109.01.7	170	0	1.13	0.008	30.3
Av.			169		1.1		
4a			118		8.03		
4b			133		15.77		
Av.			125		10.4		
5a	-65.13.1	109.01.7	25	2	2.65	7.6	38.2
5b			30		3.14		
5c			45		0.66		
5d			90		5.89		
5e			42		7.05		
Av.	-65.08.6	107.17.9	46	1	3.9	2.6	33.4

Figure 2.6. Integrated surface ice biomass across pack ice floes - East Antarctica (30°-150°E), spring 2000. Each line represents a transect on a different floe in the same area

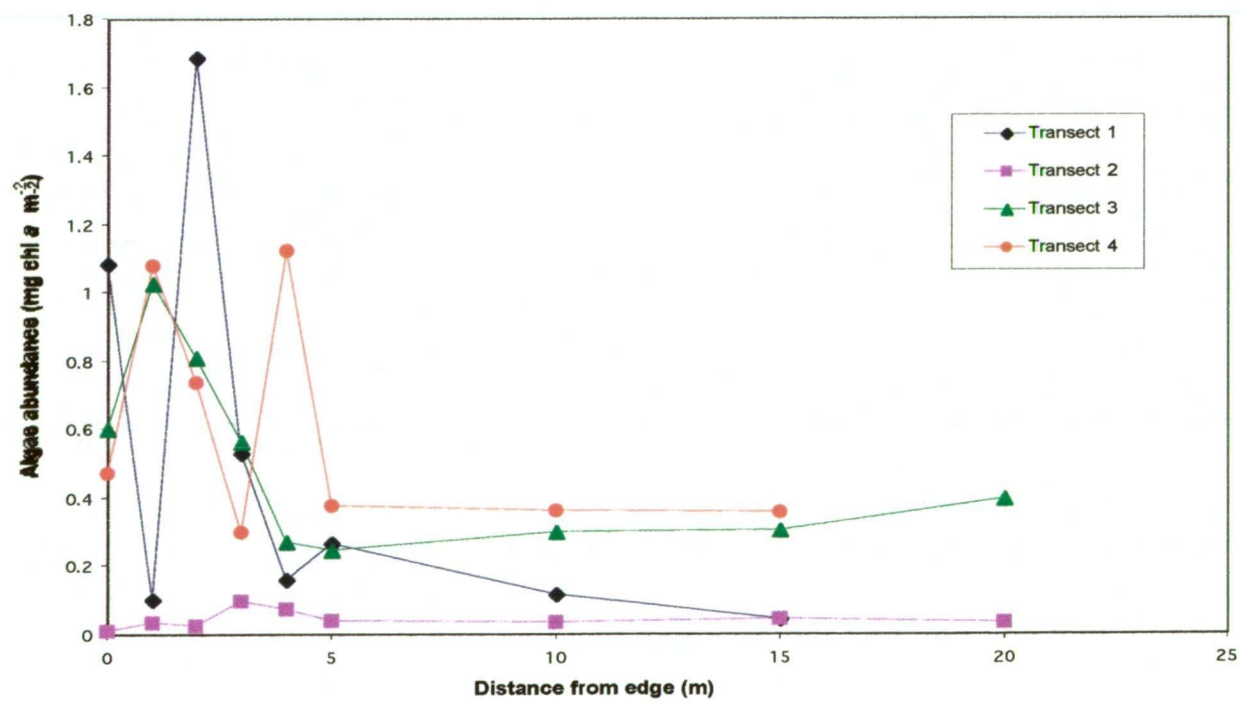


Table 2.2. Diatom biodiversity in surface ice and snow across pack ice floes

A: Edge of Floe (0 – 5 m)

Species	Known Distribution	Reference (s)
<i>Berkeleya adeliensis</i>	S	1
<i>Berkeleya Antarctica</i>	S	1
<i>Chaetoceros</i> spp.	P, O	2,3
<i>Entomoneis kjellmanii</i>	O	4
<i>Fragilariopsis angulata</i>	O	5
<i>Fragilariopsis curta</i>	P, O	2,5
<i>Fragilariopsis cylindrus</i>	P, O	2,5
<i>Fragilariopsis sublineata</i>	P, O	2,5
<i>Membraneis challengerii</i>	O	5
<i>Navicula glaciei</i>	AI	6
<i>Nitzschia lecontei</i>	O	5
<i>Nitzschia</i> cf. <i>prolongatoides</i>	P	2
<i>Nitzschia stellata</i>	O	5
<i>Plagiotropis gaussii</i>	S	5
<i>Rhizosolenia</i> spp.	P, O	2,3
<i>Thalassiosira tumida</i>	P, O	2,3

B: Floe Interior (> 5m from edge)

Species	Known Distribution	Reference (s)
<i>Berkeleya rutilans</i>	S	1
<i>Chaetoceros</i> spp.	P, O	2,3
<i>Corethron criophilum</i>	P	2
<i>Entomoneis kjellmanii</i>	O	4
<i>Fragilariopsis angulata</i>	O	5
<i>Fragilariopsis curta</i>	P, O	2,5
<i>Fragilariopsis cylindrus</i>	P, O	2,5
<i>Fragilariopsis kerguelensis</i>	P, O	2,3,5
<i>Membraneis challengerii</i>	O	5
<i>Nitzschia</i> cf. <i>prolongatoides</i>	P	2
<i>Nitzschia lecontei</i>	O	5
<i>Nitzschia stellata</i>	O	5
<i>Plagiotropis gaussii</i>	S	5
<i>Psuedonitzschia turgiduloides</i>	A	5

P=PACK ICE DIATOM

S=SEA ICE DIATOM

O=SOUTHERN OCEAN DIATOM

A=ANTARCTIC DIATOM

AI=ANTARCTIC ICE DIATOM

1=Medlin (1990)

2=Garrison & Buck (1989b)

3=Priddle & Fryxell (1985)

4=Andreoli *et al.* (1995)

5=Medlin & Priddle (1990)

2.5 Discussion

The algal biomass across the bottom of each floe (Table 1) was variable with a mean $7.7 \text{ mg Chl } a \text{ m}^{-2} \pm 4.3$. This variability is caused by the physical heterogeneity of the under surface of ice floes. For the purposes of simply characterising the biomass distribution, this data suggests that the mean biomass of the ice floe will be in the order of 80% of the maximum observed value. The bottom algal biomass was lowest in the thickest (170 cm) and thinnest (45 cm) floes and shows no clear relationship to snow thickness.

The surface assemblages are formed by seawater flooding the snow-ice interface (Meguro 1962), so floe edges are important to distribution and abundance of algae. The effect of floe edge is reflected in the pattern of algal biomass across the ice surface (Figure 2.5), which clearly displays a marked edge and interior zonation. Arrigo *et al.* (2001) also observed that biomass in surface sea ice was higher at the edges of the floe than at its centre. Biodiversity analysis (Table 2.2) also indicates a different suite of species in the edge zone compared to the interior. For generally characterising algal biomass in pack ice surface communities, this data suggests that two regions can be defined; a 5 m edge band with a mean algal biomass 50% of the maximum and the interior with 30% of the maximum.

The similarity of the algal biomass values from previous measurements, the field measurements presented here and from ice observations indicate that the measurements taken appear to be reliable, and the observation technique is consistent with the measured values. The observation technique appears to produce consistent and accurate measurements of sea ice algal biomass. However, it is not a precise method, and can only be used for broad scale estimates of biomass, such as this one. Studies of finer scale biomass distribution would require techniques with greater precision. It also suggests that the simple model method outlined above would be useful for making a more accurate estimate of algal biomass for this region than currently exists. The data collected here also suggests that the importance of bottom communities in the pack ice of this region has been underestimated by the two major estimates of algal biomass (Arrigo *et al.* 1997, Legendre *et al.* 1992).

For the purposes of this study, it will be assumed that sea ice algae remain in the ice at a constant biomass concentration until the ice disintegrates. This assumption is made to simplify the estimate of the time of demise of the ice algae community. Since the ice algae community is under the ice, it is impossible to ascertain the actual time of demise. It appears that as in the Ross Sea in spring (Arrigo *et al.* 2003), the algal accumulation in eastern Antarctica was limited mainly by the age of the ice. Micro algae would be expected to continue to increase in abundance until early December, when elevated temperatures would cause the sea ice habitat to degrade to the point where it could no longer sustain a viable microbial community (Grossi *et al.* 1987, Arrigo *et al.* 1995, Gleitz *et al.* 1996).

It is not possible to make inferences about other ice types or ice at other times of year from this work. It is expected that the algal biomass will differ greatly at other times of the yearly cycle and in ice of different ages. This work is useful for the purposes of describing the attributes of this type of ice at this time of year, for use in making a better estimate of total biomass in this region.

Chapter 3 The Estimate of Algal Biomass in East Antarctic Pack Ice

Grose, M; McMinn, A. Algal biomass in east Antarctic pack ice: how much is in the east?
In: Huiskes, A.H.L; Gieskes, W.W.C; Rozema, J; Schorno R.M.L; van der Vies, S.M; Wolff, W.J. (eds)
Antarctic Biology in a global context. Backhuys Publishers, Leiden, pp 21-25. 2002

3.1 Abstract

Total algal biomass in the eastern Antarctic pack ice zone (30-150°E) was assessed using chlorophyll *a* measurements from ice cores and calibrated observations of ice colour. Remote sensing data, viewed in GIS software, was used to calculate the ice thickness distribution and the habitat extent of each ice type. This information was used, together with measurements of the distribution of algal biomass within the ice column, to estimate total algal biomass. This was estimated to be 7.81 Tg C on 20 November 2000, 80% of which was in the bottom community. Extrapolating this result to December would result in a maximum standing algal crop of 8.51 Tg C, (95% pack ice), which is ~14% of the Antarctic ice algal biomass. These results suggest that bottom communities are far more important in the East Antarctic region than they have previously been assessed to be.

3.2 Introduction

According to recent estimates, sea ice algae of the Antarctic seasonal pack ice zone contribute 20-30% of the total annual primary production (Arrigo *et al.* 1998a, Lizotte 2001). While phytoplankton usually makes a greater contribution, the sea ice algae remain the only food source available for higher trophic levels for most of the year. Furthermore, as the ice melts in spring, much of the algae are released into the water column and often contribute to highly productive ice edge blooms that may account for a further 40% of annual production (Knox 1994). Total sea ice algal production in the Antarctic sea ice zone (SIZ) is reported to be between 30 and 70 Tg C yr⁻¹ (Arrigo *et al.* 1997, Legendre *et al.* 1992, Lizotte 2001). This production is spatially and temporally very variable, with regions and periods of high and low productivity. Biomass tends to remain low during the dark winter months and then grow rapidly with the return of the light in September to November. Ice retreat from a late October maximum reduces the aerial extent of ice communities, although the algal concentration continues to increase.

There has been no rigorous estimation of pack ice algal biomass or model of algal primary production for eastern Antarctic pack ice based on the algal distribution patterns found there. Most previous estimates of Southern Ocean sea ice algal standing crop have been based on extrapolations of measurements primarily from the Weddell Sea (Arrigo *et al.* 1997, 1998b, Legendre *et al.* 1992). In particular, we have found that in eastern Antarctica a much greater proportion of the algal biomass was located in bottom communities. The models of both Arrigo *et al.* (1997) and Legendre *et al.* (1992) assume that the only significant bottom algal biomass is found in the fast ice (1-2% of the total sea ice area) and that the distribution of surface communities follows the same pattern as that found in the Weddell Sea. The estimate of Legendre *et al.* (1992) takes the surface biomass as 4 g C m⁻² (Burkholder & Mandelli 1965) over 50% of the sea ice area, and bottom production as only occurring in fast ice, resulting in 0.63-0.70 Tg C year⁻¹ annual production. The

model of Arrigo *et al.* (1997) results in an estimate of low total production for the East Antarctic region ($0.59 \text{ g C m}^{-2} \text{ month}^{-1}$).

A better understanding of algal biomass distribution in the east Antarctic pack ice is used here to refine the estimate of total algal biomass in eastern Antarctica. This data is then used to develop a simple but more appropriate model to estimate the total biomass of sea ice algae in the east Antarctic region.

3.3 Methods

The sea ice algal biomass and distribution was estimated from ice of different thicknesses in the area $105\text{--}115^\circ\text{E}$ during November and December 2000 (see Figures 2.1 & 2.2). Each sampling site was categorized by ice and snow thickness and floe size. Biomass estimates were made both from chlorophyll *a* (Chl *a*) measurements of ice cores and from calibrated observations of ice colour. Ice cores were taken with a 13 cm diameter SIPRE corer. The bottom 20 cm of each core was sectioned as such; 0–1 cm, 1–5 cm, 5–10 cm, 10–20 cm. The melted samples were filtered onto GF/F filters and extracted in methanol for 8 hours. The Chl *a* was then measured on a Turner 10AU digital fluorometer using the acidification method of Holm-Hansen & Riemann (1978). An additional series of 3 Chl *a* biomass transects across individual ice floes was measured (Figure 3.2) to allow a correction for the effect of a concentration gradient from the edge to the interior of each floe (formed mainly by flooding of seawater from the edges).

Seventy-eight shipboard observations, at approximately hourly intervals depending on ship movement, were made of ice concentration, type, thickness, floe size, ridging, snow type and snow thickness on primary, secondary and tertiary ice types in the region between 23rd Nov and 19th Dec (following Worby & Alison 1999). An additional observation of maximum brown colour, due to algal biomass, in the bottom, interior and surface of the ice surrounding the ship was also made. Of these observations, 26 were calibrated against actual measurements of Chl *a* biomass (see Figure 2.4). The observed colour was compared to a calibrated colour chart that was prepared onboard (see Figure 2.3) and recorded. The colour chart was comprised of four biomass categories; no colour ($<3 \text{ mg Chl a m}^{-2}$), pale yellow ($\sim 4.5 \text{ mg Chl a m}^{-2}$), yellow to light brown ($\sim 10 \text{ mg Chl a m}^{-2}$) and dark brown ($\sim 30 \text{ mg Chl a m}^{-2}$). Both the measurements and observations were extrapolated to the particular ice floe to calculate an aerial measure of biomass (mg Chl a m^{-2}). A correction was made for floe edge effects for surface communities and then converted to a carbon equivalent (mg C m^{-2}) using a C: Chl *a* ratio of 38 (Palmisano & Sullivan 1983b).

The geographic extent of each ice type was estimated from interpreted remote sensing data (passive microwave images, courtesy of The National Ice Centre, Naval Ice Centre) using GIS software. This format identifies the proportion of up to three different ice types (e.g. gray ice, young ice, multiyear ice, 30–50 cm) in each $25 \times 25 \text{ km}$ grid cell, divided into discrete ice areas. Satellite data was ground-truthed from the observation data wherever appropriate. Each ice type in each ice area was examined separately, and assigned an aerial bottom and surface biomass concentration value, based on the snow and ice thickness. The assigned biomass concentration was applied to the calculated area of each ice type, allowing for ice concentration. The biomass in all the ice types for each ice area was summed, and the areas were summed to calculate the total biomass for the region.

The extent of each ice type for each month was calculated from sea ice charts (passive microwave data, courtesy of The National Ice Centre, Naval Ice Centre). Biomass in ice for the preceding and following months was extrapolated using a growth rate of $\mu = 0.1 \text{ d}^{-1}$ (Kirst & Wiencke 1995) up to a maximum of $35 \text{ mg Chl a m}^{-2}$ (Hoshiai 1981). The habitat extent of fast ice calculated from the satellite data was assigned a previously calculated average aerial biomass of $100 \text{ mg Chl a m}^{-1}$ (McMinn *et al.* 1999b). The area of pack ice for the entire Antarctic region was

also examined in this way at the time of maximum and minimum ice extent, to generate an estimate of total Antarctic algae annual production.

3.4 Results

The pack ice sampled consisted of first or multi-year ice floes of small diameter (generally 0-100 m), with abundant brash ice. From ice observations, the average thickness of ice was 96 cm and snow was 47 cm. Frazil and grease ice formed overnight, but disappeared quickly in the morning.

The total ice coverage of each the suitable ice types (excluding glacier ice, fast ice and ice less than 20 cm thick) in the East Antarctic region was at a maximum of 3.9 million km² in September and a minimum of 0.5 million km² in January. The maximum aerial extent of fast ice was 90,000 km² for the east region. The different regions of Antarctica reached a maximum extent at different weekly periods; the overall maximum extent was 13.2 million km² in late September and a minimum of 3.09 million km² in January 2001.

Bottom algal biomass in the ice cores (measured) ranged from 0.62 – 28.0 mg Chl *a* m⁻² with an average of 8.6 mg Chl *a* m⁻²; based on the colour chart these were visually observed to be 1.2 - 23 mg Chl *a* m⁻². This is comparable to values from a series of cores, measured to be 3.9-39.6 mg Chl *a* m⁻² (av. 14.0 mg Chl *a* m⁻²) from the same region in October 1998 (McMinn & Hegseth, 2003); from the Arctic, 0.1 – 14 mg Chl *a* m⁻² (Gosselin *et al.* 1997) and from Weddell Sea pack ice, 1.6 – 8.6 mg Chl *a* m⁻² in (Dieckmann *et al.* 1990).

The algal biomass of the surface communities were measured to be 0.1 to 0.5 mg Chl *a* m⁻² and visually observed to be between 0.3 to 9.6 mg Chl *a* m⁻². This also compares well with measurements made in October 1998: 0.2-5.4 (av. 1.829) mg Chl *a* m⁻² (McMinn & Hegseth, 2003). The sampled floes all had an observed colour of 0 (<3 mg Chl *a* m⁻²), reflected in the low measured values. The observed values are of the same order of magnitude used in previous estimates; 4 mg Chl *a* m⁻² (Legendre *et al.* 1992), 8 mg Chl *a* m⁻² in (observed value in November; Arrigo *et al.* 1997).

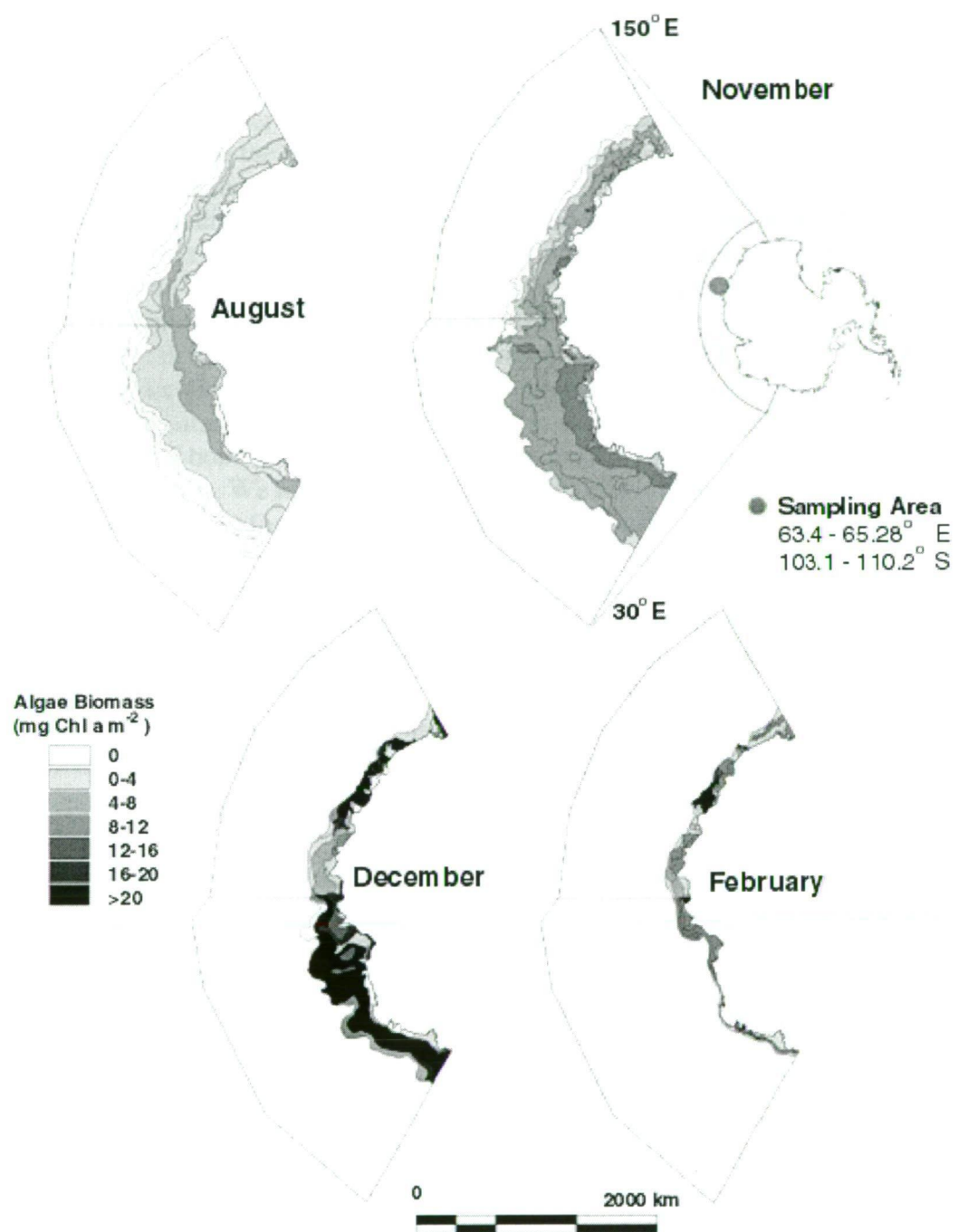
The surface assemblages are formed by seawater flooding the snow-ice interface (Meguro 1962), so floe edges are an important factor. The effect of floe edge is reflected in the pattern of algal biomass across the ice surface (see Figure 2.6), which clearly displays a marked edge and interior zonation. For the purpose of generally characterising algal biomass in pack ice surface communities, this data suggests that two regions can be defined; a 5 m edge band with a mean algal biomass 50% of the maximum and the interior with 30% of the maximum. Each observation of maximum surface brown colour was converted to mean values by correcting for the proportion of edge and interior regions. An observed floe size of 0-20 m has 75% edge zone, 25% interior, and an observed floe size 20-100m has 15% edge zone and 85% interior.

Applying the measured values, and the floe edge effect, to the habitat extent of the algae communities, using the sophisticated extrapolation technique outlined, the total biomass of algae in east Antarctic pack ice (30-150°E) was 8.6 Tg in November 2000. Using the extrapolation of growth outlined in methods, the biomass was calculated over the spring period (Table 3.1). The integrated and corrected average biomass in each ice area in the region was calculated for each month of spring, and is displayed in Figure 3.1.

Table 3.1 Total sea ice area and sea ice algal biomass parameters from east Antarctica (30-150°E) in spring 2000/2001. Data was measured in November and extrapolated forward into December and backwards to August. No values are given beyond December because the rapidly melting ice changed the natural algal habitats

	Month (Spring 2000-2001)					
	Aug	Sept	Oct	Nov	Dec	Jan
Ice Area >20cm excluding glacier ice (million km ²)	3.1	2.9	3.2	2.9	1.4	0.5
Pack – bottom biomass (Tg C)	1.41	2.11	3.04	6.51	6.74	
Pack – surface biomass (Tg C)	0.30	0.48	0.70	1.31	1.88	
Total Biomass (Tg C)	2.03	2.88	4.08	7.82	8.62	

Figure 3.1 Biomass distribution in eastern Antarctica (30-150E), Spring 2000. Biomass is an integration of surface and bottom communities estimated from ice core values and extrapolated using NOAA ice charts derived from passive microwave satellite data



3.5 Discussion

Algal communities growing on the under surface of pack ice are critically important as they provide the primary food source for grazing invertebrates during the six to nine months when the sea surface is covered with ice (Marschall 1988, O'Brien 1987, Stretch *et al.* 1988). Low light and deep mixing during this time ensures that phytoplankton biomass is minimal and that the only primary production is occurring in the relatively well-lit sea ice. Indeed, there is mounting evidence that krill, particularly the juvenile stages, depend on sea ice algae to survive the winter (Marschall 1988). Thus an appreciation of the extent of the under ice biomass will allow a better prediction of the dependent invertebrate biomass. The data presented herein shows that current models grossly underestimate the extent and significance of bottom communities in the pack ice of eastern Antarctica. The reasons for the more extensive development of bottom ice communities here is unclear but is possibly related to lower snowfall and a thinner average ice thickness.

The biomass of sea ice algae was estimated in November for this region, and then extrapolated forward and backward in time using a previously measured growth rate and calculated ice coverages from satellite data. The total biomass was found to increase through Spring and Summer, reaching a peak soon after the peak in maximum ice extent (Figure 3.2). This peak was in December, where the ice extent had reduced, but biomass was very concentrated. It is likely that we have actually underestimated the sea ice algal biomass in eastern Antarctica by selecting conservative estimates of both the C: Chl *a* ratio and the growth rate. There are very few published values of the C: Chl *a* ratios. We have used a C: Chl *a* ratio of 31, based on the published value of Palmisano & Sullivan (1983b) for McMurdo Sound fast ice. Fast ice algal communities are typically exposed to lower light climates than pack ice communities and so would be expected to have lower C: Chl *a* ratios. Other published data include values of 16-32 from Arctic pack ice (Johnsen & Hegseth 1991), our own unpublished values of 20-50 from the fast ice of McMurdo Sound and close to 90 from Ross Sea pack ice communities exposed to high light (Lizotte & Sullivan 1991). Similarly, we have conservatively selected a growth rate at the lower end of recorded values. The specific growth rate value used here of 0.1 d^{-1} was based on measurements of fast ice by Sullivan *et al.* (1985). However, much greater values have been measured from Arctic sea ice, $0.15\text{-}0.80 \text{ d}^{-1}$ (Hegseth 1992, Gilstad & Sakshaug 1990) and from Arctic phytoplankton, 1.7 d^{-1} (Kirst & Wiencke 1995).

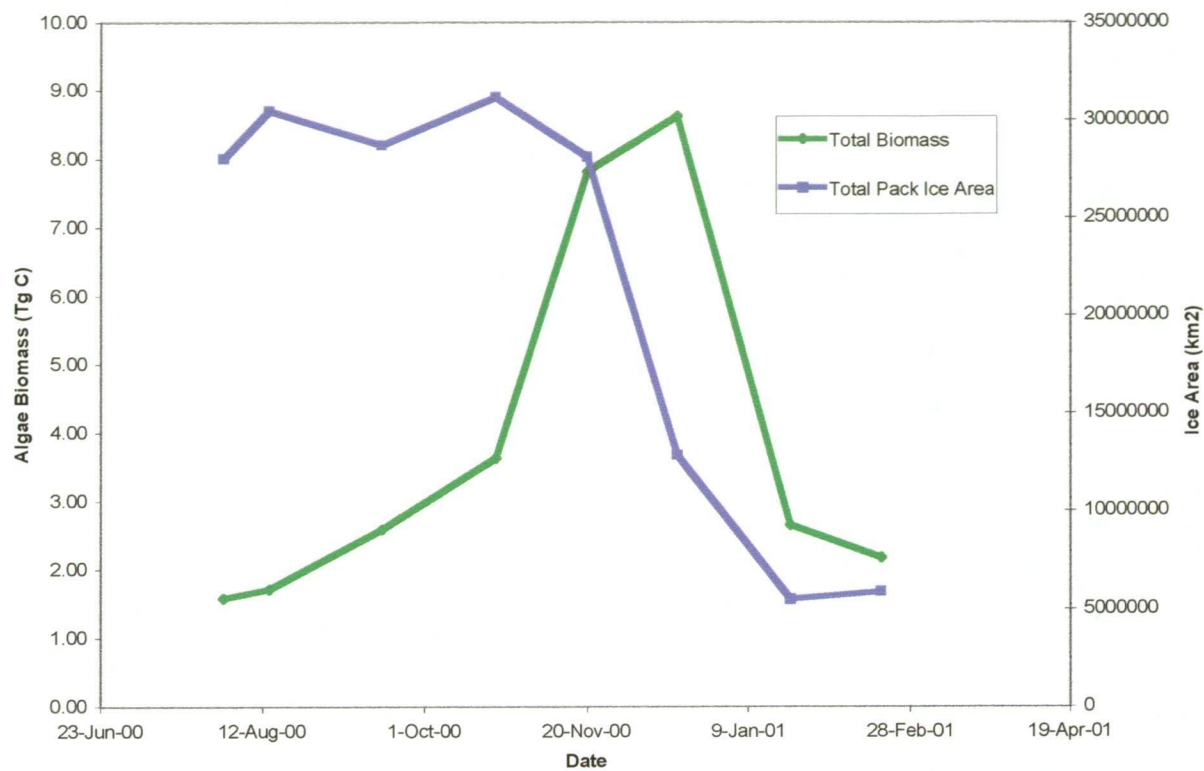
All biomass and productivity models need to be grounded in a solid observational data set. The models of Arrigo *et al.* (1997) and Legendre *et al.* (1992) represent important stages in the development of a model for the Antarctic. However, additional biomass data and distributional patterns need to be incorporated from less studied regions. This includes eastern Antarctica, the Ross Sea region and the western Pacific sector. Additional data will allow the continued refinement of the models already presented.

Our simple model results in a total estimate of production of $8.6 \text{ Tg C year}^{-1}$ in east Antarctica ($30\text{-}150^\circ\text{E}$). This is similar to the result from the sea ice model of Arrigo *et al.* (1997), which resulted in $\sim 9 \text{ Tg C year}^{-1}$ for the South Indian and SW Pacific regions ($20\text{-}160^\circ\text{E}$). The major difference in findings is that $6.75 \text{ Tg C year}^{-1}$ biomass was produced in the pack ice bottom community ($\sim 76\%$ of the total), a community previously assumed to be of negligible importance. As bottom ice algae provide a vital trophic link and are likely to be essential to over wintering krill, a closer approximation of algal biomass is essential for Southern Ocean food web models.

The maximum sea ice algal biomass in 2000, estimated for the whole of Antarctica following the same methods, is $62 \text{ Tg C year}^{-1}$, which is similar to the $63\text{-}70 \text{ Tg C year}^{-1}$ found by Legendre *et al.* (1992). This estimate of total Antarctic sea ice algal biomass is only a crude estimate, as it incorporates several assumptions; most importantly that the measurements of ice algal biomass in east Antarctica apply to the whole continent, which is known to be incorrect. The

value of this calculation is that enables a comparison to be made with other estimates. It also shows that our estimate is consistent with previous estimates.

Figure 3.2 Ice extent and total sea ice algal biomass in East Antarctica (30-150°E), Spring 2000.



Chapter 4 Discussion and Conclusions

4.1 Overview

The Antarctic marine environment is composed of an interconnected system of distinct hydrographic and biogeochemical subdivisions (Treguer and Jacques 1992), including the open ocean, frontal regions, shelf-slope waters, sea ice and marginal ice zones, and ice-free terrestrial environments. Sea ice is a dominant and distinguishing characteristic of the marine ecology in the Antarctic oceans, both in physical and biological terms. Algae in Antarctic seasonal pack ice are an important source of primary production: 20-30% of the total annual primary production, according to recent estimates (Arrigo *et al.* 1998a, Lizotte 2001). This production provides an important food source for zooplankton grazing, particularly during periods of low aquatic production such as winter. Algal biomass is also an important link in the Southern Ocean carbon cycle. So far there is no reliable estimate of total algal biomass in the different regions of Antarctica based on measurements made there.

Algae are contained within 3 broad regions in sea ice: the surface, interior and bottom. The surface and bottom communities are known to be the most abundant in algae. This study has endeavoured to make an estimate of the total algal biomass in the bottom and surface communities of seasonal pack ice in the eastern Antarctic region of 30-150°E longitude.

The first important point to clarify regarding this study is that it is not a measurement of algal biomass, it is an estimate. The final value should not be regarded as scientifically rigorous measurement but as a broad scale estimate of sea ice algae biomass in the east Antarctic sea ice zone. With many limitations on sources of data due to the remoteness and difficult nature of the environment, a fully comprehensive field survey of sea ice algae in sea ice is not yet possible, and may never be. Therefore, certain extrapolations of measurements are necessary to make broad scale estimates of total biomass. The magnitude of this extrapolation is very large in this case: measurements from a few points are extrapolated to an entire region of sea ice.

However, this extrapolation is acceptable for the purposes of this type of study. While the use of extrapolation can never lead to a strict and statistically correct measurement, they can be used to create a rough estimate or large-scale indication. This extrapolation is based on the fundamental assumption that the biomass of sea ice algae will be identical in spatially separate ice of similar nature (thickness, snow cover, age etc). While this is certainly never exactly accurate, it is assumed to be acceptable for the purposes of making this large-scale estimation.

4.2 Main conclusion

Sea ice algal biomass accumulation in the east Antarctic sea ice zone (30-150°E), was estimated in this study to be 8.6 Tg C yr⁻¹. This result is a measurement of total accumulated biomass over the yearly cycle of austral spring 2000-2001 which provides a reasonable estimate of total annual net production, assuming that it is at its maximum (Legendre *et al.* 1992). This value is in the same order as previous estimates and provides further support that algal biomass is in this order of magnitude for this region.

Of this total, 8.14 Tg C yr⁻¹ was in the pack ice, and 0.46 Tg C yr⁻¹ in the fast ice. Of the pack ice biomass, 83% was found in the bottom community (6.75 Tg C yr⁻¹) and 17% in the surface community (1.39 Tg C yr⁻¹). This suggests that the bottom community is relatively more significant in the east Antarctic region than in some other regions. Algal biomass in the bottom community is potentially more bio-available to zooplankton grazing while the ice is intact. The algal biomass in

the bottom 1cm of ice in east Antarctic pack ice is measured as 2.54 Tg C yr⁻¹ (37% of the total bottom community biomass) at the peak in December. This biomass, or a relative proportion of it in preceding months, is an available food source to zooplankton during periods of low aquatic production, such as winter.

4.3 Other conclusions, other points

In this ice at this time, the bottom community was variable in biomass due in part to the heterogenous nature of the under-surface of ice, and in part to the inherent spatial heterogeneity of ice algal distributions. From the ice core measurements, the mean bottom algal biomass was in the order of 80% of the maximum observed biomass.

In the surface community of pack ice floes, biomass of algae was heavily influenced by floe edge effects. A useful technique to characterise this floe edge effect in this ice at this time appears to be the identification of a 5 m edge band (containing a mean biomass 50% of the maximum observed), and an interior zone (containing a mean biomass 30% of the maximum observed biomass). The species composition in the surface community of ice floes was also examined and there was a similar pattern of edge zonation. In the 5 m edge zone there was a suite of 16 sea ice, Southern Ocean, pack ice and Antarctic ice species. In the interior, there was distinctly different suite of 14 sea ice, pack ice, Southern Ocean and Antarctic species.

A method of visual colour observation of sea ice as an indication of algal biomass was successfully used to collect data. The observation of yellow to brown colour on a 4-stage scale (0,1,2,and 3) in sea ice was calibrated against *in situ* measured biomass. This appears to be a useful tool for collecting broad scale data on algal biomass in sea ice from the data collected here. However, this is only an initial trial, and does not prove the usefulness of this method beyond doubt. A technique like this may be used routinely on Antarctic voyages to collect a large data set of algal biomass in ice throughout different ice types, monthly periods and different yearly cycles.

4.4 Limitations, sources of error

Fieldwork in Antarctic sea ice is difficult. This study is based on a very limited data set of relatively few different types of ice floe. The limited size of the data set is the largest source of possible error associated with a study of this nature. This error is unavoidably large but this is designed as a broad scale estimate, not a measurement of algal biomass. Therefore, no detailed error analysis is attempted for the data. The nature of sampling sea ice floes also introduces unavoidable biases. Sampling thin ice and the edges of ice floes is difficult, so there is a tendency to concentrate sampling near the centre of thicker floes. Surface samples were taken along a transect across floes starting from the edge to investigate floe edge effects. Cores were opportunistically taken in a random pattern over ice floes, covering edge and centre areas wherever possible. The sampling for this study was done opportunistically and without necessary means to avoid these difficulties, so these errors will inevitably be present.

The fluorometric analysis of Chlorophyll *a* was done following the standard procedure that has a relatively low margin of error (less than 1%), (Mantoura *et al.* 1996). This represents a minor source of error in the final result.

Remote sensing of the physical properties of sea ice does not yield perfect resolution, and represents a source of error when extrapolating a measured value of sea ice algal biomass to other areas of similar sea ice. The interpretation of sea ice remote sensing data to create the sea ice chart and GIS files used in this study is a relatively low-resolution interpretation technique. This is

another main source of inaccuracy and low precision in this study. However, the precision afforded by this type of remote sensing allows a considerably more precise estimate of biomass than an average biomass multiplied by the entire area of sea ice. A detailed error analysis of the inaccuracies introduced by the remote sensing data will not be done as it is not the intention of the study to make a rigorous measurement of biomass.

Assigning a value of algal biomass to each region of ice defined in the remotely sensed interpreted ice charts and the calculation of ice area and totalling the biomass values were done automatically. Therefore the only error associated with the calculation of the total algal biomass at the time of the fieldwork is in the measurements used to assign a biomass value to the ice regions, and errors in the ice charts themselves.

Extrapolating forward in time to the period of maximum biomass was done using conservative values for both growth rate and maximum attainable biomass (see Chapter 3). Again, the calculation of the biomass according to this growth rate and the change in sea ice area of each ice type was done automatically. Therefore, the value of maximum standing stock, which is a reasonable estimate of net annual production, is a conservative one and the only significant source of error is the measurements used to assign the value to each ice type, and in the ice charts.

4.5 Future research

This study is a broad scale estimate of algal biomass in the east Antarctic region, with many limitations and possibilities for further research. Further fieldwork is of course the obvious first step. Many more measurements of algal biomass in different types of ice at different times of year are needed to improve the reliability and versatility of an estimate such as this.

A finer spatial scale is needed in two ways; firstly finer scale measurements of algal biomass which are used to base the rules of the model on. Measurements in every ice type in every local area are needed to create a series of local scale models, rather than a regional scale model. Secondly, a finer scale of analysis in the model would be useful. This could be achieved by using finer scale remote sensing data and analysis of each cell separately, rather than an interpreted ice chart. This study was conceived as a “next step” from the continent-wide estimates of the past, towards a model that better accounts for regional differences in algal biomass. Of course, further steps are always required.

References

- Ackley, S.F; Buck, K.R; Taguchi, S; (1979) Standing crop of algae in the sea ice of the Weddell Sea region. **Deep Sea Research**. 26(3A): pp 269-281.
- Ackley, S.F (1982) Ice scavenging and nucleation: two mechanisms for the incorporation of algae into newly forming sea ice. **Eos Transactions of the American Geophysical Union**. 63 pp 65.
- Ackley, S.F; Lange, M; Wadhams, P (1990) Snow cover effects on Antarctic sea ice thickness. In: Ackley, S.F; Weeks, W.F (eds) **Sea ice properties and processes**. CRREL Monograph. 90(1): pp 16-21.
- Ackley, S.F; Sullivan, C.W (1994) Physical controls on the development and characteristics of Antarctic sea ice biological communities - a review and synthesis. **Deep Sea Research I - Oceanography Research Papers**. 41(10): pp 1583-1604.
- Allison, I; Worby, A (1994) Seasonal changes of sea-ice characteristics off East Antarctica. **Annals of Glaciology**. 20: pp 195-201.
- Andreoli, C; Tolomio, C; Moro, I; Radice, M; Moschin, E; Bellato, S (1995) Diatoms and dinoflagellates in Terra Nova Bay (Ross Sea - Antarctica) during austral summer 1990. **Polar Biology**. 15: pp 465-475.
- Archer, S.D; Leakey, P.H; Burkill, P.H; Sleight, M.A; Appleby, C.J (1996) Microbial ecology of sea ice at a coastal Antarctic site; community composition; biomass and temporal change. **Marine Ecology Progress Series**. 135: pp 179-195.
- Arrigo, K.R; Kremer, J.N; Sullivan, C.W (1993) A simulated Fast Ice Ecosystem. **Journal of Geophysical Research**. 98(C4): pp 6929-6946.
- Arrigo, K.R; Dieckmann, G.S; Gosselin, M; Robinson, D.H; Fritsen, C.H; Sullivan, C.W (1995) High resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: biomass, nutrient, and production profiles within a dense microalgal bloom. **Marine ecology progress series**. 127(1-3): pp 255-268.
- Arrigo, K.R; Worthen, D.L; Lizotte, M.P; Dixon, P; Dieckmann, G (1997) Primary Production in Antarctic Sea Ice. **Science**. 276: pp 394-397.
- Arrigo, K.R; Worthen, D.L; Schnell, A; Lizotte, M.P (1998a) Primary Production in Southern Ocean Waters. **Journal of Biophysical Research**. 103(C8): pp 15587-15600.
- Arrigo, K.R; Worthen, D.L; Dixon, P; Lizotte, M.P (1998b) Primary productivity of near surface communities within Antarctic pack ice. In: Lizotte M.P; Arrigo, K.R (eds) **ANTARCTIC SEA ICE: BIOLOGICAL PROCESS, INTERACTIONS, AND VARIABILITY**. pp 23-43.
- Arrigo, K.R; Robinson, D.H; Dunbar, R.B; Leventer, A.R; Lizotte, M.P (2001). Physical control of chlorophyll *a*, POC and TPN distributions in the pack ice of the Ross Sea, Antarctica. **Journal of Geophysical Research**. *in press*.
- Banse, K (1995) Antarctic marine top predators revisited: homeotherms do not leak much CO₂ to the air. **Polar Biology**. 15: pp 93-104.
- Bathmann, U.V; Makarov, R.R; Spiridonov, V.A; Rohardt, G (1993) Winter distribution and overwintering strategies of the Antarctic copepod species *Calanoides acutus*, *Rhincalanus gigas* and *Calanus propinquus* (Crustacea, Calanoida) in the Weddell Sea. **Polar Biology**. 13: pp 333-346.
- Boyd, C.M; Heyraud, M; Boyd, C.N (1984) Feeding of Antarctic krill, *Euphausia superba*. **Journal of Crustacean Biology**. 4(1): pp 123-141.
- Bunt, J.S (1963) Diatoms of Antarctic sea-ice as agents of primary production. **Nature**. 199(4900): pp 1255-1257

Bunt, J.S; Wood, E.J.F (1963) Microalgae and Antarctic sea ice. **Nature**. 199: pp 1254-1255.

Bunt, J.S (1964a) Primary productivity under sea ice in Antarctic waters 1. Concentrations and photosynthetic activities of microalgae in the waters of McMurdo Sound, Antarctica. **Biology of the Antarctic Seas I**. American Geophysical Union of the National Academy of Sciences - National Research Council.

Bunt, J.S (1964b) Primary productivity under the sea ice in Antarctic waters. Influence of light and other factors on photosynthetic activities of Antarctic marine microalgae. **Antarctic Research Series**. 11: pp 1-14.

Bunt, J.S (1967) Some characteristics of microalgae isolated from Antarctic sea ice. **Biology of the Antarctic seas III**. American Geophysical Union of the National Academy of Sciences - National Research Council.

Bunt, J.S (1968a) Microalgae of the Antarctic pack ice zone. **Symposium on Antarctic Biology**. Santiago, Chile, Heffer & Sons Ltd., Cambridge, England.

Bunt, J.S (1968b) Influence of light and other factors on the photosynthetic activities of Antarctic Marine microalgae. **Antarctic Research Series**. 11: pp 27-31.

Bunt, J.S; Lee, C.C (1970) Seasonal primary production in Antarctic sea ice at McMurdo Sound in 1967. **Journal of Marine Research**. 28: pp 304-320.

Burkholder, P.R; Mandelli, E.F (1965) Productivity of microalgae in Antarctic Sea Ice. **Science**. 33: pp 177-184.

Carey, A.G. Jr. (1985) Marine Ice Flora: Arctic. In: Horner, R.A (ed) **Sea Ice Biota**. Boca Raton, CRC Press: pp 173-190.

Carey, A.G. Jr. (1987) Particle flux beneath fast ice in the shallow southwestern Beaufort Sea, Arctic Ocean. **Marine Ecology Progress Series**. 40: pp 247-257.

Cavalieri, D.J; Gloersen, P; Parkinson, C.L; Comiso, J.C; Zwally, H.J (1997) Observed Hemispheric Asymmetry in Global Sea Ice Changes. **Science**. 278: pp 1104-1106.

Comiso, J.C; Zwally, H.T (1984) Concentration gradients and growth and decay characteristics of seasonal sea ice cover. **Journal of Geophysical Research**. 89: pp 8081-8103.

Comiso, J.C; Maynard, N.G; Smith, W.O Jr; Sullivan, C.W (1990) Satellite ocean colour studies of Antarctic ice edge in Summer / Autumn. **Journal of Geophysical Research**. 95: pp 9481-9486.

Daly, K.L; Macaulay, M.C (1988) Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring 1983. **Deep Sea Research**. 35: pp 21-41.

Daly, K.L (1990) Overwintering development, growth and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. **Limnology & Oceanography**. 35: pp 1564-1576.

Daly, K.L (1998) Physioecology of juvenile Antarctic krill (*Euphausia superba*) during Spring in ice-covered seas. **Antarctic Research Series 73: Antarctic sea ice biological processes, interactions, and variability**. pp 183-198.

de la Mare, W.K (1997) Abrupt mid-twentieth-century decline in Antarctic sea-ice extent from whaling records. **Nature**. 389: pp 57-60.

Dey, B; Moore, H.; Gregory, A.F (1979) Monitoring and mapping sea-ice breakup and freezeup of Arctic Canada from satellite imagery. **Arctic and alpine research**. 11(2): pp 229-242.

Dieckmann, G; Sullivan, C.W; Garrison, D (1990) Seasonal Standing Crop of Ice Algae in Pack Ice of the Weddell Sea. **Eos. Transactions of the American Geophysical Union**. 71(2): pp 79.

Dierssen, H.M; Vernet, M; Smith, R.C (2000) Optimizing models for remotely estimating primary production in Antarctic coastal waters. **Antarctic Science**. 12(1): pp 20-32.

Eicken, H; Ackley, S.F; Richter-Menge, J.A; Lange, M.A (1991) Is the strength of sea ice related to its chlorophyll content? **Polar Biology**. 11: pp 347-350.

Eicken, H (1992) The role of sea ice in structuring Antarctic ecosystems. **Polar Biology**. 12: pp 3-13.

Everson, I (1977) **The Living Resources of the Southern Ocean**. Southern Ocean Fisheries Survey Programme, Rome.

Frazer, T.K; Ross, R.M; Quetin, L.B; Montoya, J.P (1997) Turnover of carbon and nitrogen during growth of larval krill, *Euphausia superba* Dana: a stable isotope approach. **Journal of Experimental Marine Biology and Ecology**. 212: pp 259-275.

Fritsen, C.H; Ackley, S.F; Kremer, J.N; Sullivan, C.W (1998) Flood-freeze cycles and microalgal dynamics in Antarctic Pack Ice. In: Lizotte, M.P; Arrigo, K.R (eds) **Antarctic Sea Ice: Biological Processes, Interactions and Variability**. 73: pp 1-21.

Fukuchi, M; Tanimura, A; Ohtsuka, N (1985) Zooplankton community conditions under the sea ice near Syowa Station, Antarctica. **Bulletin of Marine Science**. 37: pp 518-528.

Garrison, D.L (1991) Antarctic Sea Ice Biota. **American Zoologist**. 31: pp 17-33.

Garrison, D.L; Buck, K.R (1985) Sea ice algal communities in the Weddell Sea: species composition in ice and plankton assemblages. In: Gray, J.S; Christiansen, M.E (eds) **Marine Biology of Polar Regions and Effects of Stress on Marine Organisms**. John Wiley & Sons, New York: pp 103-121.

Garrison, D.L; Buck, K.R (1989a) Protozooplankton from the Weddell Sea: abundance and distribution in the ice edge zone. **Polar Biology**. 9: pp 341-351.

Garrison, D.L; Buck, K.R (1989b) The biota of Antarctic pack ice in the Weddell Sea and Antarctic Peninsula regions. **Polar Biology**. 10: pp 211-219.

Garrison, D.L; Buck, K.R (1991) Surface-layer sea ice assemblages in Antarctic pack ice during the Austral spring: environmental conditions, primary production and community structure. **Marine Ecology Progress Series**. 75: pp 161-172.

Garrison, D.L; Ackley, S.F; Buck, K.R (1983) A physical mechanism for establishing algal populations in frazil ice. **Nature**. 306: pp 363-365.

Garrison, D.L; Buck, K.R; Fryxell, G.A (1987) Algal assemblages in Antarctic pack ice and in ice-edge plankton. **Journal of Phycology**. 23: pp 564-572.

Gilstad, M; Sakshaug, E (1990) Growth rates of ten diatom species from the Barents Sea at different irradiances and day lengths. **Marine Ecology Progress Series**. 64: pp 169-173.

Gleitz, M; Grossman, S; Scharek, R; Smetacek, V (1996) Ecology of diatom and bacterial assemblages in water associated with melting summer sea ice in the Weddell Sea, Antarctica. **Antarctic Science**. 8(2): pp 135-146.

Goodrick, S.L (1997) **On the development of Antarctic katabatic winds and their impact on ocean and ice processes in the coastal Southern Ocean with implications for primary productivity**. PhD thesis. University of Alabama, Huntsville: pp 176.

Gosselin, M; Levasseur, M; Wheeler, P.A; Horner, R.A; Booth, B.C (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. **Deep-Sea Research II**. 44(8): pp 1623-1644.

Grose, M; McMinin, A (2002) Algal biomass in east Antarctic pack ice: how much is in the east? In: Huiskes, A.H.L; Gieskes, W.W.C; Rozema, J; Schorno R.M.L; van der Vies, S.M; Wolff, W.J. (eds) **Antarctic Biology in a global context**. Backhuys Publishers, Leiden, pp 21-25.

Grossi, S.M; Sullivan, C.W (1985) Sea ice microbial communities 5, The vertical zonation of diatoms in an antarctic fast ice community. **Journal of phycology**. 21(3): pp 401-409.

- Grossi, S.M; Kottmeier, S.T; Moe, R.L; Taylor, G.T; Sullivan, C.W (1987) Sea ice microbial communities 6, Growth and primary production in bottom ice under graded snow cover. **Marine Ecology Progress Series**. 35: pp 153-164.
- Hamner, W.M; Hamner, P.P; Strand, S.W; Gilmer, R.W (1983) Behaviour of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling and molting. **Science**. 220: pp 433-435.
- Hasle, G.R (1969) An analysis of the phytoplankton of the Pacific Southern Ocean: abundance, composition, and distribution during the Bratigg Expedition, 1947-48. **Hvalradets Skrifter**. 52: pp 1-168.
- Hedgpeth, J.W (1977) The Antarctic marine ecosystem. In: Llano, G (ed.) **Adaptations Within Antarctic Ecosystems**, Proceedings of the Third SCAR Symposium on Antarctic Biology, Smithsonian Institution, Washington, D.C. pp. 3-10
- Hegseth, E.N (1992) Sub-ice algal assemblages of the Barents Sea: species composition, chemical composition and growth rates. **Polar Biology**. 12: pp 485-496.
- Heywood, R.B; Whitaker, T.M (1984) The Antarctic marine flora. In: Laws, R.M (ed) **Antarctic Ecology**. London, Academic Press. 2: pp 373-419.
- Holm-Hansen, O; Riemann, B (1978) Chlorophyll a determination: improvements in methodology. **Oikos**. 30: pp 438-447.
- Holm-Hansen, O; Huntley, M (1984) Feeding requirements of krill in relation to food sources. **Journal of Crustacean Biology**. 4(1): pp 156-173.
- Hooker, J.D (1847). **Diatomaceae**. The Botany of the Antarctic Voyage of H.M Discovery ships 'Erebus' and 'Terror', Years 1839-1843. Vol: LVI. London.
- Hopkins, T.L; Torres, J.J (1989) Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. **Deep Sea Research**. 36: pp 543-560.
- Horner, R.A (1985). Ecology of sea ice microalgae. In: Horner, R.A (ed) **Sea Ice Biota**. Boca Raton, CRC Press: pp 83-103.
- Horner, R.A (1990). Ice-associated Diatoms. In: Medlin, L.K; Priddle, J (eds) **Polar Marine Diatoms**. British Antarctic Survey, Natural Environment Research, Cambridge UK: pp 9-14.
- Horner, R.A; Syversten, E.E; Thomas, D.P; Lange, C (1988) Proposed terminology and reporting units for sea ice algal assemblages. **Polar Biology**. 8: pp 249-253.
- Hoshiai, T (1977) Seasonal change of ice communities in the sea ice near Syowa Station, Antarctica. In: Dunbar, M.J (ed) **Polar Oceans**. Arctic Institute of North America, Calgary.
- Hoshiai, T (1981) Proliferation of ice algae in the Syowa Station area, Antarctica. **Memorial National Institute of Polar Research Series E (Biol. Med. Sci.)**. 34: pp 1-12.
- Hoshiai, T; Tanimura, A (1986) Sea ice meiofauna at Syowa station, Antarctica. **Memorial National Institute of Polar Research, Special Issue**. 44: pp 118-124.
- Hoshiai, T; Tanimura, A; Watanabe, K (1987) Ice algae as food of an Antarctic ice-associated copepod, *Paralabidocera antarctica* (I.C Thompson). **Proceedings of NIPR Symposium on Polar Biology**. 1: pp 105-111
- Huntley, M.E; Lopez, M.D.G; Karl, D.M (1991) Top predators in the Southern Ocean: A major leak in the biological carbon pump. **Science**. 253: pp 64-66.
- Huntley, M.E; Nordhausen, W; Lopez, M.D.G (1994) Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter. **Marine Ecology Progress Series**. 107: pp 23-40.
- Ikeda, T; Dixon, P (1982) Body shrinkage as a possible overwintering mechanism of the Antarctic krill

Euphausia superba Dana. **Journal of Experimental Marine Biology and Ecology**. 62: pp 143-151.

Johnsen, G; Hegseth, E.N (1991) Photoadaptation of sea-ice microalgae in the Barents Sea. **Polar Biology**. 11: pp 179-184.

Kawaguchi, K; Ishikawa, S; Matsuda, O, *et al.* (1986) Overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off Ongul Islands in Lützow-Holm Bay, Antarctica. **Memoirs of the National Institute of Polar Research Special Issue**. 44: pp 67-85.

Kawaguchi, S; Satake, M (1994) Relationship between recruitment of the Antarctic krill and the degree of ice cover near the South Shetland Islands. **Fisheries Science**. 60(1): pp 123-124.

Kirst, G.O.C; Wiencke, C (1995) Ecophysiology of polar algae. **Journal of Phycology**. 31: pp 181-199.

Kittel, W; Ligowski, R (1980) Algae found in the food of *Euphausia crystallorophias* (Crustacea). **Polish Polar Research**. 1(23): pp 129-137.

Knox, G.A (1994) **The Biology of the Southern Ocean**. Cambridge University Press, Cambridge.

Kottmeier, S.T; Sullivan, C.W (1987) Seasonal primary and bacterial productivity in the pack ice as related to krill. In: CCAMLR, IOC, SCAR, SCOR (eds) **Proceedings of Scientific Seminar on Antarctic Ocean Variability and its Influence on Marine Living Resources, particularly Krill**. 2-6 June 1987, Paris pp 1-26.

Kottmeier, S.T; Sullivan, C.W (1990) Bacterial biomass and production in pack ice of Antarctic marginal ice edge zones. **Deep Sea Research**. 37: pp 1311-1330.

Kottmeier, S.T; Miller, M.A; Lizotte, M.P; Craft, L.L; Gulliksen, B; Sullivan, C.W (1985) Ecology of sea ice microbial communities (SIMCO) during the 1984 winter to summer transition in McMurdo Sound, Antarctica. **United States Antarctic Journal**. 20: pp 128-130.

Krebs, W.M; Lipps, J.H; Burckle, L.H (1987) Ice diatom floras, Arthur Harbour, Antarctica. **Polar Biology**. 7: pp 163-171.

Kudoh, S; Robineau, B; Suzuki, Y; Fujiyoshi, Y; Takahashi, M (1997) Photosynthetic acclimation and the estimation of temperate ice algal primary production in Saroma-ko Lagoon, Japan. **Journal of Marine Systems**. 11: pp 93-109.

Lancelot, C; Mathot, S; Veth, C; de Baar, H (1993) Factors controlling phytoplankton ice-edge blooms in the marginal ice-zone of the northwestern Weddell Sea during sea ice retreat 1988: field observations and mathematical modeling. **Polar Biology**. 13: pp 377-387.

Langdon, R.M; Quetin, L.B (1991) Behavioural and physiological characteristics of the Antarctic krill, *Euphausia superba*. **American Zoologist**. 31: pp 49-63.

Lascara, C.M; Hofmann, E.E; Ross, R.M; Quetin, L.B (1999) Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. **Deep-Sea Research I**. 46: pp 951-984.

Legendre, L; Le Fevre, J (1991) From individual plankton cells to pelagic marine ecosystems and to global biogeochemical cycles. In: Demers, S (ed) **Particle analysis in oceanography**. Springer, Berlin: pp 261-299.

Legendre, L; Ackley, S.F; Dieckmann, G.S; Gulliksen, B; Horner, R; Hoshiai, T; Melnikov, I.A; Reeburgh, W.S; Spindler, M; Sullivan, C.W (1992) Ecology of sea ice biota 2. Global significance. **Polar Biology**. 12: pp 429-444.

Lizotte, M.P (2001) The contributions of sea ice algae to Antarctic marine ecosystems. **American Zoologist**. 41: pp 57-73.

Lizotte, M.P; Sullivan, C.W (1991) Rates of photoadaptation in sea ice diatoms from McMurdo Sound, Antarctica. **Journal of Phycology**. 27: pp 367-373.

- Lizotte, M.P; Robinson, D.H; Sullivan, C.W (1998) Algal pigment signatures in Antarctic sea ice. In: Lizotte, M.P; Arrigo, K.R (eds) **Antarctic Sea Ice: Physical Processes, Interactions and Variability**. Antarctic Research Series. 73: 93-106.
- Lizotte, M.P (2001), *pers comm*. Via email, Senior scientist, Bigelow Marine Institute, Maine USA
- Loeb, V; Slegel, V; Holm-Hansen, O; Hewitt, R; Fraser, W; Trivelpiece, W; Trivelpiece, S (1997) Effects of sea-ice extent and krill or salp-dominance on the Antarctic food web. **Nature**. 387: pp 897-900.
- Longhurst, A.R; Bedo, A.W; Harrison, W.G; Head, E.J.H; Sameoto, D.D (1990) Vertical flux of respiratory carbon by oceanic diel migrant biota. **Deep Sea Research**. 37: pp 685-694.
- Lu, Q (1998) On mesoscale modeling of the dynamics and thermodynamics of sea ice. **Institute of Hydrodynamics and Hydraulic Engineering series**. 44: pp 1-154.
- Lu, Q; Kej, A; Rasmussen, E.B (1988) A three-level dynamic thermodynamic sea ice model. In: Sackinger, W.M; Jeffries, M.O (eds) **Port and Ocean Engineering under Arctic Conditions**. The Geophysical Institute, Fairbanks, Alaska: pp 175-186.
- Maihara, Y; Endo, Y; *et al.* (1986) Laboratory observations on molting and growth of Antarctic krill, *Euphausia superba* Dana. **Proceedings of the 8th Symposium on Polar Biology**, pp 125-127.
- Mantoura, R.F.C; Jeffrey, S.W; Llewellyn, C.A; Claustre, H; Morales, C.E (1996). Comparison between spectrophotometric, fluorometric and HPLC methods for chlorophyll analysis. **Experimental results of SCOR Working Group 78 workshops**.
- Marschall, H.P (1988) The over-wintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. **Polar Biology**. 9: pp 129-135.
- Massom, R.A; Comiso, J.C; Worby, A.P; Lytle, V.I; Stock, L (1999) Regional Classes of Sea Ice cover in the East Antarctic Pack observed from satellite and *In Situ* during a winter time period. **Remote Sensing of the Environment**. 68: pp 61-76.
- Massom, R.A; Hill, K.L; Lytle, V.I; Worby, A.P; Paget, M.J; Allison, I (2000) Effects of regional fast-ice and iceberg distributions on the behaviour of the Mertz Glacier polynya, East Antarctica. In: Jeffries, M.O; Eicken, H. [eds] **Annals of glaciology**. Papers from the International Symposium on Sea Ice and its Interactions with the Ocean, Atmosphere and Biosphere. Fairbanks, Alaska, June 2000, 33: pp. 391-398
- Mathot, S; Garrison, D.L; Lancelot, C (1996) Pelagic and Ice-Based Primary Production in the Southern Ocean. **Eos. Transactions of the Geophysical Union**. 76(3): OS143.
- Maykut, G.A; Grenfell, T.C (1975) The spectral distribution of light beneath first-year sea ice in the Arctic Ocean. **Limnology and Oceanography**. 20: pp 534-563.
- McConnville, M.J; Wetherbee, R (1983) The bottom-ice microalgal community from the annual ice in the inshore waters of East Antarctica. **Journal of Phycology**. 19: pp 431-439.
- McMinn, A; Ashworth, C (1998) The use of oxygen microelectrodes to determine the net production by an Antarctic sea ice algal community. **Antarctic Science**. 10: pp 30-35.
- McMinn, A; Skerratt, J; Trull, T; Ashworth, C; Lizotte, M (1999a) Nutrient stress gradient in the bottom 5 cm of fast ice, McMurdo Sound, Antarctica. **Polar Biology**. 21: pp 220-227.
- McMinn, A; Ashworth, C; Ryan, K (1999b) Growth and productivity of Antarctic sea ice algae under PAR and UV irradiances. **Botanica Marina**. 42: pp 401-407.
- McMinn, A; Hegseth, E.N (2003) Early Spring pack ice from the Arctic and Antarctic: how different are they? In: Huiskes, A.H.L; Gieskes, W.W.C; Rozema, J; Schorno R.M.L; van der Vies, S.M; Wolff, W.J. (eds) **Antarctic Biology in a global context**. Backhuys Publishers, Leiden, pp 182-186.
- McMinn, A; Ryan, K; Gademann, R (2003) Diurnal changes in photosynthesis of Antarctic fast ice algal communities determined by pulse amplitude modulation fluorometry. **Marine Biology**. 143: pp 359-367

- Medlin, L.K (1990) *Berkeleya* spp. from Antarctic waters, including *Berkeleya adeliensis*, sp. nov. a new tube dwelling diatom from the undersurface of sea-ice. **Beiheft zur Nova Hedwigia**. 100: pp 77-89.
- Medlin, L.K; Priddle, J (1990) **Polar Marine Diatoms**. British Antarctic Survey, Natural Environment Research Council, Cambridge: pp 214.
- Meguro, M (1962) Plankton ice in the Antarctic Ocean. **Antarctic Record**. 14: pp 1192-1199.
- Michel, C; Legendre, L; Ingram, R.G; Gosselin, M; Levasseur, M (1996) Carbon budget of sea-ice algae in spring: evidence of a significant transfer to zooplankton grazers. **Journal of Geophysical Research**. 101(C8): pp 18345-18360.
- Moloney, C.L (1992) Carbon and the Antarctic marine food web. **Science**. 257: pp 259.
- Murphy, E.J; Clarke, A; Symn, C; Priddle, J (1995) Temporal variation in Antarctic sea-ice: analysis of a long term fast-ice record from the South Orkney Islands. **Deep-Sea Research I**. 42(7): pp 1045-1062.
- Nicol, S; Allison, I (1997) The frozen skin of the Southern Ocean. **American Scientist**. 85: pp 426-439.
- Nicol, S; Pauly, T; Bindoff, N; Wright, S; Thiele, D; Hosie, G; Strutton, P; Woehler, E (2000a) Ocean circulation off East Antarctica affects ecosystem structure and sea-ice extent. **Nature**. 406: pp 504-507
- Nicol, S; Kitchener, J; King, R; Hosie, G.W; de la Mare, W.K (2000b) Population structure and condition of Antarctic krill (*Euphausia superba*) off East Antarctica (80 - 150°E) during the Austral summer of 1995/1996. **Deep Sea Research II**. 47: pp 2465-2488.
- NOAA (2001). www.natice.noaa.gov, National Snow and Ice Database.
- O'Brien, D.P (1987) Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic Spring of 1985. **Journal of Crustacean Biology**. 7: pp 437-448.
- Palmisano, A.C; Sullivan, C.W (1983a) Sea ice microbial communities (SIMCO). 1. Distribution, abundance and primary production of ice microalgae in McMurdo Sound, Antarctica in 1980. **Polar Biology**. 2: 171-177.
- Palmisano, A.C; Sullivan, C.W (1983b) Physiological response of microalgae in the ice platelet layer to ambient low light conditions. In: Siegfried, R.R (ed) **Proceedings of the fourth symposium on Antarctic biology: Nutrient cycles and food chains**.
- Palmisano, A.C; Sullivan, C.W (1985) Growth, metabolism and dark survival in sea ice microalgae. In: Horner, R.A (ed) **Sea Ice Biota**. CRC Press, Inc. Boca Raton, Florida.
- Palmisano, A.C; SooHoo, J.B; Sullivan, C.W (1985) Photosynthesis-irradiance relationships in the sea ice microalgae from McMurdo Sound, Antarctica. **Journal of Phycology**. 21: pp 341-346.
- Palmisano, A.C; SooHoo, J.B; Sullivan, C.W (1987) Effects of four environmental variables on photosynthesis-irradiance relationships in Antarctic sea-ice microalgae. **Marine Biology**. 94: pp 299-306.
- Parkinson, C.L; Gloersen, P (1993) Global sea ice coverage. In: Gurney, R.J; Foster, J.L; Parkinson, C.L (eds.) **Atlas of Satellite Observations Related to Global Change**. Cambridge University Press, Cambridge, pp 371-383
- Partington, K; Bertoia, C (2002) **Evaluation of Special Sensor Microwave / Imager Sea-Ice Products**. http://www.natice.noaa.gov/nic_science.htm. 2002.
- Pollard, D; Thompson, S.L (1994) Sea-ice dynamics and CO₂ sensitivity in a global climate model. **Atmosphere-Ocean**. 32(2): pp 449-467.
- Priddle, J; Fryxell, G (1985) **Handbook of the common plankton diatoms of the Southern Ocean: Centrales except the genus *Thalassiosira***. British Antarctic Survey, Natural Environment Research Council, Cambridge University Press: pp 159.

- Quetin, L.B; Ross, R.M (1991) Behavioural and physiological characteristics of the Antarctic krill, *Euphausia superba*. **American Zoologist**. 31: pp 49-63.
- Quetin, L.B; Ross, R.M (2001) **Growth rates of larval Antarctic krill in mid-winter in the Marguerite Bay region**. Presented at the Third U.S Southern Ocean Globec Science Investigator Meeting. 10-12 December 2001 Arlington, VA.
- Quetin L.B; Ross, R.M; Clarke, A (1994) Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. In: El-Sayed, S.Z (ed) **Southern Ocean Ecology: The BIOMASS Perspective**. Cambridge University Press, Cambridge: pp 165-184.
- Quetin L.B; Ross, R.M; Frazer, T.K; Haberman, K.L (1996). Factors affecting distribution and abundance of zooplankton with an emphasis on Antarctic krill, *Euphausia superba*. In: Ross, R.M *et al.* (eds) **Foundations for Ecological Research West of the Antarctic Peninsula**. AGU Antarctic Research Series. American Geophysical Union, Washington: pp 357-371.
- Robineau, B; Legendre, L; Kishino, M; Kudoh, S (1997) Horizontal heterogeneity of microalgal biomass in the first-year sea ice of Saroma-ko Lagoon, (Hokkaido, Japan). **Journal of Marine Systems**. 11(1-2): pp 81-91.
- Robinson, D.H; Arrigo, K.R; Itturiaga, R; Sullivan, C.W (1995) Microalgal light-harvesting in extreme low-light environments in McMurdo Sound, Antarctica. **Journal of Phycology**. 31: pp 508-520.
- Runge, J.A; Ingram, R.G (1988) Underice grazing by planktonic, calanoid copepods in relation to a bloom of ice microalgae in southeastern Hudson Bay. **Limnology & Oceanography**. 33: pp 280-286.
- Runge, J.A; Ingram, R.G (1991) Under ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in south-eastern Hudson Bay. **Marine Biology**. 108: pp 217-225.
- Schnack-Schiel, S.B. Thomas, D; Dahms, H.U; Haas, C; Mizdalski, E (1998) Copepods in Antarctic Sea Ice. In: Lizotte, M.P; Arrigo, K.R (eds) **Antarctic Sea Ice: Biological Processes, Interactions, and Variability**. Antarctic Research Series. 73: pp 173-182.
- Smith, W.O Jr. (1987) Phytoplankton dynamics in marginal ice zones. **Oceanography and Marine Biology, Annual Review**. 25: pp 11-38.
- Smith, W.O Jr.; Nelson, D.M (1986) Importance of ice edge phytoplankton production in the Southern Ocean. **BioScience**. 36(4): pp 251-257.
- Smith, R.E.H; Clement, P; Cota, G.F; Li, W.K.W (1987) Intracellular photosynthate allocation and the control of Arctic marine ice algal production. **Journal of Phycology**. 23: pp 124-132.
- SooHoo, J.B; Palmisano, A.C; Kottmeier, S.T; Lizotte, M.P; SooHoo, S.L; Sullivan, C.W (1987) Spectral light absorption and quantum yield of photosynthesis in sea ice microalgae and a bloom of *Phaeocystis pouchetii* in McMurdo sound, Antarctica. **Marine Ecology Progress Series**. 39: pp 175-189.
- Squire, V.A (1987) The physical oceanography and sea ice characteristics of the Southern Ocean. **Primer Symposium Espanol de Estudios Antarticos**. Pama de Mallorca, June-July, pp 201-226.
- Stoecker, D.K; Gustafson, D.E; Merrell, J.R; Black, M.M.D; Baier, C.T (1997) Excystment and growth of chrysophytes and dinoflagellates at low temperatures and high salinities in Antarctic sea ice. **Journal of Phycology**. 33: pp 585-595.
- Stoecker, D.K; Gustafson, D.E; Merrell, J.R; Black, M.M.D; Baier, C.T (1998) Population dynamics of microalgae in the upper land-fast sea ice at a snow-free location. **Journal of Phycology**. 34: pp 60-69.
- Stretch, J.J; Hamner, P.P; Hamner, W.M; Michel, W.C; Cook, J; Sullivan, C.W (1988) Foraging behaviour of antarctic krill *Euphausia superba* on sea ice microalgae. **Marine Ecology Progress Series**. 44: pp 131-139.
- Sullivan, C.W; Palmisano, A.C; Kottmeier, S; Grossi, S.M; Moe, R (1985) The influence of light on growth and development of the sea-ice microbial community of McMurdo Sound. In: Siegfried, W. R; Condy, P.R;

Laws, R.M (eds) **Antarctic nutrient cycles and food webs**. Springer-Verlag, Berlin: pp 78-83.

Suzuki, Y; Kudoh, S; Takahashi, M (1997) Photosynthetic and respiratory characteristics of an Arctic ice algal community living in low light and low temperature conditions. **Journal of Marine Systems**. 11: pp 111-121.

Swadling, K.M; Gibson, J.A.E; Ritz, D.A; Nichols, P.D; Hughes, D.E (1997a) Grazing of phytoplankton by copepods in Eastern Antarctic coastal waters. **Marine Biology**. 128(1): pp 39-48.

Swadling, K.M; McPhee, A.D; Riddle, M.J; Gibson, J.A.E (1997b) Antarctic zooplankton: seasonal cycles of non-crustacean fauna. **Proceedings of the 20th Symposium on Polar Biology**. Japanese National Institute of Polar Research.

Thompson, P (2000) **Ecophysiology of the Brine Dinoflagellate, *Polarella glacialis*, and Antarctic Fast Ice Brine Communities**. PhD Thesis. IASOS, University of Tasmania, Hobart.

Torres, J.J; Donnelly, J; Hopkins, T.L; Lancraft, T.M; Aarset, A.V; Ainley, D.G (1994) Proximate composition and over-wintering strategies of Antarctic micronektonic Crustacea. **Marine Ecology Progress Series**. 113: pp 221-232.

Treguer, P; Jacques, G (1992) Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. **Polar Biology**. 12: pp 149-162.

Tremblay, C; Runge, J.A; Legendre, L (1989) Grazing and sedimentation of ice algae during and immediately after a bloom at the ice water interface. **Marine Ecology Progress Series**. 56: pp 291-300.

van Franeker, J.A (1992) Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia seas, Antarctica, November 1988 to January 1989 (EPOS Leg 2). **Polar Biology**. 12: pp 93-102.

van Franeker, J.A.; Bathmann, U.V; Mathot, S (1997) Carbon Fluxes to Antarctic top predators. **Deep Sea Research II**. 44(1-2): pp 435-455.

Vezina, A.F; Demers, S; Laurion, I; *et. al.* (1997) Carbon flows through the microbial food web of first-year ice in Resolute Passage (Canadian High Arctic). **Journal of Marine Systems**. 11: pp 173-189.

Virtue, P; Nichols, P.D; Nicol, S (1994) Interpreting aspects of krill life history and survival through lipid analyses. **Proceedings of the SCAR Sixth Biology Symposium**. May 1994, Venice. pp 282.

Wadhams, P; Lange, M.A.; Ackley, S.F (1987) The ice thickness distribution across the Atlantic sector of the Antarctic ocean in midwinter. **Journal of Geophysical Research**. 92(C13): pp 14535-14552.

Walsh, K.J; O'Farrel, S.P.W; Kevin, J; McGregor, J.L (1993) **Modelling sea ice processes and accumulation rates over the Antarctic region**. Fourth International Conference on Southern Hemisphere Meteorology and Oceanography. A Joint Meeting of the American Meteorological Society and the Australian Meteorological and Oceanographic Society. Hobart, Australia.

Watanabe, K (1982) Centric diatom communities found in Antarctic sea ice. **Antarctic Record**. 74: pp 119-126.

Watanabe, K (1988) Sub-ice microalgal strands in the Antarctic coastal fast ice near Syowa Station. **Japanese Journal of Phycology**. 36: pp 221-229.

Watanabe, K; Satoh, H (1987) Seasonal variations of ice algal standing crop near Syowa Station, East Antarctica in 1984/85. **Bulletin of the Plankton Society of Japan**. 34: pp 143-164.

Welch, H.E; Bergmann, M.A (1989) Seasonal development of ice algae and its prediction from environmental factors near Resolute, N.W.T, Canada. **Canadian Journal of Fisheries and Aquatic Science**. 46: pp 1793-1804.

Werner, I (1997) Grazing of Arctic under-ice amphipods on sea-ice algae. **Marine Ecology Progress Series**. 160: pp 93-99.

Worby, A.P; Allison, I (1999) **A ship-based technique for observing Antarctic sea ice, Part I: Observational Techniques and Results**. Research Report 14, pp 63. 1999. Hobart, Australia, Cooperative Research Centre for Antarctica and the Southern Ocean, University of Tasmania.

Worby, A.P; Massom, R.A (1995) **The Structure and Properties of Sea Ice and Snow Cover in East Antarctic Pack Ice**. Research Report, pp 191. Hobart, Australia, Cooperative Research Centre for Antarctica and the Southern Ocean, University of Tasmania.

Worby, A.P; Massom, R.A; Allison, I; Lytle, V; Heil, P (1998) East Antarctic sea ice: A review of its structure, properties and drift. **Antarctic Research Series**. 74: pp 41-67.

Zwally, H.J; *et al.* (1983) **Antarctic Sea Ice, 1973-1976: Satellite Passive Microwave Observations**. NASA, Washington DC.