Sea Ice Biota: Trophic modelling of the Ross Sea

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1 Introduction

Sea ice is a dominant forcing function in the ecology of the Ross Sea (Eicken 1992; Thomas & Dieckmann 2002a; Arrigo & Thomas 2004; Knox 2007 and references therein). Ice reduces the amount of light reaching the water column and reduces heat and gas exchange and vertical mixing. The upper surface of the ice provides a habitat for a number of sea birds and mammals (Ackley et al. 2003), while at the same time, the ice itself, especially the lower part which is in contact with the water, constitutes a unique habitat for microalgae and bacteria which provide a food source for associated microfauna and meiofauna and the cryopelagic fauna of the surface water layer immediate below the ice (Aarsett 1987; Kottmeier & Sullivan 1987; Garrison 1991; Brierley & Thomas 2002; Arrigo & Thomas 2004). For example, 90% of the food items in the stomach contents of *P. borchgrevinki* were copepods and their nauplii (Hoshiai et al. 1987a). Also sea ice appears to attract mesopelagic organisms (such as fish) at night thus exposing them to foraging by surface foraging birds (Kaufmann et al. 1995). Krill are also known to be attracted to the concentrations of food underneath melting ice in some cases (see Brierley & Thomas 2002 and references therein). Some ice bacteria may be large enough (chains 10–30 μm long) to serve as food for juvenile krill since choanoflagellates forming colonies up to 18 μm diameter have been shown to serve as sources of food for krill (e.g. Kottmeier & Sullivan 1990 and references therein).

One of the most important roles that sea ice biota plays, relates to the functioning of pelagic ecosystems when sea ice melts. Ice melting can provoke strong increase in abundances of auto- and heterotrophic microbes in the water column and the development of a microalgal bloom of cells >20 um (Giesenhagen et al. 1999). Primary and bacterial production in the water column can be enhanced up to 28- and 24-fold, respectively and abundances increased by a factor of 20 and 12 respectively. Melting ice adds a number of substances to the water column: (1) fresh water that can enhance stratification; (2) nutrients and micro-elements; (3) sea ice biota, including autotrophs and heterotrophs; (4) dissolved organic matter. The relative importance of these in stimulating primary and secondary production below sea ice seems to be somewhat variable. For example, heterotrophs from the sea ice have been shown to contribute to the bloom in the upper water column beneath sea ice as it melts (see Scharek et al. 1994; Jensen & Hansen 2000). Other studies have shown that the addition of ice biota and dissolved organic matter from melting ice can stimulate primary production in the water column over and above the effect of the melting ice in enhancing stratification (Giesenhagen et al. 1999). They showed that the addition of dissolved organic matter (DOM) from ice melting mainly stimulated pelagic bacterial populations whose production went up 12-fold, but grazing by mesozooplankton in the water column prevented accumulation of nano- and microalgae following ice melt. They also confirmed, from remote sensing of surface chlorophyll concentration by ocean colour satellite sensors, that algal blooms are not always formed during ice melt.

The sea ice ecosystem is divided here into the following compartments: (1) epontic algae; (2) ice bacteria; (3) ice protozoa; (4) ice metazoa. Ice detritus is dealt with in the "bacteria and detritus" section.

1.1 Imports, Exports, Accumulations

It is important for the ecosystem model for us to determine imports, exports and accumulations of material in each of the groups. No accumulation of any trophic group in single year sea ice are allowed in the annual model; there can be no build up or loss of material averaged over a year because the ice forms and melts in this period. However, there may be import of material (organisms from the water column are incorporated into the ice as it forms), or export (build up of biomass through the year is released into the water column when the ice melts). The proportions of the annual production of the various sea-ice groups that are transferred when sea ice melts (often referred to as "seasonal transfer fractions", T^S) are not well known for the Ross Sea.

2 Epontic (ice) algae

2.1 Biomass

Sea ice autotrophs comprise most of the single celled algal higher taxa that are found in the water column although diatoms (up to 100 species) are the most conspicuous and best studied because their silica skeleton ensures they are well preserved when sampled (Lizotte 2003 and references therein). Autotrophs may be responsible for up to 50% of primary production in some parts of the Southern Ocean (Kottmeier et al. 1987; Grossi et al. 1987). Estimation of the large-scale biomass and productivity of sea ice autotrophs in the Ross Sea is complex because of variability on large and small seasonal and temporal scales. Within the Ross Sea, there are a number of different types of ice present on a microscopic scale (e.g. frazil ice, congelation ice, platelet ice, snow/slush), and on a macroscopic scale (e.g. grease ice, marginal ice zone, pack ice, multi-year ice, land-fast ice). More details are given in the Physical section. Within these ice types, there are a number of microhabitats where epontic (sea ice) algae can occur. The microhabitats include: (1) ponds on the upper surface of the ice; (2) slush or snow on the top of the sea ice; (3) between different layers within the interior of the ice; (4) interstitial algae between ice crystals; (5) within cavities (salt extrusion channels) extending upwards from the bottom surface of the ice; (6) attached to the lower surface of the ice, or in the skeletal ice layer at the water-ice interface; (7) among unconsolidated platelet ice at the bottom of the sea ice.

Autotrophic biomass and other properties of the ice-ecosystem (such as species present, primary productivity, and trophic interrelations) vary with ice habitat (Kottmeier & Sullivan 1990; Norkko et al. 2002; Garrison et al. 2003), as well as with environmental conditions (temperature, ice thickness, insolation, nutrients, trace elements etc). Sea ice is populated by the scavenging of algal cells by ice crystals during ice formation (Grossmann & Glietz 1993). In some cases, the greatest fraction of algae in sea-ice resides in the lower layers of the ice (Arrigo & Thomas 2004). For example, in the eastern ice pack in spring, 80% of epontic algal biomass was on the bottom surface of the ice (Grose & McMinn 2003), and in the Weddell Sea, most Chl-a (>90%) was restricted to the bottom 20 cm of ice (Fritsen & Sullivan 1997). By contract, in the Weddell and Scotia Seas in autumn, Kottmeier & Sullivan (1990) found highest concentrations and growth of algae to occur in surface slush and saline ponds, though these may be relatively ephemeral. Arrigo (2003) reviewed a large number of research papers on epontic algae and suggested that epontic algal biomass and production rates: (1) are higher in land-fast, multi-year ice than single

year, pack ice; (2) decrease by ice habitat in the order platelet >bottom surface >upper surface >internal.

Quantifying aspects of the sea ice ecosystem within a given ice floe depends on understanding of the physical structure of the ice, how it was formed, characteristics of the associated flora and fauna, and the environmental conditions. The spatial scales of variation in these properties can be as short as a few metres in many types of ice (Garrison & Buck 1989b). There are relatively few studies giving direct measurements of the factors relevant to estimating epontic algal biomass and production in the Ross Sea on large spatial scales, and we estimate epontic algal biomass in the Ross Sea by an indirect method, namely, by considering all information on sea ice algae in the Antarctic, and transferring this information to the particular conditions of the Ross Sea.

Arrigo (2003) summarises measurements of algal standing stock in various parts of the Antarctic (Arrigo 2003, table 5.1). He summarises maximum recorded measurements of algal concentration (mg Chl a m^{-3}) and algal density (mg Chl a m^{-2}) organised by microhabitat (surface, internal, bottom, congelation, platelet and pack), from 50 papers published between 1962 and 2003. Extremely high algal concentrations (some >1000 mg Chl a m^{-2}) from platelet ice communities are excluded, as this habitat makes up a tiny fraction of the Ross Sea. Where necessary, we converted concentration (m^{-3}) to area density (m^{-2}) using factors consistent with similar ice microhabitats for epontic algae given by Arrigo (2003).

The values given by Arrigo (2003) are maximum values measured, but we are concerned with average concentrations. Minimum concentrations of epontic algae in sea ice are often close to zero, and lower concentrations are often more common that high concentrations. Concentrations of phytoplankton in the water column are typically log distributed, and it is likely that epontic algal concentration will have a similar distribution in space. We hence estimate the average concentration from the geometric (i.e. logarithmic) mean of the maximum and minimum values. This is consistent with studies such as Palmisano & Sullivan (1983). The values from Arrigo (2003) hence suggest epontic algal chlorophyll densities of 5.1–38 mg Chl a m^{-2} (25^{th}–75^{th} percentiles), with a median value of 12 mg Chl a m^{-2}. We assume that these concentrations, made up from estimates of epontic algae in various ice habitats, apply to the whole ice column rather than requiring their superposition to account for production occurring in more than one habitat at the same time.

We can compare this range with those found in studies not included in Arrigo (2003). Garrison et al. (2003) measured ice-column integrated Chl-a concentrations in the Ross Sea in austral autumn, and found values in the range 0.02–21 mg Chla m^{-2}, with a median value of ~3 mg Chl a m^{-2}. Norkko et al. (2002) found values ranging from 0.02–0.2 mg Chl a m^{-2} in McMurdo Sound in multiyear and first year ice. Watanabe & Satoh (1987) found peaks in the chlorophyll *a* standing crop in sea ice in October–November at Syowa Station of 124 mg Chl a m^{-2}. Dieckmann et al. (1998) suggests integrated stocks of 10–12 mg Chl a m^{-2} are usual. Spring surface concentrations of epontic algae were 0.1–5 (average 1.8) mg Chl a m^{-2} (McMinn & Hegseth 2003). Subsequent to Arrigo (2003), Arrigo & Thomas (2004) and references therein suggest that most epontic algal concentrations measured have been in the range 0.5–30 mg Chl a m^{-2}.

Having obtained a reasonable estimate of algal chlorophyll density in sea ice in the Antarctic, we now convert chlorophyll density (mg Chl m^{-2}) to biomass density (gC m^{-2}) using published values for the carbon-chlorophyll ratio of epontic algae. Carbon:chlorophyll ratios for epontic algae were found to be highly variable, varying by ice type, season and location. C:Chl-a ratio of 38 gC g^{-1}Chl a for epontic algae is given by Palmisano & Sullivan (1983), Sullivan et al. (1985), Sullivan (1985). Other values are 16–32 gC g^{-1}Chl a (Arctic pack ice), 20–50 gC g^{-1}Chl a fast ice of

McMurdo sound, and close to 90 gC g^{-1}Chl a for Ross Sea pack ice communities exposed to high light (Grose & McMinn 2003; Lizotte & Sullivan 1992). Garrison et al. (2005) gives 28 gC g^{-1}Chl a (autumn) and 55 gC g^{-1}Chl a (summer). Garrison et al. (2003) give values between 23 and 94, mean of 44 gC g^{-1}Chl a for the Ross Sea, and we use these values. The range of these values is used to set approximate "error" bars on our estimates. The data is shown in Figure 1.

Although there is considerable variability (as would be expected given the range of ice and environmental conditions through the Antarctic during a year), the seasonal pattern of sea ice algal biomass concentration may be described as a function of algal concentration, time of year and daily insolation. Here, we find that the seasonal pattern is reasonably described by function of the following form (Equation 1).

$$B(t) = A_1 \cdot E(t)^{0.3} \cdot \exp\left(A_2 \cdot \sin\left(\frac{2\pi}{365}\left(t + A_3\right)\right)\right) \qquad [1]$$

Where B(t) is the epontic algal biomass (gC m^{-2}) on day-of-year t (1 January = 1), E(t) is the daily integrated photosynthetic radiation (relative arbitrary units) at day t (m), and A_1, A_2, and A_3 are empirical coefficients. Here, E(t) is calculated by integrating the cosine of the solar zenith angle between sunrise and sunset on each day (Kirk 1994), and multiplying this by the daily Earth-sun distance factor (Spencer 1971). We made no correction for variation in Fresnel reflectance from the sea or ice surface at different sun angles (Kirk 1994, Jerlov 1976). The empirical coefficients were estimated using least-squares fitting in log space to the data from the literature, taking into account the variability and number of measurements in each case. The initial results were A=[0.478, 0.971, 4.2] (r^2=0.22; N=63). We also estimated the 25th and 75th percentiles of the ratio=[measured value]/regression estimate. This ratio, 0.44–2.6, is indicative of the range of variability that may be present in sea ice algal biomass.

The fitted curve (Figure 1a) gives highest concentrations of epontic algae between November and January. A large-scale model of epontic algae by Arrigo et al. (1997, 1998b) suggest peak concentrations between October and December, so our peak may be a little late. We note that this regression gives a phase in the algal biomass through a year which is strongly positively correlated with daily insolation (incident irradiance integrated through the day), albeit with a phase lag of about a month (Figure 1b). The relationship suggests that biomass and productivity will be highly correlated, which has implications for estimating appropriate algal productivity to biomass ratios (next section). The concentrations of algal biomass during the times of complete darkness in the Ross Sea may be lower than described here because all winter data used in the regression is from the Weddell Sea and includes areas where darkness is not complete (i.e. not within the polar circle). We reduce our estimates of viable algal biomass to zero during times of total darkness for the whole Ross Sea.

We used the concentration of sea ice in the Ross Sea during a year (weighted-average method, see Physical Environment section for details) to estimate the epontic algal biomass variation (Figure 1c). The average value over a year is 0.29 gC m^{-2} (maximum of 1.7 gC m^{-2} in February) with an estimated possible range of 0.079–0.95 gC m^{-2}.

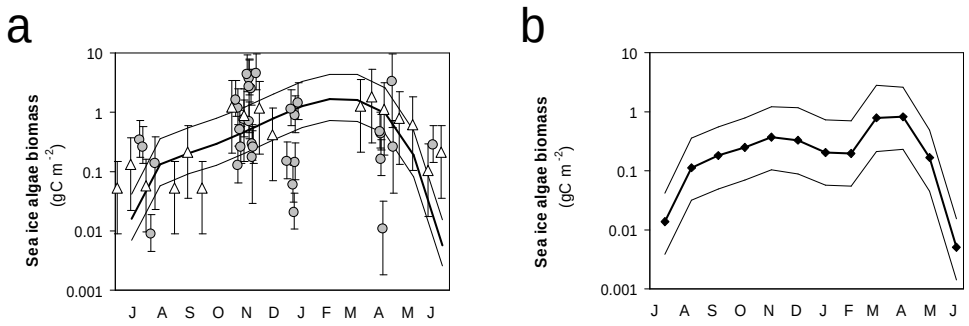

Figure 1. Characteristics of epontic algae biomass over a seasonal cycle (months of year on x-axis). **a**: Algal biomass as a function of date. Grey circles from over 50 studies summarized by Arrigo (2003). White triangles from the seasonal study of Delille et al. (1995). The regression (solid line), and estimate of 25th–75th percentile variability (lighter lines) are shown. **b**: Estimated epontic algal biomass averaged across the Ross Sea (i.e. accounting for seasonal changes in ice cover).

2.2 Production

The growth of the epontic algae is limited by three main factors: (1) ice formation processes which provide the microhabitat suitable for production; (2) light availability; (3) temperature. Micronutrients such as iron, and macronutrients such as nitrate, are not thought to limit epontic algal production (Garrison et al. 2003). Instead, Garrison et al. (2003) suggested that epontic algal biomass in the Ross Sea was primarily limited by suitable ice habitat rather than by light. Growth of epontic algae in the Prydz Bay (east Antarctica) area may begin as early as June (Everitt & Thomas 1986) – their growth probably accelerates with increasing day length. Incident irradiance is an important forcing factor in production by sea ice algae, with the combined effects of ice, and snow cover, reducing the light available for algal growth within the ice, and on its bottom surface (e.g. SooHoo et al. 1987a, b). As with marine phytoplankton, epontic algal production ceases in the absence of light between approximately 13 May and 29 July. The main peaks of epontic algal production are hence austral spring and austral autumn. Arrigo & Thomas (2004) estimated that sea ice primary production is greatest in November with about 60% occurring in November and December.

As noted above, epontic algal biomass and productivity are highly correlated, so that the value of P/B appropriate for an annual average calculation is not equal to the average of P/B values during the year. It is hence necessary to estimate epontic algal production seasonally through the year. In the absence of large scale, seasonally-resolved measurements of epontic algal growth in the Ross Sea, we estimated production by an indirect method.

We surveyed the Antarctic scientific literature to obtain a seasonal estimate of the rate of algal production in sea ice. Arrigo (2003, table 5.1) gives data on epontic algal production rates from 18 publications covering a range of Antarctic areas, generally in spring and autumn (Figure 2a). To augment this data seasonally, we used the results of a numerical model of primary production in sea ice (Arrigo et al. 1997, 1998b; Arrigo 2003). This model estimates the production for all Antarctic sea ice in five sectors: Ross Sea, Weddell Sea, Bellingshausen/Amundsen Seas, Western South Pacific Ocean, and Southern Indian Ocean (Figure 2b).

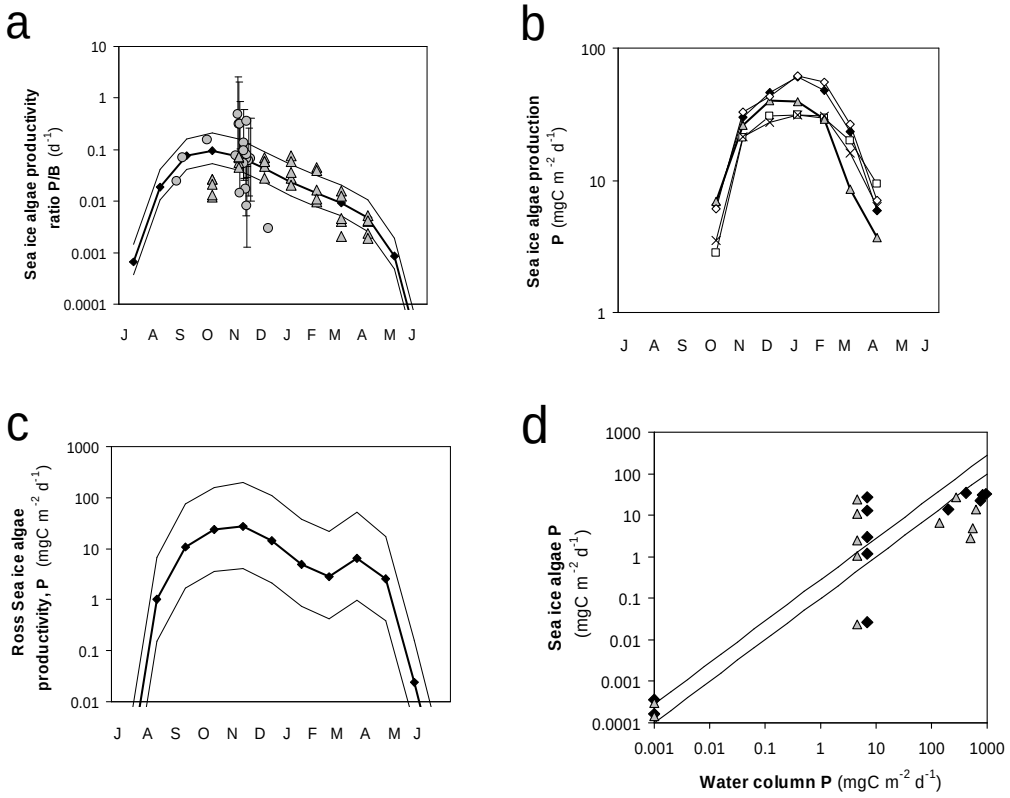

Figure 2. Characteristics of epontic algae production in the Ross Sea. **a**: Modeled epontic algal production rates in the Antarctic from Arrigo et al. (1997, 1998b). Areas shown are: Ross Sea (grey triangles), Weddell Sea (black diamonds), Bellingshausen and Amundsen Seas (white squares), Western South Pacific Ocean (X), and Southern Indian Ocean (white diamonds). Only production in single year ice is shown. **b**: Epontic algae production rate (P/B) in sea ice, with grey circles showing literature values (Arrigo 2003), grey triangles showing modeled production rates, and solid lines showing the model fitted to the data as described in the text. **c**: Daily productivity rates in the Ross Sea taking into account variations in sea ice area by month. **d**: Comparison between primary production in sea ice by epontic algae, and in the water column by phytoplankton. Black diamonds are "point" values (i.e. uncorrected for seasonal variations in sea ice area over a year), and grey triangles are average values for the Ross Sea. The values of Arrigo & Thomas (2004) are also shown (lines).

We use the combination of measurements and the modelled data of primary production to estimate a seasonal productivity for epontic algae in the Ross Sea based on the following assumptions.

(1) Where a maximum and minimum productivity rate are given in a study, we assume that the average value is the logarithmic mean of the extreme values, consistent with epontic algae having a logarithmic distribution.
(2) We estimate epontic algal productivity using the productivity:biomass ratio of epontic algae. Employing this ratio will reduce the dependence of algal productivity on habitat availability. Limitation of epontic algal production by habitat availability will be determined by considering the amount of ice cover in the Ross Sea through a year. Difference in habitat availability between floes is assumed not to affect the intrinsic rate of growth of epontic algae (i.e. their P/B ratio).

(3) We assume that the intrinsic growth rate is primarily determined by light availability, with temperature, nutrient and trace element impacts on productivity being second order effects.
(4) We assume that intrinsic growth rate of epontic algae can be approximated by Equation 2. Here, the growth rate (P/B) on day of year t is related to the daily, broad-band insolation (E, arbitrary units), which does not include the effect of clouds. We also neglect the dependency of epontic algal production on ice thickness and snow accumulation.

$$\frac{P}{B}(t) = A_1 \cdot E(t) \cdot \exp\left(A_2 \cdot \sin\left(\frac{2\pi}{365}(t + A_3) \right) \right) \quad [2]$$

The empirical coefficients in this equation were fitted to the data by least squares regression in log space. The regression gave values: A_1=0.0119, A_2=-1.52, A_3=50.9 [N=56, R^2=0.12]. We also estimated the 25th and 75th percentiles of the ratio=[measured value]/regression estimate. This ratio, 0.55–2.2, is indicative of the range of variability that may be present in sea ice algal growth rate in the Ross Sea.

This model was then applied to the estimate of daily insolation in the Ross Sea to estimate seasonal variation in P/B. Combining the seasonal variation in P/B with seasonal variation in biomass and sea ice area in the Ross Sea gives an estimate of the annual average value of production by epontic algae of 7.8 mgC m^{-2} d^{-1} (range 1.2–56 mgC m^{-2} d^{-1}) (see Figure 2a). The peak value of production is estimated at 34 mgC m^{-2} d^{-1} in November. The production values were then adjusted for the proportion of the Ross Sea that is ice covered to give Figure 2c. The annual average P/B for epontic algae in the Ross Sea is estimated to be 9.9 y^{-1} (range 5.4–21 y^{-1}). This production rate is considerably smaller than that estimated for water column phytoplankton (>30 y^{-1}).

2.3 Comparison with other data

These seasonal values of epontic algal production are similar to values reported in the literature. Production rates for internal ice algae reported by Stoecker et al. (2000) for McMurdo Sound in the summer were 0.5–12 mgC m^{-2} d^{-1}. Production rate of a bottom community of epontic algal in the spring were reported as 0.5–85 mgC m^{-2} d^{-1} (Grossi et al. 1987). Kottmeier et al. (1987) reports production rates of 23–47 mgC m^{-2} d^{-1} in pack ice between October and December. McMinn et al. (2000) found productivity rates of a fast ice bottom algal mat at Cape Evans, McMurdo Sound to be 84–430 mgC m^{-2} h^{-1}. Production levels on sunny days were so high that oxygen bubbles formed at the ice water interface. Knox (2007), and references therein, reports that pack ice algal production increases from negligible winter levels to late spring maxima of up to 35 mgC m^{-2} d^{-1}. These maxima occur in late November around much of the Antarctic. Arrigo & Thomas (2004) estimate similar peak production rates of c. 50 mgC m^{-2} d^{-1}.

The Ross Sea sector of the Antarctic in the model of epontic algal production (Arrigo et al. 1997, 1998b) covers all ice between 160°E and 135°W. As an approximate comparison, we scaled the results of the model based on sea ice extent alone. The scaled results from the model of would suggest an annual epontic algal production for the Ross Sea of c. 2.3 TgC/y. The method given above estimates an annual production of 0.3–13 TgC/y, with a mean value of 1.8 TgC/y. The presence of the large Ross Sea polynya in the Ross Sea in the main growing period for epontic algae (December–February) suggests that we would expect annual production of epontic algae in

the Ross Sea to be less than the scaled values of Arrigo et al. (1997, 1998b), so this is a credible result.

2.4 Comparison of epontic and water column algal production

Arrigo & Thomas (2004) estimated epontic algal production to be typically 10–28% of total production in the ice covered waters of the Southern Ocean. Value of epontic algal production in sea ice in the Ross Sea, not adjusted for the proportion of the study area covered in sea ice, is estimated to be 15 gC m^{-2} y^{-1}. Over the course of a year, the ratio of production in the sea ice to production in the water column (neither corrected for variations in sea ice extent) was between 0.4% and 400%, with a (log) average value of 13%. Corrected for ice area and averaged over a year, production in the sea ice was about 11% that in the water column (Figure 2d).

2.5 Imports, Exports, Accumulations

Sea ice algae seem to be a taxonomic subset of algae in the water column (e.g. Garrison & Buck 1985; Garrison et al. 1987). Although there will be some incorporation of "seed" algae into the ice as it forms in autumn, this is likely to represent a negligible transfer of viable phytoplankton biomass from water column phytoplankton to epontic algae.

When the ice melts in spring/summer, any accumulation of epontic algal biomass over the course of a year will be released into the water column. It is not clear to what extent ice algae are viable in the water column. Given that the annual average biomass of ice algae is much less than the annual average biomass of water column phytoplankton, this will not have a major impact on the annual average model. We assume that epontic algae transferred to the water column on ice melting becomes water column detritus rather than being viable. We use an initial estimate of the proportion of the annual epontic algal production transferred to the water column on ice melt of T^S=0.3. Ecotrophic efficiency (E) for epontic algae in the Ross Sea is not known, and is assumed to be 0.8 on the basis that most of the annual production of this group is likely to be consumed by sea ice biota.

3 Ice bacteria

3.1 Biomass

Like algae, sea ice bacteria occur in several microhabitats associated with sea ice, including in slush and saline ponds on the upper surface of the ice, between layers in the ice, in microcavities within the structure of the ice, and associated with brine channels extending upwards from the lower surface (e.g. Palmisano & Sullivan 1985). Sea ice is thought to be initially populated with bacteria by the attachment of bacteria onto algal cells during ice formation (Grossmann & Glietz 1993). Bacteria frozen into ice crystals cannot grow but may survive (Sullivan 1985). Kottmeier & Sullivan (1990) found ice bacteria to be up to 4 times larger in biovolume than bacteria in sea water. For example, Rivkin et al. (1989) use 40 fgC $cell^{-1}$ and Delille et al. (2002) use 60 fgC $cell^{-1}$ for ice bacteria in McMurdo Sound in the spring. Kottmeier & Sullivan (1990) give data showing average cell carbon for ice bacteria of 63 fgC $cell^{-1}$, compared to average water column value of 25 fgC $cell^{-1}$ or 15–18 fgC $cell^{-1}$ (Lochte 1997).

There is seasonal variation in bacterial cell carbon. Bacterial biovolume and cell carbon tends to be high in spring, and reach a minimum in autumn (Delille et al. 2002). A conversion factor

between biovolume and carbon of 200–400 fgC μm^{-3} seems typical (Bratbak & Dundas 1984; Bjornsen & Kuparinen 1991; Archer et al. 1996; Theil-Nielsen & Sondergaard 1998). Based on available data and this conversion factor, we estimate bacterial cell carbon as Figure 3a.

Not only do bacterial cell volumes tend to be higher in pack ice than in the water column, but bacterial abundances (in terms of cell numbers per unit volume) can be 2–19 times greater in pack ice than in seawater in the Antarctic (e.g. Kottmeier & Sullivan 1990). As a result of high biovolume and elevated cell numbers in sea ice relative to sea water, ice microhabitats can have 4–80 times more bacterial biomass per m^3 than seawater, and 16–4800 times bacterial production rates per m^3 (Kottmeier & Sullivan 1990). There is a considerable body of research on sea ice bacteria in the Antarctic, and in the Ross Sea in particular, but no seasonally and spatially measurements of bacterial biomass. We hence estimate the biomass of bacteria in ice in the Ross Sea indirectly.

A summary of all readily available published information on bacterial abundance in the Antarctic is given in Table 1. In many cases (e.g. Kottmeier & Sullivan 1990), a mean and standard deviation bacterial abundances through the ice core are reported. In others (e.g. Gowing et al. 2004), only maximum and minimum values are given, and it was necessary to estimate the mean abundance as follows. A number of studies (e.g. Sullivan & Palmisano 1984; Kottmeier & Sullivan 1990; Delille et al. 2002) give data that shows that the average bacterial abundance per m^3 of ice through a core may in fact be less than an average of the maximum and minimum values, i.e. high abundances are rather localised. Data from Sullivan & Palmisano (1984) and Kottmeier & Sullivan (1990) were used to estimate that the mean value may be approximately 0.6 the average of the maximum and minimum values through the core. The data in Table 1 are plotted in Figure 3b.

There is significant regional variation, and by habitat. In particular, bacterial concentrations tend to be highest in surface ponds, surface slush/snow, and in platelet ice at the bottom of multi-year ice. Excluding these values and considering only abundances from the interior if the sea ice, gives a seasonal pattern that is well described by a sinusoid in log-space (Equation 3). We used a least-squares, non-linear fit to the data taking into account the variability and number of replicate measurements in each case. The coefficient of determination, r^2=0.54. The 25th and 75th percentiles were also estimated as indicative of the range of variability that may be present in bacteria biomass in sea ice.

$$y = \exp\left(-0.455 + 1.33\sin\left(\frac{2\pi}{365}(x + 28.4)\right)\right) \quad [3]$$

Table 1. Published information on bacterial biomass in pack ice in the Antarctic.

Habitat	**Abundance** $x10^6$ cells ml^{-1}		**Location**	**Season**[1]	**Source**
	Low	**High**			
Land fast ice (bottom)	0.30	1.02	McMurdo	Sp	Sullivan & Palmisano (1984)
Land fast ice (upper)	0.02	0.36	McMurdo	Sp	Sullivan & Palmisano (1984)
Pack ice (cores)	0.10	3.00	Weddell/Scotia Seas	Sp	Miller et al. (1984)
Land fast ice (bottom)	0.20	0.85	McMurdo	Sp	Grossi et al. (1984)
Land fast (bottom)	0.10	0.50	McMurdo	Sp, Su	Kottmeier et al. (1987)
Land fast (platelet)	0.05	0.40	McMurdo	Sp, Su	Kottmeier et al. (1987)
Platelet ice	0.04	0.10	McMurdo Sound	Sp	Rivkin et al. (1989)
Congelation ice	0.02	0.05	McMurdo Sound	Sp	Rivkin et al. (1989)
Pack ice (cores)	0.66	1.10	Weddell/Scotia Seas	Sp	Kottmeier & Sullivan (1990)
Pack ice (cores)	3.29	4.43	Weddell/Scotia Seas	Au	Kottmeier & Sullivan (1990)
Pack ice (slush)	11.7	11.9	Weddell/Scotia Seas	Au	Kottmeier & Sullivan (1990)
Pack ice (surface pond)	17.2	24.4	Weddell/Scotia Seas	Au	Kottmeier & Sullivan (1990)
Pack ice (porewater)	0.74	1.56	Weddell/Scotia Seas	Au	Kottmeier & Sullivan (1990)
Land fast ice (surface)	0.30	1.50	Adelie Land	Sp	Delille & Rosiers (1995)
Land fast ice (bottom)	0.30	0.40	Adelie Land	Sp	Delille & Rosiers (1995)
Pack ice (platelets)	15	20	Weddell Sea	late Su	Grossmann et al. (1996)
Pack ice (infiltration layer)	0.23	1.50	Weddell Sea	Su	Gleitz et al. (1996)
Pack ice (cores)	0.50	2.33	Terre Adelie area	A	Delille et al. (2002)
Pack ice (cores)	0.08	1.75	Terre Adelie area	W	Delille et al. (2002)
Pack ice (cores)	0.12	0.75	Terre Adelie area	Sp	Delille et al. (2002)
Pack ice (cores)	0.17	1.67	Terre Adelie area	Su	Delille et al. (2002)
Pack ice (surface)	0.18	1.68	East Ross Sea	Su	Gowing et al. (2004)
Pack ice (slush)	0.15	5.94	East Ross Sea	Su	Gowing et al. (2004)
Pack ice (cores)	0.20	5.81	East Ross Sea	Su	Gowing et al. (2004)
Pack ice (bottom)	0.18	6.72	East Ross Sea	Su	Gowing et al. (2004)

[1] Season: Su=Summer, A=Autumn, W=Winter, Sp=Spring

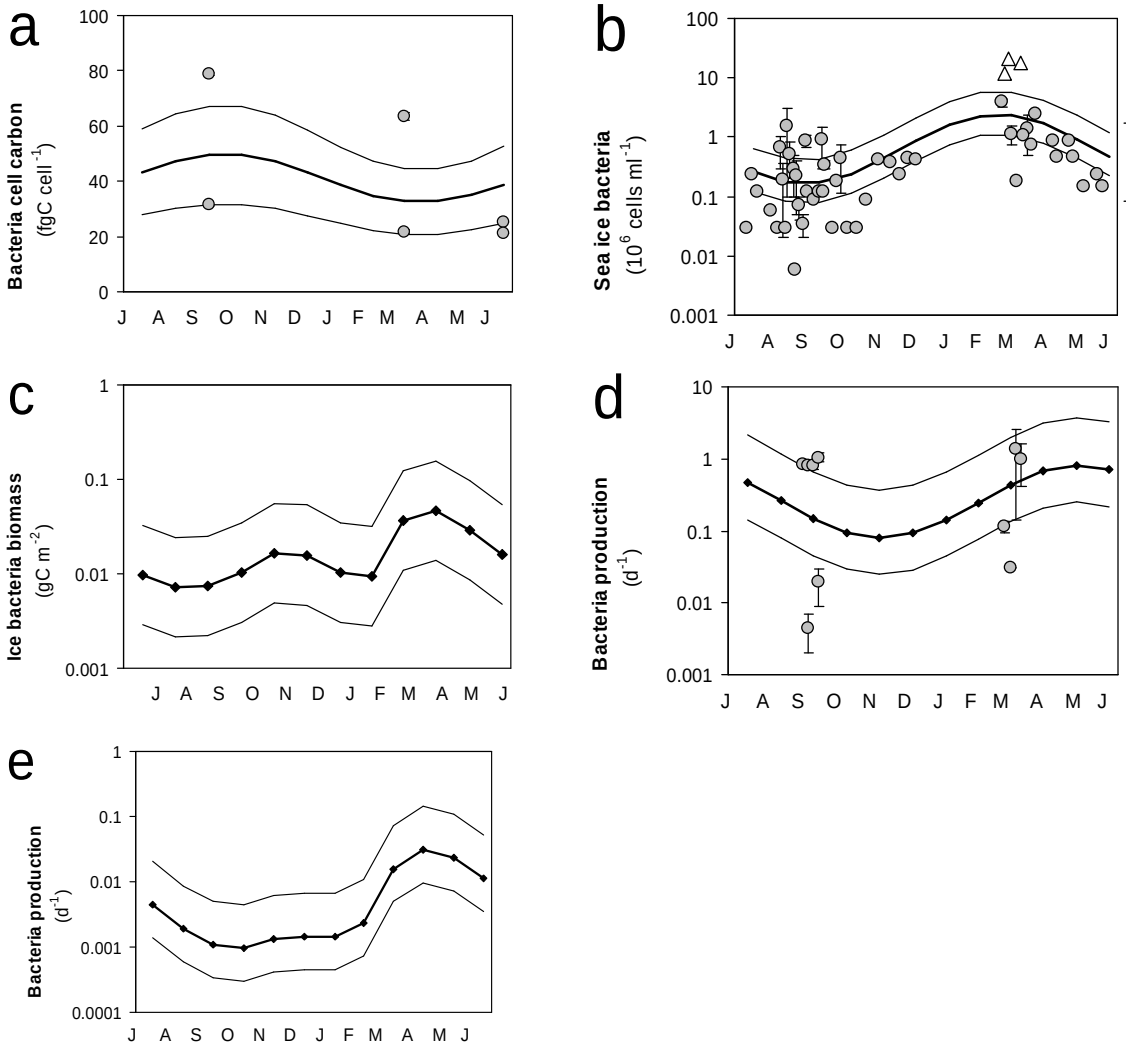

Figure 3. Characteristics of sea ice bacteria used to estimate bacterial biomass in the Ross Sea. **a**: Bacterial cell carbon as a function of season. Grey circles from Kottmeier & Sullivan (1990). **b**: Bacterial abundance in Antarctic sea ice from literature values. Pack ice values are shown as grey dots, surface snow, slush, ponds, and platelet ice are shown as open triangles and not included in the regression (solid line), or estimate of 25^{th}–75^{th} percentile variability (lighter lines). Note that different points have different weightings, depending on the variability in the reported results, and number of measurements in each dataset. **c**: Total bacterial biomass in sea ice, averaged across the Ross Sea accounting for seasonal variations in ice area. **d**: Bacterial production rates in sea ice, with grey symbols showing literature values. **e**: Bacterial production in the Ross Sea taking in account seasonal variations in sea ice area.

We assume that although bacterial concentrations in surface ponds and bottom platelet ice tend to be high, the areas associated with these habitats tend to be both small (e.g. platelet ice only occurs on multiyear ice which we estimate as c. 1% of the Ross Sea area), and relatively short lived (e.g. surface ponds will be liquid only in the late spring and summer). Hence, we neglect bacterial biomass associated with these habitats. The result of these considerations is that the biomass of bacteria in sea ice averaged over a year for the Ross Sea is 18 mgC m^{-2} taking into account seasonal variations in ice area (Figure 3c). The likely range of bacterial biomass is 5.3–60 mgC m^{-2} – a range of about an order of magnitude.

3.2 Comparison of algal and bacterial biomass in sea ice

As a semi-independent check on this estimate of the biomass of ice bacteria, we estimated the biomass of ice bacteria based on the biomass of ice algae in the Ross Sea. It has long been suggested that the distribution and rate of growth of bacteria in pack ice are coupled to the distribution and rate of growth of ice microalgae (Kottmeier & Sullivan 1990). Significant positive correlations between bacterial number, biomass and production, and Chl-a and primary production, suggest indirectly that bacterial growth and phytoplankton photosynthesis in pack ice are coupled (Kottmeier et al. 1987). Growth of bacteria in pack ice is probably stimulated by blooms of microalgae, which are triggered by sustained high surface irradiance (Grossi et al. 1984). Ice microalgae may provide bacteria with an energy source (dissolved organic matter, "ice detritus" in the model), while bacteria may help to regenerate nutrients and sustain algal growth. Uncoupling between bacterial and algal production can be observed however (e.g. Kottmeier & Sullivan 1987) as may be expected in winter when the substrate for bacterial growth may be the breakdown products resulting from the grazing down of algae at that time.

Table 2 shows some relationships reported in the literature between bacterial biomass and epontic algae in sea ice. Stewart & Fritsen (2004) also derived the relationship between bacterial biomass, *BB* (mgC m^{-3}) and epontic algal Chl *a* (*C*) for the Ross Sea sea ice as Equation 4 (R^2=0.52, n=122):

$$\log_{10}(BB) = 0.669 + 0.50\log_{10}(C) \qquad [4]$$

Table 2. Regression statistics for the relationship between $\log_{10}$(bacterial abundance, cells m^{-3}), and $\log_{10}$(epontic algae chlorophyll-a concentration, mg m^{-3}). "Y-int" is the intercept on the y-axis.

Y-int	Slope	R^2	Reference
8.7	0.786	0.88	Bird & Kalff (1984)
9.8	0.543	0.75	Cole et al. (1988)
10.5	0.149	0.1	Cota et al. (1990)
9.9	0.414	0.69	Stewart & Fritsen (2004)
9.9	0.414	0.69	Stewart & Fritsen (2004)

Figure 4 shows the comparison between bacterial biomass and chlorophyll concentration from epontic algae. The data estimated in the current study are within the ranges found in the literature, and close to the regression results. The results show that we estimate higher bacterial abundances in the winter than the regression line suggests, but this may to be expected given that the ratio of water column phytoplankton : bacterial biomass is smaller by a factor of two in winter than in spring in subantarctic water south of New Zealand (Bradford-Grieve et al. 1999).

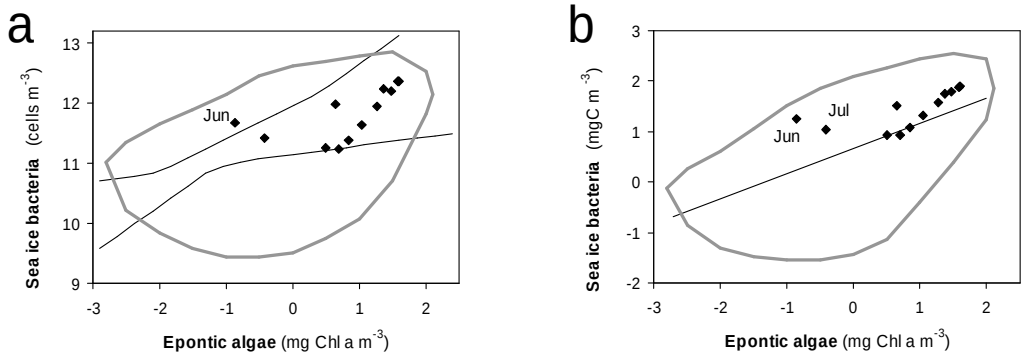

Figure 4. Bacteria and algae in sea ice. **a**: Bacterial abundance and chlorophyll concentration. The black diamonds are values estimated for the Ross Sea in the present study. The grey ring bounds values summarised by Stewart & Fritsen (2004). The lines bound the range of five regression results as given by Bird & Kalff (1984), Cole et al. (1988), Cota et al. (1990), and Stewart & Frtisen (2004). **b**: Bacterial biomass and chlorophyll concentration. The black diamonds are values estimated for the Ross Sea in the present study. The grey ring bounds values summarised by Stewart & Fritsen (2004). The lines give the range of the regression result for the Ross Sea as given by Stewart & Frtisen (2004).

3.3 Production

Although the biomass of bacteria in sea ice can be greater than in the water below ice, counts of viable cells can be lower (Sullivan & Palmisano 1984). Continued bacterial growth may be sustained through the winter by degrading particulate and dissolved organic matter within the brine pockets (Arrigo et al. 1995). Low temperatures and high brine salinities however restrict microbial activity to varying degrees (Kottmeier & Sullivan 1988; Arrigo & Sullivan 1992). Some direct measurements of growth rates of sea ice bacteria are available from the scientific literature (Table 3). Higher rates of bacterial production are typically observed in late winter and spring; this may be related to the supply and demand for organic carbon (e.g. Rivkin et al. 1989). Guglielmo et al. (2004) show that extracellular enzymatic activity in the form of aminopeptidase activity in the bottom sea ice and platelet ice in Terra Nova Bay was much higher than in the surrounding ice free waters. They suggest that rates of bacterial-mediated degradation of organic carbon possibly as high as >10 gC m^{-2} d^{-1} may exceed organic matter production by photosynthesis possibly leading to the observed accumulation of dissolved inorganic nutrients.

Growth rates of bacteria increased 100-fold (from 0.002 to 0.03 d^{-1} during onset of a *Phaeocystis* sp. Bloom in McMurdo Sound (Kottmeier et al. 1987). It is also worth noting that bacteria are capable of producing in the winter (5.2±3.4 mgC m^{-2} d^{-1}; Kottmeier & Sullivan 1987).

Table 3. Published information on bacterial production rates in pack ice in the Antarctic.

Habitat	Production (d^{-1})		Location	Season[1]	Source
	Low	High			
Congelation ice	0.002	0.007	McMurdo Sound	Sp	Kottmeier et al (1987)
Platelet ice	0.009	0.03	McMurdo Sound	Sp	Kottmeier et al (1987)
Congelation ice	0.1	0.2	McMurdo Sound	Su	Kottmeier et al (1987)
Platelet ice	0.07	0.08	McMurdo Sound	Su	Kottmeier et al (1987)
Congelation ice	0.8	0.9	McMurdo Sound	Sp	Kottmeier et al (1987)
Platelet ice	0.8	0.8	McMurdo Sound	Sp	Kottmeier et al (1987)
Congelation ice	0.7	0.9	McMurdo Sound	Sp	Rivkin et al. (1989)
Platelet ice	0.9	1.2	McMurdo Sound	Sp	Rivkin et al. (1989)
Pack ice (cores)	0.10	0.14	Weddell/Scotia Seas	Au	Kottmeier & Sullivan (1990)
Pack ice (slush)	0.03	0.03	Weddell/Scotia Seas	Au	Kottmeier & Sullivan (1990)
Pack ice (surface pond)	0.14	2.60	Weddell/Scotia Seas	Au	Kottmeier & Sullivan (1990)
Pack ice (porewater)	0.42	1.60	Weddell/Scotia Seas	Au	Kottmeier & Sullivan (1990)

[1] Season: Su=Summer, A=Autumn, W=Winter, Sp=Spring

A sinusoidal fit to the literature data on ice bacteria production rates was estimated in log-space (Figure 3e). When combined with the bacterial biomass estimates for each month, we estimate that the average production to biomass ratio for bacteria in sea ice is P/B=165 y^{-1}. We estimate that a possible range of this value is 51–750 y^{-1}, though the upper value seems high.

Bacterial production may be significantly correlated with microalgal production and biomass (Kottmeier et al. 1987; Stewart & Fritsen 2004) although not always (Lizotte 2003). A number of studies give values for the ratio of bacterial to phytosynthetic production rates in sea ice (Kottmeier et al. 1987; Kottmeier & Sullivan 1987, 1990; Rivkin et al. 1989; Grossman & Dieckmann 1994; Gleitz et al. 1996; Mock et al. 1997), giving ranges between 0.0001 and 19. For the Scotia and Weddell Seas, the highest values were found in the pore water, with ratios of 0.09–0.22 in the ice itself (Kottmeier & Sullivan 1990). Excluding the winter when epontic algal production is zero, the values estimated in the current study suggest that the ratio of bacterial to phytosynthetic production rates in sea ice vary between 0.04 and 12, with a log-mean value of 0.4. These values are reasonable.

3.4 Consumption, diet, P/Q, respiration, assimilation efficiency, ecotrophic efficiency

Sea ice bacteria in the model are assumed to consume only sea ice detritus. P/Q of ice bacteria are assumed to be similar to those of water column bacteria, i.e. P/Q=0.3. Together with our estimate of P/B, this suggests Q/B=550 y^{-1}. We assume a typical unassimilated consumption ratio of U=0.3. Together, these values suggest a respiration to biomass ratio of R/B=220 y^{-1}. It may be that a large proportion of ice bacteria are dead as for sediment bacteria (Luna et al. 2002), so we assume an ecotrophic efficiency of 0.30 for ice bacteria.

3.5 Imports, Exports, Accumulations

As ice forms in the autumn, bacteria may be incorporated into the ice from the water column. The maximum transfer of bacteria from the water column to the ice may be approximately equivalent to the biomass of bacteria in the upper 1 m of the water column which will be much less than the total biomass of bacteria in the water column. It is possible that bacteria from the water column are transferred into the ice throughout the year as water permeates the brine channels in the sea ice (e.g. by wave pumping), but this is likely to be small.

When the ice melts, any accumulation of ice bacteria that has occurred over the course of a year will be released into the water column. The proportions of sea ice bacteria that are viable in the water column are not known, but may be small as the habitats are very different. Hence, we assume accumulated ice bacteria transfers to water column detritus on ice melt. The proportion of the annual production of ice bacteria that is transferred to the water column when ice melts is not known, and we assume it is T^S=0.3.

4 Ice protozoa (0.8 – 200μm)

4.1 Introduction

Primary production within the sea ice fuels a microheterotrophic community including, as well as bacteria, a diverse group of protozoans composed of coanoflagellates, dinoflagellates, ciliates, tintinnids, foraminifera, and amoebae (e.g. Kottmeier et al. 1987). Here, we define ice protozoa as having an equivalent spherical diameter between 0.8 and 200 μm. Ice protozoa of the Ross Sea are dominated by ciliates followed by heterotrophic flagellates, dinoflagellates in autumn and summer (Lee and Fenchel 1972a; Buck et al. 1990; Garrison & Close 1993; Delille et al. 2002; Garrison et al. 2005;), and forams (Lipps et al. 1979, Dieckmann et al. 1991; Schnack-Schiel et al. 2001).

4.2 Biomass

Garrison et al. (2005) estimate a total median heterotrophic biomass in the Ross Sea and waters to about 65°S in autumn and summer of 10.1, and 65.3 mgC m^{-2}, respectively. They found that heterotrophs made up about 17% of the total microbial biomass in sea ice. A study of forams and ciliates >20 μm in sea ice of the Weddell Sea over a number of months, partly describes the annual trajectory of biomass of heterotrophs (Schnack-Schiel et al. 2001a). From work at a Terre Adélie site, west of the Ross Sea on the development of first-year sea ice protozoa from June to December (Delille et al. 2002) we can see that the work of Schnack-Schiel et al. (2001a) probably missed the maximum in development of the protozoan community which occurred in late June. Assuming that the sea ice of the Ross Sea is similar to the annual cycles obtained by combining information from all three locations, we estimated the seasonal cycle of protozoan biomass in the sea ice as Figure 5a. We note that the methodology used by Delille et al. (2002) missed small heterotrophs (<10 μm). Consequently, our estimates may be low. Taking seasonal variations in sea ice cover into account (Figure 5b), the annual average biomass of protozoa in sea ice is estimated to be 2.7 mgC m^{-2}, with a possible range of 0.7–8 mgC m^{-2}.

In the Weddell Sea, in spring, heterotrophic protozoa make up 1–93% (mean 26%) of total sea ice biomass (Garrison & Buck 1991). Our estimates suggest a proportion that varies annually between 0.1% and 23%, with a mean value of 4%.

4.3 Production

In the Arctic, microprotistan specific growth rates were 0.072–0.181 d^{-1} for heterotrophic microflagellates, and 0.041–0.135 d^{-1} for phagotrophic ciliates in May (Sime-Ngando et al. 1997) or annual P/B of 14.6–65.7 y^{-1}. These authors also calculated that heterotrophic microprotists accumulated biomass at the rate of 1.08 gC m^{-2} y^{-1}. In Antarctic sea ice ciliates of the genus *Euplotes* had growth rates such as would be expected from extrapolating the temperature growth rates function of ciliates from lower latitudes with high temperature regimes to low temperatures (Lee & Fenchel 1972). That is, at about 0°C a generation time is about 4.5 d or a doubling time of 0.22 d^{-1} or 80 y^{-1} if we assume that growth is at the same rate all year round. Given that secondary production in sea ice probably slows once the results of primary production have worked through the system, we choose P/B = 60 y^{-1}.

4.4 Consumption, Diet

Microheterotrophs are important trophic links between algal and bacterial production and larger heterotrophs (Kottmeier et al. 1987). The particles ingested by ciliates are related to the cell size of the ciliate, with ciliates <15 μm in equivalent spherical diameter being mainly bactivorous, while larger species graze on pico- and nanoplankton rather than bacteria (e.g. Fenchel 1987; Scott et al. 2001). Microzooplankton (20–200 μm) in McMurdo Sound were also found to be principally bactivorous, with only a small dietary contribution from autotrophic food (Lessard & Rivkin 1986; Buck et al. 1990). Ciliates may also graze on small cells and colloids (Scott et al. 2001). A phagotrophic athecate dinoflagellate in sea ice in the Weddell Sea ate a variety of protests but predominantly diatoms (Buck et al. 1990). Initially we assume that ice protozoa eat food in the proportion: bacteria 80%, other protozoa 10%, algae 10%.

Consumption rates of ciliates are typically measured via clearance rates, nl $cell^{-1}$ h^{-1}, using dilution experiments. Reported clearance rates of ciliates vary enormously, ranging over 5 orders of magnitude from tens of nanolitres to hundreds of microlitres per cell per h. Sherr et al. (1997) showed that at -1°C ingestion rates of ciliates from the Arctic were comparable with similar sizes ciliates in temperate waters. At lower temperatures, clearance rates are reduced. Fluorescently labelled microspheres have recently been used to investigate clearance rates of protozoa (e.g. Sherr & Sherr 1993). Using this method, Scott et al. (2001) investigated consumption rates of the sea ice ciliate *Pseudocohnilembus*. This ciliate was found to take up bacteria sized particles at the fastest rate. The uptake of bacteria-sized fluorescent microspheres led to clearance rates in the range 3.6–5.4 nl $cell^{-1}$ h^{-1}. The measurements suggest maximum consumption rates equivalent to annual Q/B of 140 y^{-1}. Production to consumption ratios for ciliates in temperate waters are often taken as c. 0.3. This ratio would suggest annual consumption, Q/B, of c. 200 y^{-1}. In the absence of direct estimates of food consumption, we take consumption by sea ice ciliates just above the average of these two values (140 and 200 y^{-1}) at 190 y^{-1}.

4.5 P/Q, Respiration, Assimilation efficiency

It is reasonable to assume that annual P/Q for ice protozoans is the same as similarly sized organisms in the water column (ciliates), namely, 0.30. The values estimated above (P/B=60 y^{-1}, Q/B=180 y^{-1}) lead to P/Q=0.32 y^{-1}, which is close. Assimilation efficiencies of ciliates in the Antarctic are assumed to be c. 80%. These three factors (P/B=60 y^{-1}, Q/B=190 y^{-1}, U=0.2), together allow us to estimate a respiration rate for Antarctic protozoans in sea ice of R/B=92 y^{-1}.

4.6 Ecotrophic efficiency

Ecotrophic efficiency (*E*) for protozoa in sea ice in the Ross Sea is not known, and is assumed to be 0.9 on the basis that the majority of the annual production of this group is likely to be consumed by direct predation.

4.7 Imports, Exports, Accumulations

Sea ice protozoa are presumed to be a taxonomic subset of the water column although data are sparse. Although there are assumed to be incorporation of "seed" protozoa into the ice as it forms, it is assumed to represent a negligible transfer of biomass from the water column to the ice. When the ice melts, any accumulation of sympagic protozoan over the course of a year will be released into the water column. As for epontic algae, the proportions of sea ice protozoa that are viable in the water column are not known and are assumed to be small, so that all seasonal transfer is to water column detritus. The proportion of the annual production of ice protozoa that is transferred to the water column when ice melts is not known, and we assume it is T^S=0.2.

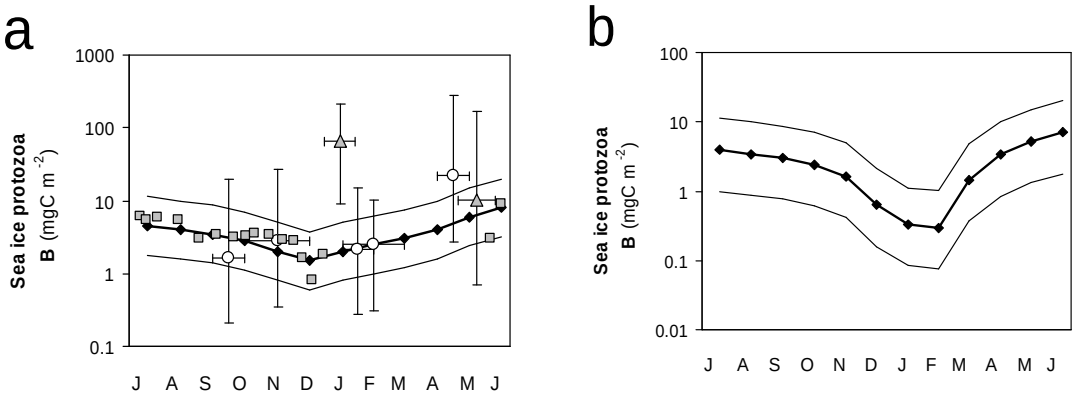

Figure 5. Sea ice protozoa in the Ross Sea. **a**: Sea ice protozoa from data in the scientific literature (grey triangles from Garrison et al. 2005; white circles from Schnack-Schiel et al. 2001a; grey squares from Delille et al. 2002). The regression line and approximate bounds on uncertainty are also shown. **b**: Sea ice protozoan biomass averaged over the Ross Sea area, taking seasonal variations in ice cover into consideration.

5 Ice metazoa

5.1 Introduction

There is a distinct metazoan fauna of sea ice that forms the link between ice algae and the water column (e.g. Lee & Fenchel 1972; Fenchel & Lee 1972; Kottmeier & Sullivan 1990; Hoshiai et al. 1991; Garrison 1991; Garrison & Buck 1991; Garrison & Mathot 1996; Schnack-Schiel et al. 2001a, b; Schnack-Schiel 2003; Arrigo & Thomas 2004). Metazoans associated with Antarctic sea ice include organisms actually living in sea ice, in the brine channels, as well as those on the underside of floes and in the underlying water. Schnack-Schiel et al. (2001) found that the bulk of the meiofauna was concentrated in the lowest parts of the sea ice, especially during winter and autumn in the Weddell Sea. However, in porous summer sea ice, sympagic organisms also occur

in high densities in upper and intermediate layers of sea ice. The sea ice habitat serves as an important nursery ground for juveniles, providing energy-rich food resources and offering shelter from predators.

The distribution of metazoa in sea ice tends to be patchy on small scales (e.g. within a given ice flow, vertically through the floe), and on large scales (e.g. between various research cruises in different parts of the Antarctic) (e.g. Schnack-Schiel et al. 2001). In some seasons in some areas, non-metazoan forams dominate (75%) the sea-ice community in terms of numerical abundance while turbellarians dominate (45%) in terms of biomass (summer, Weddell sea ice: Schnack-Schiel et al. 2001). Copepods seem to be ubiquitous members of this fauna and have life history strategies intimately linked to the seasonal sea ice (Swadling et al. 1997; Schnack-Schiel 2003). They comprise *Stephos longipes* (Schnack-Schiel et al. 1995, 2001; Swadling et al. 1997; Günther et al. 1999; Schnack-Schiel et al. 2001), *Drescheriella glacialis* (Schnack-Schiel et al. 2001; Dahms & Dieckmann 1987), harpacticoids (Hoshiai & Tanimua 1986), *Paralabidocera antarctica* (Hoshiai & Tanimura 1986; Swadling et al. 1997; Guenther et al. 1999), *Oncaea curvata* (Hoshiai & Tanimura 1986; Swadling et al. 1997), *Ctenocalanus vanus (citer)* (Hoshiai & Tanimua 1986; Swadling et al. 1997), *Oithona similis* (Swadling et al. 1997), *Drepanopus* at higher latitudes (Tucker & Burton 1989). Planktonic species such as *C. propinquus* and *M. gerlachei* do not survive incorporation into ice because of low tolerance of high salinity whereas sympagic acoel turbellarians can survive in salinities up to 75 (Gradinger & Schnack-Schiel 1998). Asteroid echinoderm larvae have also been found to be part of the ice metazoan fauna (Rivkin et al. 1986).

There are a number of adaptations that copepods make to their ice habitat. Extreme stickiness of the eggs of *Stephos longipes* makes them stick to floating ice crystals (Kurbjeweit et al. 1993). *S. longipes* occurs in all habitats (surface ponds, thick pack-ice, marginal ice zone) in late summer early autumn but was encountered in largest numbers in surface ice in summer (Schnack-Schiel et al. 1995; Schnack-Schiel et al. 2001a). Nauplii outnumbered copepodids in the surface ice and refrozen gap water, while in the gap water copepodids (mainly CI-CIII in summer and CII-CIV in autumn) comprised 70% of the total population. *Stephos longipes*, identified from nauplii (Costanza et al. 2002) along with *Harpacticus furcifer* accounted for 90% of the sympagic communities in the annual sea ice in Terra Nova Bay.

The life history of *Paralabidocera antarctica*, that has been found in annual sea ice in Terra Nova Bay (Costanza et al. 2002) and free in the water column in the southwest Ross Sea (Bradford 1971), has been described from elsewhere in the Antarctic (Tanimura 1992; Tanimura et al. 1984). This species was found in traps under fast ice near Syowa Station in November but not between May and October (Tanimura et al. 2002). These observations were related to their ice-dwelling and pelagic life-phases. *Paralabidocera antarctica* was composed mainly of nauplii showing there was a highly synchronised life cycle (Schnack-Schiel et al. 2001a; Swadling 2001). There is rapid development through the copepodid stages and a short adult life span of 2-3 weeks and adults appeared in late spring or early summer, spawned and died soon after (Tanimura et al. 1984; Swadling et al. 2004). Patterns of lipid content of adults showed that this was the fuel for mating and spawning (Swadling et al. 2000). The population underwent habitat shift to the water column at CIV stage although adults remained at the ice water interface (Swadling et al. 2000).

All developmental stages of *Drescheriella glacialis* were taken from ice cores and were not found in surface ponds, gap water and new ice (Schnack-Schiel et al. 2001a). It enters the sea ice in early autumn and over-winters as NIV stage. This species is highly adapted to its environment (Dahms et al. 1990). It has an ability to penetrate deeply into the ice. It has a tolerance of comparatively high salinity, a good swimming ability, its life history suggest an r-strategy (i.e. a

relatively short life cycle (minimum generation time 132 d), high total investment in reproduction, low investment per offspring, and continuous reproduction (Bergmans et al. 1991). This is the first record of continuous reproduction for the polar environment.

Studies in the Weddell Sea and on the Antarctic Peninsula have suggested important ecological coupling between larval krill feeding on the undersides of sea ice (Ducklow 1983; Stretch et al. 1988; Quetin & Ross 1991; Schnack-Schiel et al. 2001a, b). In McMurdo Sound, the sea ice is an important habitat for the icefish (*Pagothenia borchgrevinki)* which feeds on sea ice associated fauna (e.g., the amphipod *Paramoera walkeri*). The undersurface of ice floes often have labyrinthine channels, up to several cm in diameter, which are likely to provide opportunities for pelagic feeders to prey on ice organisms (Kottmeier & Sullivan 1990).

5.2 Biomass

There is a paucity of large-area measurements of metafaunal biomass in sea ice in general (e.g. Schnack-Schiel et al. 1998). We have no direct estimates of meiofaunal biomass for the Ross Sea. For the purposes of the present study we assume that biomass of ice fauna in the Ross Sea is similar to the Weddell Sea and other Antarctic regions where information is more complete. Some workers have given only abundance of particular species (e.g. for Syowa station - Hoshiai & Tanimura 1986). A limited number of studies have expressed their data as biomass; more often, the data is given in terms of abundances (individuals per unit volume or area of ice). Where studies give abundances of metazoan rather than biomass, it is necessary to consider the weights of individuals to estimate biomass. Individual weights of Antarctic metazoans were taken from Swadling et al. (2000), and Mayzaud et al. (2002) amongst others (Table 4). We can convert numbers of *Paralabidocera antarctica* to biomass using the number–weight relationship given by Ikeda & Fay (1981) which gives average body weight of 5.1 μg DW (dry weight). This value lies within the range of values for the copepodite stage-weight relationship given by Swadling et al. (2000) that ranges from dry weights of 3.2 μg ind^{-1} for CI to 30 μg ind^{-1} for CVI. Dry weights were converted to carbon using an empirical relationships for crustacean zooplankton: B[gC] = 0.416 ·W[gDW] (Brey 2005). This factor is similar to that of Conover & Huntley (1991) who found it to be 0.473±0.060. Schnack-Schiel et al. (2001a) gave abundances and biomass from the same samples, allowing us to estimate that the average individual weight of sea ice metazoan were 7.6 μg ind^{-1} (range: 0.9–32 μg ind^{-1}) for calanoid copepods, and 0.9 μg ind^{-1} (range: 0.6–1.4 μg ind^{-1}) for harpacticoid copepods.

Table 4. Individual weights of metazoans.

Species	Stage	DW (μg ind^{-1})	Reference
Paralabidocera antarctica	adult	16–30	Swadling et al. 2000
Paralabidocera antarctica	CIV,CV	5.1 (4.7–6.3)	Swadling et al. 2000; Ikeda & Fay 1981
Paralabidocera antarctica	nauplii	2.1	Swadling et al. 2000
Ctenocalanus citer	CV,CVI	14	Cohen & Lough 1981; Mayzaud et al. 2002
Oithona similis	CIV,CV,CVI	1.5	Atkinson 1996; Mayzaud et al. 2002
Oncaea curvata	adult	2.5	Mayzaud et al. 2002
Harpacticoid copepod	mixture	0.94	Schnack-Schiel et al. 2001a
Calanoid copepod	mixture	7.6	Schnack-Schiel et al. 2001a
Copepod egg		0.24	
Stephos longipes	copepodite	7.6	

Applying these individual weights to the abundances given by Swadling et al. (1997) suggest metafaunal biomass in sea ice in April of 58–170 mgC m^{-2}, which seems high. Schnack-Schiel et al. (2001) summarises the work of a number of authors (including the work of Grandinger, 1999), taken from six research cruises in the Antarctic between 1985 and 1997. The data give metazoan biomass of 2.3–11 mgC m^{-2}. Schnack-Schiel et al. (1998) give data leading to metazoan biomass of 0.6–53 mgC m^{-2} (average of 19 mgC m^{-2}) for the Bellingshausen and Amundsen Seas in summer. Data from Swadling et al. (2000) gives metazoan biomass of 4.4–11 mgC m^{-2} (average of 6.6 mgC m^{-2}) for the East Antarctica in spring. High metazoan abundances were found in platelet ice in the Weddell Sea, suggesting biomass values >250 mgC m^{-2} (Gunther et al. 1999). Estimating a seasonal cycle for this variation based on the data (Figure 6a), and weighting by the seasonal variation in ice cover in the Ross Sea, leads to an estimate of metazoan biomass in sea ice of 3.1 mgC m^{-2}, with an estimated range 0.8–10 mgC m^{-2} (Figure 6b).

A number of studies show, at the latitude of about 68°S off the Australian Davis Station (East Antarctic), that there was an approximate correlation between epontic algae biomass and metazoan biomass in sea ice (e.g. Swadling et al. 1997; their figure 6b). Plotting data from five studies in the Antarctic where these data are available (Gunther et al. 1999; Schnack-Schiel et al. 1989, 2001a; Swadling et al. 1997, 2000), compares well with the data estimated in the present work (Figure 6c) although some are biased towards the low side. We are not aware of measurements of metazoan abundance available for the winter period (June, July), where epontic algal biomass is assumed to fall to extremely low levels.

5.3 Production

The instantaneous growth rates of marine populations of *Paralabidocera antarctica* has been reported as 0.04–0.14 d^{-1} (Swadling et al. 2004). Hoshiai et al. (1996) state that *P. antarctica* has two growing periods a year, coinciding with the autumn and spring-summer blooms of epontic algae. The period over which the copepods can be considered to grow is estimated to be between 7 and 9 months per year, generally September – March. For example, *P. antarctica* eggs is layer in about March (Hoshiai & Tanimura 1986) and nauplia development proceeds until June. The population then remains in a steady state until September followed by continued development of the nauplii from October to November to produce copepodites (Hoshiai et al. 1996) that then move into the water column. *Stephos longipes* probably has a similar life history strategy (Atkinson 1998). Hence, we estimate a metazoan productivity (P/B) of 20 y^{-1}, with a range of 8.5–38 y^{-1}. Note that this is somewhat higher than the assumed production rate of mesozooplankton in the water column biota (P/B=8.0 y^{-1}). We may expect production of metazoa in sea ice to be greater than that in the water column, as sea ice populations tend to be biased towards nauplii and developmental stages that are commonly considered to grow at faster rates than adults. This effect may be offset somewhat by the fact that the sea-ice habitat is likely to be significantly colder and have a more variable temperature than seawater.

5.4 Consumption, Diet

The nauplii stages of the three species that make up most of the metazoan biomass found in sea ice (*Paralabidocera antarctica*, *Drescheriella glacialis*, and *Stephos longipes*), are primarily herbivorous (e.g. Hoshiai et al. 1989). However, increasing evidence suggests that copepod grazing rates derived from analysis of algal pigments in the gut often cannot match the respiratory and egg production requirements of individuals or population (Dam et al. 1993; Drits et al. 1993, 1994; Pakhomov et al. 1997). Extra food may come from carnivorous feeding on protozoan cells (Atkinson 1994, 1996), or on small zooplankters (Metz & Schnack-Schiel 1995). Therefore, it is

likely that they consume protozoa as well. Initially we assume that the diet of ice metazoa is similar to that of the mesozooplankton assemblage in the water column, namely: 30% ice protozoa; 65% epontic algae; 5% other ice metazoans.

Present knowledge of grazing as a structuring factor in the ecosystem of sea ice is reported as being poor and basic (Gradinger et al. 1999), even for Artic ice communities which are better studied than those of the Antarctic. Gradinger et al. (1999) suggests that consumption by meiofauna (i.e. protozoa and metazoa) in Arctic sea ice is of the same magnitude as primary production by epontic algae over a year, but this may not be true in the Antarctic. Gradinger (1999) states that: "the potential grazing pressure of sea ice meiofanua is low compared to daily primary production rates during the polar summer". Values given by Gradinger (1999) in Antarctic sea ice suggest ingestion rates by meiofauna of 0.7 d^{-1}. Seasonal data for the Antarctic in Gradinger (1999, Table 3) leads to Figure 6d. This estimate leads to an annual consumption rate of meiofauna in sea ice of 180 y^{-1} when seasonal variations in biomass are taken into account. Meiofauna data from Gradinger (1999) includes all sympagic heterotrophs including sea ice protozoa such as foraminifera and metazoans that have higher consumption rates than metazoa. Correcting for protozoan consumption based on values estimated previously leads to Figure 6e, our best estimate of metazoan consumption rates in sea ice. These values give an annual Q/B of 86 y^{-1}.

General allometric equations (Moloney & Field 1989) suggest maximum ingestion rates for nauplii of *Paralabidocera antarctica* with body size of c. 0.01 mgC ind^{-1} to be 2.2 d^{-1}. For all body sizes of metazoans, the maximum ingestion rate is estimated to be Q/B=1.8 d^{-1}. It is unlikely that metazoa feed at this rate year round, given that the growth of epontic algae ceases in the Antarctic winter. If we assume that vigorous feeding is restricted to 3 months (90 days) per year, the range of annual consumption rates is 60–200 y^{-1}. These values encompass the value estimated above.

5.5 P/Q, Respiration, Assimilation efficiency

The values estimated above lead to P/Q=0.27 y^{-1}. This is close to the annual P/Q for ice metazoans is the same as similarly sized organisms in the water column of 0.25–0.30.

Respiration rate of Antarctic (water column) copepods was found to be closely related to individual size (Mayzaud et al. 2002). Assuming a respiratory quotient (RQ) of 0.95 corresponding to ammonotelic species (i.e. having ammonia as the chief excretory product) Omori & Ikeda (1984), values given by Mayzaud et al. (2002) for a number of copepods in the Indian sector of the Antarctic Ocean in spring lead to R/B values of between 6 and 26 y^{-1} for individuals of weight between 10 and 4500 mg ind^{-1}. Higher respiration rates are found in smaller individuals. For comparison, the respiration rate of adult *Paralabidocera antarctica* is 1.961 µl O_2 mg dry wt^{-1} h^{-1} (Ikeda & Fay 1981). This is equivalent to a respiration rate expressed as R/B of 21 y^{-1}. The data from Mayzaud et al. (2002) would suggest a value of R/B=21 y^{-1}, so these data are consistent. For nauplii of *Paralabidocera antarctica*, the data of Mayzaud et al. (2002) gives a value of R/B=40 y^{-1}, though we note this is outside the range of data used to develop the relationship. The average of these three estimates of respiration rate is R/B=27 y^{-1}.

Assimilation efficiencies of copepods in the Antarctic are assumed to be 80% (Mayzaud et al. 2002).

These three factors (P/Q=0.3, R/B=27 y^{-1}, UA=0.25), together allow us to estimate P/B=18 y^{-1} and Q/B=61 y^{-1}, and. The fact that these are similar to our previous estimates (P/B=22 y^{-1}, and Q/B=86 y^{-1}) lends some credibility to the values. Our best estimates are taken as an average of the values produced by the two methods, i.e. P/B=20 y^{-1}, and Q/B=74 y^{-1}. The values lie between those estimated for Antarctica mesozooplankton in the water column (P/B=8.0 y^{-1}, Q/B=27 y^{-1}), and Antarctic heterotrophic microplankton in the water column (P/B=54 y^{-1}, Q/B=180 y^{-1}). As the size of metazoa in sea ice is between these two groups, this seems reasonable.

5.6 Ecotrophic efficiency

Ecotrophic efficiency (*E*) for metazoa in sea ice in the Ross Sea is not known, and is assumed to be 0.9 on the basis that the majority of the annual production of this group is likely to be consumed by direct predation.

5.7 Imports, Exports, Accumulations

It appears that the main species of copepod found in sea ice (*Paralabidocera antarctica*, *Drescheriella glacialis*, and *Stephos longipes*) use the ice habitat as an overwintering and feeding habitat for the nauplii or copepodid stage (e.g. Atkinson 1998). When the ice melts, these early stages are released into the water column where they may continue their development. Other species of Antarctic copepod (e.g. *Calanoides acutus*, *Oithona similis*, *Oithona frigida*, *Ctenocalanus citer*, *Metridia gerlachei*, *Calanus propinquus*, *Calanus simillimus*, *Microcalanus pygmaeus*, *Oncaea curvata*, *Rhincalanus gigas*) have life strategies that either do not link or are less intimately linked with the sea ice.

Although there may be some incorporation of eggs or nauplii into the ice as it forms, this is assumed to represent a negligible transfer of biomass from the water column. In contrast however, we assume that all metazoa in the sea ice at the end of the growing season are transferred into the water column. There may hence be an appreciable, positive net export of biomass from sympagic metazoa to water column mesozooplankton when averaged over a year. The proportion of the annual production of ice metazoa that is transferred to the water column when ice melts is not known, and we assume it is T^S=0.1.

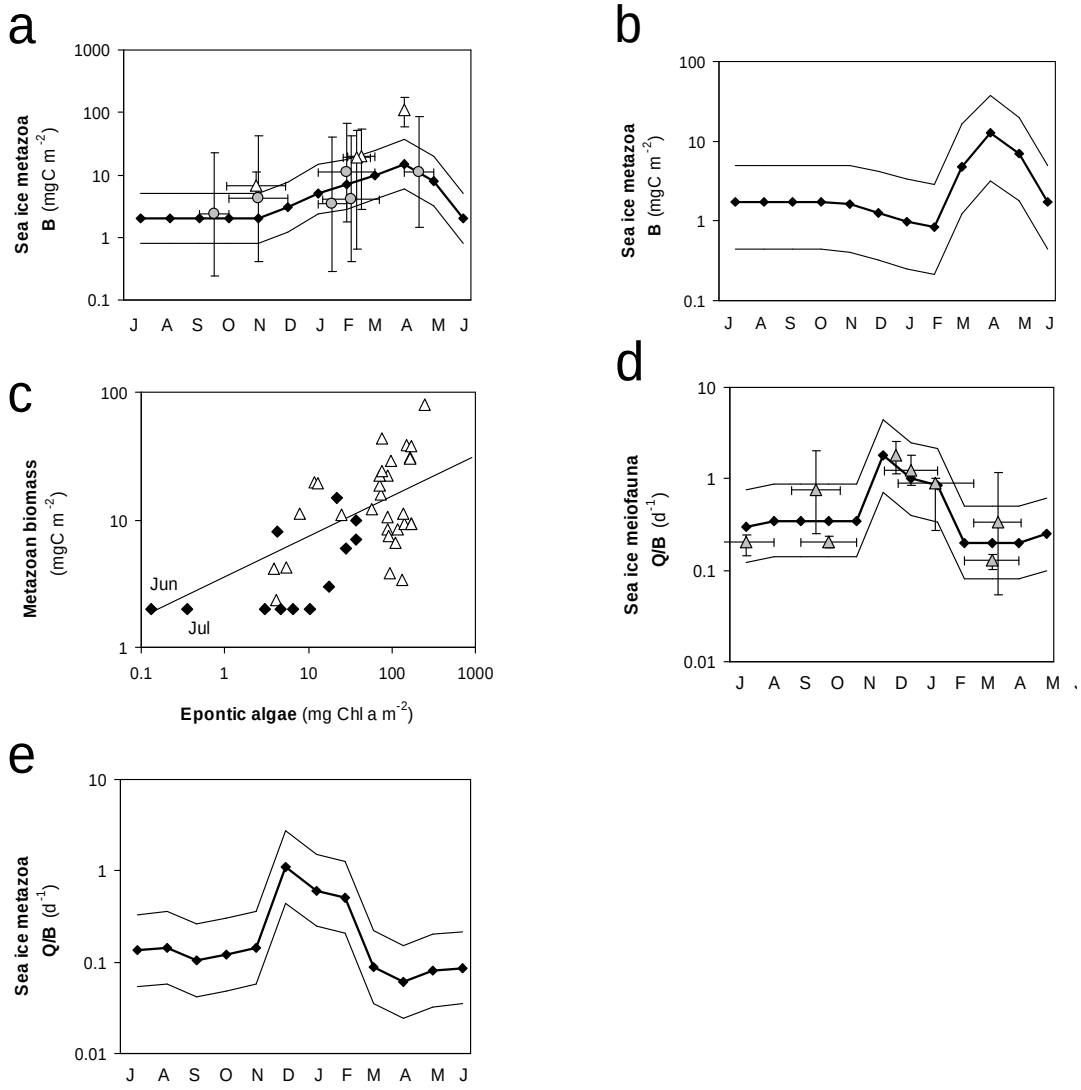

Figure 6. Sea ice metazoa in the Ross Sea. **a**: Sea ice metazoa from data in the scientific literature (grey circles from Schnack-Schiel et al. 2001a; white triangles from Swadling et al. 1997, Schnack-Schiel et al. 1998, and Swadling et al. 2000. **b**: Sea ice metazoan biomass weighted for seasonal ice cover in the Ross Sea. **c**: Comparison between epontic algae and sea ice metazoan. White triangles are data from five studies in the Antarctic (Gunther et al. 1999; Schnack-Schiel et al. 1989, 2001a; Swadling et al. 1997, 2000). The linear least-squares regression line (in log space) to the data is also shown. Black diamonds are data estimated here for the Ross Sea in various months, with June and July marked. **d**: Meiofauna consumption rates in sea ice, with grey triangles showing measurements from Gradinger (1999), and estimated allometrically based on Moloney & Field (1989). e: Estimated metazoan consumption rates based on meiofauna consumption corrected for protozoan consumption.

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