Birds: Trophic modelling of the Ross Sea

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1 Birds in the Ross Sea

The model includes bird species breeding in the Ross Sea and major visitors to the region. Eleven species of birds are known to breed in the Ross Sea study area, and in adjacent regions (Table 1: Harper et al. 1984, Ainley et al. 1984). Birds in the Ross Sea study region are divided into three groups in the trophic model: (1) emperor penguins; (2) Adélie penguins; and (3) flying birds (petrels, albatrosses, skuas). Estimates of biomass for each bird group are given by species below. Methods for estimating the other parameters needed for these birds in the model are considered below.

1.1 Methods of estimating modelling parameters

Two methods were used to estimate production for birds in the Ross Sea where insufficient information exists to allow an annual energetic model to be created (all flying birds). First, in the absence of data and the observation of Ainley et al. (1984) that many birds found in the study area in summer were not breeding, we assumed that about 40% of the adult population breeds in any year. We took egg numbers per breeding pair per year, and egg weights from the literature (Heather & Robertson 1996; Shirihai 2002) to estimate egg production per year. We then assumed egg production is about 5% of total population production, in keeping with results from the modeled penguin populations (see below). Second, we assumed that there is an allometric relationship between weight and P/B as given by Brown et al. (2004), so that P/B of various bird species scales as $W^{-0.25}$. We estimated the constant of proportionality from our models of Adélie and emperor penguins in the Ross Sea as 0.41 y^{-1} $kgWW^{-1}$ and hence estimated P/B values of the other avian species. The absolute average difference between the estimates of production by the two methods was 24.6%, with a mean difference of 10.4% (method 1 higher on average). In the absence of better independent evidence, our best estimate is given by averaging results of the two methods.

1.2 Consumption

Food consumption requirements for each species were estimated by two methods. Nagy (1987) estimated daily dry weight food consumption for seabirds according to body weight. This was converted to carbon using a ratio of 0.4 gC/g wet-weight (Vinogradov 1953). In the second method, average daily energy requirement of seabirds was taken as 2.8 times the standard metabolic rate (SMR: Lasiewski & Dawson 1967; Schneider & Hunt 1982). An assimilation efficiency of 0.75 and energy/carbon ratio of ~10 kcal/gC was used to give carbon requirements (Croxall 1987; Lasiewski & Dawson 1967; Schneider and Hunt 1982). These methods differed by less than 20% for all bird species.

1.3 Assimilation efficiencies

Jackson (1986) measured mean assimilation efficiencies (AE) of five white-chinned petrel (*Procellaria aequinoctialis*) fledglings fed on light-fish (*Maurolicus muelleri*), squid (*Loligo reynaudi*) and Antarctic krill (*Euphausia superba*). AE were found for these prey items to be (respectively) 77.9, 74.4 and 76.0%, respectively. The study states: “After correction for nitrogen retention, AE values decreased to 69.1% for light-fish, 68.0% for squid, and 67.5% for Antarctic krill. Differences in AE for different prey types may result from differential nitrogen content of the prey tissue. Assimilation efficiency values for fish and squid of a specialized feeder, the Jackass penguin, differ more than the AEs of white-chinned petrels for these food types. The generalized diet of the white-chinned petrel may account for this species’ ability to assimilate widely different prey types with similar efficiencies.” In the present study, we use 0.3 as the proportion of unassimilated food for all bird groups.

1.4 Export

If birds were to be killed by interactions with fishing vessels and removed from the region this would also represent a net export of biomass from the system. It is known that birds can be incidentally killed by fisheries activities by collision with lines and wires, or other parts of the ship, entanglement in nets, and ensnarement on hooks. Although the impacts of fishing on marine birds are not systematically observed (Tasker et al. 2000; Taylor 2000a, b), all mortality of seabirds by fishing in the Ross Sea must be reported to CCAMLR. Since 1996, direct seabird mortality from legal fishing in the Southern Ocean has dropped because of mitigation measures taken by the fishing industry. Bird mortality reported by fishing vessels in the Ross Sea is very small: less than 1–2 birds/year for the whole fishery. The numbers of birds killed by non-registered fishing vessels is not known. In the first instance in this study we assume that the amount of carbon transfer as a result of birds being killed by fishing vessels in the Ross Sea is small. It is beyond the scope of the current study to determine whether bird kill by fishing vessels is significant for individual bird populations. Birds can also become entangled in lost fishing gear, disturbed by fishing activity, or affected by pollution from fishing vessels but this will not impinge on the trophic model.

For birds that breed in the Ross Sea study area, there will be an export of biomass from the study region each year at the end of the breeding season. This export will be offset by the breeding adults moving back into the study area to breed the following year. Breeders entering the study area are likely to be heavier on average than those leaving the study area after breeding, suggesting a net import of biomass over a year. However, high mortality of juveniles between leaving the study region for the first time and re-entry as a breeding adult tends to lead to a net export of biomass. Good demographic data is available for Adélie and emperor penguins which allows us to estimate the net import/export of biomass for penguins using demographic models as explained below. Similar information is not available for other (flying) birds in the Ross Sea, but as the more abundant species breed in the study area, we use a similar value for net export for these species as for penguins (15%).

1.5 Ecotrophic efficiency

Ecotrophic efficiencies are not known for birds in the Ross Sea. Where birds are known to suffer direct predators in the study area (Adélie and emperor penguins), ecotrophic efficiencies are set so that a nominal half the mortality is due to direct predation and half due to non-predation mortality (starvation, disease etc). Where little direct predation in the study area is likely or it is not known whether this occurs, (flying birds), all mortality is assumed to be non-predation and ecotrophic efficiency calculated accordingly, taking into account net export from the area. Biomass associated with non-predation mortality of all birds is channeled to the carcass group in the model.

2 Emperor penguin

Emperor penguins (*Aptenodytes forsteri*) are one of the better studied seabirds in the Ross Sea with information available about population size and trends (e.g., Stirling & Greenwood 1970, Kooyman and Mullins 1990; Kooyman 1993), breeding (e.g., Kooyman 1993), and food and feeding (Cherel and Kooyman 1998; Burns & Kooyman 2001). An estimated 29 000–40 000 pairs of emperor penguins breed in six colonies between Cape Roget and Cape Crozier (Young 1981, Harper et al. 1984), and at Franklin Island and Beaufort Island in the Ross Sea (Burns & Kooyman 2001). There are also 6000 pairs of emperor penguins at Cape Colbeck, Marie Byrd Land (Ainley et al. 1984, Kooyman 1994), half of whose foraging area is assumed to lie within the study area. We estimate the number of emperor penguin breeding pairs in the Ross Sea to be 32 500 (Woehler 1993; Woehler & Croxall 1997; Kooyman 1994; Ainley 2002a, b). Recent work using satellite imagery to enumerate emperor penguin numbers (Barber-Meyer et al. 2007) suggests the average number of breeding pairs in 2005 and 2006 in the Ross Sea was about 36 000. This estimate tallies reasonably well in colonies surveyed using aerial photos and ground counts (Kooyman & Mullins 1990; Kooyman 1993; Kooyman et al 2007; Barber-Meyer et al. 2008).

In general, emperor penguin numbers in some colonies in the Ross Sea appear to have increased by c. 3% between 1983 and 1990 (Kooyman & Mullins 1990; Kooyman 1993), but there are differences from year to year and between colonies (Kooyman 1993). In a study of chick abundance trends, Barber-Meyer et al. (2008) suggests that the overall emperor penguin population in the Ross Sea was stable during 1983–2005, and we hence assume negligible long term, population trends in numbers of breeding emperor penguins in the Ross Sea.

It is necessary to take into account the life cycle, population structure, and seasonal movements of emperor penguins to estimate their population biomass and energetic parameters for modelling.

2.1 Life cycle

The effect of the life history of emperor penguins on foraging effort is summarised by Burns & Kooyman (2001). In autumn (Mar/Apr), adults gather in colonies for courtship and mating. The breeding adults, especially males are very fat at this time, weighing up to 40 kg (Shirihai 2002 and references therein) compared to an average weight of the emperor penguin of c. 30 kg (Kooyman et al. 2004). There tends to be an unequal sex ratio in emperor penguins at breeding sites, with more females than males (at one site, about 40% males, 60% females: Dewey 1999). This may imply a higher mortality in males than females, or that a higher proportion of males than females do not breed each year. We assume all males at the breeding colonies will breed, and that unsuccessful and non-breeding females stay in the study area. Juveniles tend to be dispersed to the north (Kooyman et al. 1996) year round.

One egg weighing approximately 515 g is layed per breeding pair in May/June. Penguins eggshells are relatively thick, with the eggshell weight being 9–15.8% as a percentage of whole fresh-egg weight for penguins (Williams et al. 1982; Boersma et al. 2004). Time to hatching is about 64 days on average, with hatching typically between mid-July and the beginning of August (Dewey 1999). Freshly hatched emperor penguin chicks weigh 120–160 g. Males fast while females forage between egg laying and hatching in (mid-July/early August). The males may lose 45% of body weight over this period of fasting than can last 115 days.

Both sexes then alternately forage (trips taking 1–3 weeks) and provision the chick for about 150 days (Dewey 1999) until Dec/Jan. Chicks weigh about 50% of adult mass (approximately

9.9–14.8 kg) at fledging (Dewey 1999; Shirihai 2002). Around late December/early January adults leave the breeding colonies to feed, and also migrate eastwards from the Ross Sea to moult on the large consolidated pack ice of the Amundsen Sea. The migration begins in Jan/Feb, and typically finishes in March (Kooyman et al. 2004). In the population model given below, we remove the adult birds from the study area for 1 month during this migration for moulting. Juveniles disperse northwards from January, and can reach beyond 60°S (Kooyman et al. 1996). Most emperor penguins make their first return to the nesting colony at about 4 years old, but age at first breeding is usually 5–6 y in males and 5 y in females (Williams 1995), with an average close to 5.5 y (Dewey 1999). In the model given below, this movement is assumed to take juveniles out of the study area from May after hatching until aged 4 years.

There are three main foraging periods, and these are associated with different foraging behaviour: (1) after egg laying (females only); (2) during chick provisioning when adults forage within 200 km of colonies (e.g. Cherel & Kooyman 1998); (3) after chick fledging and before moulting when adults travel up to 1200 km to eastern Ross Sea to forage (Kooyman et al. 1996). We assume that the majority of feeding during all of these periods is from within the Ross Sea study area.

2.2 Demographics

Typical demographic parameters and mortalities of emperor penguins for all colonies in the Ross Sea are not well known, and here we use typical values from all colonies where information is available. Median age-at-death for post-juvenile emperor penguins has been estimated at 19.9 years (Dewey 1999) though occasionally is greater than 40 years. Here we assume “average longevity” to mean the median age at death in the adult population (Barlow & Boveng 1991; Trites & Pauly 1998). Assuming the transition from juvenile to adult is at 5.5 y, and that adult mortality is constant with penguin age, we estimate an adult mortality of 0.048 y^{-1}. This is consistent with work that suggests typically around 95% adults survive from year to year (Dewey 1999).

If the male-female proportions at the colonies (40%-60%: Dewey 1999) is representative of adults in the population, and there are the same number of male and female recruits to the adult population, the male mortality is 0.058 y^{-1} and the female mortality is 0.039 y^{-1}. For a stable adult population, this implies a recruitment equivalent to about 4.8% of the biomass of the adult population per year. Egg loss and early chick mortality for one large Ross Sea colony was reported as about 5.4%, with highest chick mortality in July-September (Barber-Mayer et al. 2008). Breeding success (number of chicks fledged divided by number of eggs laid) in emperor penguin colonies seems to be highly variable (from <5% to >80%) depending on conditions, and 60% may be typical (Barbraud & Weimerskirch 2001). Mortality of chicks is highest in the first year, when it is reported that in some cases, only about 19% of young may survive their first year (Dewey 1999).

2.3 Biomass, P/B, Q/B, export estimated from a population model

We used a simple population model to estimate production of a typical emperor penguin population. This model of population numbers and biomass in the model area is seasonally and age-stage resolved, and is based on the assumption of a long-term stable population. The components in the model are: (1) eggs; (2) chicks; (3) juveniles (both sexes); (4) adult, breeding females; (5) adult, breeding males; (6) adult non-breeders (both sexes). The year is divided into 2-week blocks and growth (based on measured seasonal weights of birds) and mortality is applied to each group over each period. Consumption is calculated based on standard metabolic rate (as described above) applied to each size of animal in the population. This method hence takes into account variations in consumption rates between different parts of the population. Growth of chicks and juveniles is taken as approximately linear. Adults are not assumed to grow at all, though their weight varies substantially through periods of foraging, egg incubation, and moulting. Movement patterns of adults and juveniles are taken into account by assuming adults (breeding and non-breeding) are absent from the study area for 6 weeks, Jan/Mar, and juveniles are absent between May after hatching until aged 4 years.

In the model, we assume the population is stable with an adult mortality rate of 0.048 y^{-1}, 62% of all adult emperor penguins breeding each year (Ainley et al. 1984), a breeding success of 60%, and juvenile mortality of 1.0 y^{-1} in the first year and 0.075 y^{-1} thereafter. Other parameters are as given previously. This implies that juvenile survival in the first year after fledging is 35% which seems reasonable. In the model, for 100 adults, there are 62 breeders (31 breeding pairs), 38 adult non-breeders, an average of 34.4 juveniles, and 4.8 animals recruiting into the adult population per year. For a total of 32 500 breeding pairs in the Ross Sea, the model allows us to calculate a total population size of 105 000, and hence an annual average population biomass of emperor penguins that breed in the Ross Sea of 3900 t wet weight. Adults and juveniles spend time out of the study area during the year which is equivalent to reducing this biomass by 20%.

In the modelled emperor penguin population in the Ross Sea, production is made up of three parts: (1) production of eggs by adult breeders (3%); (2) growth of chicks during provisioning by adults (68%); (3) growth of juveniles after fledging (29%). Mortality loss in terms of biomass is in approximate proportions: eggs (0.1%), chicks (16%), juveniles (49%), adults (35%). Thus overall production is estimated to be P/B=0.11 y^{-1} where “B” refers to the entire population. Adjusting this for time spent outside the study area gives the value to use in the model of P/B=0.10 y^{-1} where “B” refers to the annual average population in the Ross Sea.

Estimates of consumption based on growth and metabolic requirements (e.g. Nagy 1987; Schneider & Hunt 1982) lead to estimates of consumption rates of 34–39 y^{-1} for adults. Jarre-Teichmann et al. (1997) estimated that emperor penguins in the Weddell Sea consumed about 1 kg of food per day giving a Q/B of about 13 y^{-1}, but this seems very low. Based on a seasonally-resolved and age structured population model given above, we estimated consumption for the whole population taking into account variations in consumption by animals of different sizes. Overall consumption of the population as a proportion of total population biomass is estimated to be equivalent to Q/B=51 y^{-1}. This takes into account the three periods of high consumption by the adults, and the low/zero consumption during courtship, mating, egg incubation and moulting. Based on this individual-based model, the individual Q/B values and approximate proportions of total consumption by group are estimated to be: (1) juveniles, Q/B=40 y^{-1}, 14% of total population consumption; (2) adults, Q/B=55 y^{-1}, 86% of total consumption. Adjusting this for time spent outside the study area gives the value to use in the model of Q/B=44 y^{-1} where “B” refers to the annual average population in the Ross Sea. For comparison, data in Robertson & Newgrain implies a P/B of 30-84-y^{-1} for individual adults parenting chicks.

The biomasses of the various stages of birds combined with their location as discussed above allow us to calculate that there is a net export of emperor penguin biomass from the Ross Sea over the course of a year, equivalent to about 1.5% of the annual average biomass, or about 14% of the annual production. Most (91%) of this export is due to juveniles leaving the study area and dying before they return aged 4 years and above, with 9% due to adults being out the study area around the moulting period.

2.4 Foraging and diet

Emperor penguins search for prey in the open water of the Southern Ocean or in ice-free polynyas (an area of open water) and tidal cracks in pack ice. They have been recorded diving to depths of 400 to 450 meters. There have been numerous studies of the diet of emperor penguins within and outside the Ross Sea (e.g. Putz 1995; Kirkwood & Robertson 1997a, b; Cherel & Kooyman 1998) which show that they eat primarily crustaceans, fish, and cephalopods. The proportions of prey they take vary seasonally and geographically, depending on the abundance of prey in the area (Ainley et al. 1992).

In the western Ross Sea, the diet of emperor penguins feeding chicks was 89–95% (by mass) fish, and 5–11% crustaceans (Cherel & Kooyman 1998). About 89% of the fish was *Pleuragramma antarcticum*, the remainder being unidentified as juveniles of channichthyid fishes. Other fish prey found in the diet in various regions include *Gymndraco acuticeps*, *Trematomus* sp., *Pagothenia* sp., *Notolepis coatsi*, and *Electrona antarctica*. Small *P. antarcticum* (<100 mm standard length) dominated the diet in the study by Cherel & Kooyman (1998), but this may have been an effect of the sampling method (Burns & Kooyman 2001). Crustaceans in the diet comprised 52% gammarid amphipods (*Abyssorchomene rossi*, *A. plebs*, *Eusirus microps*), species which are commonly found in association with sea ice (e.g. Krapp et al. 2008) and the euphausiid, *Euphasusia crystallorophias* (24%). In some areas of the Ross Sea, squid (predominantly *Psychroteuthis glacialis*) made up to 12% of diet. Note that the foraging trip of emperor penguins lasts several days and even weeks but diet values are only from the last 2–3 days of trip and may not be representative of the whole trip (Cherel & Kooyman 1998). Diets for emperor penguins initially used in the Ross Sea model are given in Table 2. Thus, the possible food items partitioned among the compartments used in the model are: Antarctic silverfish (68%), small demersal fishes (10%), cephalopods (4%), pelagic fishes (10%), *E. crystallorophias* (2%), *E.* superba (2%), other macrozooplankton (2%), ice metazoa (2%).

2.5 Predators

Antarctic giant petrels (*Macronectes giganteus*) and Antarctic skuas (*Stercorarius maccormicki*) are the primary predators of emperor penguin chicks in colonies, taking from 7 to 34% of young. Leopard seals (*Hydrurga leptonyx*) take young when they enter the sea after moulting and adults. Adults are also taken by killer whales.

3 Adélie penguin

Adélie penguins (*Pygoscelis adeliae*) are among the best studied penguin species in the world and they have been extensively studied in the Ross Sea. These studies have included reports on their breeding distribution and abundance (e.g., Reid 1964; Taylor & Wilson 1990; Taylor et al. 1990), demography and population regulation (e.g., Ainley et al. 1983, Wilson et al. 2001), breeding (e.g., Oelke, 1975, Spurr, 1975, Davis & McCaffrey 1986), diet (e.g., Paulin 1975, van Heezik 1988, Ainley et al. 1998), and foraging movement and migration (e.g., Davis et al. 1988, Davis & Miller 1990, Davis et al. 1996, Ainley et al. 2004).

Bird numbers were estimated from aerial photographs (e.g. Wilson et al. 2001 and references therein). About 30–38% of the world population of Adélie penguins are thought to reside in the Ross Sea, breeding at c. 35 rookeries. The colonies are on land, and vary in size, from a few hundred to many thousand pairs. There are two main concentrations of Adélie penguins (Harper et al. 1984; Taylor et al 1990; Ainley 2002): (1) northern Victoria Land (62% of Ross Sea pairs), (2) and the southern islands of Franklin, Beaufort and Ross (34% of Ross Sea pairs). On the Victoria Land coast, the largest colonies are at Cape Adare (169 000 pairs), Possession Island (162 000 pairs), and Cape Hallett (44 000 pairs). In the SW Ross Sea, the largest colonies are at Cape Crozier (118 000 pairs), Franklin Island (56 000 pairs), Beaufort Island (38 000 pairs) and Cape Bird (36 000 pairs). Based on Ainley (2002) we use a total value of 746 000 breeding pairs in a typical recent year in the Ross Sea. This excludes nearly 7000 breeding pairs at the Balleny Islands.

There have been long-term, substantial fluctuations in the numbers of Adélie penguins breeding throughout the Ross Sea, as well as interannual variations in numbers. Year to year variations can be as high as ±20% y^{-1} and are probably a result of variations in sea ice extent and distribution between years (Wilson et al. 2001). Long-term changes in populations have also been documented. For example, the colony at Cape Adare was estimated in 1983 from counts of aerial photographs taken on 02 December at 257 000 pairs and 282 000 pairs on 11 December 1986. It is possible that this recorded increase was simply a function of the difference in timing of the photographs, as this late in the season would see many more adults in the colony than simply one member of each breeding pair. The 1990 count recorded 170 000 pairs (a decrease of 40% from the 1986 count). The colony at Possession Island was estimated at 162 000 pairs in 1990 and 187 500 a few years earlier (a decrease of 14%). The large colony at Cape Crozier was accurately counted from aerial photographs taken at the optimal time for census in years 1985, 1986 and 1987 and had 167 000, 177 00 and 177 000 pairs respectively (data includes East Crozier) (Taylor et al 1990) compared to 118 000 pairs in 1991, a decrease of 33%. Causes for longer term trends are not well known but may be linked to longer term variations in sea ice cover. Because of the high interannual variability in surveyed numbers, differences in trends between colonies, and a lack of information on whether these changes are continuing, for the present version of the model we assume no consistent trend in Adélie penguin numbers in the Ross Sea.

3.1 Life cycle

Below, we describe a typical cycle for the Ross Sea. The description of the phases of the Adélie life cycle largely follows Ainley (2002) and references therein - we do not repeat individual references here except where the information does not appear in Ainley (2002). Much of the work is based on the well-studied populations of Adélie penguins in the SW Ross Sea at capes Royds, Bird and Crozier. There is significant variation in the colony occupation pattern within these colonies, and between these Ross Island colonies and other areas of Antarctica (e.g. Signy Island, Point Geologie, Bechervaise, Wilkes). Timing also varies with year. It should be borne in mind then that we describe the typical colony characteristics in an unspecified recent year. The annual cycle includes: (1) a pre-migratory period of feeding and fattening; (2) spring migration to the breeding colony; (3) nesting and chick rearing; (4) autumn migration from the colony; (5) heavy feeding; (6) moult; (7) overwintering.

3.2 Breeding

In spring, Adélie penguins start to migrate from the outer reaches of the pack ice towards land, where they will breed, much of the travel being by walking, tobogganning as well as swimming. The migration to the breeding colonies only occurs after the penguins have obtained a huge supply of body fat which sustains them while the southern ice pack is too consolidated to allow concentrated feeding. Adélie penguins begin to arrive at their breeding colonies (“occupation”) from about day 280 (early Oct). At this stage, only breeders tend to arrive, the males normally arriving before the females. The first egg is laid about 21 d (19–24 d) days later. The number of birds at the colony reaches a peak around day 305 (early Nov). Pairs are formed relatively quickly (1–12 d) after arrival at the colonies, and between 1 and 3 eggs (mean clutch size is 1.8) are laid per breeding pair. The first eggs are laid about 8 d after arrival of the female, and subsequent eggs are laid at about 3 d intervals thereafter. Peak egg laying in the Ross Sea typically occurs in early Nov. The eggs weigh about 114 g (101–124 g), with the shell accounting for about 13% of this. Once eggs are laid, females leave to sea for 8–14 days, with the male left incubating. Thereafter, mates alternate incubation and foraging. During foraging at this time, birds remain associated with land and ice boundaries and tend to avoid the large open water area in the Ross Sea for feeding (Ainley and Jacobs 1981; Ainley et al 1984; Ainley 2002). Non-breeders (including yearlings) remain concentrated in pack ice within 150 km of breeding colonies at this time, whereas yearlings remain even further away from the colonies. At this time, about 1/3 of the Adélie penguin population in the Ross Sea occupied waters overlying the continental shelf, with the remaining 2/3 occupying waters over the continental slope (Ainley et al 1984; Ainley 2002).

Failed breeders leave the colony while successful breeders are incubating eggs. This, and the fact that one parent of each pair is away foraging at any time, means that the population of the colony falls to about half the maximum level around late Nov. Incubation lasts 32–37 d, with peak hatching around 4 Dec. Chicks weigh about 95 g on hatching. Chicks are provisioned in two ways. First, in the guard stage lasting 22 d (16–34 d) where at least one parent stays with the chick(s) at all times. Mates alternate feeding chicks and forage approximately equally. Second, the crèche stage where both adults forage while chicks group together. This stage lasts until fledging when chicks are aged typically 52 d (range 41–64 d). While incubating, maximum foraging distances of adult Adélie penguins from breeding colonies have been measured to be about 48 km (Trivelpiece et al 1996), 20–100 km (Kerry et al. 1995), and 30–70 km (typically 40 km) around Bird Island in the SW Ross Sea (summarised in Ainley 2002).

Chick weight increases to a maximum of about 3.4 kg (2.9–3.8 kg) during provisioning by adults (Janes 1997, Lawless et al. 2001) at age 42 d, and then typically falls to 2.6 kg (2.0–3.0 kg) during fledging before departure to sea. Failed breeders, non-breeders and juveniles start to arrive through Dec, giving a second peak representing “reoccupation” around day 355. After fledging, juveniles disperse to the north to a limit of about 60°S. Juveniles gain weight exponentially to attain close to (95%) adult weight at ~3 years old. Most adult breeding birds have left the colony by late Jan.

3.3 Moulting

All Adélie penguins moult annually, and this normally occurs on pack ice rather than on land. Moulting typically starts about 9 days after chicks fledge, peaking on about day 60 (early Mar) for adults and around day 41 (early Feb) for juveniles in the Ross Sea. Voracious feeding after leaving the colony and before moulting, helps build up fat reserves to sustain them through the fasting accompanying moulting. This feeding between the nesting colonies and ice pack refugia usually occurs in relatively ice free waters, but may entail use of minke whale breathing holes a few hundred metres apart if ice is fast. The exact locations of Adélie penguin moult areas vary with ice distribution from year to year. Some penguins from SW colonies in the Ross Sea tend to move east to pack ice in the Amundsen Sea off Marie Byrd Land (Ainley 2002; Ainley et al 1984). Some birds from the Victoria Land colonies move north to a small area of persistent pack ice near the Balleny Islands (Davis et al 1996). Adult and juvenile moulting takes about 19 d during which time typical adult weight falls from 6.9 to 3.7 kg, and typically juvenile weight falls from 5.5 to 3.1 kg. These weights may be compared with typical adult breeder sizes of 5.713 kg (males) and 5.119 kg (females) (Emmerson et al. 2004).

3.4 Winter distribution

After moulting, penguins disperse widely. Ship-board surveys and satellite tracking show that Adélie penguins can move out of the study area during the winter (Davis et al. 1996, Ainley 2002). Adélie penguins tend to remain associated with or in close proximity to pack ice, close to but not at the outermost edge. They are likely to be associated with ice concentrations 15-80 % representing loose but stable concentrations of ice floes (Wilson et al. 2001, Ainley 2002 (summarises AMERIEZ winter studies)). There are occasional sightings of Adélie penguins at sea far north of the edge of pack ice although some of these are almost certainly misidentified chinstrap penguins). Adélie (and other penguins) are visual feeders and typically dive to the depth of 1% penetration of light (Ainley 2002; Wilson et al. 1993). This may mean they remain north of the Antarctic circle in winter (Ainley 2002; Fraser & Trivelpiece 1996). Here, we assume that all Adélie penguins are at sea and absent from the Ross Sea study area between May and August inclusive (4 months).

3.5 Demography and mortality

Average age-at-death of Adélie penguins is about 9.0 years, with the oldest Adélie penguin recorded in the wild being about 20 y. Estimates of survivorship vary significantly between years and colonies, as survival of Adélie penguins in the Ross Sea is affected from year to year by food, predation, weather, and ice conditions. Annual survival rates are reported (Ainley 2002; Ainley & DeMaster 1990) to be approximately 0.40 (first year), 0.67 (years 2 and 3), and 0.92 (thereafter). In the population model used here, we use similar survival rates which lead to a stable population given our choice of other parameters. These survival rates are 0.40 (first year), 0.71 (years 2 and 3), and 0.92 (thereafter).

Adélie penguins reach close to adult weight after 3 years and become reproductively mature at about 3-5 y. We take the age of recruitment from juveniles to the adult population to be at age 3 y. A proportion of the adult population does not breed in a given year because of environmental, physiological and other factors (e.g., losing partner), which varies depending on local conditions. The proportion breeding per year is highly dependent on age, with only 8% of 3 year old attempting to breed, c. 85% of adults aged 7-12, and >90% of birds older than 13 y attempting to breed. Average age at first breeding in the Ross Sea, corrected for mortality and cohort size, is about 5.5 y in the Ross Sea and more than 90% of first breeders are aged 4–7 y. Assuming a typical adult annual survivorship (0.92) and based on data in Ainley (2002), the population-weighted proportion of adults (aged 3 and over) attempting to breed each year is 74.3%.

Breeding success (fledged chicks per egg) is a combination of clutch size, hatching success, and fledging success. On average over 26 seasons and 7 sites in the Ross Sea, 51% of eggs produced a fledged chick, though breeding success in this period and sites varied between 26–68%. Typical clutch size is 1.9. Typical percentage of eggs hatching is 69% but is variable (37–88%). Typical proportion chicks surviving to fledging is 77% (47–96%) (all Ainley 2002 and references therein).

3.6 Consumption, diet and foraging

Diets for Adélie penguins in the Ross Sea used in the model are given in Table 2. The proportions of different prey items, by weight, taken by Adélie penguins in the Ross Sea is known to vary by season, year, and by breeding colony (Ainley et al. 1998). Adélie penguins are typically considered as specialist krill predators but in fact fish (especially juvenile *Pleuragramma antarcticum*) can be a seasonally dominant prey item of Adélie penguins in the Ross Sea and are energetically more valuable than krill (Ainley et al. 2003). Ainley et al. (2003) present data that shows that penguins in the southwest Ross Sea were not foraging in slope waters but were feeding in neritic waters. In the summer in open waters of the Ross Sea, krill dominates the diet (Ainley et al. 1984; van Heezik 1988; Davis et al. 1988). Over the continental slope off Victoria Land, *E. superba* may make up 98% of the diet. Further south over the continental shelf in the Ross Sea, Ainley (2002) summarises research (van Heezik 1998; Ainley et al. 1998; and others) showing that *Pleuragramma antarcticum* and *Euphasusia crystallorophias* are both important in the diet of Ross Sea Adélie penguins during the summer chick provisioning period. Stable isotope studies of chick toenails shows that this is a useful tool to synoptically describe diets over a large area (Ainley et al. 2003). The diet here was made up of a mixture of *P. antarcticum* (39-79%) and *E. crystallorophias* (25-99%), with amphipods and bivalves being minor prey items (e.g. Ainley et al. 2003). *P. antarcticum* tend to dominate in areas where foraging occurred in open water adjacent to pack ice or ice concentrations were lower (Ainley et al. 2003), whereas *E. crystallorophias* dominated Adélie diet when the pack ice was extensive.

Few studies have investigated the diet of Adélie penguins in winter. Although not relevant to this study, as we assume that all Adélie penguins are absent the Ross Sea study area for 4 months between May and August, Ainley et al. (1992), found that (in descending order of importance by mass), winter prey of Adélie penguins were squid, krill (*Euphausia superba*) and fish. It is likely that during the winter north of the Ross Sea, Adélie Penguins eat squid and fish, with fish dominating when in neritic waters (Ainley 2002a). We suggest initially that diets contain Antarctic silverfish (50%), small demersal fish (5%), cephalopods (1%), *E. crystallorophias* (30%), *E. superba* (9%), other macrozooplankton (2%), ice metazoa (2%), macrobenthos (1%).

3.7 Biomass, P/B, Q/B estimated from a population model

We used a population model of a typical Adélie penguin colony to assess total population numbers, biomass, production and consumption rates in 2-week blocks, and the seasonal variation in these quantities. The model is stage structured and age structured for breeding adults, and is similar to the model for emperor penguins described above. We assume that the Adélie penguin population is comprised of the following types: (1) adult breeding birds with nests likely to have been included in years census, including successful breeders and failed breeders, separated into males and females; (2) adult non-breeders – birds in adult plumage more than 3 years old that may or may not have previously bred, but are not breeding this year; (3) pre-breeders or “wanderers” – birds in adult plumage aged between 2 and 3 y that have never established nests or bred; (4) yearlings – juvenile birds in immature plumage less than 15 months old that have left the rookery); (5) chicks (between hatching and fledging); (6) eggs. The year is divided into 2 week periods, and each stage of penguin breeding has an activity associated with each period. These include nesting, laying, egg incubation, foraging, provisioning chicks, crèche (chicks only), moulting (adults only), and fledging (chicks only). Production (egg laying or growth), consumption, and mortality are calculated for each stage for each period.

The parameters described above lead to a stable population where annual recruitment rates equal total mortality loss over the year. In this modelled population, total population biomass is equivalent to 9.6 kg per breeder. Total production for the population is equivalent to P/B=0.24 y^{-1}. Average proportion of numbers (biomass) by stage over a year are: (1) adult breeders, 0.39 (0.47); (2) adult non-breeders, 0.13 (0.17); (3) pre-breeders, 0.13 (0.14); (4) yearlings, 0.13 (0.11); (5) chicks, 0.22 (0.11). This is equivalent to 2.0 million adult birds, 1.0 million juveniles (yearlings and pre-breeders). The average annual total population biomass in the Ross Sea is estimated at 14.4 thousand tonnes. Production arises from three parts, with values showing proportions of total production: (1) production of eggs by breeders, 0.03; (2) growth of pre-breeders, 0.07; (3) growth of yearlings, 0.18; (4) growth of chicks, 0.72. Mortality due to predation, in terms of biomass, is distributed across the population as: (1) adults 0.25; (2) pre-breeders, 0.23; (3) yearlings, 0.42; (4) chicks, 0.11; (5) eggs, 0.01. Most of the population production hence arises during the chick provisioning period, but it is the yearlings (between leaving the rookeries and 15 months old) that are the most significant stage (in terms of total biomass) to predators.

Food requirements for each size of bird were calculated according the energy requirements estimated by Schneider and Hunt (1982). These estimates were summed for all birds in the model population (as above) to give a total population consumption equivalent to Q/B=69.8 y^{-1}. Average proportion of consumption by stage over a year are: (1) adult breeders 0.59; (2) adult non-breeders, 0.18; (3) pre-breeders 0.12; (4) yearlings, 0.09; (5) chicks, 0.02. For comparison, considering the adults alone, the two methods described in section 2.3 led to Q/B values of 60–66 y^{-1}.

We assume that juveniles after fledging, aged 1-3 years, spend about 20% of their time in pack ice in the Ross Sea study area. Adults (both breeders and non-breeders) are assumed to spend the equivalent of about 8 months a year in the Ross Sea, the rest of the time (over winter especially) being dispersed in pack ice to the north of the study area. These assumptions allow us to calculate an equivalent annual average biomass, P/B and Q/B value for Adélie penguins in the study area. Biomass is reduced by about 45%, whereas P/B increases to 0.36 y^{-1} and Q/B increases to 81.1 y^{-1}. The increase in these energetic parameters appropriate for modelling the population in the study area rather than the whole population arises because the chick stages are entirely resident in the Ross Sea, and these have faster turnovers than the rest of the population. The biomasses of the various stages of penguins combined with their location (in Ross Sea, dispersed to north) allow us to calculate that there is a net export of Adélie penguin biomass from the Ross Sea over the course of a year, equivalent to about 5.3% of the annual average biomass, or about 15% of the annual production. This figure is quite low because most of the penguins leaving the Ross Sea in autumn return to the area the following spring. Most of this export is due to fledglings (juveniles between fledging and aged 2 years) leaving the study area and dying before they return aged 4 years and above. The relatively small *net* export of biomass is due to the deaths of penguins while outside the area being offset by the increase in weight of the returning birds compared to those leaving.

4 Flying birds

4.1 Petrels

Six species of petrels breed in the vicinity of the Ross Sea. In order of abundance, petrels in the Ross Sea are reported (Ainley et al. 1984) as: Antarctic petrel (*Thallassoica antarctica*), snow petrel (*Pagodroma nivea*, *P. confusa*), Wilson's storm petrel (*Oceanites oceanicus*), and Antarctic fulmar (*Fulmarus glacialoides*). Two species of petrel are restricted to the northern Ross Sea: Antarctic prion (*Pachyptila desolata*), and cape petrel (*Daption capensis*). Five species of petrel, more associated with northern waters, may be infrequent visitors to the Ross Sea region: southern giant petrel (*Macronectes giganteus*), mottled petrel (*Pterodroma inexpecta*), sooty shearwater (*Puffinus griseus*), short-tailed shearwater (*Puffinus tenuirostris*), and black-bellied storm-petrel (*Fregetta tropica*). Of these, only the southern giant petrel is likely to range as far south as the Ross Sea proper, the other generally being restricted to north of the Polar Front.

Reliable and detailed information on the numbers and distribution on petrels (and other flying birds) in the Ross Sea is very limited and is derived indirectly from counts of flying birds from ships (e.g. Ainley 1984). The total petrel population has been estimated to number "millions of pairs" (Harper et al. 1984). Young (1981) gives total petrel densities of about 11.3 birds/km^2 for the Ross Sea i.e. a total petrel number of about 8 million. The considerations below give a total petrel population of the Ross Sea of 6.9 million in the summer which is reasonably close. The estimate annual average biomass is dominated by Antarctic petrel (75%), snow petrel (24%), with <1% due to the other species (Ainley et al. 1984). We assume that all petrel and albatross populations in the Ross Sea have no consistent, long-term trends. Other basic information on petrels and albatrosses (e.g. adult weights, egg numbers, foraging ranges) was taken from a number of basic references (e.g. Watson 1975; Shirihai 2002; Heather & Robertson 1986).

Diet of petrels in the Ross Sea depends on two factors. First, their mode of feeding (dipping, diving, surface-seizing or pursuit plunging) determines what prey may be taken by each species. Second, location of feeding (e.g. oceanic water, continental slope water, shelf water) and time of year affect prey availability (Ainley et al. 1984). Most petrels in the Ross Sea are essentially surface feeders. Petrels feed on a mixture of prey including: fish (mainly *Pleuragramma antarcticum*), squid, and crustacea (*E. crystallorophias*, and amphipods). Ainley et al. (1992) showed that petrels, especially snow petrels and Antarctic petrels are somewhat selective in their feeding, ignoring krill when fish are available. The preponderance of *P. antarcticum* in snow petrel (and skua) diets (Ainley et al. 1984) also argues against purely opportunistic feeding although seabirds exploited prey largely according to ranked availability (Ainley et al. 1992). By weight of prey, fish and squid are major dietary components, and there seems to be little segregation in prey type by petrel species (Harper et al. 1984). Diet is likely to vary seasonally, but we lack an understanding of how prey availability changes during the year and how changes affect petrel diet over a year. No material (e.g., offal, discarded bycatch) may be discarded from fishing vessels in areas under CCAMLR jurisdiction so this does not appear as a component of their diet.

4.1.1 Antarctic petrel

Antarctic petrels (*Thallassoica antarctica*) are associated with coastal Antarctic waters, and stay within or close to the pack ice year-round. The northern limit is reported as 56°S in summer and 48°S in winter (Shirihai 2002). Individual weights of adults are 650–675 g. The total circumpolar population may be 10–20 million individuals with concentrations in West Antarctica and Victoria Land. Antarctic petrels are colonial, establishing large nesting colonies (1000 – 1 million birds) on low snow-free cliffs. Birds arrive at the colonies in early to mid-October, eggs are laid in late November, and chicks depart late February to mid March. Probably the largest breeding colonies (with millions of pairs) in the vicinity of the Ross Sea may be more than 100 km inland of the coast in the Fosdick and Rockefeller mountains on King Edward VII peninsula, Marie Byrd Land in the eastern Ross Sea (Ainley et al. 1984). Broady et al. (1989) reports approximately 10 000 pairs breeding on Mount Paterson in the Rockefeller Mountains.

On the basis of observations at sea, Antarctic petrels are thought to dominate non-penguin avian biomass in the Ross Sea at some times of the year (Ainley et al. 1984). Observations from US Coast Guard vessels in December between 1976 and 1979 indicate that there may be about 3.9 million Antarctic petrels in the Ross Sea region at this time of year, of which, c. 95% feed in the Ross Sea itself (Ainley et al. 1984: 38, figure 23, Ainley 1985). Ainley et al. (1985) corrected this number for birds assumed to be incubating eggs, and obtained an estimate of the total Ross Sea Antarctic petrel population of 5.0 million. Peak observed densities observed at sea were as high as 306 birds/km^2 and occurred along the continental slope (Ainley et al. 1984). Ainley et al. (1984) reports that “by late January and February, a large proportion of the Antarctic petrel population had shifted away from the slope waters toward the northeast”. We hence estimate that this number of birds is present for only 2.5 months of the year (Dec/Feb), and that Antarctic petrels disperse to the north of the Ross Sea at other times of the year.

The food of Antarctic petrels in the Ross Sea is likely to be crustaceans (krill especially), cephalopods (especially *Psychroteuthis glacialis*), and small fish, taken principally by surface-seizing (Ainley et al. 1984). We initially assume a diet of: pelagic fishes (35%), cephalopods (10%), *E. superba* (30%), *E. crystallorophias* (20%), other macrozooplankton (5%).

4.1.2 Snow petrel

There are two species of snow petrel in the Ross Sea: lesser snow petrel (*Pagodroma nivea nivea*) and the greater snow petrel (*P. nivea confusa* or *Pagodroma nivea major*). Information on biology and ecology of both species is relatively scarce, especially so for the greater snow petrel. The lesser snow petrel is thought to dominate in terms of numbers, and breeds in the Morozumi Range, and at least eight other sites in Victoria Land (Greenfield et al., 1989). In addition, two small colonies of lesser snow petrel are known from Marie Byrd Land (Greenfield et al. 1989). The greater snow petrel tends to breed in mixed colonies with the lesser petrel, with the only known "pure" breeding colony on the Balleny Islands (Robertson et al. 1980, Jouventin & Viot 1985, Shirihai 2002). Weights are 200-378 g (lesser snow petrel) and 317-570g (greater snow petrel).

Snow petrels remain within or close to the pack ice, ranging northwards in the non-breeding season, but rarely being recorded north of 60°S (Shirihai 2002). Ainley et al. (1984) suggested that the total population of snow petrels in the greater Ross Sea area was about 2.0 million birds. This figure was obtained by correcting at-sea observations from ships in December for numbers assumed to be incubating eggs at this time of year (Ainley et al. 1984). The ratio of greater to lesser snow petrels in this population is not known, so we assume it to be 90% lesser and 10% greater snow petrels. About 90% of birds are estimated to be feeding in the Ross Sea at any time (Ainley et al. 1984). Snow petrels tend to be associated with the edge of sea-ice (Ainley et al. 1984) and so we assume that this number of birds remains in the Ross Sea for the approximate 4 months of the year that ice cover is broken.

Diet of snow petrels over the continental shelf is reported as cephalopods (9.8%), *E. crystallorophias* (2%), and pelagic fish (75%), taken principally by dipping, surface-seizing, surface-diving, and pursuit diving (Ainley et al. 1984). Over the continental slope *Euphausia superba* dominated the diet and a few macrozooplankton crustacean were also taken (Ainley et al. 1984). Therefore the diet of this species probably varies approximately according to the prevalence of prey items. Here, diet of snow petrels is taken as pelagic fishes (75%), cephalopods (10%), *E. crystallorophias* (5%), *E. superba* (5%), other macrozooplankton (5%).

4.1.3 Wilson's storm petrel

Wilson's storm petrel (*Oceanites oceanicus*) is known to breed on Scott Island and Possession Island (Peter Wilson pers. obs.) and in at least eight locations in Victoria Land, with the majority apparently breeding at sites in the vicinity of Cape Adare and Cape Hallett (Ainley et al. 1984). Based on observations at sea in December, Ainley et al. (1984) estimates a Ross Sea population of 420,000, similar to the 400 000 birds given by Harper et al. (1984). Ainley et al. (1984) suggests that about 95% of this population feeds over continental slope region adjacent to their breeding colonies in the Ross Sea in summer, and that densities and numbers may stay at these levels between December and February. After breeding, Wilsons' storm petrels are known to migrate to the northern hemisphere, heading north in April and returning in Nov/Dec (Heather & Robertson 1996). Here we assume they are present in the study area for 4 months/year.

Wilson's storm petrel, over the continental slope, takes *E. superba* (48%), *E. crystallorophias* (7%), macrozooplankton (5%), cephalopods (30%), pelagic fish (10%) (Ainley et al. 1984). In the South Atlantic this species fed mostly on pelagic fish (Ainley et al. 1992). Here, we take the diet of Wilson's storm petrel to be: pelagic fishes (45%), *E. superba* (30%), *E. crystallorophias* (10%), other macrozooplankton (5%), cephalopods (10%).

4.1.4 Antarctic fulmar

Antarctic or southern fulmar (*Fulmarus glacialoides*) breed only at the Balleny Islands, with about 2000–3000 birds in the Ross Sea region (Ainley et al. 1984, 2004). Of these, we estimate that only about 20% of their foraging takes place in the study region (Ross Sea proper). We assume these birds remain in the Ross Sea only in summer (3 months), dispersing northwards for the rest of the year. Their food is reported *as E. superba* (92.5%), cephalopods (6%), penguin carcasses (1.5%) by Ainley et al. (1984), but probably includes pelagic fish, *E. crystallorophias*, and other macrozooplankton. Here, we take the diet of Antarctic fulmar as: pelagic fishes (40%), *E. superba* (42%), *E. crystallorophias* (5%), cephalopods (6%), carcasses (2%).

4.1.5 Antarctic prion

About 200 pairs of Antarctic prions (*Pachyptila desolata*) are known to breed on Scott Island in the Ross Sea (Harper et al. 1984). This implies a total population of the order of 1000 birds. Some of these may feed in the Ross Sea at some times of the year, though Ainley et al. (1984) reported them staying well north of the study area in December. We assume that 20% of this population feeds in the Ross Sea for 4 months of the year that it is largely ice free. The diet of Antarctic prion is reported as mainly pelagic fish (Ainley et al. 1992), euphausiids, other macrozooplankton, mesozooplankton (Reid et al. 1997), and small cephalopods taken by hydroplaning or surface scooping (Cherel et al. 2002). Here, the diet is taken as: pelagic fishes (75%), cephalopods (5%), *E. superba* (5%), *E. crystallorophias* (5%), other macrozooplankton (5%), mesozooplankton (5%).

4.1.6 Cape petrel

Cape petrels (*Daption capensis*) breed at both the Balleny Islands and Scott Island with perhaps 2000–3000 Cape petrels (c. 500 breeding pairs) comprising the local population of the Ross Sea (Harper et al. 1984). There are c. 5000 breeding pairs of Cape petrels on New Zealand subantarctic islands (Heather and Robertson 1996) but we consider these are unlikely to feed in the Ross Sea. Cape petrels are likely to be found in the Ross Sea in summer/early autumn only (4 months/year), moving north to temperate waters in winter and spring. Indeed, Ainley et al. (1984) found very few cape petrels in the Ross Sea in December. Diet is reported as euphausiids and other crustaceans, cephalopods and to a lesser extent, fish and carrion. . Here, the diet is taken as: pelagic fishes (53%), cephalopods (10%), *E. superba* (10%), *E. crystallorophias* (10%), other macrozooplankton (10%), mesozooplankton (5%), carcasses (2%).

4.1.7 Southern giant petrel

The southern giant petrel (*Macronectes giganteus*) is also called southern giant fulmar. There are southern giant petrel breeding colonies on the Antarctic mainland Adélie coast, and on Macquarie Island. They are almost never observed in the Southern Ross Sea (Peter Wilson, pers. com). Ainley et al. (1984) reported about 3000–5000 southern giant petrels in the Ross Sea in the summer, and we assume that these birds forage in the Ross Sea for 3 months of the year. Southern giant petrels are predatory scavengers, with penguins and petrels (eggs, chicks and ailing adults) providing the majority of their food. They may also scavenge seal remains and take cephalopods, fish and crustaceans from shallow diving. Here, the diet is taken as: small demersal fishes (5%); silverfish (5%); pelagic fishes (10%); cephalopods (10%); megabenthos (5%); macrobenthos (5%); carcasses (60%).

4.2 Albatrosses

Two species of albatross are known to be present in the Ross Sea: the black browed albatross (*Diomedea melanophris*) and the light mantled sooty albatross (*Phoebetria palpebrata*), though neither breeds in the study area.

4.2.1 Black browed albatross

The black browed albatross (*Diomedea melanophris*) is the commonest albatross species in the world, with about 3 million birds (Taylor 2000b). They breed on New Zealand subantarctic islands including Auckland, Campbell and Antipodes islands, and Heard and Macquarie islands. Black browed albatrosses disperse widely around the Southern Ocean and temperate seas, but generally stay north of pack ice. Very small numbers of black browed albatrosses were found in the vicinity of the Ross Sea in summer by Ainley et al. (1984), generally remaining to the north of the slope. It is likely that none are there at other times. We estimate a nominal 100 birds in the Ross Sea for 3 months of the year. The diet of the black browed albatross includes fish, squid, and to a lesser extent, crustaceans (mainly euphausiids) and salps which they take by surface feeding and shallow plunging (Heather & Robertson 1996). Here, the diet of black bowed albatross is taken as: small demersal fishes (5%); silverfish (35%); pelagic fishes (20%); cephalopods (10%); *E. superba* (5%); *E. crystallorophias* (5%); other macrozooplankton (5%); carcasses (15%).

4.2.2 Light mantled sooty albatross

The light mantled sooty albatross (*Phoebetria palpebrata*) breeds on offshore New Zealand subantarctic islands including Auckland, Campbell and Antipodes islands. The size of the global population is poorly known, but probably numbers less than 8000 pairs (Taylor 2000a) in New Zealand, and c. 23 000 birds worldwide (Heather & Robertson 1996). The birds range widely through the Southern Ocean to the Antarctic coast, and light-mantled sooty albatrosses breeding on Macquarie Island commute to polar waters to feed (Weimerskirch & Robertson, 1994). Ainley et al. (1984) found light mantled sooty albatrosses in the Ross Sea in December, with densities up to 0.2 birds/km^2 over the continental slope. We estimate a nominal 100 birds are found in the Ross Sea for 3 months of the year. Light mantled sooty albatross feed on fish, squid, and krill mainly taken from the ocean surface with some shallow plunging. Some carrion, such as small seabirds, may also be taken (Heather & Robertson 1996). Here, the diet of light browed albatross is taken as: small demersal fish (5%); silverfish (35%); pelagic fish (20%); cephalopods (10%); *E. superba* (5%); *E. crystallorophias* (5%); other macrozooplankton (5%); carcasses (15%).

4.3 Skuas

Two species of skua are present in the Ross Sea sector of the Antarctic: south-polar skua (*Catharacta maccormicki*), and southern skua (*Catharacta lonnbergi*). However, the nearest southern skua breeding colonies to the study area are the Balleny Islands and these are unlikely to feed in the Ross Sea proper so will not be considered further. South polar skuas have been studied extensively in the Ross Sea with topics including breeding (e.g., Young, 1963, Spellerberg 1971), territory (Young, 1972), food (Young 1994, Mund & Miller 1995); and demography (Ainley et al. 1990). South polar skuas appear to breed throughout the area bordering the Ross Sea wherever snow- and ice-free land is available (Harper et al. 1984).

4.3.1 South polar skua

Major concentrations of south polar skuas occur near Adélie penguin colonies, although they also nest in many other places (Harper et al. 1984). For instance, only 16 of the known 55 skua breeding sites in the Ross Sea are associated with penguin colonies (Ainley et al 1986). Counts are only available for Cape Adare, Cape Hallett and the McMurdo Sound area. About 1500 pairs breed on Ross Island with the Cape Crozier population by far the largest; and this may be a large proportion of the Ross Sea region total population (Spellerberg 1967, Harper et al. 1984, Ainley et al. 1986). Young (1981) suggested about 1400 breeding pairs of skuas were in the Ross Sea. Taken together, these surveys suggest 1800–2500 pairs in the Ross Sea, and approximately 11 000 birds (assuming 40% of the population breeds in any year). South polar skuas arrive at breeding colonies mid-October and leave in February to mid-March. In the non-breeding season, birds leave the study area altogether, so we assume they remain in the study area for 6 months per year.

Population decreases of south polar skua near human activities have occurred in the past (Harper et al. 1984; Pascoe, 1984). For example, there has been a significant reduction of skua numbers in the McMurdo Sound region since the closure of the rubbish dump associated with the research base. Surveys in the 1980s also found evidence of dump feeding at other skua colonies that have not been recently surveyed, and it is likely that these have also declined in number (Ainley 2002b), though we assume these populations have now stabilised.

South polar skua prey on eggs and young of breeding penguins, as well as feeding on Antarctic and snow petrel eggs and chicks, adult fish (especially *Pleuragramma antarcticum*,), and krill (*Euphausia crystallorophias* with some *E. superba*) by surface feeding, scavenging or pirate feeding (Mund & Miller 1995; Ainley et al. 1984). Skua can also take seal remains and parts of other carcasses. Information on overall diet of skuas is ambiguous as Mund & Miller (1995) conclude that the birds they studied fed mainly on penguin chicks and eggs, implying fish a lesser part of the diet whereas Ainley et al. (1984), from the data sources cited, record skua as feeding on Crustacea and fish. Mund & Miller (1995) note that, where *Pleuragramma antarcticum* was taken the fish were large and possibly benthic. From the observations on feeding methods (Ainley et al. 1984) we have to assume these larger *P. antarcticum* were pirated from other predators because skuas are not known to "dive" or "plunge". We initially assume a diet of: small demersal fishes (10%); silverfish (15%); pelagic fishes (5%); cephalopods (5%); *E. crystallorophias* (5%); *E. superba* (5%); other macrozooplankton (5%); carcasses (50%).

4.4 Combined parameters for flying bird trophic group

Values of biomass, production, consumption, and diet fractions for all petrels, albatrosses and skua were summed. The total annual average biomass of flying birds was estimated to be 860 tWW, equivalent to 1.4E-4 gC m^{-2}.

We estimated productivity rates of flying birds using the methods explained earlier, namely, based on scaling egg production, and using an allometric relationship between production and bird size. These two methods gave values of P/B that differed by 16% on average for flying birds The combined value for the flying bird compartment is P/B=0.55 y^{-1}. For comparison, Crawford et al. (1991) used P/B=0.2 y^{-1} for southwest African seabirds and Wolff (1994) used 0.07 y^{-1} for northern Chile seabirds which does not see high enough.

For different species of flying birds, Q/B was estimated based on two methods as explained earlier in this document, namely, based on daily dry weight food consumption for seabirds according to body weight (Nagy 1987), and based on standard metabolic rate (Lasiewski & Dawson 1967; Schneider & Hunt 1982). The value of Q/B estimated by the two methods differed by 6%. The values of Q/B estimated in this way varied between 56 and 189 y^{-1}, with larger birds having smaller Q/B values. The combined value of Q/B for flying birds is 115 y^{-1}. For comparison, van Franeker (1992), estimated food required per bird per day from equations given by Furness & Monaghan (1987) to range from 21% of wet weight body mass for large birds to 83% of body weight for small birds, approximately equivalent to Q/B 77–303 y^{-1}.

Diet for the flying bird component of the model was estimated by combining the diets for the individual species in proportion to their estimated consumption in the study area. The overall proportions of prey items in the diet are summarized in Table 2.

5 Summary of model parameters for birds

A summary of the parameters used by the model for birds is given in Table 1 and Table 2.

6 Acknowledgements

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Table 1. Tabulation of information and calculations of biomass, P/B and Q/B for the birds found for some or most of their life in the Ross Sea study area. B=biomass, P=production, Q=consumption, X=export (as fraction of annual production in study area). “Time” and “Area” refer to months spent in the Ross Sea modelling area per year.

		Mean weight (kgWW)	**Breeding pairs**	**Summer number**	**Time (months)**	**Area (%)**	**Biomass (tww)**	**Biomass (mgCm^{-2})**	**P/B (y^{-1})**	**Q/B (y^{-1})**	**X (fraction)**
Emperor penguin	*Aptenodytes forsteri*	27.9	32512	104877	10.8	88	313021	4.91E-01	0.10	44	0.145
Adélie penguin	*Pygoscelis adeliae*	4.4	745711	2006977	8.3	80	14362	1.25E+00	0.36	81	0.150
Flying birds		0.50		7430950			860	1.35E-04	0.55	115	0
Antarctic petrel	*Thallassoica antarctica*	0.65		5000000	2.5	95	643	1.01E-01	0.52	109	0.15
Lesser snow petrel	*Pagodroma nivea*	0.33		1800000	4	90	176	2.76E-02	0.64	134	0.15
Greater snow petrel	*Pagodroma confusa*	0.44		200000	4	95	28	4.41E-03	0.57	122	0.15
Wilson's storm-petrel	*Oceanites oceanicus*	0.04		410000	4	90	4.3	6.76E-04	1.1	253	0.15
Antarctic fulmar (silver-grey petrel)	*Fulmarus glacialoides*	0.80		2500	3	100	0.50	7.85E-05	0.49	103	0.15
Antarctic prion	*Pachyptila desolata*	0.15		1000	4	20	0.01	1.57E-06	0.75	167	0.15
Cape petrel (Snares cape pigeon)	*Daption capensis*	0.45		2500	4	30	0.11	1.77E-05	0.56	122	0.15
Southern giant petrel	*Macronectes giganteus*	4.5		4000	3	20	0.90	1.41E-04	0.26	63	0
Black-browed albatross	*Diomedea melanophris*	3.0		100	3	100	0.08	1.18E-05	0.33	71	0
Light-mantled sooty albatross	*Phoebetria palpebrata*	2.8		100	3	100	0.07	1.08E-05	0.35	72	0
South-polar skua	*Catharacta maccormicki*	1.4	2150	10750	6	100	7.3	1.14E-03	0.31	89	0.15

Table 2. Tabulation of diet information for the birds found for some or most of their life in the Ross Sea study area. The proportion of the diet made up of each prey item is shown. Proportions of diet less than 0.5% have been set to zero.

	Predators		
	Emperor penguin	Adélie penguin	Flying birds
Prey group	Proportion of prey in diet	Proportion of prey in diet	Proportion of prey in diet
Small demersal fishes	0.10	0.05	0
Silverfish	0.68	0.50	0.40
Pelagic fishes	0.10	0	0.05
Cephalopods	0.04	0.01	0.09
Euphausia crystallorophias	0.02	0.30	0.16
Euphausia superba	0.02	0.09	0.23
Other macrozooplankton	0.02	0.02	0.03
Mesozooplankton	0	0	0.01
Ice metazoa	0.02	0.02	0.02
Macrobenthos	0	0.01	0
Carcasses	0	0	0.01
TOTAL	1.00	1.00	1.00

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