

Benthos: Trophic modelling of the Ross Sea

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1 Introduction

Although the Ross Sea benthos has been extensively studied from the late 19th century to present-day (e.g., Borchgrevink 1901; Littlepage & Pearse 1967; Bullivant & Dearborn 1967; Bullivant 1967a, b; Dayton & Oliver 1977; Lipps et al. 1979; Battershill 1989; review by Starmans et al. 1999; Gambi & Bussotti 1999; Barry et al. 2003; Rehm et al. 2006), large-scale estimates of benthic biomass in the Ross Sea is limited. Sampling methods and lack of calibration of numbers to biomass are at the base of difficulties in arriving at consolidated mega- and macrobenthos biomass data.

Some key features of the Antarctic benthos are given below (e.g., Arntz et al. 1997).

- There are distinct differences between various benthic subsystems (<30m, shelf, slope, deep water).
- Distribution of benthic macrofauna biomass is very patchy. There are areas of the Ross Sea that contain extraordinarily high benthic faunal abundances and others that have relatively low biomass.
- Some benthic production is linked to surface production, at other times it is decoupled.

Two types of method have been used commonly to study the benthic ecosystem of the Ross Sea: “remote” and “direct” measurements. Diver-swum transects give an indication of the spatial distribution of macro and mega-benthic fauna in terms of abundance (numbers of individuals) and diversity (number and types of species) but are restricted to shallow waters (<50 m). In deeper water, sampling using “remote” methods such as camera (video or still) systems have been used to obtain data on what is living on, or extending from, the sediment surface. Camera resolution can be an impediment to observing smaller individuals in the frames. Remote measurements do not directly measure biomass or production of different organisms and are usefully combined with direct sampling (e.g., Cummings et al. 2003; Mitchell & Clark 2004; Hanchet et al. 2008).

If box or other corers are used, then a much smaller area is sampled and smaller organisms enumerated. However, it is generally not possible to sample densely enough to elucidate the patchiness in the distribution of benthos biomass. Also, it is common for workers to use different mesh sizes to separate benthic organisms from sediment making combining different studies difficult or impossible.

1.1 The benthic ecosystem sub-model

The conceptual structure of the benthic ecosystem used in this study is based on a widely-used but simple energetic model of benthic communities (e.g., Smith 1987, 1989; Christiansen et al. 2001; Gage 2003; Piepenburg et al. 1995; Nodder et al. 2003; Bradford-Grieve et al. 2003). The conceptual model of the Ross Sea benthos used in the present study has three components: (1) megabenthos; (2) macrobenthos; (3) meiobenthos. Benthic bacteria and benthic detritus are

included in the generic bacteria and detrital model groups. We use a definition here of megabenthos >20 mm in size, macrobenthos 0.5–20 mm, and meiobenthos <0.5 mm.

It is unclear whether a more detailed subdivision of the benthic community would benefit the overall trophic model. Jarre-Teichmann et al. (1997) developed a trophic model of the benthic shelf community of the eastern Weddell Sea, dividing the benthic macrofauna into the following compartments: Crinoidea, Holothuroidea, Ophiuroidea, Mollusca, Bryozoa, Polychaeta, Asteroidea, Porifera, Echinoidea and Tunicata/Hemichordata. Such a detailed subdivision of the benthic community is not common in trophic models, because the benthos tends to be relatively poorly characterised in terms of biomass, and spatial and/or temporal variability. Data also becomes progressively scarcer as the water depth increases, especially in Southern Ocean regions.

The structure and function of the benthic ecosystem and the characteristics of the benthic-pelagic coupling are typically unevenly distributed at a range of spatial scales, depending on factors including substrate, water depth, ice-cover, and proximity to primary producers (macroalgae, phytoplankton, epontic algae). Some of the environmental factors that are likely to exert some control on benthic faunal biomass also have a temporal variation (especially ice cover and primary production). The complexity of the relationship between benthic faunal density and environment, and the patchiness of the distribution, makes it difficult to estimate a “characteristic” biomass, structure and function of the Ross Sea benthic fauna. As a starting point, we estimate megafaunal and macrofaunal biomass for the coastal and offshore regions of the Ross Sea separately as explained below. For meiobenthos, we use a relationship between meiofaunal biomass and depth.

2 Megabenthos

2.1 Weights and carbon content conversions

We require knowledge of weights of individual megabenthic organisms to convert measured abundances (ind/m²) to biomass density. The wet mass of several taxa are greatly biased by water content, massive inorganic outer shells and/or inorganic carbon-rich (CaCO₃) skeletal material, and variable amounts of organic carbon as a percentage of wet and dry weights (Rowe 1983). Some of the megabenthos is not appropriately enumerated in terms of abundance of individuals, including structure forming “massive” organisms and colonial species. For two groups (porifera, ectoprocta), measurements of abundances are in terms of area cover, and these are converted to biomass using an estimate of wet weight per m² for that organism.

As yet, the weight relationships of Ross Sea benthos has been worked out only for some shallow water hard bottom organisms in Terra Nova Bay (Gambi et al. 1994), soft bottom shallow water polychaetes (Gambi et al. 1997), the shallow water nemertean *Parborlasia corrugatus* (Heine et al. 1991), the echinoid *Sterechinus neumayeri* (Brey et al. 1995) and benthic littoral communities (Cattaneo-Vietti et al. 2000). In addition, because of the limited resolution of underwater imagery, many benthic taxa measured remotely cannot be identified to species level, making estimation of “typical” sizes from the literature uncertain. Here, typical individual weights were obtained by weighing specimens collected from the Ross Sea on the recent New Zealand IPY-CAMLR voyage (Hanchet et al. 2008) and shown in Table 1.

Table 1 also shows typical individual weight, area weights, and conversion factors between wet-weight and carbon, as wet weights must be converted to organic carbon content for modelling. Wet-weight to carbon conversion factors were taken from a number of publications including

Vinogradov (1953) (various groups), Galeron et al. (2000) (various groups), Dayton et al. (1974) for Porifera, and Brey (2005) for Holothurians. Proportions of carbon associated with living material rather than inorganic skeletal material were estimated as by Lundquist & Pinkerton (2008).

Table 1. Typical weights and living carbon content of Ross Sea non-coastal megabenthos. Biota are grouped. * indicates values are per % of cover rather than per individual.

Group	Comment	Typical weights gWW/ind (* gWW/%)	gC/gWW	Proportion living	gC living/ind (* gC living/%)
Asteroid	Sea star	41.4	0.110	1	4.555
Ophiuroid	Brittle star	5.6	0.064	1	0.357
Echinoid	Urchin	2.0	0.043	0.2	0.017
Holothurian	Sea cucumber	30.0	0.056	1	1.687
Crinoid	Soft coral	13.5	0.064	1	0.867
Arthropod shrimp	Benthic shrimp	4.4	0.106	1	0.464
Mollusc	Gastropod	15.5	0.096	0.2	0.297
Annelida	Worm	6.6	0.090	1	0.594
Pycnogonid	Sea spider	2.0	0.104	0.5	0.105
Porifera	Sponge	64.3*	0.070	0.1	0.453*
Hydrocoral	Hard coral	119.0	0.020	0.1	0.238
Hydroid	Hydroid (individual)	6.6	0.142	1	0.934
Ascidian	Chordata	37.8	0.017	1	0.642
Alcyonacea	Soft coral	59.9	0.073	1	4.343
Pennatulacea	Sea pen (octocoral)	7.0	0.052	0.2	0.072
Gorgonacea	Gorgonian coral	10.0	0.052	0.1	0.052
Hexacoral	Anenome	68.2	0.054	1	3.685
Bryozoa	Bryozoan-hydroid complex	15.3*	0.093	0.1	0.143*

2.2 Biomass

Biomass of megabenthos in the Ross Sea is estimated from three sets of data.

First, there are a number of studies of the near-shore Ross Sea megabenthos in waters shallower than 30 m depth. The majority of studies of megafauna have been conducted in the McMurdo Sound and Terra Nova Bay regions (Dayton et al. 1969, 1970, 1974, 1994; Dayton & Oliver 1977; Oliver & Slattery 1985; Battershill 1989; Dayton 1990; Lenihan 1992; Lenihan & Oliver 1995; Brey et al. 1995; Chiantore et al. 1998; Cattaneo-Vietti et al. 2000; Gambi et al. 2000; Heilmayer et al. 2003). Even though waters less than 100 m deep make up <1% of the total Ross Sea study region, these are considered separately because shallow waters may contribute a disproportionate amount to the total megabenthic biomass of the Ross Sea. Biomasses and densities of the molluscan species in Terra Nova Bay are reported in Cattaneo-Vietti et al. 2000 (see Table 4 in that paper). Their study found the Antarctic scallop (*Adamussium colbecki*) to be the most common species of mollusc in Terra Nova Bay, with densities up to 59 ind m⁻² (25 average). The study showed that the bivalve assemblage was diverse, with *A. colbecki* making up only 12% of the mollusc individuals (by number) on average. *A. colbecki* was also found to be common further south in McMurdo Sound, where abundances up to 85 ind m⁻² occur at between 4–15 m (Stockton 1984). Typical dry weights of tissue of individuals are 0.2–4 gDW ind⁻¹ for shell heights between 20 and 80 mm (Heilmayer & Brey 2003). A population median individual size may be c.50 mm (Heilmayer et al. 2003) and an average individual weight may be of the

order of 1.3 gDW ind⁻¹. This gives an average biomass density of *A. colbecki* of 30 gDW m⁻² in Terra Nova Bay and McMurdo Sound. This range of density is low compared to estimates of biomass of *A. colbecki* at New Harbour, McMurdo Sound, where biomass measurements range from 59–66 gDW m⁻² (Brey & Clarke 1993), and to up to 120 gDW m⁻² for a 20–40 m population with densities of around 60 ind m⁻² (Road Bay, Terra Nova Bay; Chiantore et al. 1998). Carbon is assumed to make up about 34% of dry weight of molluscs (Brey 2005). Hence, a lower bound on the density of *A. colbecki* alone is estimated to be of the order of 11 gC m⁻² in parts of Terra Nova Bay and McMurdo Sound. Benthic megafauna in Terra Nova Bay and McMurdo Sound regions also include the regular urchin *Sterechinus neumayeri* in addition to exceedingly high densities of the infaunal bivalve *Laternula elliptica* that have been found at Faraglione (Terra Nova Bay) at depths below 25 m (S. Thrush, N. Andrew and G. Funnell, unpublished data). These studies would hence suggest megafauna biomass densities in some coastal areas may be substantially greater than 11 gC m⁻², though this includes inorganic carbon in the shell.

Second, we consider data from the ROAVERRS (Research on Ocean/Atmosphere Variability and Ecosystem Response in the Ross Sea) research cruise studying megabenthos of deeper Ross Sea (Figure 1a). This voyage sampled two areas: (1) along the coast from Cape Adare and Terra Nova Bay, out to 500 m depth; and (2) in the Ross Sea from 300 to 1200 m depth (Barry et al. 2003). Barry et al. (2003, see Table 10) gives data on the abundance of benthic megafauna over large areas of the Ross Sea from this program. Dr Jim Barry has kindly provided these data from 55 stations in the Ross Sea to this study. Data were gathered using a towed camera system but organism size or biomass were not measured. We assume that the abundances given by Barry et al. (2003) include the major contributors to the biomass of the megabenthos, though note that smaller organisms may be under-represented.

Third, data were obtained from the NIWA Deep-water Towed Imaging System (DTIS) on the New Zealand IPY-CAML voyage to the Ross Sea (Hanchet et al. 2008). This voyage completed tows of the video imaging system on the Ross Sea shelf (8 tows), slope (8 tows), deep water within the study area (2 tows), and deep water north of the study area (8 tows): Figure 1b. “Shelf” is all areas landward of the 600 m depth contour; “slope” is depths 600–1800 m in the shelf region; and “deep” is all areas >1800 m in depth in the study area, and deeper than 1000 m to the north of the study area. Data on major megabenthic groups were obtained in “real-time” onboard the vessel. More extensively processed data from the voyage will be available in due course, but these preliminary data are the best available results at present (April 2009). The data were merged onto the common set of megabenthic groups given in Table 1. ROAVERRS data are likely to be more quantitative, as the optical resolution of the images are higher and the still images have been subject to more detailed processing than the underway IPY-CAML video data. To reconcile the IPY-CAML video data with the ROAVERRS data, we calculated log-average values for each benthic group of biota from the region of overlap in the Ross Sea shelf (73–77°S, 167°E–180°). Log-averages were used to reduce biasing of the average by occasional high values. This overlap consisted of 9 IPY-CAML stations and 31 ROAVERRS stations. Where the ratio of the log-averages for a particular group between the two surveys was between 0.1 and 10, we adjusted the IPY-CAML data by this value. This was the case for Asteroid, Ophiuroid, Echinoid, Holothurian, Crinoid, Mollusc, Annelida, Pycnogonid, Hydrocoral, Ascidian, Alcyonacea, Pennatulacea, Gorgonacea and Hexacoral groups. The abundances of Arthropod_shrimp and Hydroid groups measured by IPY-CAML on the shelf were very much lower than those measured by ROAVERRS (factor of 190 for Arthropod shrimp and 26 for Hydroids). This is probably because the resolution of the video data from IPY-CAML is sufficient to see animals greater than about 5 cm in size whereas the still images used on ROAVERRS data mean that individuals >2 cm are likely to be counted. Both these groups include many small individuals in the 2–5 cm size range. We used only data from ROAVERRS on the shelf, and unadjusted data

from IPY-CAMLR on the slope and shelf. We acknowledge that biomass values for Arthropod_shrimp and Hydroid may consequently be underestimated on the slope and deep water. No area coverage measurements of Porifera and Ectoprocta are currently available from the IPY-CAML voyage so we used individual counts along the transects as an indicator of abundances of these groups adjusted to match the log-average percentage cover values from the ROAVERRS voyages. Final estimates of biomass for all groups are given in Table 2.

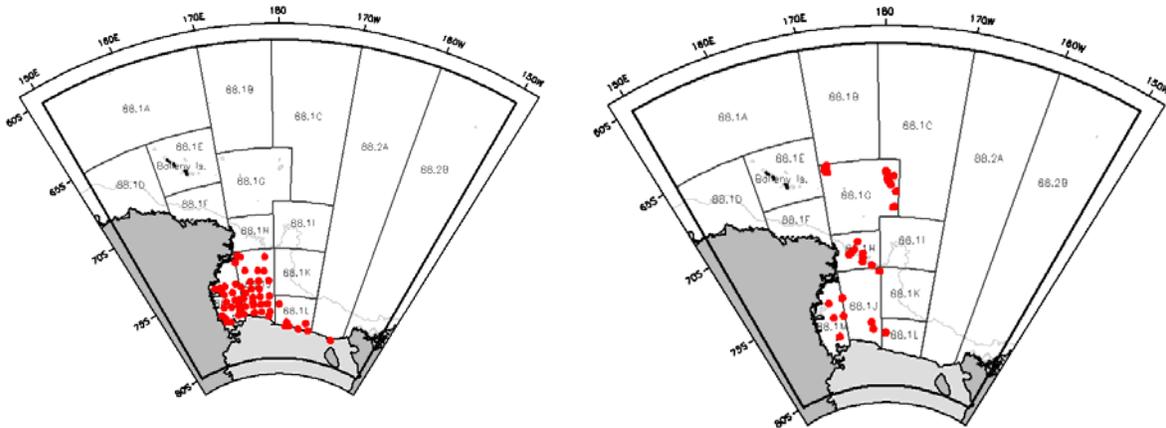


Figure 1. Location of stations from the **a:** ROAVERRS and **b:** IPY-CAML benthic surveys of the Ross Sea region.

Combining these data in the appropriate proportions for the study area of the trophic model allows us to estimate megabenthic faunal abundance for the whole study region (Table 2). The average abundance of benthic individuals in the present trophic model study region was 0.15 individuals/m². Our data show that the benthic megafauna of the deeper Ross Sea was dominated in terms of carbon biomass by anemones (22.0%), holothurians (16.1%), ophiuroids (12.1%), and porifera (10.6%). Combining these components gives an average megafaunal biomass density for the non-coastal waters of the Ross Sea of 1.4 gC m⁻².

Table 2. Biomasses of benthic megafauna in the Ross Sea region by area. “Shelf” is all areas landward of the 600 m depth contour. “Slope” is depths 600–1800 m in the shelf region, and “deep” is all areas >1800 m in depth.

Region		Shelf	Slope	Deep	All	
Area (km ²)		421 897	75 206	139 895	636 998	
Group	Comment	B (gC m ⁻²)	B (% total)			
Asteroid	Sea star	0.089	0.077	0.017	0.072	5.1
Ophiuroid	Brittle star	0.219	0.149	0.027	0.169	12.1
Echinoid	Urchin	0.001	0.000	0.000	0.001	0.0
Holothurian	Sea cucumber	0.316	0.006	0.077	0.227	16.2
Crinoid	Soft coral	0.118	0.004	0.004	0.079	5.7
Arthropod shrimp	Benthic shrimp	0.088	0.004	0.011	0.061	4.4
Mollusc	Gastropod	0.001	0.000	0.000	0.001	0.1
Annelida	Worm	0.202	0.000	0.007	0.136	9.7
Pycnogonid	Sea spider	0.001	0.000	0.000	0.001	0.1

Porifera	Sponge	0.196	0.122	0.019	0.148	10.6
Hydrocoral	Hard coral	0.000	0.001	0.000	0.000	0.0
Hydroid	Hydroid (individual)	0.101	0.000	0.000	0.067	4.8
Ascidian	Chordata	0.044	0.002	0.003	0.030	2.1
Alcyonacea	Soft coral	0.012	0.000	0.001	0.008	0.6
Pennatulacea	Sea pen (octocoral)	0.011	0.002	0.000	0.008	0.5
Gorgonacea	Gorgonian coral	0.010	0.001	0.001	0.007	0.5
Hexacoral	Anenome	0.306	0.749	0.074	0.307	22.0
Bryozoa	Bryozoan-hydroid complex	0.115	0.001	0.000	0.076	5.5
ALL		1.829	1.118	0.241	1.396	100

The overall assessment of the density of megafauna in the Ross Sea depends on the relative areas dominated different faunal assemblages: the high biomass coastal areas, and the lower biomass offshore and deeper waters. Information on the patchiness of different benthic communities in the Ross Sea is not well known. Here, we assume that high megafaunal biomass (typified by Terra Nova Bay and McMurdo Sound studies) is typical of 20% of waters less than 100 m deep (c. 0.15% of the study area). The values estimated from Barry et al. (2003) are used for all other areas. These considerations give an average megafaunal biomass for the Ross Sea of 1.42 gC m⁻², 1.9% from the coastal areas, 85.1% from the non-coastal shelf, 9.3% from the slope, and 3.7% from the deep ocean benthos.

2.3 Production

Larger animals such as *Adamussium colbecki* and *Sterechinus neumayeri* are long lived and slow growing implying low P/B ratios (Berkman et al. 2004; Brey et al. 1995). Estimates of growth and age of *A. colbecki* have varied considerably. Recently, however, mark-recapture information from individuals in New Harbour, indicate that *A. colbecki* life spans may be century-scale (Berkman et al. 2004), implying low P/B values. Hielmayer et al. (2003) estimate (somatic) P/B=0.2 y⁻¹ for *A. colbecki*. Brey & Clarke (1993), and references therein, give (somatic) P/B values for megabenthic species in the Ross Sea of 0.04–0.20 y⁻¹, ascribing low benthic productivities in the Antarctic relative to non-polar regions to low food input and low temperatures. General macrofaunal P/B can be estimated from the relationship described by Brey & Gerdes (1998) based on water temperature. Using a temperature of between -1.9°C and +2.0°C, P/B is calculated to be 0.36 y⁻¹. Jarre-Teichmann gives P/B=0.30 y⁻¹ for the benthic mollusc *Lissarca notorcadensis*, similar species to which are found in Terra Nova Bay (Cattaneo-Vietti et al. 2000). The urchin *Sterechinus neumayeri* is the most abundant regular urchin in the Antarctic, and is known to grow very slowly, taking about 40 y to reach a diameter of 70 mm (Brey et al. 1995). Somatic P/B for this species was estimated to be 0.07 y⁻¹ in the Weddell Sea (Brey 1991). Five species of bryozoans (*Cellarinella* sp.) in the Antarctic are estimated to grow at a rate equivalent to an average of P/B=0.18 y⁻¹ (Barnes et al. 2007). Jarre-Teichmann et al. (1997, and references therein) estimated P/B values for megabenthos in the Weddell Sea as: 0.17 y⁻¹ (Ophiuroidea), 0.10 y⁻¹ (Holothuroidea), 0.08 y⁻¹ (Asteroidea), 0.10 y⁻¹ (Crinoidea), 0.07 y⁻¹ (Echinoidea), 0.60 y⁻¹ (Polychaeta and other worms), 0.59 y⁻¹ (benthic decapods), 0.04 y⁻¹ (Cnidaria), 0.30 y⁻¹ (Hemichordata), 0.03 y⁻¹ (Porifera), 0.10 y⁻¹ (Tunicata), 0.31 y⁻¹ (benthic molluscs). Bowden et al. (2006) gives data suggesting an annual average P/B for Antarctic polychaetes of 1.6 y⁻¹. Combining these productivities in proportion to the estimated biomasses of these biota in the Ross Sea gives an average P/B of 0.25 y⁻¹ for Ross Sea megabenthos.

2.4 Consumption

Consumption by megabenthos will be calculated from gross efficiency (P/Q). This ratio was given for subantarctic mega and macrobenthos combined (Bradford-Grieve et al. 2003) as P/Q=0.35. Hielmayer et al. (2003) estimated consumption by *A. colbecki* in Terra Nova Bay of 6000 kJ m⁻² y⁻¹ and production of 609 kJ m⁻² y⁻¹, allowing us to estimate P/Q=0.10. We use a value of P/Q for megabenthos in the Ross Sea between these values of 0.20. These give an estimate of Q/B for megabenthos of 1.2 y⁻¹. Unassimilated consumption for megabenthos is assumed to be 0.3 as Jarre-Teichmann et al. (1997).

2.5 Diet

Chiantore et al. (1998) using sedimentation estimates from Albertelli et al. (1998), suggest that only about 17% of the annual food requirements of *A. colbecki* in this Terra Nova Bay population is provided by sedimentation. Ice algae, macroalgal detritus and lateral advection of organic matter from the open Ross Sea are likely to be important food sources for *A. colbecki* (Hielmayer et al. 2003). Brey et al. (1995) estimated consumption by *S. neumayeri* along the coast of the Ross Sea at three stations: (1) Cape Evans Q=10.9 gC m⁻² y⁻¹; (2) McMurdo Station Q=4.0 gC m⁻² y⁻¹; (3) New Harbour Q=3.0 gC m⁻² y⁻¹. This corresponds to 21, 12 and 30%, respectively, of the estimated sedimentation and benthic macroalgal production at these locations. The remainder may come from locally produced material (phytoplankton, zooplankton) filtered from the water column. The infaunal bivalve *L. elliptica* is described as a suspension feeder, feeding mostly on material of planktonic origin (including settling ice algae), and on resuspended material (Ahn 1993; Norkko et al. unpublished).

There is also likely to be some intra-group predation within the mega. For example, known predators of juveniles and adults of the Antarctic scallop include ophiuroids, sea stars, nemertean, and gastropod, whereas the sea anemone *Isotella antarctica* is known to prey on *Sterechinus* (Dayton et al. 1970, Amsler et al. 1999). Known predators of the bivalve *L. elliptica* in Terra Nova Bay and McMurdo Sound regions include the ophiuroids *Ophiosparte gigas* and *Ophionotus victoriae*, the sea star *Diplasterias brucei*, and the gastropod *Trophon longstaffi*.

Barry et al. (2003, see Table 10) give data on megafaunal abundance by feeding type: deposit-feeders, filter-feeders and predators. If we assume that consumption (gC y⁻¹) is proportional to abundance (number of individuals per m²) then we can estimate that consumption by megabenthic fauna in the Ross Sea is dominated by filter feeders (87%), with a smaller proportion of deposit feeders (11%) and 2% predators. Based on combined data from CAML-IPY and ROAVERRS, the ratio by weight is 65:30:5 for filter:deposit:predators. It is not known what proportion of the diet of detritus or filter feeders is from bacteria compared to actual detritus – here we assume a nominal 75-25 split (Moodley et al. 2002; Josefson et al. 2002; see also section on “Bacteria & Detritus”). Suspended detritus being consumed by filter feeders is assumed to be entirely benthic detritus rather than water-column detritus in the sense that “water column detritus” is that produced and consumed well away from the benthos. As a first estimate for modelling, we propose using a megabenthos trophic compartment diet of: 23% benthic detritus, 70% benthic bacteria, 3% meiobenthos; 3% macrobenthos; 1% carcasses.

2.6 Ecological Efficiency

Ecological efficiency (i.e. non-predation-related mortality) for Antarctic megabenthos is not known. Hielmayer et al. (2003) estimated *A. colbecki* production in Terra Nova Bay at 609 kJ m⁻²

y^{-1} , and consider that about $433 \text{ kJ m}^{-2} \text{ y}^{-1}$ is transferred to its predators, implying an ecological efficiency of 0.71. This is substantially higher than used by Jarre-Teichmann et al. (1998) for benthic molluscs of 0.27. Here we propose using an ecological efficiency of 0.7 as an initial estimate.

3 Macrobenthos

3.1 Individual weights of macrobenthos

Information on the individual weights of various species of benthic macrofauna is required to convert densities of individuals to biomass. These characteristic weights vary by location and organism but here we estimate a typical value from many weights. From Gambi et al. (1994) we estimate a mean weight of 53.0 mgWW/ind. Gerdes et al. (1992) measured an individual macrobenthic weight in the Weddell Sea of 58.5 gWW/ind. Data from ROAVERRS (Barry et al. 2003; Barry unpublished data) on numbers and wet weight of macrobenthos (75 stations) gives an average individual weight of 29.8 mgWW/ind. Assuming 0.043 gC/gWW (Brey 2005), the ROAVERRS data gives an average weight of 1.3 mgC/ind for macrobenthos, which we use here.

3.2 Biomass

Benthic macrofauna are defined here as organisms between 0.2 and 20 mm in size. A strict size-based demarcation between mega and macro benthic fauna range is not always possible, for example, when observation is remote (e.g., video or camera observation). General information on the benthic macrofauna of the Ross Sea is given in: Bullivant 1967a,b; Dearborn 1967; Gambi et al. 1994, 1997; Cattaneo-Vietti et al. 1999, 2000; Chiantore et al. 1998, 2000). The majority of studies of macrofauna in the Ross Sea have been conducted in the McMurdo Sound and Terra Nova Bay regions e.g., Cattaneo-Vietti et al. 2000a,b; Rosso & Sanfilippo 2000; Gambi et al. 2000; Cantone et al. 2000; Norkko et al. 2004. Relatively few studies have investigated the benthic macrofauna of the deeper waters of the Ross Sea, two exceptions being Gambi & Bussotti (1999) who visited three locations in the non-coastal Ross Sea in 1994–1995, and the ROAVERRS series of voyages (Barry et al. 2003). More recently, the Research Vessel *Italica* visited coastal areas in vicinity of Cape Hallett, Cape Adare, Coulman Island and Cape Russell in 2004, and carried out transect-based sampling of stations 100–500 m deep (Cummings et al. 2005). Also in 2004, the Research Vessel *Tangaroa* visited areas from Cape Adare to Cape Hallett, and sampled five across-shelf transects, targeting three depth strata (50–250, 250–500 and 500–750 m; Mitchell & Clark 2004). The IPY-CAMLR voyage also sampled benthic macrofauna (Hanchet et al. 2008). Samples from these latter voyages are still being processed.

Here, we use macrobenthic data for the coastal zone and deeper water separately. In shallow areas off Terra Nova Bay, macrobenthic communities were found to include similar animal taxa, with polychaetes, molluscs and peracarid crustaceans especially abundant (Gambi et al. 1994). Relative and absolute biomass of various macrofauna are highly variable depending on sediment type and other local conditions. This variability means that estimates of macrofaunal biomass will tend to have a large uncertainty in the absence of large-area surveys of macrofaunal biomass. Gambi et al. (1994) summarise comparisons between numbers and biomass of macrobenthos from a number of studies in various Antarctic and subantarctic areas (see Table IV in Gambi et al. 1994). Biomass of macrofauna in Terra Nova Bay was reported as being c. 3.7 gDW m^{-2} for waters shallower than 50 m. We assume a ratio of 0.38 gC/gAFDW and 0.9 gAFDW/gDW for macrobenthos (Brey 2005), giving a macrofaunal biomass density of 1.2 gC m^{-2} for these coastal

areas. This value is taken to be applicable to waters less than 50 m deep which make up c. 0.5% of the study area.

For all waters deeper than 50 m we use macrobenthic data from the ROAVERRS research cruises to the Ross Sea (Barry et al. 2003), which took 75 benthic core samples which were analysed for macrobenthic numbers and biomass (Figure 2). These data have kindly been made available to this study by Dr Jim Barry.

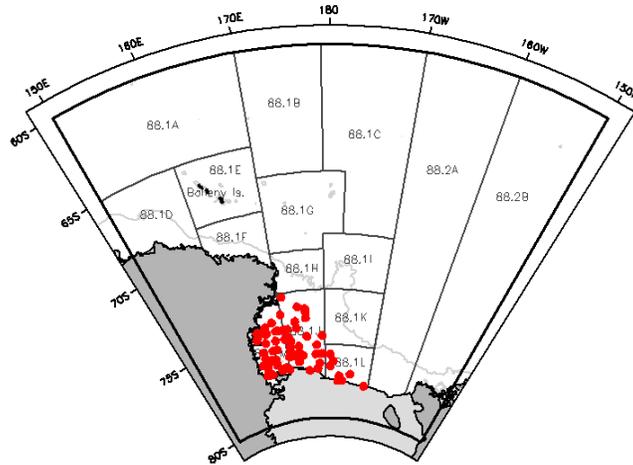


Figure 2. ROAVERRS core samples for macrobenthos (N=75).

The log-mean macrofauna biomass from ROAVERRS is 11.4 gWW/m², equivalent to 0.49 gC m⁻² (Brey et al. 2005). Work from subantarctic waters (Nodder unpublished data) suggests that macrofaunal numbers decrease with depth proportional to approximately $\exp(-0.0012z)$ where z is the depth in metres. Applying this relationship to the Ross Sea to account for the depth distribution of macrobenthos biomass gives an average density of 0.42 gCm⁻² for non-coastal waters over the study area. Combining the shallow and deep water stations gives an estimate of total benthic macrofaunal biomass for the Ross Sea of 0.43 gC m⁻².

For comparison in terms of numbers, data from ROAVERRS suggests a log-mean macrobenthic abundance of 462 ind/m², a log-mean being used to reduce the biasing effect of a few, high biomass stations. Dayton & Oliver (1977) measured macrofauna abundance of 1960 ind m⁻² at a single station of depth 500 m in the Ross Sea. Gambi & Bussotti (1999) measured polychaete abundances of 430–1047 ind m⁻². These abundances are at the lower end of abundances recorded in the Scotia Arc and Antarctic Peninsula (Gambi & Bussotti 1999). For comparison in terms of biomass, macrobenthos based on data from the South Atlantic sector of the Antarctic around 53–56°S (Gerdes et al. 1992; Gerdes & Montiel 1999) is in the range of 47–704 gWW m⁻², approximately equivalent to 2–24 gC m⁻² (Rowe 1983), so considerably higher than estimated here. Mean macrofaunal biomass for the Chatham Rise was estimated at 0.21 gC m⁻² (based on data given by: Probert & McKnight 1993; Probert et al. 1996; Nodder et al. 2003).

3.3 Production

A P/B ratio for benthic macrofauna can be estimated from the relationship given by Brey & Gerdes (1998) showing a general increase in annual community P/B with water temperature. Bottom water temperature in McMurdo Sound is consistently at -1.92°C (always less than 0°C) but further north in Terra Nova Bay it can reach 2°C. The regression equation of Brey & Gerdes

gives $P/B=0.36 \text{ y}^{-1}$ and this value is used here. In temperate waters, $P/B=1.83 \text{ y}^{-1}$ was given by Cartes & Maynou (1998) for polychaetes, whereas Feller & Warwick (1988) suggest that a range of $0.7\text{--}4 \text{ y}^{-1}$ is possible. For subantarctic waters, Probert (1986) suggests a P/B ratio of 1.0 y^{-1} is reasonable, but that 0.4 y^{-1} is possible. P/B for polychaetes in the Weddell Sea was taken as 0.85 y^{-1} (Jarre-Teichmann et al. 1998).

3.4 Consumption

Consumption by macrobenthos is usually estimated using the gross efficiency (production/consumption ratio), and we will follow this approach here. Bradford-Grieve et al. (2003) used a ratio of $P/Q=0.35$ for subantarctic waters as for mesozooplankton, but this seems too high. We suggest that a value of $P/Q=0.25$ is reasonable for the Ross Sea macrobenthos. Unassimilated consumption for macrobenthos is assumed to be 0.2 as Bradford-Grieve et al. (2003).

3.5 Diet

The diets of Antarctic polychaetes (which are assumed to dominate the Ross Sea macrobenthos in terms of biomass) are largely unknown. In the Weddell Sea, Jarre-Teichmann et al. (1998) state that about 3% of polychaetes are polynoid and prey on other polychaetes, amphipods and detritus, but the bulk are sedentary species and may be assumed to feed mainly on benthic bacteria and detritus directly. In the present study we assume that benthic bacteria predominate over direct consumption of benthic detritus (Moodley et al. 2002; Josefson et al. 2002). As a first estimate for modelling, we propose using a diet of the macrobenthos trophic compartment of: 5% other macrobenthos; 21% benthic detritus; 64% benthic bacteria; 10% meiobenthos.

4 Meiobenthos

Meiofauna (benthic infauna $63 \mu\text{m}\text{--}0.5 \text{ mm}$) in Antarctica are generally not well studied (Arntz et al. 1994; Soltwedel 2000). An exception is the extensive research on foraminifera in New Harbour, McMurdo Sound, Ross Sea (reviewed by Gooday et al. 1996). Foraminifera are a large component of the benthic community in this area ($3600\text{--}12,200 \text{ m}^{-2}$; Gooday et al. 1996), and are likely to be important in the cycling and decomposition of nutrients and seafloor organic matter and the consumption of bacteria (e.g., Bernhard & Bowser 1992; Pawlowski et al. 2005). Off King George Island (Antarctic Peninsula), de Skowronski & Corbisier (2002) found the meiobenthos to be dominated by nematodes (>60%), copepods, nauplii and polychaetes, with mean densities of about $3.5\text{--}4.0 \times 10^6 \text{ ind m}^{-2}$. These studies found large variations in meiofaunal abundance in space, but reasons for the differences were not clear. Meiofaunal densities for the Ross Sea have been measured as $0.2\text{--}1.2 \times 10^6 \text{ ind m}^{-2}$ (deep sea: Fabiano & Danovaro 1999) and $4.6\text{--}5.7 \times 10^6 \text{ ind m}^{-2}$ (coastal: Danovaro et al. 1999). To convert meiofaunal density in terms of individuals to biomass requires information on the characteristic weights of meiofauna individuals. Representative individual weights are likely to vary with water depth, region, environmental variables such as ice cover, primary production, detrital flux rate, and possibly season. As a holding value, we assume a “typical” meiofaunal organism weight for the whole Ross Sea of $4.4 \times 10^{-5} \text{ mgAFDW ind}^{-1}$ (Soltwedel 2000). This assumption leads to estimates of biomass density between 0.01 and $0.25 \text{ gAFDW m}^{-2}$. Soltwedel (2000: figure 4) summarises available meiofaunal biomass measurements for the Antarctic region. A relationship between meiofaunal biomass density and depth is obtained, which predicts densities of between $0.06\text{--}0.16 \text{ gAFDW m}^{-2}$ for the Ross Sea study area (depths $0\text{--}3000 \text{ m}$). The average value for the Ross Sea, obtained using this relationship and the bathymetry of the study region is $0.12 \text{ gAFDW m}^{-2}$. We

assume that carbon makes up about 38% of AFDW (Brey 2005), giving an estimate of meiofaunal biomass for the Ross Sea of 0.044 gC m⁻². This value falls within the meiofaunal biomass density envelope reported for a variety of temperate and tropical continental margins around the world (e.g., Figure 2 in Soltwedel 2000; Feller & Warwick 1988).

Annual P/B ratios of meiofauna vary considerably, between about 2.5–15 y⁻¹, but 10 y⁻¹ is often taken as an average value for subantarctic waters (Feller & Warwick, 1988; Probert 1986). Nevertheless, production may be lower in the Ross Sea. Annual P/Q for benthic meiofauna was given as 0.31 y⁻¹ (Pomeroy 1979), whereas Probert (1986) gives a P/Q of between 0.1–0.3 y⁻¹. A value of P/Q=0.3 y⁻¹ will be assumed initially for the Ross Sea. The prime source of food for the meiobenthos is assumed to be benthic bacteria (71%), direct consumption of benthic detritus (24%) with some cannibalistic contribution from other meiobenthos (5%). Unassimilated consumption for meiobenthos is assumed to be 0.2.

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