

Bacteria and detritus: Trophic modelling of the Ross Sea

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1 Overview

An overview of how bacteria and detritus are handled in the model is given in Figure 1. There are three bacteria groups:

- (1) Sea-ice bacteria;
- (2) water-column bacteria;
- (3) benthic bacteria.

There are four detritus groups:

- (1) sea ice detritus;
- (2) water-column detritus;
- (3) benthic detritus;
- (4) carcasses.

Transfers between detrital and bacterial groups, not due to consumption or death are:

- (1) transfer of bacteria on ice melt to the water column;
- (2) transfer of detritus on ice melt to the water column;
- (3) sinking of detritus through water column to the sea floor;
- (4) long-term burial of benthic organic matter.

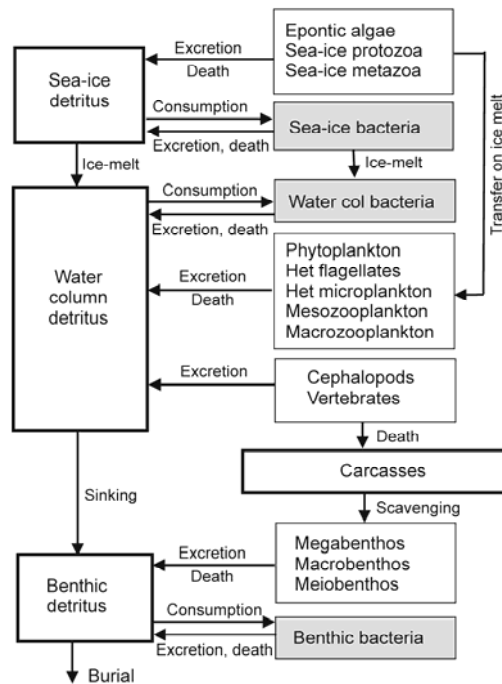


Figure 1. Detritus and bacteria in the Ross Sea ecosystem model. The three bacteria groups are shown in grey. The four detrital groups have thicker bounding boxes.

1.1 Transfers when sea-ice melts

No accumulation of biomass is allowed in the sea-ice compartments between years. The vast majority of ice is assumed to melt each year so that the material in the sea-ice at that time of year is transferred into the water column. It is assumed that the living material is viable in the water column: sea ice bacteria are transferred to water column bacteria; epontic algae are transferred to water column phytoplankton; sea ice protozoa (0.8–200 μm) are transferred 50% to heterotrophic microplankton (20–200 μm) and 50% to heterotrophic flagellates (2–20 μm); sea ice metazoa (>0.2 mm) are transferred to water column mesozooplankton (0.2–20 mm).

1.2 Detrivores: consumption of detritus or bacteria?

It is not clear to what extent Antarctic detrivores consume detrital material directly rather than consuming bacteria. For example, some studies suggest that water column and benthic detritus is consumed directly only by bacteria and protozoa, and that other detritivorous organisms feed largely on bacteria (Moodley et al. 2002; Josefson et al. 2002). There is evidence, though, that copepods and microzooplankton in the water column and microprotozoa in sediments may feed directly on detritus in sediments (Kemp 1990; Fabiano et al. 2000b). Here, we assume that a nominal 25% of detritivorous consumption is of detritus directly, and 75% is of bacteria (see section on benthos).

1.3 Carcasses

The trophic group labelled “Carcasses” is made up of non-living organic matter from animals that have not been directly predated and have not been excreted as a waste product. It hence includes

bodies of animals that have died for reasons other than predation (including disease, starvation, excess-parasite load), as well as parts of animals that died due to predation but were not consumed at the time (i.e. “messy eating”). It does not include vegetation of any kind, exudants, faecal material, moulted feathers, shed scales etc. Such material is classified in the model as “detritus”. The purpose of this group in the model is to separate material that can be consumed by scavengers from material that is largely broken down by bacterial decomposition.

2 Bacteria in the water column

2.1 Biomass

Measurements of bacterioplankton biomass and growth dynamics in the full water column of the Ross Sea were given in a number of papers by Ducklow (Ducklow 1999; Ducklow et al. 2000, 2001; Monticelli et al. 2003). Concentrations of bacteria were typically highest at the surface, decreasing to low levels at c. 300 m. Measurements from Ducklow et al. (2001) give an effective depth of bacteria (the ratio of water column integrated average bacteria biomass to surface bacteria concentration) of about 260 m. For bacterial productivity, the depth is about 240 m. Measurements by Ducklow in the Ross Sea were used to estimate an annual cycle of bacterial biomass and production (Figure 2). The bacterial bloom lagged behind the phytoplankton bloom by about one month, with standing stocks of bacterial biomass rising from a minimum in late October to a maximum in early February. Bacterial biomass appeared to be limited by DOC flux in the surface 0–50 m. The fact that there was substantial bacterial biomass (and growth) in the 15–300 m layer indicates a supply of labile organic matter for bacteria below the euphotic zone between October and April. Near Terra Nova Bay, it appeared that bacterivory by protists may have produced a rapid decline in bacterial biomass from mid January to early to mid February (Monticelli et al. 2003). Water column average (0–300 m) bacterial biomass was between 0.06–1.22 gC m⁻².

To obtain an annual average biomass, we assume that winter values are half the minimum measured by Ducklow. We must also make an allowance for the proportion of the Ross Sea which is covered with sea ice, as bacterial biomass can be substantially reduced (to ¹/₂₀ th) beneath sea ice (Edwards et al. 1998) which we use here. The annual average value for bacterial biomass in the Ross Sea is hence estimated to be 0.23 gC m⁻².

Our estimate lies within the range of values given in other studies. Using a depth of 260 m (see above), measurements by Ducklow et al. (2000, 2001) are equivalent to average densities of 0.2–4.7 mgC m⁻³. In the austral summer, bacterial concentrations in the Ross Sea coastal zone were 2.4–24 mgC m⁻³ (Umani et al. 2004). Laws et al. (2000) suggest bacterial concentrations of 9.6 mgC m⁻³ are typical of the summer in the Ross Sea. Work in another part of the Southern Ocean (Bellinghousen Sea: Edwards et al. 1998) shows that bacterial carbon concentrations were typically between 2.4 mgC m⁻³ (under ice) and 47 mgC m⁻³ (open ocean). Fritsen & Sullivan (1997) found low bacteria concentrations (<2 mgC m⁻³) in the water below sea ice in the Weddell Sea. Lochte et al. (1997) give concentrations near the Polar Front of between about 5–8 mgC m⁻³. Becquevort (1997) gave bacterioplankton concentrations in the range 2–9 mgC m⁻³ in the southern Polar Front and in the marginal ice zone of the Ross Sea. Hodson et al. (1981) gave 0.065–0.65 x10⁶ cells ml⁻¹.

Our estimate of bacteria biomass is about 49% of autotroph biomass in the Ross Sea, on average, over an annual cycle. Lochte et al. (1997) give bacterial biomass as 23–37% of phytoplankton biomass in the Polar Front. Ducklow et al. (2000) show that in the Ross Sea variations in bacterial

biomass through the year do not necessarily follow phytoplankton biomass – there is often a lag between the two, leading to bacterial biomass:phytoplankton biomass ratios between 4–81%. Our estimate lies within these bounds.

Finally, we note that it is not known what proportion of bacteria cells in the water column of the Ross Sea are viable (i.e. actively consuming detritus and “producing”) - this may be relatively low. For example, in subantarctic waters off the Kerguelen Islands, Razouls et al. (1997) found that at some times only ~10% of bacteria cells were viable.

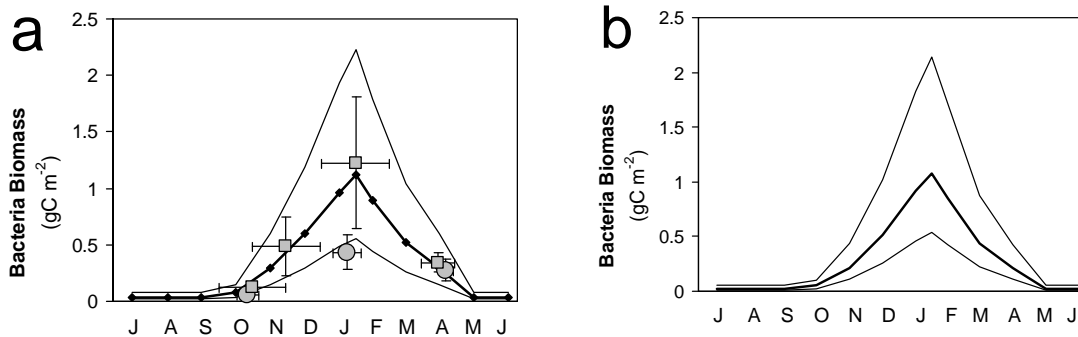


Figure 2. Bacterial biomass in the Ross Sea as described in the text. **a:** Average bacterial biomass for Ross Sea open-ocean waters. Grey symbols represent measured values of bacterial biomass (see text). **b:** Biomass for the study area as a whole, corrected for sea-ice cover. The heavy centre lines indicate our best estimates of the values, and the upper and lower lines indicate the approximate range of acceptable values.

2.2 Production

Production by bacteria in the Ross Sea was estimated based on measurements presented in a series of papers by Ducklow (Ducklow 1999; Ducklow et al. 2000, 2001). Measurements of bacterial production in the Ross Sea through the growing season were used to estimate an annual cycle of bacterial production (Figure 3). Water column integrated production of bacteria reach a peak in January/February (of ~0.17 gC m⁻² d⁻¹) and fell to low levels in the winter. Becquevort & Smith (2001) give some corroborating information on seasonal events in the Ross Sea polynya: bacterial production rates were low until late November, then, increased after mid December (Figure 3). We assume that winter values are half the minimum measured by Ducklow et al. (2000, 2001). As for bacterial biomass, bacterial production is likely to be reduced by 95% below sea ice compared with ice-free waters (Edwards et al. 1998). The annual average bacterial production for the Ross Sea water column is hence estimated to be 8.3 gC m⁻² y⁻¹. This leads to a P/B value for water column bacteria in the Ross Sea of 35 y⁻¹.

This bacterial production is low compared to other systems. For example, P/B=87 y⁻¹ for bacteria in subantarctic waters was estimated by Bradford-Grieve et al. (2003). Bacterial production is generally assumed to be equivalent to about 25–30% of simultaneously estimated phytoplankton primary production rates across a wide range of marine and freshwater ecosystems of varying trophic status (Ducklow et al. 2000). The annual average ratio of bacterial to phytoplankton production for the Ross Sea was 14%. Low productivity of bacteria in Antarctic waters relative to higher-latitude systems has been observed before. For example, Lochte et al. (1997) measured bacterial productivity, biomass, consumption and respiration of bacteria near the Polar Front, in

the southern Antarctic Circumpolar Current and Marginal Ice Zone. The values (range) they found for bacteria were $P/B=20 \text{ y}^{-1}$ ($3.0\text{--}39 \text{ y}^{-1}$). Kirchman et al. (2001) found that fluxes of dissolved organic carbon (DOC) were low in the Ross Sea compared to standing stocks and fluxes of particulate material, and this may explain low productivities of bacteria in the study region.

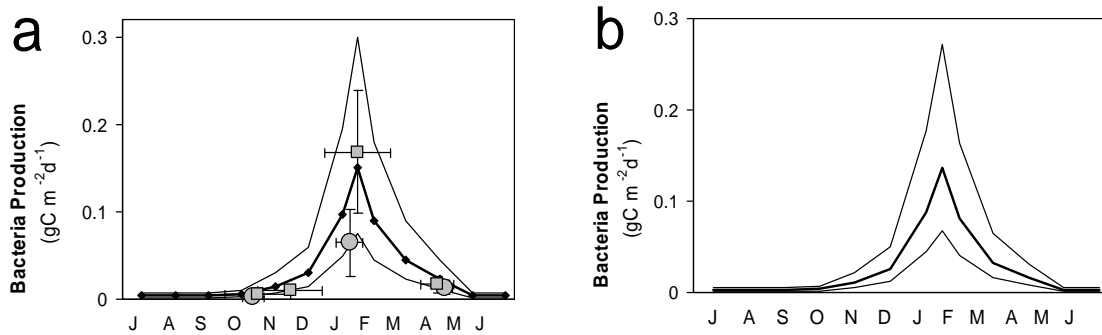


Figure 3. Bacterial production in the Ross Sea as estimated in the text. **a:** Bacterial production for open-ocean waters. Grey symbols represent measured values of bacterial production (see text for details). **b:** Production for the study area as a whole. The heavy centre lines indicate our best estimates of the values. The upper and lower lines indicate the approximate range of acceptable values.

2.3 Consumption

Bacteria in the water column consume detrital and dissolved organic material in the water column. Consumption by bacteria is typically quantified via growth efficiency (P/Q) values. Bradford-Grieve et al. (2003) used $P/Q=0.23$ for bacteria in subantarctic waters off New Zealand. Lochte et al. (1997) measured values in the Polar Front, in the southern Antarctic Circumpolar Current and Marginal Ice Zone, and reports $P/Q=0.30$ ($0.28\text{--}0.31$), and $P/R=0.43$ ($0.38\text{--}0.44$). Carlson et al. (1999) reported that *Phaeocystis* can be utilised quickly by bacterioplankton at growth efficiencies of 9–38%. Growth efficiencies (P/Q) for open ocean bacteria feeding on dissolved organic matter in the Southern Ocean was reported as 0.26–0.30 (Kaehler et al. 1997), which was reported as being consistent with work of Lignell (1990). Here, we propose using a P/Q for bacteria in the water column of 0.30. This gives an estimate of $Q/B=118 \text{ y}^{-1}$. We have not been able to locate any estimates of unassimilated consumption for water column bacteria in the Ross Sea and here we assume a value of $U=0.3$.

3 Benthic Bacteria

3.1 Biomass

There are a number of papers on sediment bacterial characteristics in the Ross Sea and the nearby Antarctic shelf (Smith et al. 1989; Fabiano & Danovaro 1998; Bowman et al. 2003; Bowman & McCuaig 2003). White et al. (1993) reviewed the information on Antarctic microbial communities in general. We base our estimate of benthic bacterial biomass (and productivity) on data from sediment cores taken from three ROAVERRS (Research on Ocean/Atmosphere Variability and Ecosystem Response in the Ross Sea) research voyages (Barry et al. 2003). This

voyage sampled benthic bacterial numbers and activity from 171 cores over the Ross Sea shelf (Figure 4). Dr Jim Barry has kindly provided these data to this study.

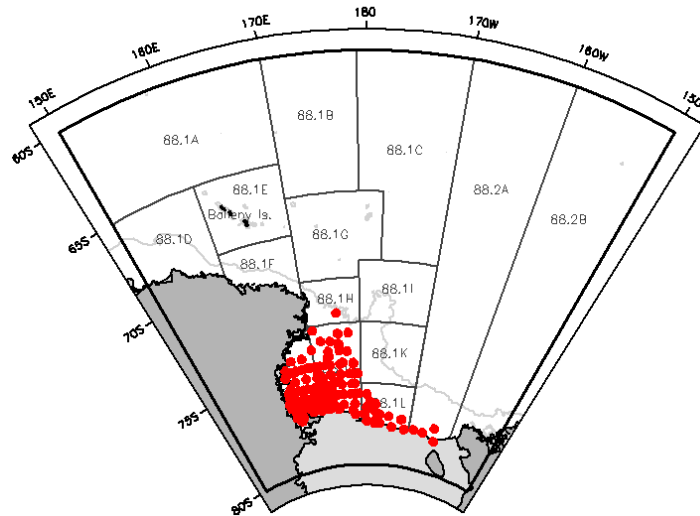


Figure 4. ROAVERRS sediment cores taken in the Ross Sea (data courtesy of Dr Jim Barry).

We estimate an average carbon content of Antarctic benthic bacteria of 91 fgC/cell as for Terra Nova Bay (Fabiano et al. 2000). Information from only the top cm of sediment was available from ROAVERRS (Barry et al. 2003). We used measurements of the depth distribution of bacteria in Ross Sea sediments from Fabiano & Danovaro (1998) to calculate the ratio between the near surface concentration of bacteria (gC m^{-3}) and the depth integrated concentration (gC m^{-2}). The average ratio from the two stations of Fabiano & Danovaro (1998) is 0.12 m (0.09–0.15 m). We assume that this ratio between near-surface and depth-integrated bacterial concentration is applicable to the whole Ross Sea shelf. Hence, we can use near surface concentration data from ROAVERRS to estimate the depth integrated benthic bacterial biomass. The values we estimate are 3–800 gC m^{-2} , with a median value (to account for the long-tailed distribution of bacterial biomass) of 47 gC m^{-2} . We assume a decrease in bacterial biomass with depth as $z^{-0.5}$ as for sediment community oxygen consumption (Gage 2003; Nodder et al. 2003) which allows us to calculate mean benthic bacterial biomass for the whole study area of 40 gC m^{-2} .

We compare these results with other published studies. Taking the density of Antarctic soft sediment (sand/mud) to be approximately 1.8 g cm^{-3} , sediments at New Harbour, McMurdo Sound were found to have concentrations of bacteria of c. $2.1 \times 10^9 \text{ cells g}^{-1}$ (Smith et al. 1986), approximately equivalent to 44 gC m^{-2} . The two open water stations studied by Fabiano and Danovaro (1998) had benthic biomasses of 16 and 8.4 gC m^{-2} , whereas, coastal sediments in Terra Nova Bay had bacterial biomasses of 3.3–24 gC m^{-2} (Fabiano et al. 2000) which lie within the range of values derived from the data of Barry.

We do not know how benthic bacterial biomass changes with season in the study area, and so assume these mainly summer data are representative of the annual average as some studies have shown that there is not a strong seasonal change in bacterial concentrations (e.g. Delille's 1995 work on a 2-y study of Kerguelen Island sediment at 49.5°S). Also, a seasonal study was made of bacterial populations in the coastal sediment at Signy Island (61°S) in the South Atlantic (Tanner & Herbert 1981) which showed no very strong seasonal changes but there was a minimum in bacteria numbers in June/July. Included in these were proteolytic and denitrifying bacteria with showed maxima around the time of the spring/summer bloom.

3.2 Production

We assume that activity (production) of benthic bacteria is concentrated in the surface 1 cm, consistent with modelling results (Talin et al. 2003) and some field studies (Haglund et al. 2003) that suggest benthic activity decreasing rapidly with depth in the sediment, though we note other field studies that do not show such a decline (Fallon et al. 1983). Measurements of sediment bacteria production from 171 ROAVERRS cores hence suggest a range of production values equivalent to P/B of 0.004–16 y^{-1} . The median of these values (used to account for the long-tailed distribution of bacterial P/B values) is P/B=0.71 y^{-1} . For comparison, growth rate, Bradford-Grieve et al. (2003) estimated P/B=1.0 y^{-1} for subantarctic waters off New Zealand, so this estimate seems reasonable. We note the P/B value for sediment bacteria is much lower than for bacteria in the water column.

3.3 Consumption

Non-living organic matter (OM) deposited in marine sediments from settling of marine snow is composed of a mixture of material, some of which is labile (directly consumable by benthic organisms) and some refractory. Sedimenting OM is largely composed of refractory, high-molecular-weight compounds and particles unsuitable for direct utilization by bacteria (Fabiano et al. 2000; Fabiano & Donovano 1998 and references therein). The degradation and utilization of organic polymers by bacteria occurs by extracellular enzyme activity (EEA). Coastal polar regions may be characterised by relatively low EEA activity in the water column and, coupled with high sedimentation rates, may result in an accumulation of detritus of high nutritional quality in the sediments that could potentially support large microbial biomasses. High latitude bacterial biomasses are comparable with those of temperate latitudes but very low bacterial productivity suggests that a large fraction of the bacterial assemblage is inactive.

Here, we estimate consumption by benthic bacteria via P/Q (growth efficiency). For bacteria, P/Q could range from 0.33–0.66 (Kemp 1994 and references therein) with the lower growth efficiencies occurring when growth is supported by relatively refractory material. It is possible that in some parts of the Ross Sea study area, P/Q for benthic bacteria could be at the higher range for part of the year because of the substantial sedimentation that occurs from the *Phaeocystis* sp. bloom (DiTullio et al. 2000). Here, we taking P/Q=0.5, which leads to a consumption estimate for benthic bacteria of Q/B=1.4 y^{-1} .

3.4 Unassimilated consumption and ecotrophic efficiency

We have not been able to locate any estimates of unassimilated consumption for benthic bacteria in the Ross Sea and here we assume a value of U=0.3. It is likely that a large proportion of sediment bacteria in Antarctic sediments are dead. Luna et al. (2002) found that dead cells comprise 70–74% of sediment bacteria in coastal sediments in the Mediterranean. Therefore, we will assume an ecotrophic efficiency of 0.30.

3.5 Sediment community respiration

We now use these estimates of benthic bacterial energetics to estimate sediment community respiration and compare this to published, directly measured values, assuming that bacterial biomass is in approximate steady state (e.g. DeLille 1995), so that ingested bacterial biomass

should be respired and represented in the measurement of total bacteria-mediated system metabolism.

Values of biomass, P/B and Q/B calculated previously for sediment bacteria can be used to estimate respiration using the relationship $R=Q(1-U)-P$. Respiration by benthic bacteria is hence estimated to be $11 \text{ gC m}^{-2} \text{ y}^{-1}$. Respiration by mega, macro and meiobenthos is estimated to be 9.5% of this value based on values estimated in the benthic section, giving an estimate of total benthic (non-megafaunal) respiration of $12.4 \text{ gC m}^{-2} \text{ y}^{-1}$.

Benthic respiration measurements (sediment community oxygen consumption, SCOC) have been made during the *Phaeocystis* bloom in the Ross Sea during large sedimentation events (DiTullio et al. 2000) and reported in Grebmeier et al. (2003). Sediment respiration values measured in the deep cold high salinity waters of the Ross Sea ranged from $0.00\text{--}8.41 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ over spring and summer (Grebmeier et al. 2003) although these data were not reported with the depth at which the measurements were taken. Higher sediment respiration rates were observed when the polynya was more open in 1996 than during high ice cover in 1997. Sediment oxygen uptake was only significantly correlated with depth and ^{13}C in the surface sediment, and bore no significant relationship to infaunal abundance or biomass. During medium ice cover average sediment oxygen uptake was $2.4\pm 1.1 \text{ mmol m}^{-2} \text{ d}^{-1}$ (Grebmeier et al. 2003). Applying the relationship given in Figure 5 to the Ross Sea study region gives an estimate of average SCOC of $2.31 \text{ mmol m}^{-2} \text{ d}^{-1}$.

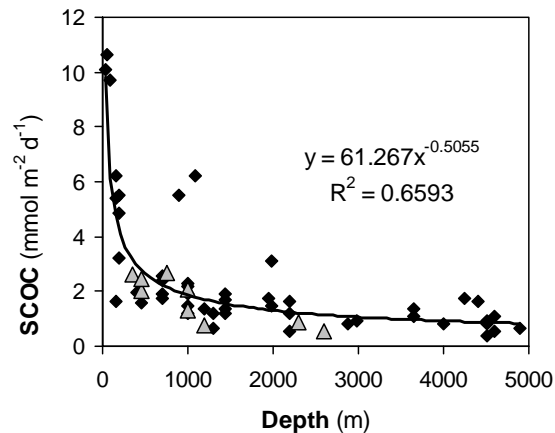


Figure 5. Sediment community oxygen consumption changes with depth. Black diamonds from Gage (2003) fig 11.10 for NE and NW Atlantic. Grey triangles measurements by Nodder et al. (2003) in the subantarctic Pacific at c. $45^{\circ}\text{S } 180^{\circ}\text{E}$.

Carbon remineralization by the benthic community was calculated by assuming a respiration quotient of 0.85 for mixed carbohydrate and lipid components (Hargrave 1973; Smith 1987, 1989). This suggests a sediment respiration of $8.6 \text{ gC m}^{-2} \text{ y}^{-1}$ if the respiration is approximately constant year round which we first assume it is. These two estimates of sediment respiration for the study area ($12.4 \text{ gC m}^{-2} \text{ y}^{-1}$ from estimates of biomass and activity, and $8.6 \text{ gC m}^{-2} \text{ y}^{-1}$ from extrapolating oxygen consumption measurements) are within 30%. The comparison suggests that the values used in the model for biomass and energetics of benthic bacteria may be slightly too high.

4 Bacteria in sea ice

Trophic parameters for bacteria in sea ice in the Ross Sea are given in the section on sea ice ecology and summarised in Table 1.

5 Water column detritus

5.1 Introduction

The primary production process results in the accumulation of living and dead organic material. In contrast to some more temperate latitudes (e.g. the North Atlantic), phytoplankton production in the Ross Sea results in a predominant (70–99%) production of particulate organic carbon relative to dissolved organic matter (Carlson et al. 2000). Dissolved organic carbon (DOC) is composed of all material that will pass through a 0.22 μm filter. The residue of particles $>200 \mu\text{m}$ is known as particulate organic carbon (POC) and is made up of phytoplankton, bacteria, microzooplankton, phytodetritus, faecal material and other non-living cellular material (Accornero & Gowing 2003). Some organic material may be leaked, directly (or indirectly due to the activities of grazing animals) into the environment as DOC. There are hence three pools of organic material in the water column: living particulate (including bacteria, phytoplankton, and zooplankton), non-living or detrital particulate organic material and dissolved organic carbon (DOC). For the purposes of the model we define “detritus” as being the sum of the standing stocks of non-living POC and all DOC. Most field data measured total particulate organic carbon (POC) which includes living components, so that the quantities of detritus can only be arrived at by subtraction of the living components.

There is an extensive literature on the seasonal concentration and flux of POC and DOC in the Ross Sea, for example: Accornero et al. 2003a, b; Andrews et al. 1999; Asper & Smith 1999, 2003; Becquevort & Smith 2001; Buesseler et al. 2003; Carlson et al. 2000; Cochran et al. 2000; Collier et al. 2000; DeMaster et al. 1992; Fabiano et al. 2000a; Gardner et al. 2000; Giordano et al. 1999; Gonzalez 1992; Gowing et al. 1995, 1996, 2001; Jaeger et al. 1996; Langone et al. 1998; Langone et al. 2000; Nelson et al. 1996; Schalk et al. 1993; Smith & Dunbar 1998; Sweeney et al. 2000a; Umani et al. 2002. In addition, here is a whole edition of the journal Antarctic Research Series (Vol 78) available on biogeochemistry of the Ross Sea (DiTullio & Dunbar 2003).

5.2 Water column detrital POC

Integrated standing stocks of particulate organic matter (POC) in the water column in the Ross Sea, 0–200 m, vary from 2.4 g m^{-2} in early spring to a maximum of 84 gC m^{-2} in summer (Gardner et al. 2000 and references therein). For approximately 7 months, from April to November, there is minimum POC. These data are corrected for the living component by subtracting phytoplankton, bacterial and heterotrophic protozoa biomass (Smith et al. 2000). The non-living fraction of POC in the Ross Sea peaks in concentration in February, lagging the phytoplankton biomass peak by about 1 month in the upper 200 m (Carlson et al. 1999). These figures suggest that the non-living detrital POC makes up 66–99% of the total water column POC. The annual average standing stock of non-living detrital POC is estimated to be 18.3 gC m^{-2} . For comparison, in Terra Nova Bay, in February 0–100 m, POC was measured in the range 10–25 gC m^{-2} (Umani et al. 2002, see also Fabiano et al. 2000a) lay within the range of values reported by Gardner et al. (2000). Bounds are estimated to be between 0.4–2.5 this estimate.

We note that only a proportion of the detrital POC may be usable for microbial metabolism. For example, Fabiano & Pusceddu (1998) found that about 70% of POC is total biopolymeric carbon (tBPC) (sum of protein, carbohydrate and lipid carbon) and about 50% of tBPC is hydrolyzable biopolymeric carbon (hBPC) and apparently available for microbial metabolism. However, the very large seasonal variation in POC to near zero levels in winter, suggest that the majority of POC in the water column is usable by biota. Here, we estimate that the winter concentration of detrital DOC (5.4 gC m^{-2}) represents the refractory component, with the remainder being labile. The labile annual average concentration of non-living detrital POC is hence estimated to be 12.9 gC m^{-2} (Figure 6a).

5.3 Water column DOC

In the Ross Sea seasonal variations in DOC of approximately 1.14 molC m^{-2} (13.7 gC m^{-2}) have been measured to occur in the surface 250 m (Ducklow et al. 1999; Carlson et al. 2000). Carlson et al. (2000) measured relatively consistent background levels of refractory deep water DOC of 6.27 molC m^{-2} (75 gC m^{-2}) through the year which are unlikely to be available to the biological system. We estimate an annual average standing stock of labile DOC of 3.5 gC m^{-2} (Figure 6b). Bounds are estimated to be between 0.4–2.5.

The seasonal variation in the labile water column detritus for the model is shown in Figure 6c. This has an average value of 16.4 gC m^{-2} .

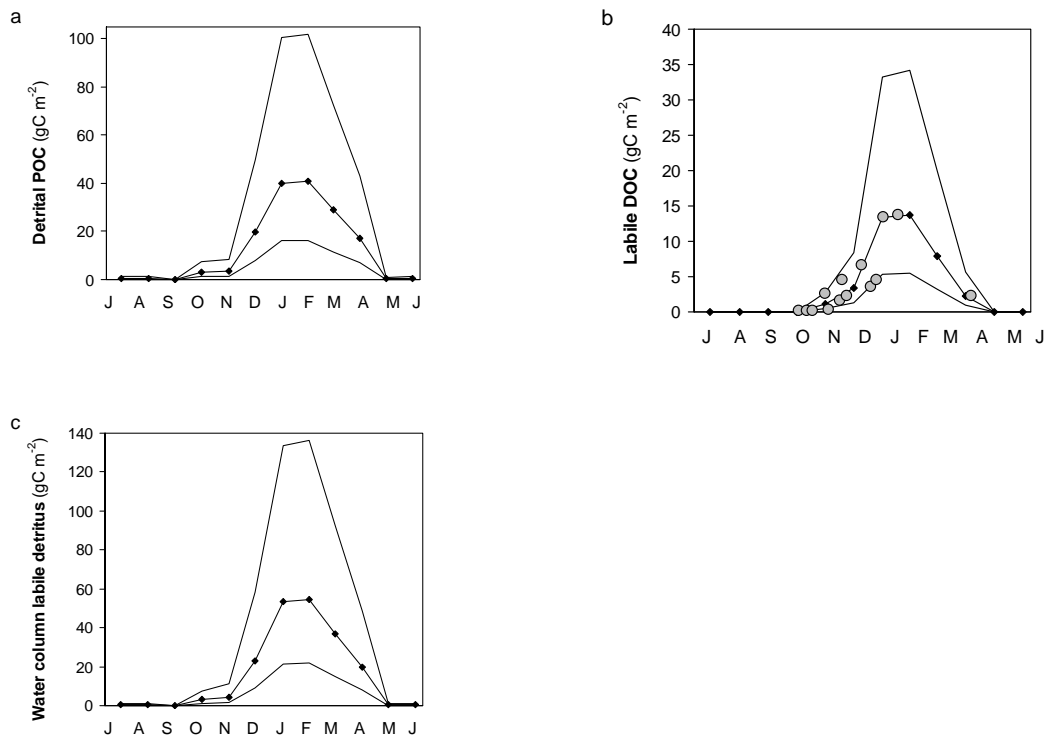


Figure 6. **a:** Detrital particulate organic matter from Gardner et al. (2000) and Smith et al. (2000). **b:** Labile dissolved organic carbon (DOC) based on Carlson et al. (2000); **c:** Estimated total labile detritus in the water column. Estimated confidence bounds are factors of 0.4–2.5 the central estimate.

6 Ice detritus

Gleitz et al. (1996) and Gunther et al. (1999) present reviews of the seasonal changes in the biogeochemistry and ecology of sea-ice algae. Newly formed sea-ice typically has high concentrations of inorganic carbon, low DOM and high nutrients. As primary production by epontic algae occurs, nutrients decline while DOM is accumulated (provided there is limited exchange between the sea-ice and underlying sea). Grazing and bacterial activity can then remineralize nutrients and lead to the growth of small algal species (Knox 2007).

Measurements of sea-ice POC from 69° to 78°S in November 1998 were made by Arrigo et al. (2003: Fig. 12). Values from Arrigo et al. (2003) were used to estimate concentrations of POC (after correcting for ice thickness from Arrigo et al. 2003) of 0.30–1.8 gC m⁻³, with an average of 0.91 gC m⁻³. Garrison et al. (2003) measured POC in the pack ice of the Ross Sea in May and June 1998. POC was positively correlated with chl *a* (which had lowest values south of 72°S) in both frazil and congelation ice. These two ice types were the only ones evident south of 72°S (see their figure 3). These data are summarised (µg l⁻¹) in their Table 2. Figures given by Garrison et al. (2003) suggest a mean POC of 0.55–1.6 gC m⁻³. Kattner et al. (2004) give data on POC and DOC, in the Weddell Sea, 1-15 m from ice flow borders, spaced through ice, for mid February to March 1997. In the Weddell Sea, POC in layered flows in summer/early autumn was equivalent to 4.3 gC m⁻³ and DOC of 3.6 gC m⁻³. Kennedy et al. (2002) give POC in sea ice in Jan/Feb in the Weddell Sea. They record POC of 2.1 gC m⁻³ for intact floes, and 10.0 gC m⁻³ overall for layered flows (see their Table 1) and noted the highly variable POC. Measurements of DOC in sea ice in the Amundsen and Bellingshausen Seas are given in Thomas et al. (2001). They show that DOC in melted ice cores was 1.3–2.5 gC m⁻³ (non-brine), which was about 30 times greater than in the water column. This DOC was composed on average of 30% carbohydrates. There was no strong relationship between DOC and chlorophyll *a* although there were generally higher concentrations of DOC in warm, porous summer second year sea ice compared with colder autumn first-year ice. Here, we use an average of these values which gives an annual average POC concentration of 1.7 gC m⁻³, and an annual average DOC concentration of 2.5 gC m⁻³ (Figure 7a).

Concentrations of POC and DOC in sea-ice were summed, and converted to a Ross Sea average by correcting for average sea-ice concentration over the study area and estimated ice thickness. See the section on the physical environment of the Ross Sea for details these estimates. From this we subtract estimated biomasses of sea-ice algae, protozoa, metazoan and bacteria to give an estimate of non-living organic carbon for the study area. Our final annual average estimate is 2.6 gC m⁻². We estimate a possible range of uncertainty of 0.88–7.9 gC m⁻² (Figure 7b). The proportion of the total annual input of detrital material in the sea ice habitat that is transferred to the water column when ice melts (as opposed to being remineralised by sea ice bacteria) is not known, and we initially assume it is $T^S=0.3$ as a starting point for the model.

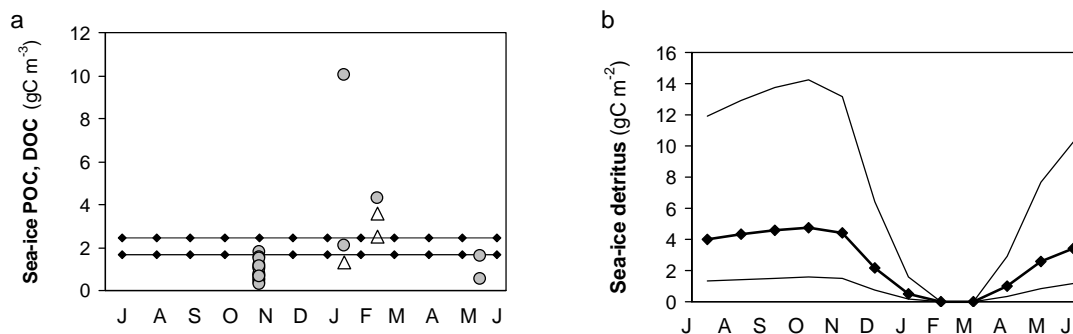


Figure 7. a: Detrital particulate organic matter (POC) and detrital dissolved organic carbon (DOC). Grey circles are in situ measurements of POC and white triangles are DOC. Data are from Arrigo et al. (2003), Garrison et al. (2003), Kattner et al. (2004) Kennedy et al. (2002) Thomas et al. (2001). Black lines are annual average estimates (upper: DOC, lower: POC). **b:** Annual variation in areal density of total detrital material in sea ice corrected for biomass of sea-ice biota, sea ice thickness and seasonal variations in Ross Sea average sea-ice concentration.

7 Benthic detritus

The standing stock of benthic detritus is not used in the model: only flows to and from the benthic detritus are used. Although we expect that surface sediment quantity and quality would change seasonally in the Ross Sea, only summer surface sediment data are available so we cannot obtain an estimate of the seasonal cycle of organic matter in benthic sediments. Hence, we do not estimate a carbon biomass for benthic detritus.

8 Detrital flows

8.1 Detrital flux to the sea floor

The non-living components of the POC can aggregate to form “marine snow”, where different types of detrital particles are bound together loosely by transparent exopolymers (Allredge & Jackson 1995). This marine snow sinks through the water column, during which the non-living fractions of POC and DOC may be remineralised by bacteria (and possibly other organisms). Degradation and utilization of organic material by bacteria in the water column during sedimentation occurs by extracellular enzyme activity (EEA). Coastal polar regions may be characterised by relatively low EEA activity in the water column, so that a proportion of water column detritus sinks to the sea-bed to form benthic detritus. Nelson et al. (1996) integrated data on the cycling of organic carbon and biogenic silica in the Southern Ocean with estimates of water column and sedimentary fluxes on the Ross Sea continental shelf. They concluded that there is no detectable decomposition of sinking organic material between 250 m and the sea floor, so that the majority of decomposition in the water column occurs between 50–250 m (see also Sweeney et al. 2000; Azzaro et al. 2006).

The contribution that faecal pellets make to downwards flux of organic carbon in the southern Ross Sea varies from 3.8–58.8% (Accornero & Gowing 2003c). From late January to late February a significant part of the material produced in the euphotic zone sank out in faecal pellets, suggesting that grazing was the most important biological process supplying sinking organic particles to the sea floor at that time. At the end of the productive period faecal pellets

appeared to have been formed by coprophagy or the consumption of detritus or flagellates. Very low pellet fluxes in the winter and spring and early summer suggest physical factors and food webs retain pellets in surface waters.

The peak of total vertical POC flux to sediment traps in the Ross Sea is separated from the peak in total POC in the water column 0–100 m by 3 months at 200 m and 3.75 months at about 470 m (Gardner et al. 2000). The timing of the peak sedimentation event is postulated by Longone et al. (2003) to be associated with the development of a seasonal minimum in sea water density suggesting that deep convective mixing of late summer surface waters forces a seasonal particle settling event. Collier et al. (2000) show that export of organic matter to 200 m in spring and summer was very low indicating that the ongoing phytoplankton bloom was being stored or recycled in the upper water column. There was a major pulse of biogenic silica export in autumn 1.5 months after the ice started to form. The correlation of this event with lithogeneous particles, excess Fe, and with the early breakdown of katabatic winds suggests that this event was related to Fe fertilization of diatom production and export. The largest flux of organic matter during 1996–97 was associated with the pteropod *Limacina helicina* and occurred under the ice in late autumn just after the diatom pulse. It is thought that this pulse represents the die-out of this herbivore after POC had declined to very low levels. Collier et al. (2000, p 3509) suggest that production, biomass and export of organic carbon is largely uncoupled. They speculate that this is because of the very slow settling rate of *Phaeocystis antarctica* (see Asper & Smith 1999), low grazing of this species (Leventer & Dunbar 1996 and other references), and microbial remineralisation in the upper water column. Substantial flux at the time of ice melting showed up only in silica fluxes (but only at one of the stations in the north central Ross Sea) but hardly showed in the organic carbon fluxes (Collier et al. 2000).

Variability in detrital flux between regions of the Ross Sea has been demonstrated from limited data. Collier et al. (2000) show that flux in the southern Ross Sea was generally twice that in the north. At the northern station the average annual flux to 460 m was $1.43 \text{ mmol m}^{-2} \text{ d}^{-1}$, whereas at the southern station average annual flux to 481 m and 465 m was 3.26 and $2.8 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively although values may be underestimations related to the functioning of sediment traps near the sea floor. The average total vertical C flux for the Ross Sea at 100 m (obtained by extrapolation of the measurements) was estimated as $26 \text{ gC m}^{-2} \text{ y}^{-1}$ (Buesseler et al. 2003) for the seven month period between October and May (the “growing season”). This estimate may be compared with the annual average supply to depths > 200 m of $47 \text{ gC m}^{-2} \text{ y}^{-1}$ for a Ross Sea bounded by the 1000 m isopleth (Sweeney et al. 2000b). Buesseler et al. (2003) note that this estimate of export is significantly higher than sediment trap results which may be explained by errors in POC measurement and/or by lowered efficiency of bottom-tethered sediment traps. Trap data from Collier et al. (2000) suggest annual flux rates of only c. $3.7 \text{ gC m}^{-2} \text{ y}^{-1}$. Nelson et al. (1996) estimate that only $5.1 \text{ gC m}^{-2} \text{ y}^{-1}$ is delivered to the sea floor. Sediment trap data from DeMaster et al. (1996) in the Ross Sea leads to annual carbon flux to the sea bed of $1.2\text{--}9.1 \text{ gC m}^{-2} \text{ y}^{-1}$. We initially assume that the annual contribution to the water column detrital pool to the sea floor is $10 \text{ gC m}^{-2} \text{ y}^{-1}$ with a range of $2\text{--}50 \text{ gC m}^{-2} \text{ y}^{-1}$ for the study area. The seasonal variation is assumed to follow data from (Collier et al. 2000) summarised in Smith et al. (2007), scaled to this annual average value (Figure 8).

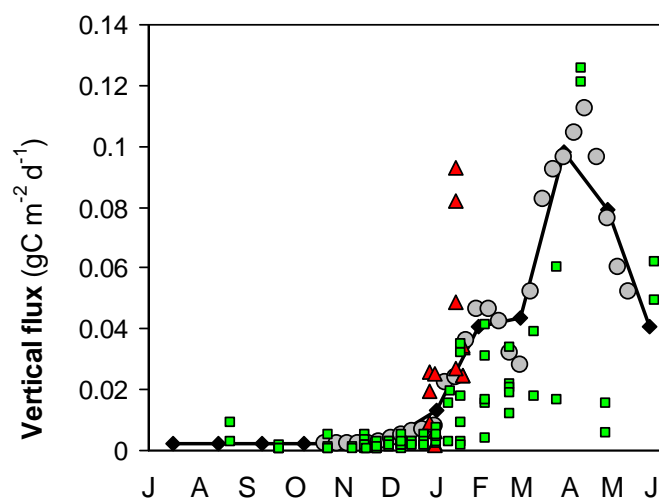


Figure 8. Vertical flux rates for the study area. Data shown are: grey circles, Smith et al. (2007), scaled to estimates from Buesseler et al. (2003) and Sweeney et al. (2000b) as described in the text; red triangles from Smith & Dunbar (1998), not scaled; green squares, Collier et al. (2000), not scaled.

1.1. Burial

A proportion of benthic detritus may be buried and represents an export of carbon from the system. It has been shown that benthic detrital biomass can accumulate in some years and be consumed in others (Gage 2003). Short-term (interannual) variations may be superimposed on long-term (decadal) accumulation rates.

Data on nutrient efflux and sediment accumulation of organic carbon in the Ross Sea presented by Nelson et al. (1996) calculates that the preservation efficiency (permanent burial) of organic carbon (accumulation rate/flux to the sediment surface) integrated over the Ross Sea is 4.9%. More than 95% of the organic matter reaching the sea floor is decomposed in the surface sediments, largely by benthic bacteria.

A different picture may be appropriate for shallow waters because the sedimentation of basically unprocessed POC is probably consumed by “suspension-feeder rich” communities (Barry et al. 2003). Benthic megafauna are important in the coupling between the water column and sea floor. For example, the Antarctic scallop, *Adamussium colbecki*, has been shown to be able to process about 14% of total downward carbon flux from the water column to the sediments. Faeces returned to the seabed have good energy values and can be used by deposit feeders (Chiantore et al. 1998). Whether benthic detritus accumulates or reduces over time is hence probably controlled by a combination of sedimentation rates and benthic heterotrophic activity.

9 Summary: all bacteria and detrital compartments

Values for bacteria in the trophic model of the Ross Sea as a whole are calculated by combining parameters for bacteria in the water column, benthic sediments and sea-ice (Table 1).

Table 1. Summary parameters for bacteria in the trophic model. Columns labelled %P and %Q are proportions of total production and consumption respectively by the various components.

	B (gC m ⁻²)	P/B (gC m ⁻² y ⁻¹)	Q/B (gC m ⁻² y ⁻¹)	P/Q	U	%P	%Q
Water bacteria	0.23	35	71	0.50	0	21.0	21.0
Ice bacteria	0.018	165	329	0.50	0	7.5	7.5
Benthic bacteria	39.9	0.71	1.4	0.50	0	71.5	71.5
All bacteria	40.1	1.0	2.0	0.50	0	100	100
Vertical detrital flux to sea floor	10	gC m ⁻² y ⁻¹ (see text; wide uncertainty 2–50 gC m ⁻² y ⁻¹)					
Burial	4.9%	of flux to sea floor (Nelson et al. 1996)					

Water column bacteria are hence estimated to be responsible for nearly half the total production and consumption by bacteria in the Ross Sea. Benthic bacteria, with their higher biomass but lower activity, are estimated to account for about 37% of all bacterial production and consumption in the study area, with ice bacteria responsible for the remaining 14%. The proportions for consumption and production are identical because the three groups of bacteria have the same growth efficiencies (P/Q). We note that these figures imply that there is insufficient vertical flux of organic matter to supply the needs of bacteria in the sediments (only 64% met by vertical flux). Such a shortfall has been observed in other studies (e.g. Smith 1987; Nodder et al. 2003), one potential explanation being that benthic organisms (primarily the benthic bacteria) are able to use dissolved organic carbon from water permeating the sediments.

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