

## Zooplankton: Trophic modelling of the Ross Sea

M.H. Pinkerton, J. Bradford-Grieve

National Institute of Water and Atmospheric Research Ltd (NIWA), Private Bag 14901, Wellington, New Zealand.

Email: [m.pinkerton@niwa.co.nz](mailto:m.pinkerton@niwa.co.nz); Tel.: +64 4 386 0369 ; Fax: +64 4 386 2153

### 1 Introduction

In this section we deal with:

- Ice (crystal) krill (*Euphausia crystallorophias*)
- Antarctic krill (*Euphausia superba*)
- Macrozooplankton other than euphausiids (>20 mm)
- Mesozooplankton (0.2–20 mm)
- Heterotrophic microplankton (20–200 µm)
- Heterotrophic flagellates (2–20 µm)

### 2 *Euphausia crystallorophias*

#### 2.1 Distribution and development

*Euphausia crystallorophias* is found preferentially in the shallower parts of the western Ross Sea (Makarov et al. 1991; Brinton et al. 2000; Azzali & Kalinowski, 2000; Sala et al. 2002; Azzali et al. 2006), and in the eastern parts (Ackley et al. 2003). Distribution information (Azzali et al. 2006; Ackley et al. 2003) suggests that the seaward distribution of this species ends at the shelf break. In the west, north of 74°S, this species was found only in small numbers and only in shallow waters in the neritic zone.

*E. crystallorophias* appears to feed vigorously during summer, with high growth rates. During winter (from April at least until August) growth slows (Kirkwood 1996; Nicol et al. 2004), presumably because consumption reduces, as food availability decreases. Littlepage (1964) records the lipid content of *E. crystallorophias* from May 1961 – January 1962. Lipids made up to 36% of body dry weight during late summer and early winter, but decrease at a constant rate throughout the winter to a low of 9% just prior to the major plankton bloom between December–February. *E. crystallorophias* appears to spawn in November to early December, and there seems to be no build up of lipids prior to reproduction. It appears therefore, that stored lipids serve to sustain metabolism during the winter period when food availability is low. The period of reproduction of *E. crystallorophias* seems to be timed to ensure that diatoms are available to the early larval stages. The development of Ross Sea polynya may be important in the early start to spawning of *E. crystallorophias* compared with *E. superba* (Makarov et al. 1991). *E. crystallorophias* take about 2 years to reach adulthood, completing larval development under the sea ice during the Antarctic winter (Kirkwood, 1996; see also Pakhomov & Perissinotto, 1997). The mean time for the eggs of *E. crystallorophias* eggs to develop to furcilia stage VI was 236 days – this is twice the time that *E. superba* takes to develop. The reason for this may be the low temperatures or the low levels of food available. According to Nicol et al. (2004) low food abundance during winter leads to a decreased growth rate, significantly increased intermoult period, and a switch to carnivorous/detrital diet. This species is more dependent on stored lipids to overwinter than *E. superba* (Ju & Harvey 2004).

## 2.2 Biomass

Our estimates of *E. crystallorophias* biomass in the Ross Sea are taken from the study of Sala et al. (2002) in January and February 2000. Sala et al. (2002) show that *E. crystallorophias* is distributed on the continental shelf of the Ross Sea and close to the Ross Ice Shelf in numbers that were twice the density of *E. superba* although the latter species is much larger. Samples were taken using a Hamburg Plankton Net with a mouth opening of 5 m<sup>2</sup> using double oblique deployment towed at 3 knots approximately. Sala et al. (2002) reports wet-weight biomass densities (gww/1000 m<sup>3</sup>) of *E. crystallorophias* in column 11 of Table 1 in Sala et al. (2002). Wet-weight densities of *E. crystallorophias* up to between 0.02–474 gWW/1000m<sup>3</sup> were found, with an average value for *E. crystallorophias* and *E. superba* combined of 294 gWW/1000m<sup>3</sup>.

We estimated annual average carbon biomass for *E. crystallorophias* for the Ross Sea study region from the values given by Sala et al. (2002) as follows. First, we converted measured densities of wet-weight of *E. crystallorophias* to concentrations of carbon. Two methods of converting to carbon were applied. First, we used the relationship of Weibe (1988):  $\log_{10}(W) = -1.537 + 0.852 \log_{10}(C)$  where  $W$  = wet weight (g m<sup>-3</sup>), and  $C$  = carbon concentration (mgC m<sup>-3</sup>). This leads to a carbon:WW ratio of about 3–6%. Second, we took body carbon content of *E. crystallorophias* to be 40.9–45% of total dry weight (Ikeda & Kirkwood, 1989). Dry weight is often assumed to be c. 13% of wet weight (Bradford-Grieve et al. 2003). Weibe (1988) give a relationship for converting wet weight to dry weight of zooplankton:  $\log_{10}(D) = -2.002 + 0.950 \log_{10}(W)$  where  $W$  = wet weight (g m<sup>-3</sup>), and  $D$  = dry weight (mgC m<sup>-3</sup>). This relationship suggests dry weight is c. 12% of wet weight for the *E. crystallorophias* biomass concentrations measured in the Ross Sea. These suggest a carbon:WW ratio of about 5.5%. For typical concentrations of *E. crystallorophias* given by Sala et al. (2002), the two methods differed by ~40%, with the first method (Weibe 1988) giving lower values than the second (Ikeda & Kirkwood 1989). We used an average of the two methods, with an average value of 3.8%.

Next, we used the carbon concentrations to estimate integrated water column carbon biomass. We assumed that the *E. crystallorophias* density tabulated was an average over the maximum fishing depth for the trawl. The depths of the oblique tows were from the surface to between 17–299 m. This means that the measurements made were often not sampling the whole population as O'Brien (1987) shows that diel vertical migrations of *E. crystallorophias* occur between the surface and at least 100 m off Enderby Land and most of the population was below 40 m between 0600–2400 h. The maximum depth of *E. crystallorophias* in the Ross Sea is not known, though Nordhausen (1994) shows *E. crystallorophias* deeper than 200 m in the Gerlache Strait in winter.

The time of day when the tows were carried out is not given by Sala et al. (2002). Here, we assume: (1) that *E. crystallorophias* density is constant to 100 m or the maximum fishing depth, whichever is deeper; (2) that there are negligible *E. crystallorophias* below 200 m or at the seabed, whichever is shallower; (3) that between these depths, *E. crystallorophias* density decreases linearly with depth. These considerations suggest that the tows reported by Sala et al. (2002) are measuring 47% of the *E. crystallorophias* in the water column on average.

Data from Italian surveys of krill presented in Sala et al. (2002) and later summarised in Azzali et al. (2006) did not extend east of 175°30'W so that concentrations of *E. crystallorophias* over the Ross Sea shelf to the east of the area were not measured. To calculate an average biomass of *Euphausia crystallorophias* over the whole study area we divided the stations sampled by Sala et al. (2002) into three groups depending on depth: stations shallower than 500 m, between 500 and

1000 m, and deeper than 1000 m. We make the assumption that the stations visited by Sala et al. (2002) have *E. crystallorophias* densities that are representative of waters of similar depths in the whole of the study region because Sala et al. (2002) visited stations over a large area (70°–77°S, 164°E–176°W) in an approximately regular grid. Makarov et al. (1991) surveyed larval abundance of *E. crystallorophias* and *E. superba* in the Ross Sea in 1982, and values east of 176° appear comparable with values further west at similar depths. We note that measurements of *E. crystallorophias* biomass in these eastern waters would improve confidence in our estimates of average *E. crystallorophias* biomass for the study area. We calculated an estimate of the mean *E. crystallorophias* biomass within each of the three depth groups. Sala et al. (2002) reports that the spatial distribution of *E. crystallorophias* biomass was frequently patchy, and samples taken from these assemblages were characterised by values of biomass that are typically small, with a few very large exceptions. As the means of such data may be oversensitive to extreme values, McConnaughty & Conquest (1992) suggested that biomass of aggregated stocks should be calculated using the geometric mean. The estimator was calculated by exponentiating the mean of the  $\ln(x+1)$  – transformed data and subtracting one. This estimator may provide more effective assessment of the overall density of overdispersed stocks. Zero catches were included in the calculation to allow for the fact that *E. crystallorophias* and *E. superba* populations are almost entirely separate in space in the Ross Sea (Sala et al. 2002). The data show that *E. crystallorophias* is most abundant on average in water between 500 and 1000 m deep (average biomass of 0.97 gWW m<sup>-2</sup>). *E. crystallorophias* was reasonably abundant in the shallow water. The study area comprises 29% water shallower than 500 m, 41% of water depths between 500 and 1000 m, and 30% water deeper than 1000 m. The average *E. crystallorophias* biomass densities for the three depth groups were combined in these proportions. Our estimate of *E. crystallorophias* average biomass density for the whole study region is 0.70 gWW m<sup>-2</sup> consistent with Azzali et al. (2006) who worked up the same data in a different way. This result implies a total wet weight of 440 000 t of *E. crystallorophias* in the study region during the summer.

Measurements of *E. crystallorophias* density by Sala et al. (2002) were made in the summer (Jan/Feb 2000), and ideally we would take into account the seasonal variation in *E. crystallorophias* abundance to estimate an annual average density. *E. crystallorophias* lives to the age of 5 years or more, but a representative annual cycle of *E. crystallorophias* abundance in the Ross Sea is not known. Azzali et al. (2006) present data from Italian surveys of krill in the Ross Sea in November, December and January, but because these are in different years, it is not possible to estimate a seasonal cycle from the data. *E. crystallorophias* appears to spawn in November to early December and completes its larval development under the sea ice during the Antarctic winter (Kirkwood 1996; see also Pakhomov & Perissinotto 1997). Mortality is likely to be higher for larval *E. crystallorophias*, and decrease with age. Without further information, it is not possible to estimate seasonal variations in *E. crystallorophias* biomass in the Ross Sea, and we assume that it is approximately constant through the year.

Next, we consider whether the measurements by Sala et al. (2002) in the summer 2000 are typical of the long-term average krill abundance in the study region, as krill abundance is known to vary considerably from year to year. Pakhomov & Perissinotto (1997) show abundances of larval *E. crystallorophias* varying by several orders of magnitude between years in the Cooperation Sea. Atkinson et al. (2004) reviewed time series of krill abundance through the Southern Ocean, and showed interannual variability of about an order of magnitude (factor of 100 was common). Atkinson et al. (2004) also showed a >50% decline in the total krill abundance through the Southern Ocean in the period 1926–2003. Unfortunately, there are few data on the abundance of *E. crystallorophias* in the Ross Sea, and Atkinson et al. (2004) was unable to assess trends in krill abundance here. Problems with assessing interannual variations in krill abundance include: (1) different researchers, equipment and methodologies of carrying out abundance assessments in

different years; (2) differences in the timing of the work; (3) variations in changes in krill abundance with season in different years; (4) inherent patchiness of krill abundance makes abundance estimation difficult. Lascara et al. (1999) report 5-fold variations in krill abundance off the Antarctic Peninsula in mid-January during the period 1990 and 1993, measured by a consistent method. Our ability to detect long-term changes, or assess interannual variations in krill abundance in the Ross Sea is limited by reliable, regular and consistent sampling. Azzali et al. (2006) present data from Italian surveys of krill in the Ross Sea in 1994, 1997 and 2000. These results suggest that the average biomass of *E. crystallorophias* from the surveys in 1997 and 2000 is a factor 1.5 higher than the value measured in 2000 and given by Sala et al. (2002). We hence increase our estimate of biomass by this factor to 682 000 tWW.

Data on the abundance of *E. crystallorophias* will become available from analysis of acoustic data from the 2008 New Zealand IPY-CAML survey of the Ross Sea (O'Driscoll et al. 2009). Biomass estimates were made from multifrequency acoustic data (12, 38, 70 and 120 kHz), mark-identification from midwater and demersal trawls, and computed tomography scans of frozen specimens for target strength (O'Driscoll et al. 2009). A preliminary estimate of the biomass of *E. crystallorophias* in the study area in Feb/Mar 2009 was hence 562 000 tWW, which was noted as being similar to a 2005 Japanese acoustic-based estimate of *E. crystallorophias* in the study area of 600 000 t (O'Driscoll et al. 2009). We take our best estimate of *E. crystallorophias* biomass in the study area as the adjusted Sala et al. (2002) values (682 000 t) equivalent to 0.041 gC m<sup>-2</sup>.

Finally, Sala et al. (2002) suggests 90% confidence intervals of approximate factors of 0.39 (low limit) and 2.43 (high limit) from *E. crystallorophias* densities. We assume that our method of using the values given by Sala et al. (2002) to estimate water column averages, spatial averages for the study region, carbon from wet weight, and annual averages have added an extra error of a factor of 0.5 (low) and 2 (high). This hence gives possible uncertainties on our estimate from factors of 0.20 to 4.8.

### **2.3 Food and condition**

Gut content analysis shows that *E. crystallorophias* are omnivores (O'Brien, 1987; Pakhomov et al. 1998). In December, micro and mesozooplankton were the dominant components of the diet of *E. crystallorophias*, comprising 75% of identifiable items (Pakhomov et al. 1998). But in January heterotrophic component of diet decreased sharply and phytoplankton cells accounted for 68% of total number of food particles. They deduce that this species has a predominantly carnivorous habit during spring but at the onset of the spring phytoplankton bloom this species switches to a truly omnivorous habit. Some consumption of other macrozooplankton by *E. crystallorophias* is also likely. We assume, initially, that the prey of *E. crystallorophias* over the course of a year in the Ross Sea is: 35% heterotrophic microplankton; 21% heterotrophic flagellates; 30% phytoplankton; 5% epontic algae; 6% ice protozoa; 6% ice metazoan (mainly amphipods and copepods in the ice habitat through the winter).

### **2.4 Production, P/B**

In the Southern Ocean euphausiids typically have P/B values between 1.24–4.75 y<sup>-1</sup> (Cartes & Maynou 1998). The appropriate P/B value for *E. crystallorophias* depends on the population structure. For adult populations, P/B values are of the order 0.8–1.2 y<sup>-1</sup>, depending somewhat on whether exuviae (shed cuticles) are included in the definition of “production”. In trophic balance studies such as this, “production” is all organic material that is available for consumption by predators, or which flows to detritus. This would include exuviae, so we would expect P/B values

of 1.0–1.2  $y^{-1}$  for adults. If larvae are included, the average P/B values for the population will be higher as these animals grow faster than the adults. The growth model for *E. crystallophias* given by Pakhomov & Perissinotto (1996) gives P/B values ( $y^{-1}$ ) of approximately 6.8 (larval), 2.3 (juveniles), 0.9 (sub-adults) and 0.3 (adults). Sala et al. (2002) reports that *E. crystallophias* in the Ross Sea was composed of 35.9% juveniles, 31.5% sub-adults, and 32.4% adults. The larval component was not measured by Sala et al. (2002), and is probably most appropriately included in the zooplankton compartment rather than the krill trophic component.

We estimate that the average P/B values of the population will be approximately 1.8  $y^{-1}$ , with a possible range of 0.9–3.6  $y^{-1}$ . Improved insight into production by krill in the Ross Sea may be obtained by the development of an age-structured population model. Much of the information necessary to develop such a model is available: growth rates in ice krill have been measured (Pakhomov & Perissinotto 1996); relationships between weight and length is given by various studies (Siegel 1987; Rakusa & Stepnik 1980; Pakhomov et al. 1998; Zhong & Wang 1993; Pakhomov & Perissinotto 1996, 1997).

## **2.5 Consumption, Q/B**

Consumption rates by *E. crystallophias* are given by Pakhomov & Perissinotto (1997), and Pakhomov et al. (1998) in terms of  $\mu\text{gC}$  per individual per day, based on gut pigment measurements, evacuation rates and an assumed carbon-chlorophyll ratio. We converted these to annual Q/B values using information on the average weight of the *E. crystallophias* stages from Pakhomov & Perissinotto (1996), and Pakhomov et al. (1998). Values from Pakhomov & Perissinotto (1997) in the Cooperation Sea give Q/B of 27  $y^{-1}$  (larvae), 5–13  $y^{-1}$  (juveniles) and 0.8–2.9  $y^{-1}$  (sub-adults and adults). Values from Pakhomov et al. (1998) suggest Q/B for adults between 3.9–4.7  $y^{-1}$ . Weighting these values in proportion to the relative abundances of the components as given by Sala et al. (2002) for the Ross Sea, gives a best estimate of Q/B of 13.2  $y^{-1}$ . We suggest an acceptable range of 6.6–26.4  $y^{-1}$ .

## **2.6 Unassimilated consumption**

Assimilation efficiency for *E. crystallophias* is assumed to be similar to *E. superba*, ranging from 70–92% (Meyer et al. 2003), giving  $U$  as c. 0.2.

## **2.7 Ecotrophic efficiency**

Ecotrophic efficiency ( $E$ ) for *E. crystallophias* in the Ross Sea is not known, and is assumed to be 0.95 on the basis that the vast majority of the annual production of this species is likely to be consumed by direct predation.

# **3 Euphausia superba**

## **3.1 Development and Distribution**

*Euphausia superba* females probably spawn between December and February and possibly over most of the summer months (Baker 1959, in: Everson, 1984) over a wide range of depths (see also Miller & Hampton 1989; Atkinson et al. 2008; Kawaguchi et al. 2007). Timing of breeding is somewhat variable from year to year. This long breeding season maybe because of the wide

latitudinal range over which the species is found. The eggs then sink and hatch at depth, probably to about 850–1000 m or even to 2000 m (Marr 1962). After hatching, larvae develop as they ascend the water column and arrive near the surface at the first calyptopis stage (the developmental ascent takes about 2–4 weeks) to feed about 30 days after spawning. Total development from egg to final larval stage takes about 130 days. Voronina (1995) found peak concentrations of larvae were located at 250–300 m. Adults appear to be found at any depth between the surface and more than 1000 m (Marin et al. 1991), though high concentrations are often found close to the surface at 15–130 m depth in Gerlache Strait (Nordhausen, 1994; Zhou et al. 1994). Daly & Macaulay (1991) believe that the seasonal behaviour and distribution of *E. superba* is designed by the need to acquire food and avoid predators. Seasonal sea ice plays an integral role in the ecology of krill. Ice-edge blooms are an important and predictable food supply, particularly for reproducing adults and first-feeding larvae. Ice floes provide protection for larvae and juveniles, and sea ice biota, a widespread food source, are important to the survival of larvae during winter (Brierley et al. 2002; Ross et al. 2004). The shortest possible life cycle of *E. superba* (egg to egg) is c. 2 years, assuming that growth periods are only for 4–6 months of the year (Ikeda, 1985). *Euphausia superba*'s life span is probably about 4–7.5 years; this prolonged life is presumed to provide for improved fecundity of female krill.

In the Ross Sea *E. superba* (Antarctic krill) were encountered above the continental slope as shown in Figure 17.1 (Makarov et al. 1992; Azzali & Kalinowski 2000; Sala et al. 2002; Azzali et al. 2006) and north of 74°S in the eastern Ross Sea (Ackley et al. 2003). Large quantities of *Euphausia superba* have been recorded near the Balleny Islands and in the northern parts of the Ross Sea (Timonin 1987; Voronina & Maslennikov 1993; Azzali & Kalinowski 2000). Penguin diet samples recently obtained by Landcare Research at Hallett Station, near the shelf break in the Ross Sea, suggests that major densities of *E. superba* occur in the study region (Ainley pers. com.). Low concentrations of *E. superba* noted by Marr (1962) may be attributed to inadequate sampling (Ainley pers. com.). Makarov et al. (1991) shows high larval densities close to 2000 m contour between 180° and 165°W. In the vicinity of the Balleny Islands, these large densities are possibly associated with one or more of the water types (the Antarctic Circumpolar Current, Offshore Antarctic Current, and the mixed waters from both in the Ross Gyre) present in the area. Voronina (1995) notes that on a transect along 67°S *E. superba* developmental stages were only found north of the western Ross Sea near the Balleny Islands. This suggests that successful breeding and survival of larvae had occurred only in this region. The style of life history of *E. superba*, in which eggs sink to greater than 850 m, is probably the reason why this species does not breed in the inner (shallower) parts of the Ross Sea. The penetration of this species into the Ross Sea may be limited by the southward transport of individuals by Antarctic Surface Waters. Veronina & Maslennikov (1993) interpreted the distribution of *E. superba* to have some relationship to the hydrography of the region, but the description of this relationship is not very clear in their paper, and the quoted supporting papers are not easy to obtain, and are in Russian.

### 3.2 Biomass

We estimated biomass of *Euphausia superba* for the Ross Sea in a similar way as for *E. crystallophias*, described above, based on values given by Sala et al. (2002), Figure 17.1. Wet weight densities of *E. superba* varied between 0.04 and 1500 gww/1000 m<sup>3</sup>. First, we converted measured densities of wet-weight of *E. superba* to concentrations of carbon using an average of the methods of Weibe (1988) and Ikeda & Kirkwood (1989). The conversion values are very similar to data on elemental composition of *E. superba* near Antarctic Peninsula in July–August given by Huntley et al. (1994). These data include dry weight vs length ( $\log DW = -3.250 + 3.270 \log L$ ), and carbon vs dry weight ( $\log DW = 0.508 + 0.917 \log C$ ), where DW, and C are in mg

and L is in mm. The relation between dry weight and body length in winter was indistinguishable from that in summer. The same is true for the relationships between DW and body C. These values imply that carbon makes up c. 37% of dry weight, and c. 3.8% of wet weight. As before, data from Italian surveys of krill presented in Sala et al. (2002) and later summarised in Azzali et al. (2006) did not extend east of 175°30'W so that concentrations of *E. superba* over the eastern Ross Sea shelf slope were not measured.

The population, as captured by Sala et al. (2002) using a 5 m<sup>2</sup> net with mesh of 1000 µm (1 mm), was devoid of larval stages, had scarce juveniles and was composed primary of larger stage adult stages. The information that exists on the possible vertical distribution of *E. superba* (e.g., Marin et al. 1991; Nordhausen, 1994) means that the data reported by Sala et al. (2002) may have sampled only a small part of the potential population because most samples were taken above 100 m. We assume that *E. superba* has a deeper depth distribution than *E. crystallophias*, and assume that: (1) that *E. superba* biomass density is constant to 100 m or the maximum fishing depth, whichever is deeper; (2) that there are negligible *E. superba* below 200 m or at the sea-bed, whichever is shallower; (3) that between these depths, *E. superba* density decreases linearly with depth. These considerations suggest that the tows reported by Sala et al. (2002) are measuring 37% of the *E. superba* in the water column on average. We cannot test these assumptions until acoustic results are available from the Italians. These assumptions imply water column concentrations of *E. superba* up to 264 gWW m<sup>-2</sup> were present in the Ross Sea.

To calculate an average density of *Euphausia superba* over the whole study area we used the same three depth groupings of the stations sampled by Sala et al. (2002) as before: stations shallower than 500 m, between 500 – 1000 m, and deeper than 1000 m. Makarov et al. (1991) shows that *E. superba* larval densities in the Ross Sea east of 176°W are generally comparable with values to the west at similar depths. We hence make the assumption that the stations visited by Sala et al. (2002), in the region 70°–77°S, 164°E–176°W, have *E. superba* densities that are representative of waters of similar depths in the whole of the study region. We calculated an estimate of the mean *E. superba* biomass within each of the three depth groups using the same estimator used for *E. crystallophias*, as both krill species are overdispersed in point net measurements. Zero catches were included. As expected, most *E. superba* biomass occurs in waters deeper than 1000 m. The average *E. superba* biomass densities for the three depth groups were combined as explained previously. Our estimate of *E. superba* average biomass is 1.3 gWW m<sup>-2</sup>.

As before, we recognise the need to consider seasonal variations in the distribution or abundance of *E. superba* as this may change the average biomass in the study region over a year. Lascara et al. (1999) presented a dataset of seasonal *E. superba* distribution from a series of four research cruises west of the Antarctic Peninsula, and summarised previous seasonal measurements in this region. The measurements may be used to estimate the seasonal variation in krill abundance off the Antarctic Peninsula. However, measurements reported by Lascara et al. (1999) were made in different Antarctic areas, in different years, and often by different researchers, and are hence subject to considerable uncertainty. *E. superba* live to the age of five years or more, so that large variations in adult biomass through the year may be unlikely. Azzali et al. (2006) reports results from four voyages in November, December and January, but because these are from different years, the data do not give useful information on seasonal variations in biomass of *E. superba* in the Ross Sea. Here, we take the survey of Sala et al. (2002) in January to be representative of the annual average biomass of *E. superba*.

Variations in the abundance of *E. superba*, between years, is related to sea ice cover in some regions (Brierley & Watkins 2000; Priddle et al. 1988). Azzali et al. (2006) show data from four

Italian surveys of zooplankton in the Ross Sea in 1994 (two voyages), 1997 and 2000. The average biomass from the recent (1997 and 2000) surveys is 1.9 times higher than that from the 2000 survey alone (Sala et al 2002) and we hence increase our estimate of average density of *E. superba* by this factor to give an estimate of *E. superba* total biomass of 1 540 000 tWW which we use here. This is equivalent to a carbon density of 0.092 gC m<sup>-2</sup> for the study area.

For comparison, This is similar to the biomass estimate of 1 400 000 t obtained on the 2005 Japanese acoustic survey as reported in O'Driscoll et al. (2009).based on preliminary analysis of acoustic data from the 2008 New Zealand IPY-CAML survey of the Ross Sea (Hanchet et al. 2008), the biomass of *E. superba* in the study area is estimated to be only 424 000 tWW (O'Driscoll et al. 2009) – only 28% of our value. The estimate of *E. superba* biomass from the New Zealand IPY-CAML survey is of uncertain accuracy because the survey concentrated on the Ross Sea shelf and northern areas where *E. superba* densities are known to be lower (O'Driscoll et al. 2009), and this estimate will not be used here.

The maximum *E. superba* density of 264 gWW m<sup>-2</sup> and spatial average of 4.2 gWW m<sup>-2</sup>, may be compared to work in other Southern Ocean areas. Hampton (1985) report a mean biomass of 31 gWW m<sup>-2</sup> in the South Atlantic from a large number of swarms. Marr (1962) estimates krill density to be 2.5–29 gWW m<sup>-2</sup> in the Weddell and East Wind zones. Daly & Macaulay (1988) estimate 1–68 gWW m<sup>-2</sup> under the ice and 10–100 gWW m<sup>-2</sup> in open water (from acoustic and net sampling in Weddell Sea). Hewitt et al. (2002) estimates average densities of 11.2–150 gWW m<sup>-2</sup> for a number of CCAMLR strata, mostly from the Scotia Sea region. The values in the Ross Sea hence seem reasonable, albeit towards the low end of *E. superba* densities in the Southern Ocean.

### 3.3 Food and condition

For the Southern Ocean in general, *E. superba* are essentially herbivorous, especially during the austral spring and autumn when phytoplankton blooms occur (Smetacek et al. 1990; Clarke & Leakey, 1996; Miller, 2003; Miller & Hampton, 1989; Genhai, 1989; Genhai et al. 1993). In the Marginal Ice Zone in Bellingshausen Sea, Cripps & Hill (1998) showed that diatoms were main diet item in the open ocean and suspended material from the water column (dinoflagellates) were fed on under the pack ice. In the Lazarev Sea, heterotrophic organisms were consumed in proportions ranging from 17–99% (mean 79% ± 21 SD) of the mass of gut contents (Perissinotto et al. 2000; Atkinson & Snyder 1997). They may feed on ice (epontic) algae in winter months (Quetin et al. 1994; O'Brien 1987).

*E. superba* have also been shown to be carnivorous (Cripps & Atkinson, 2000; Huntley et al. 1994; Nordhausen et al. 1992; Zhou et al. 2004), or omnivorous (Price et al. 1988; Atkinson & Snyder 1997; Nishino & Kawamura 1994; Schnack 1985; Ju & Harvey 2004). Hernandez-Leon et al. (2001) show that *E. superba* feed on phytoplankton during the day and switch to carnivory at night, in February, and that is accompanied by an inverse relationship between vertical distribution of krill and non-krill zooplankton. Krill were at about 100 m during the day and migrated downwards at night coinciding with the upward migration of *Metridia gerlachei* at night. High polyunsaturated fatty acid content of *E. superba* around South Georgia (Cripps et al. 1999; Cripps & Atkinson 2000) confirms omnivorous feeding of krill during non-bloom periods. However, *E. superba* is less dependent on stored lipids to overwinter compared to *E. crystallophias* (Ju & Harvey 2004).

In summary, *E. superba* appear able to use whatever food is available, and food selection is likely to be flexible in response to the availability of different food sources. Krill seem to switch from



herbivory of water column phytoplankton in spring/summer, to omnivory (water column zooplankton, and epontic algae) through the winter. Some consumption of other macrozooplankton by *E. superba* is also likely. We assume, initially, prey of *E. superba* over the course of a year in the Ross Sea is: 22% heterotrophic microplankton; 35% heterotrophic flagellates; 30% phytoplankton; 6% epontic algae; 2% ice protozoa; 5% ice metazoa (mainly amphipods and copepods in the ice habitat through the winter).

### 3.4 Production, P/B

The appropriate P/B value for *E. superba* depends on the population structure, as smaller, younger individuals consume more and grow faster as a proportion of their body weight than larger individuals. As for *E. crystallophias*, exuviae should be included in our estimates of production for krill. Ross et al. (2000) point out that growth varies with food quality and quantity, and so will vary seasonally. Average length of *E. superba* may decline through winter, though it is not known if this is due to starvation, body shrinkage, or changes to the population structure (Huntley et al. 1994; McClatchie et al. 1991; Quetin & Ross, 1991). In the species profile for *E. superba* for CCAMLR, Miller (2003) states that it has not been satisfactorily verified that growth of *E. superba* follows a predictable pattern.

When larval production is included (P/B for larvae is about  $4.6 \text{ y}^{-1}$ ) the mean ratio for all developmental stages may increase to as high as  $5.0 \text{ y}^{-1}$ . Cartes & Maynou (1998) give P/B values for euphausiids between  $1.24\text{--}4.75 \text{ y}^{-1}$ . P/B for 150 d growing season was given as 2.77 for krill aged 1+, 1.19 for 2+ group or 1.53 total (Miller et al. 1985). The value of P/B averaged over a year is likely to be lower than these values for the growing season. Others have worked on P/B for *E. superba* (Siegel 1986, 2000a; Veronina 1983, 1998; Tseitlin 1989; Menushutkin 1993) and values range from  $0.53\text{--}1.86 \text{ y}^{-1}$ .

Sala et al. (2002) reports that *E. superba* in the Ross Sea in the summer was composed of 84% adults, 15% sub-adults and 1% juveniles. Krill larvae are not included in this trophic component. We assume here that the average P/B values of the population will be approximately  $1.1 \text{ y}^{-1}$ , with a possible range of  $0.50\text{--}2.2 \text{ y}^{-1}$ .

### 3.5 Consumption, Q/B

Consumption may decrease during winter as prey availability reduces. Huntley et al. (1994) apply several scenarios to a model of krill physiology and conclude that krill are capable of finding enough food, feeding and growing in winter. This model also predicts the daily carbon ration as a proportion of body carbon for growing krill for krill of 20, 30 and 40 mm length, giving values of Q/B between  $5.3\text{--}10.4 \text{ y}^{-1}$ . As these values are for the winter period, annual average values will be somewhat greater. Meyer et al. (2003) suggest mean daily carbon rations for juvenile stages that lead to Q/B values of  $55\text{--}102 \text{ y}^{-1}$ , but see also Samyshev & Lushev (1983), Pakhomov et al. (2004). Assuming that juvenile consumption is greater than adult consumption by a factor of approximately 5 (as for *E. crystallophias*), we estimate that the *E. superba* population in the Ross Sea has an annual averaged Q/B value of c.  $7.5 \text{ y}^{-1}$ , with possible bounds  $3.8\text{--}15 \text{ y}^{-1}$ .

### 3.6 Unassimilated consumption

Assimilation efficiency *E. superba* ranges from 70–92% (Meyer et al. 2003), giving  $U$  as c. 0.2.

### 3.7 Ecotrophic efficiency

Ecotrophic efficiency ( $E$ ) for *E. superba* in the Ross Sea is not known, and is assumed to be 0.95 on the basis that the vast majority of the annual production of this group is likely to be consumed by direct predation.

## 4 Macrozooplankton other than krill

Macrozooplankton in the Ross Sea include: Coelenterata (*Dipulmaris antarctica*, *Calyropsis borchgrevinkii*, *Nausithoe* sp.), Pteropoda (*Clione limacina*, *Limacina helica*), Amphipoda (*Hyperiella dilatata*, *H. macronyx*, *Cylopus lucasii*), Euphausiacea (*Euphausia superba*, *E. crystallorophias*, *Thysanaessa macrura*), Chaetognatha (*Sagitta gazellae*, *Eukrohnia hamata*), Salpidae (*Salpa gerlachei*) and also some polychaeta, ostracoda, mysids, and decapoda. More details on macrozooplankton species in the Ross Sea is given by Bradford-Grieve & Fenwick (2001) in their review of biodiversity. Non-krill biomass is estimated from data made available by Dr V. Barkhatov (TINRO, Vladivostok) (Appendix 1).

### 4.1 Biomass

Measurements of macrozooplankton abundance across the Ross Sea shelf from Russian research voyage in February–March 1982 are unpublished but have been provided by Dr Barkhatov and processed as part of this study. Details are given in Appendix 1. Non-krill biomass varied from 0.14–301 mgC m<sup>-2</sup> (mean 25.1 mgC m<sup>-2</sup>). Gelatinous zooplankton (e.g., salps) were rarely found in the Ross Sea, at least in February–March 1982 although *Salpa gerlachei* was recorded at 3 stations (21, 27, 38) over the continental slope. Hopkins (1987) also found that salps were not a major component of the trophic structure of the midwater ecosystem of McMurdo Sound. Barkhatov's data lead to an estimate of annual average non-krill biomass in the study area of 0.037 gC m<sup>-2</sup> for the model. The estimates of krill biomass from the Russian data provided by Dr Barkhatov give geometric average values for krill density of 0.055 gC m<sup>-2</sup>, which is more than 3 times lower than the average density of all krill estimated from the Italian surveys (Sala et al. 2002; Azzali et al. 2006; and see preceding sections). The Russian sampling did not cover the areas of highest *Euphausia superba* concentrations to the north of the Ross Sea slope (Figure 3), and that these concentrations make up a large proportion of the total krill biomass in the study region, the lower estimate derived from the Russian data is explicable. We do not adjust the value of non-krill macrozooplankton derived from the data of Barkhatov, but note that our estimate may be biased low.

### 4.2 Production, P/B

Production/biomass ratios for non-krill macrozooplankton are taken from the literature. The krill, *Nematoscelis megalops* has P/B = 5–6 y<sup>-1</sup> (Lindley, 1982). Cartes & Maynou (1998) use P/B = 8.1 y<sup>-1</sup> for peracarids. Here, we assume productivities are lower because of the low temperatures, and seasonality of food availability. We propose using a similar P/B value at the higher end of that of krill, i.e. 2.0 y<sup>-1</sup>, with a range of 1–4 y<sup>-1</sup>.

### 4.3 Diet, Consumption, Q/B

Non-krill, non-salp macrozooplankton are likely to include phytoplankton, microzooplankton, and mesozooplankton with copepods dominating the diet (Barange et al. 1991; Froneman et al. 1996). The feeding and predation impact of carnivorous macrozooplankton (>20 mm) on mesozooplankton (2–20 mm) in the sub-Antarctic waters of the southwest Indian Ocean was studied by Froneman et al. (2002). The carnivore component consists of mainly decapods, amphipods, chaetognaths, euphausiids and some gelatinous zooplankton. It is likely that the diet of macrozooplankton in general consists primarily of mesozooplankton as well as phytoplankton and microzooplankton. Epontic algae, and ice microfauna (mainly amphipods and copepods in the ice habitat) are also likely to form food for macrozooplankton through the winter, especially the more herbivorous salps and large pteropods. Some consumption of macrozooplankton by other macrozooplankton species is likely. The exact proportions of phytoplankton and zooplankton in the diet of macrozooplankton are not known, and will vary with macrozooplankton species (especially the proportion of salps), depth, location, season, and interannually. Here, we assume initially prey of salps and other non-krill macrozooplankton over the course of a year in the Ross Sea is: 5% other macrozooplankton; 35% mesozooplankton; 20% heterotrophic microplankton; 3% heterotrophic flagellates; 30% phytoplankton; 4% epontic algae; 1% ice protozoa; 2% ice metazoa.

In the absence of consumption data for cold water species we propose to use a value at the upper end of the possible range of values found for krill in Antarctic waters, of  $Q/B=15 \text{ y}^{-1}$ , with a range of  $7\text{--}30 \text{ y}^{-1}$ .

### 4.4 Unassimilated consumption

Assimilation efficiency for non-krill macrozooplankton in the Ross Sea are assumed to be similar for *E. superba*, giving  $U$  as c. 0.2.

### 4.5 Ecotrophic efficiency

Ecotrophic efficiency ( $E$ ) for non-krill macrozooplankton in the Ross Sea is not known, and is assumed to be 0.95 on the basis that the vast majority of the annual production of this species is likely to be consumed by direct predation.

## 5 Mesozooplankton

Mesozooplankton in the Ross Sea are defined as having a size approximately 0.2–20 mm. The mesozooplankton component typically dominates the biomass of the plankton (c. 67%: Hopkins 1971), but is slower growing and consumes less as a proportion of its mass than the microzooplankton. Several large copepod species dominate zooplankton biomass in Antarctic waters (e.g. Voronina 1998; Mayzaud et al. 2002b). These species are: *Calanus propinquus*, *Calanoides acutus*, *Rhincalanus gigas* and *Metridia gerlachei*. Other smaller species such as *Ctenocalanus citer*, *Microcalanus pygmaeus*, and *Oithona* spp. are numerically very important.

Another potentially important component of the Ross Sea mesozooplankton in some seasons is the pteropods. Knowledge of these molluscs in Antarctic waters has been summarised by Hunt et al. (2008), based on data mainly from the South Atlantic sector of the Antarctic. Six species of

pteropoda are typical of the Southern Ocean. In the Ross Sea, the most common species are the gymnosome *Clione limacina* and the thecosome *Limacina helicina antarctica*. Combined *Limacina helicina* and *C. limacina* made up to 171–1398 ind. m<sup>-3</sup> (greatest numbers were in the surface 25 m) and were 9.2–78% by numbers of the total zooplankton in Terra Nova Bay with *L. helicina* being a major contributor to these densities (Pane et al. 2004). Hopkins (1987) noted that *L. helicina* could reach 300 indiv m<sup>-3</sup> and was 23% of the biomass in McMurdo Sound

## 5.1 Biomass

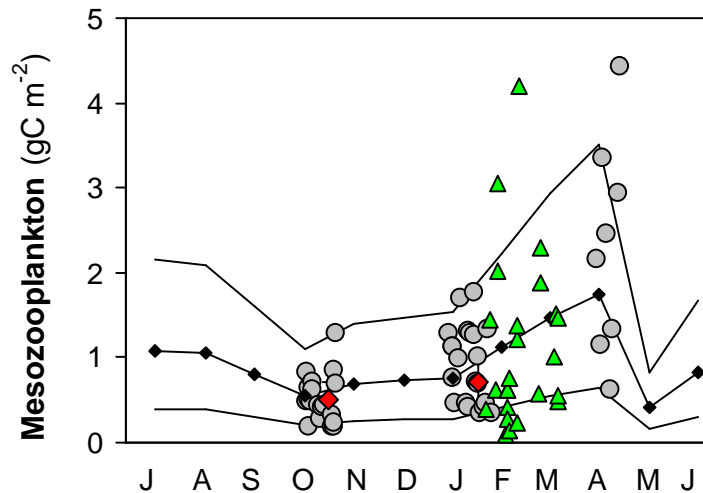
The estimates of mesozooplankton biomass presented here are based on “Zooplankton Displacement Volume” measurements made at a number of coastal and open ocean stations through the central part of the Ross Sea as part of the AESOPS/JGOFS programme (see [http://www1.who.edu/jgdms\\_info.html](http://www1.who.edu/jgdms_info.html)). The zooplankton data has not been written up. We have approval from Dr Walker O. Smith Jnr (Virginia Institute of Marine Sciences, College of William and Mary, Gloucester Pt., VA 23062, USA) to use these data. Data were collected at the standard AESOPS stations on three cruises: (1) October to November 1996, Voyage 96-4A; (2) January to February 1997, Voyage 97-1; and (3) April 1997, Voyage 97-3. Data from the tows with net mesh of 330 µm were used. We note that any samples taken with nets coarser than 200 µm will miss the smaller copepods such as *Oithona* and *Oncaea*. Nevertheless, the total biomass captured by nets <330 µm were generally the same (Hopkins 1971: Table 3). For each tow on each voyage, the displacement volume of zooplankton  $V$ , (ml m<sup>-3</sup>) was converted to a zooplankton carbon concentration,  $C$  (mgC m<sup>-3</sup>) using the relationship of Weibe (1988).

The tows generally covered about 70% of the total water depth. To account for the part of the water column not sampled, we assume that zooplankton density was constant from the lowest measurement to the sea bed. This gave estimates of zooplankton density in the Ross Sea between 0.2 and 5.0 gC m<sup>-2</sup>. These are approximately equivalent to wet-weight densities of 2–50 gWW m<sup>-2</sup>. Next, we used these values to estimate the variation in mesozooplankton abundance in the Ross Sea through the year. The seasonal abundance of zooplankton in the Pacific sector of the Southern Ocean is best known from data sets collected by the *Eltanin* and *Discovery* (Hopkins 1971). This seasonal cycle was scaled to fit the values estimated from the AESOPS data in the Ross Sea. Tagliabue & Arrigo (2003) present models that suggest seasonal cycles of mesozooplankton abundance may vary through the Ross Sea, but field data to confirm this are very limited.

There can be differences in mesozooplankton abundances in waters with and without sea ice cover. For example, Robins et al. (1995) found that in the Marginal Ice Zone and under Pack ice mesozooplankton biomass was reduced to 0.38 of the open water biomass in spring in the Bellingshausen Sea. Here, we assume that mesozooplankton abundances measured in the water column when ice cover is lowest in summer were representative of the average biomass found in the region at this time. We also assume that the stations occupied by the AESOPS voyages are representative of the Ross Sea as a whole. The 51 stations span longitudes 165°W to 175°E, and latitudes 74°–78°S. To the authors’ knowledge, there are few spatially extensive, quantitative surveys of zooplankton abundance of the Ross Sea to test this assumption. Therefore, the annual average mesozooplankton concentration for the Ross Sea is estimated to be 0.94 gC m<sup>-2</sup>, with a possible range of 0.35–1.9 gC m<sup>-2</sup>. Our estimates of mesozooplankton biomass can be compared with data collected during other studies. In general, these other studies are largely consistent with our estimates of mesozooplankton biomass for the Ross Sea, as summarised below.

- (1) In the Ross Sea Hicks (1974) measured integrated zooplankton biomass in January ranging from 9.4–29.1 gC m<sup>-2</sup> in McMurdo Sound, south of Hut Point on Ross Island in mid to late January, converted using the relationships of Weibe (1988). Mean biomass was 21 gC m<sup>-2</sup>. This is two orders of magnitude greater than the model results of Tagliabue & Arrigo (2003), and a factor of ~20 greater than we have found for the Ross Sea as a whole. Phytoplankton concentrations are greater close to the coast than offshore in the Ross Sea, so this is not necessarily inconsistent with our estimate. The outer Ross Sea was sampled with 500 µm mesh net 1989–1990 to near the bottom in summer (Sertorio et al. 2000). Biomass of copepods varied from 0.02–0.48 gC m<sup>-2</sup> in the NW Ross Sea (WW converted to C as Weibe, 1988). Again, this is consistent with our estimate.
- (2) Seasonal carbon distribution of copepods integrated over 0–1000 m in Weddell Sea given by (Schnack-Schiel et al. 1998) were 1.7 gC m<sup>-2</sup> in late winter early spring, 3.7 gC m<sup>-2</sup> in autumn, consistent with our estimates above. Large calanoids *C. propinquus*, *C. acutus*, *M. gerlachei*, *Euchaeta antarctica* and small *M. pygmaeus* accounted for 60–70% of biomass while small poecilostomatoid *Oncaea* and cyclopoid *Oithona* comprised about 20% of biomass.
- (3) Voronina et al. (1980a, b) report modelling studies on two common Antarctic copepods, *Calanoides acutus* and *Rhincalanus gigas*. The biomass cycle of *Calanoides acutus* in the 0–1500 m layer peaks in July and is at a minimum in January-February (Voronina et al. 1980a). For *Rhincalanus gigas* (Voronina et al. 1980b) the total biomass in the 0–1500 m layer has peaks in biomass in May–June and November. The minimum in August is related to the dying-off of females after spawning. The maximum abundance of copepods (not biomass) from models occurs in March–April and may vary six fold between years and locations. Concentrations varied between 2.2–10.5 gWW m<sup>-2</sup>, approximately equivalent to 0.1–0.5 gC m<sup>-2</sup>.
- (4) Hopkins (1971) gives an average mesozooplankton density of about 0.9 gC m<sup>-2</sup> for the entire Pacific sector of the Southern Ocean.
- (5) Fukuchi et al. (1985) in 1982 at Syowa Station sampled through the sea ice, down to 660 m, from May until December using a mesh size of 350 µm on the lower part of the net (the upper part was 1000 µm). Mesozooplankton concentrations peaked here at 25 mgWW m<sup>-3</sup> in September. The average biomass in this study was 8.9 gWW m<sup>-2</sup>. These are approximately equivalent to 1.2 and 0.4 gCm<sup>-2</sup>.
- (6) A study by Zvereva (1975) at Molodezhnaya Station sampled zooplankton through a hole in the ice in 1965–66 from surface to the sea floor (309 m) between July to December, and between the surface and 85 m in January–February. A maximum in wet weight was recorded in late July and August. The average value over the study was 10.9 gWW m<sup>-2</sup>, approximately equivalent to 0.5 gC m<sup>-2</sup>.
- (7) Huntley & Zhou (2000) as reported in Tagliabue & Arrigo (2003) report depth-integrated zooplankton biomasses of 0.5±0.2 gC m<sup>-2</sup> in the Ross Sea in October/November and 0.7±0.3 gC m<sup>-2</sup> in January/February. Our average value lies within their range of 0.3–1.0 gC m<sup>-2</sup>.
- (8) Unpublished Russian mesozooplankton data from the Ross Sea (February-March) in 1982 integrated over 0-200 m ranges from 0.09–17.31 gC m<sup>-2</sup> (Appendix 1). These data

are from samples collected with a Juday Net and are used courtesy of Dr Barkhatov. Although a few values are very high, the ln-mean (calculated in units of gWW) of 1.2 gC m<sup>-2</sup> lies within the data presented in Figure 1.



**Figure 1.** Annual cycle of mesozooplankton biomass in the Ross Sea. The central solid line with black diamonds is a scaled version of the data on zooplankton abundance in the Pacific sector of the Southern Ocean in the upper 1000 m (Hopkins 1971). The grey circles are zooplankton areal biomass densities calculated from the results of AESOPS JGOFS programme. Red diamonds are Ross Sea zooplankton biomass measurements of Huntley & Zhou (2000) as reported in Tagliabue & Arrigo (2003). Green triangles are unpublished data from Barkhatov (Appendix 1). The thinner lines indicate approximate bounds on the seasonal pattern of mesozooplankton concentration equivalent to the 10–90<sup>th</sup> percentiles of the AESOPS data.

## 5.2 Production, P/B

Production by mesozooplankton will not be steady year round in the Antarctic because primary production is negligible through winter and many species of mesozooplankton enter a low-production stage through this time. For example, both *Calanoides acutus* and *Rhincalanus gigas* pass the winter in diapause. Voronina et al. (1980a, b) calculated the productivity of two common Antarctic copepods, *Calanoides acutus* and *Rhincalanus gigas*. For *Calanoides acutus* in the 0–1500 m layer Voronina et al. (1980a) describe an annual pattern of production with low production from May–December and production which peaks in February–March. Voronina et al. (1980a) estimated an annual average P/B of 4.5 y<sup>-1</sup>. Population growth for *Rhincalanus gigas*, based on a modelling study by Voronina et al. (1980b) in the southern Antarctic region, led to an annual average P/B of 5.3 y<sup>-1</sup>. Schnack et al. (1985) estimate that copepod daily P/B during November/December ranged from 0.02–0.20 d<sup>-1</sup>, with average daily P/B=0.123 d<sup>-1</sup> in the period measured.

For pteropods, there is a relationship between shell weight and dry tissue weight for *L. helicina* in the subarctic Pacific (Fabry 1989). The study estimated that daily CaCO<sub>3</sub> production, calculated by the instantaneous growth rate method, is 12.6 mg CaCO<sub>3</sub> m<sup>-2</sup> d<sup>-1</sup> for individuals

with  $155 \text{ mg m}^{-2} \text{ CaCO}_3$ . Therefore carbonate P/B was  $0.0813 \text{ d}^{-1}$  or  $9.9 \text{ y}^{-1}$  assuming that growth occurs over 4 months of the year. A lower P/B =  $5 \text{ y}^{-1}$ , is estimated for *Clio pyramidata*.

Here, we initially use a value for P/B for mesozooplankton in the Ross Sea of  $4.8 \text{ y}^{-1}$ . This is the average of the production values given above, weighted for their approximate contributions to mesozooplankton biomass (77% copepods, 23% pteropods). For comparison, the P/B ratio for mesozooplankton for low productivity water is about  $12 \text{ y}^{-1}$  (Shushkina et al. 1998).

### 5.3 P/Q, Respiration, assimilation efficiency

Measurements of respiration, food assimilated, and biomass have been made for Antarctic copepods (Schnack et al. 1985). The mean proportion of consumed food assimilated was 0.68, ranging from 0.51–0.93. We therefore set the proportion of unassimilated food at 0.3 as is typical for ecotrophic models of mesozooplankton (e.g. Bradford-Grieve et al. 2003).

Average daily R/B was measured at 0.042 (Schnack et al. 1985). Assuming respiration occurs at this rate for 365 days per year (probably true except for species which enter diapause such as *Calanoides acutus* and *Rhincalanus gigas*), then annual R/B would be  $15.3 \text{ y}^{-1}$ . Values from Schnack et al. (1985) imply an average daily R/Q value of 0.37 (range 0.04–0.56) which is close to the value for R/Q = 0.5 often assumed for mesozooplankton (Laws et al. 2000). Average daily P/Q was measured at 0.307 (Schnack et al. 1985), close to the value of 0.3 often used for the growth efficiency of mesozooplankton (Laws et al. 2000; Bradford-Grieve et al. 2003) and this will be used here.

### 5.4 Ecotrophic efficiency

Ecotrophic efficiency ( $E$ ) for mesozooplankton in the Ross Sea is not known, and is assumed to be 0.99 on the basis that the vast majority of the annual production of this group is likely to be consumed by direct predation.

### 5.5 Diet

Mesozooplankton in the Antarctic are generally omnivorous, taking both autotrophic and heterotrophic material from the water column and underside of sea ice (e.g. Metz & Schnack-Schiel 1995; Pasternak & Schnack-Schiel 2001; Cripps & Hill 1998). The proportions of items in the diet of mesozooplankton will vary seasonally, and there are also variations in diets between different mesozooplankton species and different sized individuals (Hopkins 1987). In general, phytoplankton generally dominates mesozooplankton diet in summer, with carnivory dominating in winter when phytoplankton biomass is very low (Metz & Schnack-Schiel 1995, Øresland 1991; Huntley & Nordhausen 1995).

Smaller zooplankton species and smaller individuals tend to eat a high proportion of phytoplankton, with progressively greater proportions of protozoans and metazoans being consumed by larger mesozooplankton species (Hopkins 1987). For example, experiments show that *Oncaea curvata* is surface rather than pelagic feeder (Boxshall 1981) and ingests large, non-motile food particles such as aggregates or gelatinous *Phaeocystis* colonies, with diatoms also being an acceptable food, but did not feed carnivorously (e.g. on heterotrophic microplankton or flagellates) (Metz 1998). *Oncaea curvata* can be a dominant copepod Antarctic species in terms of numbers, and in the vicinity of the shelf, often also in terms of biomass (Metz 1998).

*Calanoides acutus* and *Rhincalanus gigas* fed mainly on diatoms in open water in summer (Metz & Schnack-Schiel 1995; Pasternak & Schnack-Schiel 2001).

In contrast, under pack ice in summer, *Oithona similis* was measured as being predominantly carnivorous, consuming mostly ciliates, especially, non loricate ciliates (Urban-Rich et al. 2001). In summer, microzooplankton met only 17, 19 and 24% of the total carbon requirements of *Rhincalanus gigas*, *Calanus propinquus* and *Metridia gerlachei*, respectively (Froneman et al. 1996). Metz & Schnack (1995) also demonstrate carnivorous feeding in *C. propinquus* and *M. gerlachei*. These species are often representative of the whole population as *Metridia gerlachei* can be a large component of coastal zooplankton and *Calanoides acutus* and *Rhincalanus gigas* can dominate open ocean Antarctic zooplankton biomass (e.g. Schnack et al. 1985).

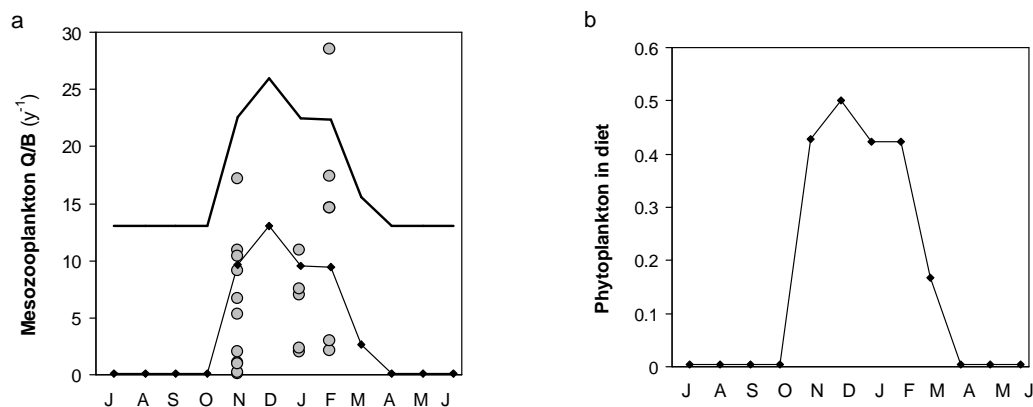
Trophically, thecosome pteropods are considered to be dominantly herbivores, capturing food with a mucous net. Because they can be at least 23% of the biomass in surface waters (Hopkins 1987) they are an important contributor to mesozooplankton grazing on phytoplankton. Here, we initially use the diet proportions of mesozooplankton: 5% mesozooplankton, 17% heterotrophic microplankton, 54% heterotrophic flagellates, and 25% phytoplankton.

## 5.6 Consumption

Consumption by Antarctic mesozooplankton varies significantly with season, with generally much higher consumption rates in austral spring and summer than in winter. In austral summer *Oithona similis* consumed up to 0.9 body weight in terms of carbon (C)  $\text{d}^{-1}$  (Lonsdale et al. 2000) which is exceptionally high. *Oncaea curvata* is reported as consuming up to 0.18  $\text{d}^{-1}$  at natural food densities (Metz 1998). Daily food intake by large calanoid copepods ranges between  $<0.1$  and  $0.2 \text{ d}^{-1}$  when feeding on naturally occurring phytoplankton concentrations of  $0.1\text{--}2 \text{ mg Chl-}a \text{ m}^{-1}$  (Metz & Schnack-Schiel 1995, and references therein). Other studies give feeding rates of mesozooplankton in the Antarctic between October and February of between  $0.001$  and  $0.3 \text{ d}^{-1}$ , with a median value of  $0.03 \text{ d}^{-1}$  (Dubischar & Bathmann 1997a,b; Mayzaud et al. 2002a,b; Froneman et al. 1996; Drits et al. 1993; Metz & Schnack-Schiel 1995). The overall food intake of large copepods, estimated from collated experimental data (Schnack et al. 1985; Drits et al. 1993; Metz & Schnack 1995; Ward et al. 1995; Froneman et al. 1996), is calculated to be lie within  $10\text{--}39 \text{ y}^{-1}$ , using the assumption that omnivorous feeding occurs for c. 150 days of the year and carnivorous feeding for 215 days of the year. Based on values of  $P/Q=0.3$  (above) and  $P/B=4.8 \text{ y}^{-1}$  (above), we estimate a  $Q/B$  value of  $16 \text{ y}^{-1}$  which is towards the centre of this range.

The estimated seasonal cycle in consumption and diet are shown in Figure 2. This was obtained by fitting the seasonal biomass of phytoplankton to the consumption rates of phytoplankton from the literature (Dubischar & Bathmann 1997; Mayzaud et al. 2002b; Froneman et al. 1996; Drits et al. 1993; Metz & Schnack-Schiel 1995). The consumption rate of microzooplankton by mesozooplankton was estimated to be constant through the year and at a level to give the annual  $Q/B$  required. The proportion of the diet from phytoplankton was then calculated (Figure 2b). In this way, we estimate that the consumption is equivalent to the summer feeding rate being maintained for about 3.6 months with no feeding at other times.





**Figure 2. a:** Consumption of mesozooplankton. The grey dots are literature values of feeding rates of mesozooplankton on phytoplankton, and the thin line is the consumption of phytoplankton fitted to the median values of these measurements based on the shape of the phytoplankton seasonal biomass line and expressed as annual equivalent. The thick line is the total consumption rate of mesozooplankton. **b:** Estimated proportion of phytoplankton in the diet of mesozooplankton, again, assuming consumption of phytoplankton follows the seasonal change in phytoplankton biomass as estimated in this study.

Pteropods may be responsible for a large proportion of mesozooplankton community grazing in summer and autumn (Hunt et al. 2008), but quantitative estimates of their contribution is not well known. An estimate of the consumption rate of *Limacina helicina* can be obtained as follows to compare with that of copepods. *L. helicina* is reported as ingesting 100–900 ng(pig) ind<sup>-1</sup> d<sup>-1</sup> (Pakhomov & Froneman 2004) The average dry weight of *Limacina helicina* was 0.29 mg ind<sup>-1</sup> (Pakhomov & Froneman 2004). We assume that carbon content of pteropods is c. 40% of dry weight as for macrozooplankton (Weibe 1988), and that the carbon:chlorophyll ratio of the particles consumed is 120 gCg<sup>-1</sup>Chl-*a* as for phytoplankton. If consumption varies annually so that it is equivalent to about 4 months of feeding at the summer rate and none at other times, we can estimate an average annual Q/B between 13–113 y<sup>-1</sup>, which encompasses our estimate of Q/B=16 y<sup>-1</sup>, but suggests this may be at the lower end of the possible range.

## 6 Heterotrophic microplankton

### 6.1 Species included in this group

Heterotrophic microplankton in this study is defined as heterotrophic organisms in the microplankton size range, or between 20–200 µm in size. Heterotrophic dinoflagellates, tintinnids and other ciliates, copepod nauplii, with a minor component of larvae and eggs of micro metazoans, make up this compartment (Lessard & Rivkin 1986; Umani et al. 1998; Caron et al. 2000). In coastal waters, larval stages of echinoderms, polychaetes, nemerteans (ribbonworms), and other benthic invertebrates can be present (Lessard & Rivkin 1986). Heterotrophic microplankton species observed in the Ross Sea tend to be typical of Antarctic waters (Stoecker et al. 1995; Monti & Fonda Umani 2000; Fonda Umani et al. 1998; Gowing & Garrison 2003). In Terra Nova Bay in summer, Fonda Umani et al. (1998) report that heterotrophic microplankton included heterotrophic dinoflagellates, tintinnids, aloricate ciliates, larvae and eggs of invertebrates. Heterotrophic dinoflagellates included species belonging to the *Protoperidinium* genus (Dodge & Priddle 1987; Elbrachter & Zolfel 1993), especially *P. antarcticum* (Lessard & Rivkin 1986), *Gyrodinium lachrymal* (Lessard & Swift 1986), and *Gymnodinium* sp. (Bjornsen &

Kuparinen 1991). Ciliates included oligotrichs, tintinnid, *Radiolaria*, and *Foraminifera*. A reduction in both abundance and species diversity of heterotrophic microplankton was observed from the polynya to the northernmost stations still covered by ice, as well as from the surface to the bottom (Monti & Fonda Umani 2000).

Cell numbers of heterotrophic microplankton, typically enumerated from preserved samples (Sherr & Sherr 1993; Landry et al. 2002) are converted to units of carbon. Carbon biomass ( $C$ ,  $\mu\text{gC}$ ) of various groups of heterotrophic microplankton can be estimated from cell biovolume ( $BV$ ,  $\mu\text{m}^3$ ) using the conversion factors:

Dinoflagellates	$C = BV \times 0.13$	(Edler 1979)
Tintinnids	$C = BV \times 0.053 + 444.5$	(Verity & Langdon 1984)
Ciliates, other than tintinnids	$C = BV \times 0.14$	(Putt & Stoecker 1989)
Other groups	$C = BV \times 0.08$	(Beers & Stewart 1970)

## 6.2 Biomass

There is an absence of large area, seasonally-resolved measurements of heterotrophic microplankton biomass in the Ross Sea. The most complete data we have found is that of Dennett et al. (2001) (see also Gowing & Garrison 2003), who measured the biomass of heterotrophic microplankton at 12–22 stations along  $76.5^\circ\text{S}$  between  $168^\circ\text{E}$  and  $178^\circ\text{W}$  on four separate research voyages between early spring and autumn. Biomass of heterotrophic microplankton in the water column is assumed to remain low throughout winter. The annual average biomass of heterotrophic microplankton from Dennett et al. (2001) was calculated to be  $0.58 \text{ gC m}^{-2}$ .

In order to evaluate this estimate, we propose using a second method to estimate heterotrophic microplankton biomass, based on autotrophic biomass, and the ratio of annual average heterotrophic microplankton biomass to annual average autotrophic biomass. If we make the assumption that there is broad consistency through the Ross Sea in time and space between autotrophic and heterotrophic biomass we can estimate heterotrophic biomass using the fact that the spatial and seasonal variation of autotrophic biomass is relatively well known (see Phytoplankton section). We estimate the ratio of annual average heterotrophic microplankton biomass to annual average autotrophic biomass in three ways.

1. Dennett et al. (2001) presents measurements of zooplankton biomass in the southern Ross Sea at four times of the year (Nov, Dec, Feb, May), which can be used to estimate an annual average microzooplankton biomass of  $0.58 \text{ gC m}^{-2}$ .
2. Ducklow et al. (2006) present data on microzooplankton biomass in the Ross Sea from Nov/Dec 1997 which can be used to estimate a (seasonally-adjusted) annual value of  $0.33 \text{ gC m}^{-2}$ .
3. We combined three independent estimates of the ratio of annual average heterotrophic microplankton biomass to annual average autotrophic biomass ( $B_{\text{micro}}/B_{\text{phyto}}$ ). First, Dennett et al. (2001) gives data allowing us to estimate  $B_{\text{micro}}/B_{\text{phyto}}$  to be 0.28. Second, measurements of heterotrophic microzooplankton biomass in the surface 100 m of Terra Nova Bay in summer (Jan/Feb 1988) are reported by Fonda Umani et al. (1998). On average, heterotrophic dinoflagellates made up 49% of the biomass of the heterotrophic microplankton trophic groups, tintinnids 28%, aloricate ciliates 13%, and eggs/larvae 9%. Median heterotrophic microplankton biomass was  $1.8 \text{ gC m}^{-2}$ . This is higher than the annual average biomass because the measurements were made only in the more productive summer period, and because productivity (and biomass) tend to be higher

along the Ross Sea coast. Chlorophyll was also measured by Fonda Umani et al. (1998). Assuming a carbon:chlorophyll ratio of 80, the values lead to  $B_{\text{micro}}/B_{\text{phyto}}=0.19$  (median), and a 10–90% range of 0.10–0.90 at different stations and depths (N=36). Third, the ratio of annual total heterotrophic microplankton biomass (2–200  $\mu\text{m}$ ) to annual average autotrophic biomass was found to be 0.50 based on data in Landry et al. (2002). This value is consistent with similar work in the Antarctic region. Work in another part of the Southern Ocean (Bellinghousen Sea: Edwards et al. 1998) shows that the ratio of heterotroph biomass to autotroph biomass varies significantly (0.37–4.6) in relation to the position of the edge of the pack ice. Using values for the fraction of this autotrophic biomass in the 20–200  $\mu\text{m}$  size range from Dennett et al. (2001), we estimate that  $B_{\text{micro}}/B_{\text{phyto}} = 0.34$ . These three estimates (0.28, 0.19, 0.34) are consistent with values given by Becquevort et al. (1992) in the Weddell Sea, where protozooplankton comprised c. 0.23 of the total microbial biomass. Using an average factor of 0.27, we estimate the mean heterotrophic microplankton biomass to be  $0.29 \text{ gC m}^{-2}$ .

We propose using an average of these three values (0.58, 0.33, 0.29) as an initial estimate of biomass, i.e.  $0.40 \text{ gC m}^{-2}$ .

### 6.3 Diet

Lessard & Rivkin (1986) studied the clearance rates of microzooplankton in the 20–200  $\mu\text{m}$  size range in McMurdo Sound, and found a marked preference for bacteria and bacterivores over autotrophs and herbivores. The heterotrophic dinoflagellate *P. antarcticum*, ciliates, and invertebrate larvae ingested almost exclusively bacteria and bacterivores. Data in Lessard & Rivkin (1986) does not allow us to estimate diet proportions, but the general result contrasts with that of Bradford-Grieve et al. (2003), and other work in temperate and tropical waters (e.g. Fenchel 1987; Roman & Rublee 1981; Lessard & Swift 1985) which found that most microzooplankton preferentially grazed autotrophic food. In particular, ciliates  $>15 \mu\text{m}$  in equivalent spherical diameter are thought to graze on pico- and nanoplankton rather than bacteria (e.g. Scott et al. 2001). Here, we assume that heterotrophic microzooplankton in the Ross Sea ingest a mix of particles, in approximate proportions: 20% heterotrophic flagellates; 40% phytoplankton; 40% water column bacteria.

### 6.4 Consumption, Q/B

We are not aware of studies on feeding rates for heterotrophic microplankton in the Ross Sea. In their comparison of the Ross Sea and West Antarctic Peninsula food-webs, Ducklow et al. (2006) used an inverse model (Daniels et al. 2006) to estimate microzooplankton grazing in Nov/Dec, having identified no suitable direct measurements of this parameter. The inverse model (Ducklow et al. 2006, figure 10) suggested only 4.4% of the primary production (which was dominated by colonial *Phaeocystis* production at this time of year) was grazed by microzooplankton. Using data from Ducklow et al. (2006), this leads us to estimate a consumption rate for microzooplankton of  $Q/B=44.7 \text{ y}^{-1}$ . Safi et al. (2007) present grazing rates for the  $<200 \mu\text{m}$  fraction in Antarctic waters (south of the Polar Front) in Nov/Dec, leading to estimates of  $Q/B$  of 78 (66–99)  $\text{y}^{-1}$  if rates were maintained at these levels year round. Here, we will use an average of the values from Safi et al. (2007) and Ducklow et al. (2006) giving  $Q/B=61 \text{ y}^{-1}$  as our initial estimate of microzooplankton consumption in the Ross Sea.

## 6.5 P/Q, Respiration, Assimilation efficiency

Gross growth efficiencies (i.e. P/Q) of flagellates and ciliates are typically assumed to be 0.35 (Laws et al. 2000). Respiration/consumption for microzooplankton is given as ~0.3 (Laws et al. 2000). Assimilation efficiency [(ingestion – excretion)/ingestion] of heterotrophic microplankton is taken to be 0.70 (e.g., Bradford-Grieve et al. 2003).

## 6.6 Ecotrophic efficiency

Ecotrophic efficiency (*E*) for heterotrophic microzooplankton in the Ross Sea is not known, and is assumed to be 0.99 on the basis that the vast majority of the annual production of this group is likely to be consumed by direct predation.

## 6.7 Production, P/B

Little appears to have been published on growth rates of heterotrophic microzooplankton in the Ross Sea. A ciliate production rate of P/B=110 y<sup>-1</sup> is near the mean of estimates from a number of studies tabulated by Kiørboe (1998) although growth rates of up to 330 y<sup>-1</sup> for ciliates have been measured (Verity et al. 1993). Work in New Zealand subantarctic waters (Bradford-Grieve et al. 2003) suggests P/B of 88 y<sup>-1</sup> for heterotrophic microplankton 20–200 μm. Klaas (1997) assumes a daily specific growth rate of 0.1 d<sup>-1</sup> in Antarctic waters equivalent to P/B of 18–36 y<sup>-1</sup> for growth lasting 6–12 months per year. An annual average production rate of P/B=21 y<sup>-1</sup> is consistent with annual average values of Q/B=61 y<sup>-1</sup> and P/Q=0.35 as estimated above and we propose to use this as our initial estimate.

## 6.8 Transfers between groups due to growth

There will be a transfer of biomass from the heterotrophic microzooplankton group to the mesozooplankton group due to growth of individuals. The magnitude of this transfer is unknown but is likely to be small. Here, we use a growth transfer parameter describing the fraction of the annual production of heterotrophic microzooplankton which is transferred to mesozooplankton as  $T^s=0.01$ . This transfer is equivalent to only 2% of the intrinsic annual production of mesozooplankton so will not significantly affect the model.

## 7 Heterotrophic flagellates

Heterotrophic flagellates are defined as heterotrophic organisms in the nanoplankton size range (2–20 μm). Becquevort (1997) found that ciliates were an insignificant fraction of this size range in the Southern Ocean. Cell numbers of heterotrophic flagellates (Becquevort 1997; Landry et al. 2002) are converted to carbon units from biovolumes (*BV*, μm<sup>3</sup>). The conversion was carried in log-space following the modified Strathmann (1967) equations of Eppley et al. (1970):

$$\log_{10}C = 0.94 \cdot \log_{10}BV - 0.60$$

Alternatively, biovolumes are converted to cell carbon using a conversion factor that may be influenced by the fixation and staining method as well as by taxon (e.g. Becquevort 1997). Various ratios in the literature range have been proposed and these range from 0.08 to 0.22 pgC

$\mu\text{m}^{-3}$  (Becquevort 1997, and references therein). Becquevort (1997) suggests that  $0.14 \text{ pgC } \mu\text{m}^{-3}$  is appropriate for dionflagellates fixed with gluteraldehyde.

## 7.1 Biomass

Biomass of heterotrophic flagellates in the Ross Sea varies spatially and seasonally. The biomass of heterotrophic nanoplankton at 12–22 stations along  $76.5^{\circ}\text{S}$  between  $168^{\circ}\text{E}$  and  $178^{\circ}\text{W}$  was measured by Dennett et al. (2001) from four research voyages spanning early spring and autumn. Mean annual biomass of heterotrophic flagellates from these data is estimated to be  $0.34 \text{ gC m}^{-2}$ . We assume winter biomass of heterotrophic flagellates in the Ross Sea is small, as it has been found to be in winter in the Weddell and Scotia Seas (Garrison et al. 1993).

An alternate method of estimating biomass of this trophic group is via our previous estimate of phytoplankton biomass. The relationship between heterotrophic flagellate biomass and autotroph (phytoplankton) biomass in the Ross Sea is complex and potentially variable, both seasonally and spatially. For example, it is known that the large bloom of *Phaeocystis antarctica* in the Ross Sea polynya is impacted minimally by zooplankton grazing, whereas the smaller diatom bloom in the adjacent Terra Nova Bay polynya is more readily grazed (Taglabue & Arrigo 2003). This suggests that the ratio of grazers to producers could be variable. However, if we assume that taking all areas of the Ross Sea and all seasons together, there is generally a positive correlation between autotrophic and heterotrophic nanoplankton biomass, we can estimate the biomass of heterotrophic nanoplankton from an estimate of autotrophic biomass. Figure 6 of Becquevort (1997) supports this assumption. The data shows that there is a strong linear correlation ( $R=0.81$ ) between protozooplankton biomass ( $<20 \mu\text{m}$ ) and the biomass of producers (bacteria and autotrophic flagellates). We calculate the ratio of heterotrophic flagellate biomass to phytoplankton biomass from a number of data sets.

1. The average ratio of mean heterotrophic flagellate biomass to phytoplankton biomass based on the data of Becquevort (1997) in the marginal ice zone of the Ross Sea is 0.24.
2. The average ratio of annual mean heterotrophic flagellate biomass to autotrophic biomass based on the data of Dennett et al. (2001) is 0.16.
3. The ratio of total heterotrophic biomass ( $2\text{--}200 \mu\text{m}$ ) to autotrophic carbon in the vicinity of the Polar Front at  $170^{\circ}\text{W}$  had a median value of 0.50 ( $N=29$ ) and varied with a 10–90% range of 0.22–0.93 (Landry et al. 2002). The ratio of heterotrophic microplankton ( $20\text{--}200 \mu\text{m}$ ) biomass to autotroph biomass in Terra Nova Bay in summer was c. 0.2 (Fonda Umani et al. 1998). See the section on “Heterotrophic microplankton” for more details of this work. These results together suggest a ratio of heterotrophic flagellate biomass to autotroph biomass of 0.3.

We take our best estimate of the ratio of heterotrophic flagellate biomass to autotroph biomass to be an average of these three values (0.24, 0.16, and 0.31), i.e. 0.24. With an estimated average annual phytoplankton biomass for the study area of  $1.1 \text{ gC m}^{-2}$ , we hence estimate a mean heterotrophic flagellate biomass of  $0.26 \text{ gC m}^{-2}$ . This is very similar to the value estimated based on data of Dennett et al. (2001) of  $0.30 \text{ gC m}^{-2}$ . An average of the two values is  $0.36 \text{ gC m}^{-2}$  which we use here. This values lies within the spring range of heterotrophic nannoplankton biomass in the western Ross Sea of  $0.003\text{--}0.39 \text{ gC m}^{-2}$  (Vanucci & Bruni 1998). If we assume heterotrophic flagellate biomass is approximately uniformly distributed between the surface and 100 m (Fonda Umani et al. 1998), this is equivalent to an average heterotrophic flagellate surface concentration of  $3.6 \text{ mgC m}^{-3}$ . This is within the range of found by Becquevort (1997) which

noted a biomass of nanoprotozooplankton of c. 2 mgC m<sup>-3</sup> (ranging from 1–5 mgC m<sup>-3</sup>) in ice-covered waters of the Atlantic sector of the Antarctic in early spring.

## 7.2 Diet

Heterotrophic flagellates are part of the “microbial loop”, usually feeding almost exclusively on the small fraction of primary producers such as cyanobacteria, other heterotrophic nanoflagellates, and bacteria (Caron et al. 2000). Flagellates less than 5 µm in size are principally bacterivorous while heterotrophic dinoflagellates feed on bacteria and autotrophic flagellates (Becquevort 1997). Initially, we estimate the diet of heterotrophic flagellates to be: 78% phytoplankton, 15% bacteria, and 7% other heterotrophic flagellates (from Becquevort 1997). Bacteria are considered to be a slightly more important component of the diet of heterotrophic flagellates in the Ross Sea than in subantarctic waters, where Bradford-Grieve et al. (2003) estimated the diet proportions to be: 7% heterotrophic flagellates; 78% phytoplankton; 15% water column bacteria.

## 7.3 Production, P/B

We have not been able to find any measurements of the growth rate of heterotrophic flagellates in the Ross Sea. We propose to estimate this quantity using assumed values for the growth efficiency of heterotrophic flagellates (P/Q) and measurements of Q/B in the Ross Sea. The values given below (Q/B=180 y<sup>-1</sup>, P/Q=0.5) lead to estimates of P/B of 62 y<sup>-1</sup>.

There is a wide range of growth values in other cold waters reported in the scientific literature. The value estimated here is towards the extreme low end of these values. Mean production of heterotrophic flagellates in subantarctic waters off New Zealand in August and January–February was P/B=290 y<sup>-1</sup>, calculated from dilution grazing experiments (Dr J. Hall. NIWA, pers. comm.). Growth rates of heterotrophic microflagellates of P/B >700 y<sup>-1</sup> have been measured when conditions are not limited by iron (Chase & Price 1997), but are or 255–424 y<sup>-1</sup> (Chase & Price 1997) for subarctic Pacific in low iron conditions. Values of P/B <360 y<sup>-1</sup> have been observed in other regions when prey concentrations are low (e.g. see Tortell et al. 1996).

## 7.4 Consumption, Q/B

Becquevort (1997) records maximum ingestion rates of various prey items by various heterotrophic flagellates (flagellates <5 µm, flagellates >5 µm, and dinoflagellates) as a proportion of body weight. In the data of Becquevort (1997), dinoflagellates tend to have much higher consumption rates than flagellates, but comprise only a minor part of the biomass of heterotrophic flagellates (c. 4%). Based on data given by Becquevort (1997) we calculate that the maximum rate of ingestion of bacteria by the heterotrophic flagellates, in the marginal ice zone of the Ross Sea was 0.0030 µgC<sup>-1</sup> h<sup>-1</sup>. Similarly, the maximum rate of ingestion of autotrophic flagellates by heterotrophic flagellates was 0.016 µgC<sup>-1</sup> h<sup>-1</sup>. We assume that maximum ingestion rate of heterotrophic flagellates by heterotrophic flagellates is approximately equal to the ingestion rates of autotrophic flagellates by heterotrophic flagellates. Combined with information on the relative biomass of flagellates and dinoflagellates biomass in the nanoplankton, these values give an estimate of consumption rate of 0.021 µgC<sup>-1</sup> h<sup>-1</sup>. If the feeding rates measured by Becquevort (1997) between October and November were maintained through the year, the annual Q/B would be 177 y<sup>-1</sup>. It is likely that consumption rates of heterotrophic flagellates will vary with the availability of food items. The abundance of food items (bacteria and autotrophic

flagellates) will probably decrease from those at the time of the study of Becquevort (1997), and hence it is likely that the annual average Q/B for heterotrophic flagellates will be lower than the value of 177 y<sup>-1</sup> estimated here.

### 7.5 P/Q, Respiration, Assimilation efficiency

Gross growth efficiencies (i.e. P/Q) of heterotrophic flagellates are typically assumed to be 0.35 (Laws et al. 2000) which we use here, although we note that Becquevort (1997) assumes a gross growth efficiency for heterotrophic flagellates of 30% in the marginal ice zone, i.e. P/Q=0.30. Respiration/consumption for microzooplankton is given as ~0.3 (Laws et al. 2000). Assimilation efficiency [(ingestion – excretion) / ingestion] of heterotrophic flagellates in low iron conditions is given as 0.84 by Chase & Price (1997) which give U=0.16 used here.

### 7.6 Ecotrophic efficiency

Ecotrophic efficiency (*E*) for heterotrophic flagellates in the Ross Sea is not known, and is assumed to be 0.99 on the basis that the vast majority of the annual production of this species is likely to be consumed by direct predation.

## 8 Summary of parameters

Parameters for krill, non-krill macrozooplankton, mesozooplankton, heterotrophic microzooplankton and heterotrophic flagellates are given below in Table 1 and Table 2. Where required in the model, parameters are combined by combining these parameters in appropriate proportions according to biomass.

**Table 1.** Summary of parameters for zooplankton in the trophic model. Wet weight biomasses, in addition to average carbon densities used in the model, are also given for krill and macrozooplankton.

	<b>B</b>	<b>B</b>	<b>P/B</b>	<b>Q/B</b>	<b>P/Q</b>	<b>U</b>
	gC m <sup>-2</sup>	tWW	gC m <sup>-2</sup> y <sup>-1</sup>	gC m <sup>-2</sup> y <sup>-1</sup>		
<i>Euphausia crystallorophias</i>	0.041	682 369	1.8	13	0.14	0.20
<i>Euphausia superba</i>	0.092	1 541 097	1.1	8.3	0.13	0.20
Other macrozooplankton	0.037	623 421	2.0	15	0.13	0.20
Mesozooplankton	0.94	...	4.8	16	0.30	0.25
Heterotrophic microplankton	0.40	...	21	61	0.35	0.30
Heterotrophic flagellates	0.30	...	62	177	0.35	0.16

**Table 2.** Summary of diets for zooplankton in the trophic model.

<b>Prey</b>	<b>Predator (proportions in diet)</b>					
	<i>E. crystal-</i> <i>orophias</i>	<i>E. superba</i>	Other macro- zooplankton	Meso- zooplankton	Heterotrophic microplankton	Heterotrophic flagellates
Other macrozoo			0.05			
Mesozooplankton			0.35	0.02		
Het. microplankton	0.21	0.22	0.20	0.15		
Het. flagellates	0.35	0.35	0.03	0.43	0.20	0.07
Phytoplankton	0.30	0.30	0.30	0.40	0.40	0.78
Ice metazoa	0.06	0.05	0.02			

Ice protozoa	0.03	0.02	0.01			
Ice algae	0.05	0.06	0.04			
Bacteria (water)					0.40	0.15

## 9 Acknowledgements

Funding for this work was provided by the New Zealand Foundation for Research, Science and Technology (C01X0505: “Ross Sea sustainability”). We thank Dr Walker O. Smith Jnr (Virginia Institute of Marine Sciences, College of William and Mary, Gloucester Pt., VA 23062, USA) for approval to access AESOPS/JGOFS zooplankton data. We are grateful to Dr Vladislav Barkhatov (TINRO, Vladivostok) for unpublished macrozooplankton and mesozooplankton data (Appendix 2).

## 10 References

- Ackley, S.F.; Bengtson, J.L.; Boveng, P.; Castellini, M.; Daly, K.L.; Jacobs, S.; Kooyman, G.L.; Laake, J.; Quentin, L.; Ross, G.; Siniff, D.B.; Stewart, D.B.; Stirling, I.; Torres, J.; Yochem, P.K. 2003. A top-down, multidisciplinary study of the structure and function of the pack-ice ecosystem in the eastern Ross Sea, Antarctica. *Polar Record* 39(210): 219-230.
- Atkinson, A.; Siegel, V.; Pakhomov, E.A.; Rothery, P.; Loeb, V.; Ross, R.M.; Quetin, L.B.; Schmidt, K.; Fretwell, P.; Murphy, E.J.; Tarling, G.A.; Fleming, A.H. 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology progress Series* 362: 1-23.
- Atkinson, A.; Synder, R. 1997. Krill-copepod interactions at South Georgia, Antarctica. I. Omnivory by *Euphasia superba*. *Marine Ecology Progress Series* 160: 63-76.
- Atkinson, A.; Siegel, V.; Pakhomov, E.; Rothery, P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100-103.
- Azzali, A.; Kalinowski, J. 2000. Spatial and temporal distribution of krill *Euphausia superba* biomass in the Ross Sea (1989–1990 and 1994). In: Faranda, F.M.; Guglielmo, L.; Ianora, A. (eds.) *Ross Sea Ecology*. Berlin, Springer-Verlag. p. 433–456.
- Azzali, M.; Leonori, I.; De Felice, A.; Russo, A. 2006. Spatial-temporal relationships between two euphausiid species in the Ross Sea. *Chemistry and Ecology (Suppl.)* 22: 219-233.
- Baker, A. 1959. The circumpolar continuity of Antarctic plankton species. *Discovery Report* 27: 201-218.
- Barange, M.; Gibbons, M.J.; Carola, M.; 1991. Diet and feeding of *Euphausia hanseni* and *Nematoscelis megalops* (Euphausiacea) in the northern Benguela Current: ecological significance of vertical space partitioning. *Marine Ecology Progress Series* 73: 173-181.
- Becquevort, S.; Mathot, S.; Lancelot, C. 1992. Interactions in the microbial community of the marginal ice zone of the northwestern Weddell Sea through size distribution analysis. *Polar Biology* 12(2): 211-218.
- Becquevort, S. 1997. Nanaprotozooplankton in the Atlantic sector of the Southern Ocean during early spring: biomass and feeding activities. *Deep Sea Research II* 44(1-2): 355-373.
- Beers, J.R.; Stewart, G.L. 1970. Numerical abundance and estimated biomass of microzooplankton. In: J.D.H. Strickland (ed.) *The ecology of the plankton off La Jolla, California, in the period April through September, 1967. Part V1. Bulletin of the Scripps Institution of Oceanography* 17: 67-87.
- Bjørnsen, P.; Kuparinen, J., 1991. Growth and herbivory by heterotrophic dinoflagellates in the Southern Ocean, studied by microcosm experiments. *Marine Biology* 106: 1–9.
- Boxshall, G.A. 1981. Community structure and resource partitioning – the plankton. Forey, P.L. (ed.) “The evolving Biosphere”. Cambridge, The University Press, pp 143-156.



- Bradford-Grieve, J.; Fenwick, G. 2001. A review of the current knowledge describing the biodiversity of the Ross Sea. Final research report for Ministry of Fisheries, Research Project ZBD2000/01 Objective 1 (in part). 93 pp.
- Bradford-Grieve, J.M.; Probert, P.K.; Nodder, S.D.; Thompson, D.; Hall, J.; Hanchet, S.; Boyd, P.; Zeldis, J.; Baker, A.N.; Best, H.A.; Broekhuizen, N.; Childerhouse, S.; Clark, M.; Hadfield, M.; Safi, K.; Wilkinson, I. 2003. Pilot trophic model for subantarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer efficiency system. *Journal of Experimental Marine Biology and Ecology* 289: 223-262.
- Brierley, A.S. et al. 2002. Antarctic krill under sea ice; elevated abundance in a narrow band just south of the ice edge. *Science* 295: 1890-1892.
- Brierley, A.S.; Watkins, J.L. 2000. Effects of sea ice cover on the swarming behaviour of Antarctic krill, *Euphausia superba*. *Canadian Journal of Fisheries and Aquatic Sciences* 57(3): 24-30.
- Brinton, E.; Ohman, M.D.; Townsend, A.W.; Knight, M.D.; Bridgeman, A.L. 1999/2000: Euphausiids of the World Ocean. Paris, UNESCO, distributed by ETI, University of Amsterdam. Macintosh version (1999), ISBN 3-540-14770-5, Windows version (2000), ISBN 3-540-14673-3. Approx. 600 Mbytes.
- Caron, D.A.; Dennett, M.R.; Lonsdale, D.J.; Moran, D.M.; Shalaponok, L. 2000. Microzooplankton herbivory in the Ross Sea, Antarctica. *Deep-Sea Research II* 47: (15-16): 3249-3272.
- Cartes, J.E.; Maynou, F. 1998. Food consumption by bathyal decapod crustacean assemblages in the western Mediterranean: predatory impact of megafauna and the food consumption-food supply balance in the deep-water food web. *Marine Ecology Progress Series* 171: 233-246.
- Chase, Z.; Price, N.M. 1997. Metabolic consequences of iron deficiency in heterotrophic marine protozoa. *Limnology and Oceanography* 42: 1673-1684.
- Clarke, A.; R.J.G. Leakey 1996. The seasonal cycle of phytoplankton, micronutrients and the microbial community in a near shore Antarctic marine ecosystem. *Limnology and Oceanography* 45: 55-63.
- Cripps, G.C.; Atkinson, A. 2000. Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*. *Canadian Journal of Fisheries and Aquatic Science* 57(3): 31-37.
- Cripps, G.C.; Hill, H.J. 1998. Changes in lipid composition of copepods and *Euphausia superba* associated with diet and environmental conditions in the marginal ice zone, Bellingshausen Sea, Antarctica. *Deep-Sea Research I* 45: 1357-1381.
- Cripps, G.C.; Watkins, J.L.; Hill, H.J.; Atkinson, A. 1999. Fatty acid content of Antarctic krill *Euphausia superba* at South Georgia related to regional populations and variations in diet. *Marine Ecology Progress Series* 181: 177-188.
- Daly, K.L.; Macaulay, M.C. 1988. Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring 1983. *Deep Sea Research I* 35: 1564-1576.
- Daly, K.L.; Macaulay, M.C. 1991. Influence of physical and biological mesoscale dynamics on the seasonal distribution and behaviour of *Euphausia superba* in the Antarctic marine ice zone. *Marine Ecology Progress Series* 79: 37-66.
- Daniels, R.M.; Richardson, T.L.; Ducklow, H.W. 2006. Food web structure and biogeochemical processes during oceanic phytoplankton blooms: An inverse model analysis. *Deep-Sea Research II* 53: 532-554.
- Dennett, M.R.; Mathot, S.; Caron, D.A.; Smith Jr, W.O.; Lonsdale, D. 2001. Abundance and distribution of phototrophic and heterotrophic nano- and microplankton in the southern Ross Sea. *Deep Sea Research II* 48, pp. 4019-4038.
- Dodge, J.D.; Priddle, J. 1987. Species composition and ecology of dinoflagellates from the Southern Ocean near South Georgia. *Journal of Plankton Research* 9(4): 685-697.

- Drits, A.V.; Pasternak, A.F.; Kosobokova, K.N. 1993. Feeding, metabolism and body composition of the Antarctic copepod *Calanus propinquus* Brady with special reference to its life cycle. *Polar Biology* 13: 13–21.
- Dubischar, C.; Bathmann, U.V. 1997. Metazooplankton grazing across frontal systems in the Southern Ocean. *Deep-Sea Research Part II* 44: 415–433.
- Ducklow, H.W.; Fraser, W.; Karl, D.M.; Quetin, L.B.; Ross, R.M.; Smith, R.C.; Stammerjohn, S.E.; Vernet, M.; Daniels, R.M. 2006. Water-column processes in the West Antarctic Peninsula and the Ross Sea: Interannual variations and foodweb structure. *Deep-Sea Research Part II* 53(8-10): 834–852.
- Edler, L. 1979. Recommendations on methods for marine biological studies in the Baltic Sea. *Baltic Marine Biology Publication* 5: 1–38.
- Edwards, D.D.; McFeters, G.A.; Ventatesan, M.I. 1998. Distribution of *Clostridium perfringens* and fecal sterols in a benthic coastal marine environment by the sewage outfalls from McMurdo Station, Antarctica. *Applied and Environmental Microbiology* 64(7): 2596–2600.
- Elbracter, M.; Zolfel, M., 1993. Taxonomy and ecology of heterotrophic ice-flagellates. In: Spindler, M., Dieckmann, G., Thomas, D. (Eds). The Expedition ANTARKTIS X/3 of RV Polastern in 1992. *Berichte zur Polarforschung* 121: 26–29.
- Eppley, R.W.; Reid, F.M.H.; Strickland, J.D.H. 1970. Estimates of phytoplankton crop size, growth rate and primary production. *Bulletin of the Scripps Institution of Oceanography* 17: 33–42.
- Everson, I. 1984. Zooplankton. In: Antarctic Ecology. Volume 2. Laws (ed.) pp 463–490. Academic Press, London.
- Fabry, V.J. 1989. Aragonite production by pteropod mollusc in the subarctic Pacific. *Deep-Sea Research* 36(11A): 1735–1751.
- Fenchel T. 1987. Ecology of Protozoa. Berlin, Springer-Verlag. 197 p.
- Fonda Umani, S.F.; Monti, M.; Nuccio, C. 1998. Microzooplankton biomass distribution in Terra Nova Bay, Ross Sea (Antarctica). *Journal of Marine Systems* 17: 289–303.
- Froneman, P.W.; Pakhamov, E.A.; Gurney, L.J.; Hunt, B.P.V. 2002. Predation impact of carnivorous macrozooplankton in the vicinity of the Prince Edward Island archipelago (Southern Ocean) in austral autumn 1998. *Deep-Sea Research II* 49(16): 3243–3254.
- Froneman, P.W.; Pakhomov, E.A.; Perisinotto, R.; McQuaid, C.D. 1996. Role of microplankton in the diet and daily ration of Antarctic zooplankton species during austral summer. *Marine Ecology Series* 143: 15–23.
- Fukichi, M.; Tanimura, A.; Ohtsuka, H. 1985. Marine biological and oceanographical investigations in Lutzow-Holm Bay, Antarctica. Antarctic Nutrient Cycles and Food Webs, W.R. Siegfrieds (ed), Berlin, Springer, 52–59.
- Garrison, D.L.; Buck, K.R.; Gowing, M.M. 1993. Winter plankton assemblages in the ice edge zone of the Weddell and Scotia Seas: composition, biomass and spatial distributions. *Deep-Sea Research I* 40(2): 311–338.
- Genhai, Z. 1989. Diet analysis of Antarctic krill *Euphausia superba* Dana. *Acta Oceanologica Sinica* 8(3): 457–462.
- Genhai, Z.; Chen, S.; Zhao, G. 1993. Study on nano- and microalgae in adjacent waters of the Antarctica. 3. Species composition of nano- and feces of *Euphausia superba* Dana in adjacent waters of the South Shetland Islands. *Antarctic Research/Nanji Yanjiu. Shanghai* 5(2): 43–51.
- Gowing, M.M. Garrison, D.L. 2003. Larger microplankton in the Ross Sea: Abundance, biomass and flux in the austral summer. *Antarctic Research Series* 78: 243–260.
- Hampton, I. 1985. Abundance, distribution and behaviour of *Euphausia superba* in the Southern Ocean between 15° and 30° E during FIBEX. In: Siegfried, W.R.; Condy, P.R.; Laws, R.M. (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin, pp. 294–203.

- Hanchet, S.M.; J. Mitchell; D. Bowden; M. Clark; J. Hall; R. O'Driscoll; M. Pinkerton; D. Robertson. 2008. Preliminary report of the New Zealand RV Tangaroa IPY-CAML survey of the Ross Sea region, Antarctica, in February–March 2008. CCAMLR document WG-EMM-08/18.
- Hernandez-Leon, S.; Portillo-Hahnefeld, A.; Almeida, C.; Becognee, P.; Moreno, I. 2001. Diel feeding behaviour in the Gerlache Strait, Antarctica. *Marine Ecology Progress Series* 223: 235-242.
- Hewitt, R.; and 16 co-authors. 2002. Setting a precautionary catch limit for Antarctic krill. *Oceanography* 15(3): 26-33.
- Hicks, G.R.F. 1974. Variation in zooplankton biomass with hydrographical regime beneath the seasonal ice, McMurdo Sound, Antarctica. *New Zealand Journal of Marine and Freshwater Research* 8(1): 67-77.
- Hopkins, T.L. 1971. Zooplankton standing crop in the Pacific sector of the Antarctic. In: Llano, G.A. & Wallen, I.E. (eds), *Biology of the Antarctic Seas IV*. American Geophysical Union, Washington D.C. *Antarctic Research Series* 17: 347-362.
- Hopkins, T.L. 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology* 96: 93-106.
- Hunt, B.P.V.; Pakhomov, E.A.; Hosie, G.W.; Siegel, V.; Ward, P.; Bernard, K. 2008. Pteropods in Southern Ocean ecosystems. *Progress in Oceanography* 78: 193-221.
- Huntley, M.; Zhou, M. 2000. US JGOFS Data System: Southern Ocean zooplankton displacement volumes from MOCNESS tows. U.S. JGOFS. Available (January 2009) from: <http://usjgofs.who.edu/jg/dir/jgofs/>
- Huntley, M.E.; Nordhausen, W. 1995. Ammonia cycling by Antarctic zooplankton in winter. *Marine Biology* 121(3): 457-467.
- Huntley, M.E.; Nordhausen, W.; Lopez, M.D.G. 1994. Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter. *Marine Ecology Progress Series* 107: 23-40.
- Ikeda, T. 1985. Life history of Antarctic krill *Euphausia superba*: A new look from an experimental approach. *Bulletin of Marine Sciences* 37: 599-608.
- Ikeda, T.; Kirkwood, R. 1989. Metabolism and body composition of two euphausiids (*Euphausia superba* and *E. crystallorophias*) collected from under the pack-ice off Enderby Land, Antarctica. *Marine Biology* 100: 301-308.
- Ju, S.-J.; Harvey, H.R. 2004. Lipids as markers of nutritional condition and diet in the Antarctic krill *Euphausia superba* and *Euphausia crystallorophias* during austral winter. *Deep-Sea Research II* 51(17-19): 2199-2214.
- Kawaguchi, S.; T. Yoshida; L. Finley; P. Cramp; S. Nicol, 2007. The krill maturity cycle: a conceptual model of the seasonal cycle in Antarctic krill. *Polar Biology* 30(6): 689-698.
- Kjørboe, T., 1998. Population regulation and role of mesozooplankton in shaping marine pelagic food webs. *Hydrobiologia* 363(1-3): 13-27.
- Kirkwood, J.M. 1996. The development of *Euphausia crystallorophias* in Ellis Fjord, Vestfold Hills, Antarctica. *Polar Biology* 16: 527-530.
- Klaas, C. 1997. Microprotozooplankton distribution and grazing impact in the open waters of the Antarctic Circumpolar Current. *Deep-Sea Research II* 44: 375-393
- Landry, M.R.; K.E. Selph; S.L. Brown; M.R. Abbott; C.I. Measures; S.M. Vink; C.B. Allen; A. Calbet; S. Christensen; H. Nolla. 2002. Seasonal dynamics of phytoplankton in the Antarctic Polar Front region at 170°W. *Deep Sea Research Part II* 49: 1843-1865.
- Lascara, C.M.; Hoffman, E.E.; Ross, R.M.; Quetin, L.B. 1999. Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. *Deep-Sea Research I* 46(6): 951-984.

- Laws, E.A.; Falkowski, P.; Smith, W.O. Jr.; Ducklow, H.W.; McCarthy, J.J. 2000. Temperature effects on export production in the open ocean. *Global Biogeochemical Cycles* 14: 1231-1246.
- Lessard, E.J.; Rivkin, R.B. 1986. Nutrition of microzooplankton and macrozooplankton from McMurdo Sound. *Antarctic Journal of the US* 21: 187-188.
- Lessard, E.J.; Swift, E. 1985. Species-specific grazing rates of heterotrophic dinoflagellates in oceanic waters, measured with a dual-label radioisotope technique. *Marine Biology* 87, 289-296.
- Lessard, E.J.; Swift, E. 1986. Dinoflagellates from the North Atlantic classified as phototrophic or heterotrophic by epifluorescence microscopy. *Journal of Plankton Research* 8: 1209-1215.
- Lindley, J.A. 1982. Population dynamics and production of euphausiids. 4. *Euphausia krohni*, *Nematoscelis megalops* and *Thysanoessa gregaria*, and eight rare species in the North Atlantic Ocean. *Marine Biology* 71(1): 1-6.
- Littlepage, J.L. 1964. Seasonal variation in lipid content of two Antarctic marine Crustacea. In: Carrick, R.; Holdgate, M.; Prévost, F. (eds) *Biologie Antarctique*, Pp. 463-470, Herman, Paris.
- Lonsdale, D.J.; Caron, D.A.; Dennett, M.R.; Schaffner, R. 2000. Predation by *Oithona* spp. on protozooplankton in the Ross Sea, Antarctica. *Deep Sea Research Part II* 47(15-16), 3273-3283.
- Makarov, R.R.; Men'shenina, L.L.; Timonin, V.P.; Shurunov, N.A. 1991. Ecology of larvae and reproduction of Euphausiidae in the Ross Sea. *Biologiya Morya* 3: 156-162. [Translation from Russian. Original Article published 1988]
- Makarov, R.R.; Men'shenina, L.L.; Solyankin, E.V. 1992. Euphausiid larvae in the eastern part of the Weddell Gyre. *Oceanology* 32(2): 276-284.
- Marin, V.H.; Brinton, E.; Huntley, M. 1991. Depth relationships of *Euphausia superba* eggs, larvae and adults near the Antarctic Peninsula, 1986-87. *Deep-Sea Research* 38(8-9A): 1249-1249.
- Marr, J. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Report* 32: 33-464.
- Mayzaud, P.; Razouls, S.; Errhif, A.; Tirelli, V.; Labat, J.P. 2002a. Feeding, respiration and egg production rate of copepods during austral spring in the Indian sector of the Antarctic Ocean: role of the zooplankton community in carbon transformation. *Deep-Sea Research* 49(6): 1027-1048.
- Mayzaud, P.; Tirelli, V.; Errhif, A.; Labat, J.P.; Razouls, S.; Perissinotto, R. 2002b. Carbon intake by zooplankton. Importance and role of zooplankton grazing in the Indian sector of the Southern Ocean. *Deep-Sea Research II* 49: 3169-3187.
- McClatchie, S.; Rakusa-Suszczewski, S.; Filcek, K. 1991. Seasonal growth and mortality of *Euphausia superba* in Admiralty Bay, South Shetland Islands, Antarctica. *ICES Journal of Marine Science* 48: 335-342.
- McConnaughty, R.A.; Conquest, L.L. 1992. Trawl survey estimation using a comparative approach based on lognormal theory. *Fishery Bulletin* 91: 107-118.
- Menushutkin, V.V. 1993. Model of population of Antarctic krill. In: Voronina, N.M. (ed.) *Pelagic ecosystems of the Southern Ocean*, Moscow, pp. 182-185. (In Russian).
- Metz, C. 1998. Feeding of *Oncaea curvata* (Poecilostomatoida, Copepoda). *Marine Ecology Progress Series* 169: 229-235.
- Metz, C.; Schnack-Schiel, S.B. 1995. Observations on carnivorous feeding in Antarctic calanoid copepods. *Marine Ecology Progress Series* 129: 71-73
- Meyer, B.; Atkinson, A.; Blume, B.; Bathmann, U.V. 2003. Feeding and energy budgets of larval Antarctic krill *Euphausia superba* in summer. *Marine Ecology Progress Series* 257: 167-177.

- Miller, D. 2003. Species profile Antarctic Krill (*Euphausia superba*). Unpublished CCAMLR document, version 5: 21 May 2003, CCAMLR Secretariat, 82 pp.
- Miller, D.G.M.; Hampton, I. 1989. Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): A review. Biological Investigation of Marine Antarctic Systems and Stocks (BIOMASS) Vol. 9, SCAR / SCOR, Cambridge, England, Scott Polar Research Institute. 199 p.
- Miller, D.G.M.; Hampton, I. 1989. Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): a review. International Council of Scientific Unions. Scientific Committee on Antarctic Research. BIOMASS scientific series; 166.
- Miller, D.G.M.; Hampton, I.; Henry, J.; Abrams, R.W.; Cooper, J. 1985. The relationship between krill food requirements and phytoplankton production in a sector of the Southern Indian Ocean. In: Siegfried, W.R.; Condy, P.R.; Laws, R.M. (eds), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin, pp. 362-371.
- Monti, M., Fonda Umani, S., 2000. Distribution of the main microzooplankton taxa in the Ross Sea (Antarctica): austral summer 1994. In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), Ross Sea Ecology. Springer-Verlag, Berlin, pp. 275- 289.
- Nicol, S.; S. Kawaguchi, 2004. Developing conceptual models of elements of the Antarctic marine ecosystem: Antarctic krill (*Euphausia superba*). Unpublished paper for CCAMLR. WG-EMM-04/05, 25 June 2004.
- Nicol, S.; Virtue, P.; King, R.; Davenport, S.R.; McGaffin, A.F.; Nichols, P. 2004. Condition of *Euphausia crystallorophias* in East Antarctica in winter in comparison to other seasons. *Deep-Sea Research II* 51(17-19): 2215-2224.
- Nishino, Y.; Kawamura, A. 1994. Feeding ecology of Antarctic krill (*Euphausia superba* Dana). *Bull. Fac. Bioresour. Mie Univ./Miedai Seibutsushigen Kiyo* 249-264.
- Nordhausen, W. 1994. Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macroura* in Gerlache Strait and Crystal Sound, Antarctica. *Marine Ecology Progress Series* 109: 131-142.
- Nordhausen, W.; Huntley, M.; Lopez, M. D. G. 1992. RACER: Carnivory by *Euphausia superba* during the Antarctic winter. *Antarctic Journal of the United States* 27: 181-183.
- O'Brien, D. P. 1987. Direct observations of the behaviour of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985. *Journal of Crustacean Biology* 7: 437-448.
- O'Driscoll R.L.; Macaulay, G.J.; Gauthier, S.; Pinkerton, M.; Hanchet, S. 2009. Preliminary acoustic results from the New Zealand IPY-CAML survey of the Ross Sea region in February-March 2008. *CCAMLR SG-ASAM-09-05*. 37 p.
- Øresland, V. 1991. Feeding of the carnivorous copepod *Euchaeta antarctica* in Antarctic waters. *Marine Ecology Progress Series* 78: 41-47.
- Pakhomov, E.A.; Atkinson, A.; Meyer, B.; Oettl, B.; Bathmann, U. 2004. Daily rations and growth of larval krill *Euphausia superba* in the Eastern Bellingshausen Sea during austral autumn. *Deep-Sea Research II* 51(17-19): 2185-2198.
- Pakhomov, E.A.; Froneman, P.W. 2004. Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during the austral summer 1997/1998 – Part 2: Grazing impact. *Deep-Sea Research II* 51: 2617-2631.
- Pakhomov, E.A.; Perissinotto, R. 1996. Antarctic neritic krill *Euphausia crystallorophias*: Spatio-temporal distribution, growth and grazing rates. *Deep-Sea Research II* 43: 59-87.
- Pakhomov, E.A.; Perissinotto, R. 1997. Spawning success and grazing impact of *Euphausia crystallorophias* in the Antarctic shelf region. In: Antarctic communities: species, structure and survival. Battaglia B.; J. Valencia; D.W.H. Walton (eds). Cambridge University Press Cambridge 187-192.

- Pakhomov, E.A.; Perissinotto, R.; Froneman, P.W. 1998. Abundance and trophodynamics of *Euphausia crystallorophias* in the shelf region of the Lazarev Sea during austral spring and summer. *Journal of Marine Systems* 17: 131-324.
- Pasternak, A.F.; Schnack-Schiel, S.B. 2001. Feeding patterns of dominant Antarctic copepods: an interplay of diapause, selectivity, and availability of food. *Hydrobiologia* 453/454: 25–36.
- Perissinotto, R.; Gurney, L.; Pakhomov, E.A. 2000. Contribution of heterotrophic material to diet and energy budget of Antarctic krill, *Euphausia superba*. *Marine Biology* 136: 129-135.
- Price, H.R.; K.R. Boyd; Boyd, C.M. 1988. Omnivorous feeding behaviour of the Antarctic krill *Euphausia superba*. *Marine Biology* 97: 67-77.
- Priddle J.; Croxall, J.P.; Everson, I. et al. 1988. Large-scale fluctuations in distribution and abundance of krill – a discussion of possible causes. In: Sahrhage D. (ed.) Antarctic Ocean resources and Variability, Springer-Verlag, Berlin.
- Putt M.; Stoeker D.K. 1989. An experimentally determined. carbon:volume ratio for marine ‘oligotrichous’ ciliates from estuarine and coastal waters. *Limnology and Oceanography* 34: 1097-1103.
- Quetin, L.B. and Ross R.M., 1991. Behavioural and physiological characteristic of the Antarctic krill, *Euphausia superba*. *American Zoologist* 31: 49-63.
- Quetin, L.B.; R.M. Ross; A. Clarke. 1994. Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. In: S.Z. El-Sayed (Ed). Southern Ocean Ecology: The BIOMASS Perspective. Cambridge University Press, Cambridge, 165–184.
- Rakusa-Suszczewski, S.; Stepnik, R. 1980. Three species of krill from Admiralty Bay (King George, South Shetlands), in summer 1978/79. *Polar Archiv für Hydrobiologie* 27(2): 273–284.
- Robins, D.B.; Harris, R.P.; Bedo, A.W.; Fernancez, E.; Fileman, T.W.; Harbour, D.S.; Head, R.N. 1995. The relationship between suspended particulate material, phytoplankton and zooplankton during the retreat of the marginal ice zone in the Bellingshausen Sea. *Deep-Sea Research II* 42(4-5): 1137-1158.
- Roman, M.R.; Rublee, P.A. 1981. A method to determine in situ grazing rates on natural particle assemblages. *Marine Biology* 65: 303-309.
- Ross, R.M.; Quetin, L.B.; Baker, K.S.; Vernet, M.; Smith, R.C. 2000. Growth limitation in young *Euphausia superba* under field conditions. *Limnology and Oceanography* 45(1): 31-43.
- Ross, R.M.; Quetin, L.B.; Newberger, T.; Oakes, S.A. 2004. Growth and behaviour of larval krill (*Euphausia superba*) under the ice in late winter 2001 west of the Antarctic Peninsula. *Deep-Sea Research II* 51(17-19): 2169-2184.
- Safi, K.A.; Griffiths, F.B.; Hall, J.A. 2007. Microzooplankton composition, biomass and grazing rates along the WOCE SR3 line between Tasmania and Antarctica. *Deep Sea Research I* 54: 1025-1041.
- Sala, A.; Azzali, M.; Russo, A. 2002. Krill of the Ross Sea: distribution, abundance and demography of *Euphausia superba* and *Euphausia crystallorophias* during the Italian Antarctic Expedition (January-February 2000). *Scientia Marina* 66(2): 123-133.
- Samyshev, E.Z.; A.I. Lushev. 1983. Food ration and its components in Antarctic krill. *Oceanology* 23(6): 763-766.
- Schnack, S.B. 1985. Feeding by *Euphausia superba* and copepod species in response to varying conditions of phytoplankton. In: Antarctic Nutrient Cycles and Food Webs. Siegfried, W.R., P.R. Condy and R.M. Laws (eds). Springer-Verlag, Berlin, Germany, 311-323.
- Schack-Schiel, S.B.; Hagen, W.; Mizadlski, E. 1998. Seasonal carbon distribution of copepods in the eastern Weddell, Sea, Antarctica. *Journal of Marine Systems* 17(1-4): 305-311.
- Schnack, S.B.; Smetacek, V.; Bodungen, B. v.; Stegmann, P. 1985. Utilization of phytoplankton by copepods in Antarctic waters during spring. In: Gray, J.S.; Christiansen, M.E. (eds). Marine Biology of Polar Regions and Effects of Stress on Marine Organisms. Chichester, John Wiley & Sons. p. 65-81.

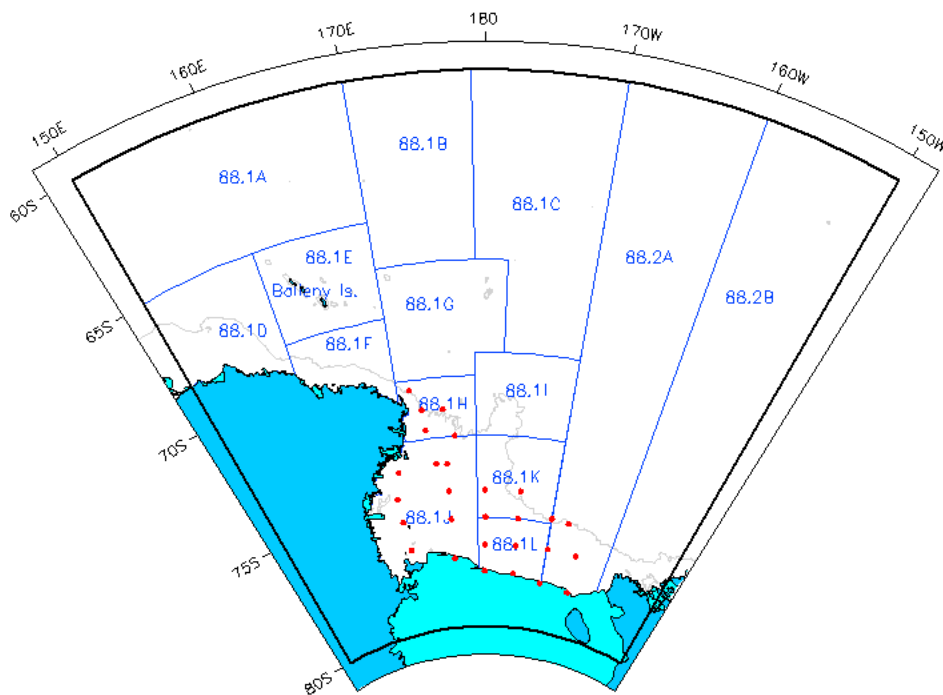
- Scott, F.J.; Davidson, A.T.; Marchant, H.J. 2001. Grazing by the Antarctic sea ice ciliate *Pseudocohnilembus*. *Polar Biology* 24: 127–131.
- Sertorio, T.Z.; Licandro, P.; Ossola, C.; Artegaiani, A. 2000. Copepod communities in the Pacific Sector of the Southern Ocean in early summer. In: Ross Sea Ecology, Faranda, F.M.; Gulielmo, L.; Ianora, A. (eds.), Springer, Berlin. Pp. 292-307.
- Sherr, E.B.; Sherr, B.F. 1993. Preservation and storage of samples for enumeration of heterotrophic protists. p. 207-212, In: P. Kemp, B. Sherr, E. Sherr, and J. Cole (eds), Current Methods in Aquatic Microbial Ecology, Lewis Publ., NY..
- Shushkina, E.A.; Vinogradov, M.E.; Lebedeva, L.P. 1998. Biotic balance in the ocean and estimation of the organic matter flux from epipelagic zones on the basis of satellite and expeditionary data. *Oceanology* 38: 628-635. (Translation from Russian).
- Siegel, V. 1986. Structure and composition of the Antarctic krill stock in the Bransfield Strait (Antarctic Peninsula) during the Second International BIOMASS Experiment (SIBEX). *Archiv fuer Fischereiwissenschaft* 37: 51-72.
- Siegel, V. 1987. Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Marine Biology* 96: 483-495.
- Siegel, V. 2000a. Krill (Euphausiacea) life history and aspects of population dynamics. *Canadian Journal of Fisheries and Aquatic Science* 57(3): 130-150.
- Smetacek, V.; Scharek, R.; Nothig, E.-M. 1990. Seasonal and regional variation in the pelagial and its relationship to the life history of krill. In: K.R. Kerry and G. Hempel (eds). Antarctic Ecosystems: Ecological Change and Conservation. Springer-Verlag, Heidelberg: 103-114.
- Stoecker, D.K.; Putt, M.; Moisan, T. 1995. Nano- and microplankton dynamics during the spring *Phaeocystis* sp. bloom in McMurdo Sound, Antarctica. *Journal of the Marine Biological Association of the UK* 75: 815-832.
- Strathmann, R.R. 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasmic volume. *Limnology and Oceanography* 12: 411–418.
- Tagliabue, A.; Arrigo, K.R. 2003. Anomalously low zooplankton abundance in the Ross Sea: An alternative explanation. *Limnology and Oceanography* 48(2): 686-699.
- Timonin, V.P. 1987. Distribution pattern and age composition of larval *Euphausia superba* Dana in the Pacific and Indian Ocean sectors of the Antarctic Ocean. *Biologo-Okeanograficheskie Issledovaniya Tikhookeanskogo Sektora Antarktiki* 119-135.
- Tortell, P.D.; Maldonado, M.T.; Price, N.M. 1996. The role of heterotrophic bacteria in iron-limited ocean ecosystems. *Nature* 383(6598): 330-332.
- Tseitlin, V.B. 1989. Biomass and production of Antarctic krill. In: Ponomareva, L.A. (ed.) Complex studies of the plankton of the Southern Ocean, Institute of Oceanology, Academy of Sciences, Moscow. pp. 118-122. (In Russian).
- Umani, S.F.; Monti, M.; Nuccio, C. 1998. Microzooplankton biomass distribution in Terra Nova Bay, Ross Sea (Antarctica). *Journal of Marine Systems* 17(1-4): 289-303.
- Urban-Rich, J.; Dagg, M.; Petersen, J. 2001. Copepod grazing on phytoplankton in the Pacific sector of the Antarctic Polar Front. *Deep-Sea Research II* 48(19-20): 4223-4246.
- Vanucci, S.; Bruni, V. 1998. Presence or absence of picophytoplankton in the western Ross Sea during spring 1994: a matter of size definition? *Polar Biology* 20: 9-13.
- Verity, P.G.; Langdon, C. 1984. Relationship between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *Journal of Plankton Research* 66: 859-868.
- Verity, P.G.; Stoecker, D.K.; Sieracki, M.E.; Nelson, J.R.; 1993. Grazing, growth and mortality of microzooplankton during the 1989 North Atlantic spring bloom at 47°N, 18°W. *Deep-Sea Research I* 40: 1793-1814.
- Voronina, N.M. 1983. Biomass and production of Antarctic krill (*Euphausia superba* Dana). *Oceanology* 23(6): 760-761.

- Voronina, N.M. 1995. Euphausiid larvae in the southern part of the Pacific sector of Antarctic in February to March, 1992. *Oceanology* 35 (5): 725-732. [English language edition 1996.]
- Voronina, N.M. 1998. Comparative abundance and distribution of major filter-feeders in the Antarctic pelagic zone. *Journal of Marine Systems* 17: 375-390.
- Voronina, N.M.; Maslennikov, V.V. 1993. Plankton as an indicator of water transport in the Antarctic. *Okeanologiya* 33(5): 717-720.
- Voronina, N.M.; Menshutkin, V.V.; Tseytlin, V.B. 1980a. Production of the common species of Antarctic copepods, *Calanoides acutus*. *Oceanology* 20(1): 90-93.
- Voronina, N.M.; Menshutkin, V.V.; Tseytlin, V.B. 1980b. Model investigations of the annual production cycle of the abundant copepod species *Rhincalanus gigas* and estimate of its production in the Antarctic. *Oceanology* 20(6): 709-713.
- Ward, P.; Atkinson, A.; Murray, A.W.A.; Wood, A.G.; Williams, R.; Poulet, S.A. 1995. The summer zooplankton community at South Georgia: biomass, vertical migration and grazing. *Polar Biology* 15: 195-208.
- Weibe, P.H. 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. *Fishery Bulletin* 86(4): 833-835.
- Zhong, X.; Wang, R. 1993. Distribution and larval development of *Euphausia crystallorophias* in the Prydz Bay region, Antarctica. *Antarctic Research/Nanji Yanjiu. Shanghai* 5(4): 32-39.
- Zhou, M.; Nordhausen, W.; Huntley, M.E. 1994. ADCP measurements of the distribution and abundance of euphausiids near the Antarctic peninsula in winter. *Deep-Sea Research I* 41: 1425-1445.
- Zhou, M.; Zhu, Y.; Petersen, J.O. 2004. *In situ* growth and mortality of mesozooplankton during the austral fall and winter in Marguerite Bay and its vicinity. *Deep-Sea Research II* 51: 2099-2118.
- Zvereva, Zh. A. 1975. Seasonal changes of Antarctic plankton in the Molodezhnaya and Mirny Region. In: "Geographical and seasonal variability of marine plankton." Leningrad, Zoological Institute, Academy of Sciences, USSR. 303 pp.



## Appendix 1: Biomass estimation from Barkhatov data

Dr Vladislav Barkhatov (TINRO, Vladivostok) kindly provided unpublished macrozooplankton and mesozooplankton data that was collected between 5 February – 26 March 1982 from the research vessel “Mys Junony”, using an Isaacs-Kidd midwater trawl and Juday Net, respectively. 1982 was a year when there was extensive open water in the Ross Sea. Twenty-five stations were sampled from 0-100, 100-200 and often 200-500m (Figure 3). At a number of stations, samples were taken from near the sea floor, but 7 stations had a depth between 700 more than 1000 m.



**Figure 3.** Stations at which Barkhatov data are available and used here (red circles).

The more conspicuous species found in these samples were: Coelenterata (*Dipulmaris antarctica*, *Calycopsis borchgrevinki*, *Nausithoe* sp.), Pteropoda (*Clione limacina*, *Limacina helica*), Amphipoda (*Hyperiella dilatata*, *H. macronyx*, *Cylopus lucasii*), Euphausiacea (*Euphausia superba*, *E. crystallorophias*, *Thysanaessa macrura*), Chaetognatha (*Sagitta gazellae*, *Eukrohnia hamata*), and Salpidae (*Salpa gerlachei*).

Integrated non-salp macrozooplankton wet weight was converted to carbon biomass using an average of the relationships of Weibe (1988) and Ikeda & Kirkwood (1989). Salp wet weight was converted to units of carbon using the observations of Dubischar et al. (2006) which indicate that for *Salpa* dry weight is about 4% of wet weight and carbon content about 8.5% of dryweight. Mesozooplankton wet weight was converted to carbon biomass using the relationship of Weibe (1988).

Integrated biomass from the surface to the sea floor is estimated from the 1982 data assuming that decreases in macrozooplankton biomass decreases linearly with depth from the deepest measurement to 200 m. We use the same approach for mesozooplankton, assuming negligible

biomass of mesozooplankton below 200 m consistent with acoustic data in the region (O'Driscoll 2006; O'Driscoll & Macaulay 2003).