

Whales: Trophic modelling of the Ross Sea

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1 Introduction and Species

For the purposes of modelling, we divide whales in the Ross Sea into 5 compartments: (1) orca (killer whales); (2) sperm whales; (3) “other toothed whales” including southern bottlenose whale and Arnoux's beaked whale”; (4) minke whales; (5) “other baleen” whales including blue, sei, fin, and humpback whales. We first detail the overall methods used to determine model energetic parameter values before giving specific information for the separate whale trophic compartments. A summary of whale parameters for the Ross Sea is given in Table 1.

2 Methods

2.1 Biomass carbon conversion

We assume that the carbon content of toothed and baleen whales in the Ross Sea is 10% of wet weight (0.1 gC/gWW), the same carbon content as fish (Vinogradov 1953), following previous trophic modelling work (e.g., Bradford-Grieve et al. 2003).

2.2 Long-term biomass trends

In the work presented, we assume that long-term changes in biomass per year are small for all species of whale (Trites et al. 2004).

2.3 Consumption

We used up to 5 methods to estimate the food requirements of cetaceans in the Ross Sea. At the outset, it is important to note that some methods estimate annual average feeding rates, whereas others estimate feeding rates in the Antarctic in the summer. For baleen whales, feeding rates in the summer may be 2.5 times or more the annual average (Reilly et al. 2004).

Method 1 is based on Innes et al. (1986) working of data from Sergeant (1969) and has been used by a number of other studies (e.g. Reilly et al. 2004). Daily prey consumption Q_{WW} (kgWW d⁻¹) is estimated as $Q_{WW}=0.42W_{kg}^{0.67}$ where W_{kg} is the average body wet-weight (kg). The estimate is based on feeding rates of captive small cetaceans and hence estimates annual average consumption.

Method 2. Daily consumption rates for baleen whales feeding in the Antarctic in summer have been estimated directly by examining stomach fullness of dead animals, and estimating digestion rate and the number of feedings per day (Tamura 2001; Tamura et al. 1997; Ichii & Kato 1991; Nemoto 1970; Zenkovich 1970; Klumov 1963). Armstrong & Siegfried (1991) also estimated feeding rates of minke whales (only) in the Antarctic using both stomach fullness and energy

budget methods. There is a wide range of estimates of daily consumption because of variations in the amount found in a “full stomach”, number feeds per day, and the time of sampling relative to feeding. Consequently, we only use this method for minke whales for which the most reliable and extensive data exist. The approximate range of feeding rates for this species is 3.2–4.1% body weight per day. Note that these are summer feeding rates, and this level of feeding would be unlikely to be maintained year round. These are converted to annual feeding rates before combining with other estimates, as described below.

Method 3. A number of methods estimate consumption of mammals based on the amount of food required to supply sufficient energy to satisfy their metabolic, growth and reproductive needs. Sigurjonsson & Vikingsson (1997) give relationships for annual average daily ration of baleen and toothed whales based on both feeding rates of captive cetaceans (based on Innes et al. 1986) and energy budgets. Their results were intended to be applicable to balaenopterids in the North Atlantic near Iceland. The relationships are $Q_{ww}=206.25W^{0.783}/1110.3$ (baleen) and $Q_{ww}=206.25W^{0.783}/1300$ (toothed whales).

Method 4. To estimate consumption of cetaceans in method 4, we used the relation between animal weight and daily consumption developed by Innes et al. (1987). For toothed whales: $Q=0.258 \cdot W^{0.69}$, where Q is daily consumption kg/d or WW prey, and W is the animal wet weight in kg. For “other marine mammals”, which we apply to seals and baleen whales, $Q=0.123 \cdot W^{0.80}$ (symbols as above). These relationships give mean consumption rates and were based on a compilation of published data for captive and wild marine mammals. There is conflicting evidence on whether the food requirements of Antarctic mammals is significantly greater than that of terrestrial mammals of a similar size (see Riedman, 1990 and references therein). Some studies have shown metabolic rates for polar mammals to be 1.5–3 times higher than terrestrial mammals in more temperate regions (e.g., Costa et al. 1986). Other work found that metabolic rates of polar mammals were only slightly higher (1.1–1.2 times) than those of a terrestrial mammal of similar size (Riedman 1990). The relationships of Innes et al. (1987) give values similar to consumption rates for terrestrial mammals of the same size. Here, we increase the values given by the relationship of Innes et al. (1987) by a middle value of 1.3.

Method 5. Here, we use an estimate of standard (or basal) metabolic rate from Lockyer (1981a): $SMR=70.5 \cdot W^{0.7325}$. This results in basal metabolic rates 11–19% lower than those given by $SMR=70 \cdot W^{0.75}$ (Kleiber 1975; Lavigne et al. 1986) but is considered more reliable. SMR is the resting or basal rate of animals; the average daily energy expenditure of animals will be higher than the SMR, especially if the animals are undergoing exertion such as extended swimming or foraging (Lockyer 1981a). The active metabolism is estimated to be about 2–5 times SMR (Kenney et al. 1997 and references therein). However, Lockyer (1981a) estimated that the daily energy expenditure of large baleen whales, averaged over a year, is only 1.3 times the SMR, and we use this factor for all cetaceans. Lockyer (1981a) gives assimilation efficiencies for Antarctic baleen whales of 79–83%, and we use 80% for all cetaceans.

Conversion factors between energy, carbon, dry- and wet-weights vary between studies and with species. For fish, 0.95–1.3 kcal/gWW is reported (Steimle & Terranova 1985; Croxall et al. 1985; van Franeker et al. 1997). For crustaceans, 0.93–1.1 kcal/gWW is reported (Lockyer 1981a; Croxall et al. 1985). We used weight conversion factors of 0.108 gC/gWW (fish: Schneider & Hunt 1982) and 0.030–0.055 gC/gWW (zooplankton: Weibe 1988; Ikeda & Kirkwood 1989). We use these to estimate 10.2 kcal/gC (fish) and 18.3 kcal/gC (crustaceans). These were combined according to the estimated diets of the individual cetacean species.

Differences between these methods (an average of all of five methods for minke whales, and an average of four methods (omitting method 2) for other baleen whales and all toothed whales) are of the order of 17% (baleen) and 27% (toothed), and so are considered reasonably consistent.

Our estimates of annual average Q/B for baleen whales ranged from 2.6 y^{-1} (blue whale) to 6.0 y^{-1} (minke whale). For toothed whales, the range for annual average Q/B was 4.9 y^{-1} (sperm whale) to 11.6 y^{-1} (Southern bottlenose whale). These are annual average consumption rates i.e. the feeding rates which would occur if feeding were evenly spread over the whole year. Baleen whales are known to feed more intensively in the Antarctic in summer than at other times of the year. Reilly et al. (2004) and Sigurjonsson & Vikingsson (1997) use the values of Lockyer (1981a) for the relative feeding rates in the summer and rest of the year where it is taken that baleen whales feed intensively in the Antarctic for about 120 d/y and consume at a rate approximately $1/10^{\text{th}}$ of this at other times of the year. In this case, the Q/B value appropriate for the model (i.e. the rate of feeding while in the Ross Sea) will be approximately 2.5 times as great as the annual average Q/B value. These Q/B values for the feeding rates in summer when the whales are present in the study area are 6.6 y^{-1} (blue) to 15.2 y^{-1} (minke whale).

These estimated feeding rates for baleen whales in summer agree well with estimates from previous studies which have attempted to estimate consumption rates for particular baleen whale species in the Antarctic in summer. Mori & Butterworth (2004) used values equivalent to Q/B=15 y^{-1} (minke whale) and 8.3 y^{-1} (blue whale) in their model. Trites (2003) quotes estimates for Q/B for marine mammals of between 11–18 y^{-1} . Recently, Hill et al. (2007) estimated consumption rates for baleen whales based on Reilly et al. (2004) who used a revised form of the model from Innes et al. (1986). The values range from 13 y^{-1} for minke whales to 6.9 y^{-1} for a group made up of blue and sei whales.

For toothed whales we averaged the results of four methods (Innes et al. 1986, 1987; Sigurjonsson & Vikingsson 1997; Lockyer 1981a) to obtain an estimate of the annual average feeding rate. These methods give reasonably consistent estimates of consumption (mean absolute variation from average of 27%). We assume that feeding by toothed whales is more intense in the summer in the Antarctic than in other areas at other times of the year, though by a much smaller amount to the increase in feeding intensity in summer for baleen whales. For example, Nemoto et al. (1985) examined sperm whales from Japanese whaling expeditions to the Antarctic in the 1951/52 season and found little increase in blubber thickness in sperm whales in the summer. Instead of feeding being a factor 2.5 higher in summer than the annual average as for baleen whales, we use a factor of 1.05. We hence estimate summer consumption rates of 9.7 y^{-1} (orca), 5.1 y^{-1} (sperm whale), 12.0 y^{-1} (other toothed whales).

2.4 Production

Annual production of whales was estimated in two ways for all species of whales:

Method 1. If the weight and number of whale populations is assumed to not change significantly from year to year, then the annual production (the biomass that is available for transfer out of the trophic compartment) may be estimated to be made up of two parts: (1) calves surviving to adulthood that replace loss due to adult mortality; (2) calves dying before reaching adulthood. The average weight of a calf dying before reaching adult size is taken as the geometric average of the birth weight and adult weight. This implicitly assumes a constant mortality rate with age and a linear growth rate. A declining mortality rate with age, and a decreasing growth rate with age, will tend to act to cancel each other out, so that this assumption is reasonable as a first

approximation. Typical per capita birth rates for baleen whale species are taken from Hill et al. (2007) as half the maximum per capita recruitment rates (i.e. at low population levels where all animals breed) from their table 13. These range from 0.045 (blue and sei whales, minke whales) to 0.06 (fin whales). For comparison, Mori & Butterworth (2004) give the range of maximum per capita birth rate for blue and minke whales between 0.05–0.20 y^{-1} . We estimated a value of 0.05 for orca (see below), 0.02 for sperm whales, and a higher value of 0.1 for the smaller southern bottlenose whale and Arnoux's beaked whale. The proportion of calves surviving to adult is poorly known but we assume here it has a value of about 40–60%, similar to orca (Olesiuk et al. 1990), being lower for smaller whales.

Method 2. Banse & Mosher (1980) relate production to animal biomass as: $P/B=12.9 \cdot M_s^{-0.33}$ where M_s is the animal weight expressed as an energy equivalent (kcal), and P/B is the annual value (y^{-1}). Fish are reported as having an energy density of about 1 kcal/gWW (Schindler et al. 1993). Mammals are likely to have a higher energy content as a result of their fat-rich blubber. Although the biochemical analysis of blubber of whales varies, 60% blubber is likely (Lavigne et al. 1986 and references therein; Koopman 2007) implying an energy content of about 9 kcal/g. Assuming such high-lipid tissues make up about 40% of the whale's body weight, we estimate a total energy density for whales of 4.2 kcal/g. This method gives P/B values that are about 31% on average different from values by the first method.

In the absence of a method to distinguish between these, we take an average of methods 1 and 2. This gives P/B for whales of between 0.019 y^{-1} (blue whale) and 0.067 y^{-1} (Southern bottlenose whale) which seem reasonable as Trites (2003) gave a range of P/B=0.02–0.06 y^{-1} for baleen and toothed whales.

2.5 Export

Movement of whales (baleen especially, but also toothed) into the Antarctic from tropical latitudes in the austral summer is generally understood to be primarily for feeding (Kasamatsu et al. 1995; Knox 2007). As the whales feed they accumulate fat reserves through thickening of their blubber which acts as an energy store for the rest of the year. The increase in feeding rates in the study region compared to the annual average is estimated to be a factor of 2.5 (baleen whales), and 1.2 (toothed whales), as explained in the section on consumption above. Assuming that mortality rates are approximately the same in the Ross Sea in summer as at other times of the year, this means that there will be a net export of organic matter from the study region associated with the whales leaving the region heavier than when they arrived. This export, expressed as a fraction of the production in the study area can be estimated as below:

$$\frac{X_{Ross}}{P_{Ross}} = \frac{\alpha \cdot \frac{Q}{B}(1-U) - \frac{R}{B} - \frac{P}{B}}{\alpha \cdot \frac{Q}{B}(1-U) - \frac{R}{B}}$$

Here, X_{Ross} is the export from the study area expressed as a fraction of the production in the study area (P_{Ross}), α is the factor by which the annual average feeding rate (Q/B) is increased in the study area, U is unassimilated consumption (assumed constant between areas), R/B is the respiration rate (assumed constant between areas), and P/B is the annual average production rate. For a population neither increasing nor decreasing in size, loss due to mortality over a year is balanced by net production, so that the numerator represents the increase in biomass of the population while in the study area after accounting for mortality loss. This increase in biomass is exported at the end of the summer when the whales leave the area. Based on the numbers for

individual species estimated below, X/P is estimated to be 0.994 for baleen whales, and 0.87–0.91 for toothed whales.

2.6 Unassimilated consumption

In the present study, we use $U=0.2$ as the proportion of unassimilated food for all cetacean groups (Bradford-Grieve et al, 2003). Unassimilated consumption is channelled to water column detritus in the model.

2.7 Ecotrophic efficiency

Ecotrophic efficiencies (E) are not known for cetaceans in the Ross Sea but as the vast majority of production is exported and predators are whales are few, ecotrophic efficiencies are estimated as being very close to unity. All biomass associated with non-predation mortality in the study area is channelled to the carcass group in the model.

3 Orca/killer whale

3.1 Introduction, species

Orca or killer whales (*Orcinus orca*) are probably the most cosmopolitan of all cetaceans, being found from ice edges to the equator, in both hemispheres. Orca have generally been considered to constitute a single species throughout the world (Rice 1998) even though since the 1970s several groups of researchers independently concluded that, based on differences in morphology, ecology and acoustic repertoire, there were three recognisably different forms of orca in the Antarctic (Pitman & Ensor 2003, and references therein): type A, type B and type C. Recent work suggests that all three different types of orca may occur in the Ross Sea (Pitman et al. 2001; Pitman & Ensor 2003; Pitman 2003). It has been suggested that type-B and type-C orca are separate species from *Orcinus orca* (Pitman & Ensor 2003; Pitman 2003), though this is still a subject of scientific debate. Type A is the typical form of *O. orca*, being the largest of the Antarctic orca, black and white, without a visible dorsal cape. Type-B and type-C orca have dorsal capes, and are a lighter grey colour rather than black. The white colour is often tinged yellow, probably due to a diatom film. The eyepatch size and shapes differ between the three types (Pitman & Ensor 2003). Type-B and type-C are shorter than type-A orca by about 1 m in total length. The groups are also distinguished by their diet and feeding strategies: type A predate on whales, type B predate on seals, and type C are fish eaters. This is discussed further below.

3.2 Abundance, distribution, movement

The Antarctic population of orca was reported as 160 000 (Hammond 1983; Northridge 1984), though this may have been an overestimate as the population around Antarctica (south of 60°S) has more recently been estimated at 70 000 animals (Klinowska, 1991). Orca are the most abundant of the toothed whales in the Ross Sea, with an estimated 3500 individuals (Ainley 1985). Orca are usually found within 800 km from the coast (Klinowska, 1991) and this seems to hold in the Ross Sea.

It appears that the distribution and social organisation of orca in the Ross Sea sector is bimodal. Pods of type-A whales seem to occur mainly over the continental slope, and may be associated

with the Antarctic Slope Front (Ainley 1985). The majority of orca actually in the Ross Sea study area are thought to be mainly type-B and type-C whales, with type-C reported as being by far the most common form in the McMurdo area (Pitman & Ensor 2003). Type B and C orca occur in separate pods over the continental shelf and within the pack ice edge in the Ross Sea (Ainley 1985). Their occurrence in the Ross Sea was associated with the vicinity of the ice edge in the western Ross Sea near Ross Island (Ainley 1985; Andrews et al. 2008).

The migratory status of type-B and type-C orca are unknown. It is generally thought that orca move out from pack-ice regions during winter, or at most, keep to marginal ice zones (Thomas 2004), though there is some evidence that they overwinter in the Antarctic (Pitman & Ensor 2003, and references therein). All whales in ice covered water require sufficient areas of open water to surface and breathe. Where polynyas and leads persist it is possible that whales reside in pack ice for long periods. Thomas (2004) details two reported sightings of orca within winter pack ice in the Antarctic, both in August. On one occasion, 60 orca were spotted with 120 minke whales in pools of open water that were cut off from the open sea by 65 km of compacted sea ice. On another occasion, a group of 40 orca of mixed ages were spotted in leads of water, 400 km south of the ice edge. In addition, Van Dam & Kooyman (2004) reported that during a cruise to the Ross Sea in May and June 1998 just two killer whales were seen on the same day at 73°S over the Ross Sea shelf slope, 580 km from the ice edge. There have also been sightings of orca in Arctic winter sea ice off west Greenland and western Alaska (Thomas 2004). So, although it is certainly possible that some Type B and C orca overwinter in the Ross Sea, it is unproven that most of the summer population does so. Here, we assume that Ross Sea orca are mainly type C and remain in the study area for the summer only (3 months of the year).

3.3 Population model

We used a simple age-structured population model for type-B and type-C orca in the Ross Sea in order to estimate the average weight of an individual in the population and for comparison with the methods for estimating consumption, and production described earlier. The model is based on a von Bertalanffy growth-function (length at age), a length-weight relationship, and a parameterization of age-dependent mortality. The population model aims to represent a typical recent year in the Ross Sea and we do not model fluctuations from year to year in response to actual changes in oceanographic conditions or orca behaviour/ecology. The entire orca population is treated together and we do not resolve sub-populations. The population is assumed to be in steady state, as no long-term trends in orca populations in the Ross Sea are known. The model separates males from females, and adults from calves (<1 y old).

3.4 Growth, length at age

Here we estimate growth and sizes of type-B and type-C orca which are assumed to be the dominate types in the Ross Sea. A number of studies give maximum lengths of orca in the Antarctic and most data are thought to relate to type-A orca (see Pitman & Ensor 2003, and references therein). Type-A male orca in the Antarctic are significantly larger than those given above, growing to 6.7–8.2 m (maximum 9.5 m) and females to 5.2–7.3 m (Fad, 1996). Mikhalev et al. (1981) report maximum lengths of 9.0 m and 7.7 m for male and female (respectively) Antarctic orca, and it is assumed that these refer to type-A whales. Compared to previous data, these figures suggest that type-A Antarctic orca are larger than northern hemisphere orca by about 1.1 m (males) and 0.6 m (females), or by about 15%. Specific data on body lengths of type B and C animals are not available, but Pitman & Ensor (2003) suggest that males are probably about 1.1 m shorter than type A, and females about 0.6 m shorter, giving typical maximum length estimates

for adult male and female type-B and type-C orca of 6.3 and 5.6 m respectively. The largest individuals at the 95% confidence level would be expected to be about 7.2 m (male) and 6.4 m (female). These lengths are remarkably similar to those for northern hemisphere orca, and it is reasonable to assume that the von Bertalanffy growth parameters K and L_{inf} for northern hemisphere orca apply to those around the Antarctic. Length-age data for northern hemisphere orca was available from Norwegian coastal whalers during the period 1938–67 and 1978–81 (Christensen 1984) and are quite consistent with data from a number of other studies (Asper & Cornell 1977; Duffield & Miller 1988; Hoyt 1990; Clark et al. 2000). Data suggest typical maximum lengths of 5.5–7.1 m (male) and 4.8–6.4 m (female). The data show that females grow more quickly than males, reaching a given proportion of the maximum weight about 2 years earlier.

3.5 Weight at length

Adult male type-A orca are reported as weighing up to approximately 8000 kg, and females as weighing up to 4000 kg (Baird 2000), though these will be much higher than average weights of type B and C orca. Based on data from the live-capture fishery for *Orcinus orca* in British Columbia and Washington in the 1960s and 1970s, Bigg & Wolman (1975) calculated the relationship between body length and weight in both sexes of orca as $W=29.65L^{2.577}$ where W is the weight (kg) and L is length (m). This relationship just lies within the 95% confidence intervals for the length-weight relationship given by Clark et al. (2000) for captive orca. There is a clear indication that captive orca are heavier for a given length than wild animals. Here, we assume that the weight-at-length relationship for type-C Antarctic orca is similar to that for non-captive northern hemisphere whales as given by Bigg & Wolman (1975) with an adjustment to reconcile neonate weights to Antarctic measurements (Mikhalev et al. 1981; Ross 1984; Christensen 1984). Based on lengths of adult type-C orca in the Ross Sea given above, this implies maximum adult weights of 3450 kg (male) and 2600 kg (female).

3.6 Demographics: Mortality

Natural mortality rates of orca in the Antarctic are not well known. In our model of orca, we estimated the natural mortality of orca using the model of Siler (1979) described by Barlow & Boveng (1991) and used by Trites & Pauly (1998) assuming that mortality is made up of a juvenile mortality rate which decreases exponentially with age, a base natural mortality rate that is independent of age, and a mortality associated with senescence which increases exponentially with age. Based on observations of the northern and southern resident communities of orca in the coastal waters of British Columbia and Washington State (Olesiuk et al. 1990) the maximum longevity of wild orca is likely to be 50–60 y (males) and 80–90 y (females), and reported that mean age of wild orca in British Columbia waters was 29.2 years (male) and 50.2 years (female). These values are in contrast with Trites & Pauly (1998) who suggested that 50 y was an appropriate estimate of the maximum longevity for orca of both sexes. Here, we take different values of mortality for males and females, and use values at the lower end of those found by Olesiuk et al. (1990) of 50 y (male) and 80 y (female). The adjusted model of Trites & Pauly (1998) for orca gives an average age at death of adults of 50.2 y (females) and 29.2 y (males), and maximum longevity of 88.3 y (female) and 51.8 y (male) consistent with results in Olesiuk et al. (1990).

3.7 Production

Mortality rates given in the previous section imply an annual birth rate of 5.1% is needed to ensure a stable population. This is close to estimates of annual birth rate of 4–5% (Dahlheim

1981). In the northern hemisphere, orca may have higher birthing rates in the autumn, although calving seems to occur year round (Olesiuk et al. 1990). Term-size fetuses were prevalent in Antarctic catches of orca taken in January–March (Anderson 1982), which suggested a possible peak in parturition in late summer. The presence of a calf within a group of 40 orca in August, 400 km south of the ice edge indicates that the whales may have given birth with the pack ice (Thomas 2004). It seems plausible therefore that Antarctic orca have peak birthing rates in late summer/early autumn but that births occur year round. Data from Olesiuk et al. (1990) gives a seasonal variation in pregnancy rates through the year by around a factor of 1.5.

Estimates of annual pregnancy rates in orca range 13.7–39.2% with the lower estimates probably more reliable (www.orca.online.fr/kwhales.htm). Estimates of the gestation period in the wild suggest about 12–16 months, with 15 months the best estimate (Nishiwaki & Handa 1958; Christensen 1984; Perrin & Reilly 1984; Anderson 1982) though Olesiuk et al. (1990) considers the measured gestation period in captivity of 17 months (Walker et al. 1988) to be a better estimate. Sex ratios at birth are assumed to be 1:1, but the ratio of male to female births has been reported at 0.48:1 and 0.83:1 for the northeast Pacific (Balcomb *et al.*, 1982; Bigg, 1982), and 1.34:1 for the Marion Islands (Condy *et al.*, 1978). Prenatal loss, as in other mammals, is assumed to be 10–30% (e.g. Hendrickx & Peterson 1997).

The population model for Type-C orca in the Ross Sea led to an estimate of overall production equivalent to P/B of 0.032 y^{-1} . The two methods for estimating production described earlier gave higher values of P/B of 0.039 and 0.056 y^{-1} , with a mean of 0.047 y^{-1} which we use in the modelling for consistency. Model production was made up of adult growth (72%), calf growth (8%), and reproduction (20%). Mortality (in terms of biomass) is given in proportions of adult mortality (93%), calf mortality (6%), prenatal mortality (1%). The mean weight of an individual within a population depends on the age (and hence length and weight) frequency distribution in the population, which in turn depends on the age-structured mortality and birth rates. The allometric estimate was used in the modelling for consistency with other species.

3.8 Consumption

Prey consumption was estimated for orca of various sizes to calculate an average for the population as a whole. For each size of animal in the population, consumption was estimated in four ways as described in the original section, using methods 1, 3, 4, 5 based on Innes et al. (1986), Sigurjonsson & Vikingsson (1997), Innes et al. (1987), and Lockyer (1981a) respectively. Younger and smaller individuals in a population grow faster than older, larger animals and hence consume more per unit body weight. Younger animals will contribute more to the mean consumption of the population than they contribute to the mean weight of animals in the population. The overall estimate of Q/B for orca consumption in the summer calculated in this way was 10.7 y^{-1} , quite close to our previous simple estimate of 9.7 y^{-1} . We use the model-based estimate of consumption because this takes into account non-adult orca which are likely to feed at a higher rate for their weight. For comparison, based on metabolic rates and assimilation efficiency for killer whales in the Aleutian Islands, Williams et al. (2004) estimates Q/B=11 y^{-1} , and Trites (2003) gives 11–18 y^{-1} , which are very close to our values.

3.9 Feeding and diet

Amongst other differences, the three types of orca in the Ross Sea specialize in different types of prey. Type-A orca are thought to predate mostly on minke whales and are likely to migrate from the lower latitudes to Antarctic waters during the austral summer in pursuit of the minke whale,

and then move north again when the minke whales migrate in the autumn (see: Kasamatsu & Joyce 1995; Stewart et al. 2003; Pitman & Ensor 2003 and references therein). Type-A orca feed by seizing prey, and are known to prey on squid, fish, penguins, seals and other whales in the Antarctic (Smith et al. 1981; Northridge 1984; Fischer & Hureau 1985; Knox 2007). In Antarctic waters, minke whale remains were identified as the primary item found in the stomachs of orca taken by whalers in the 1960s and early 1970s (Shevchenko 1975; Yukhov et al. 1975). However, these minke whales may not have been taken in Antarctic waters: Shevchenko (1975) concluded that most attacks on large whales (minke, sperm, fin, sei) occur in warm waters and not at high latitudes. Springer et al (2003) recently suggested that overexploitation of large whales by industrial whaling may have led orca to switch from preying on baleen whales to smaller mammals. Mehta et al. (2007) also concluded that large whales are not an important sources of food for (type-A) orca, though they do take juvenile whales.

Satellite-tracked movements of a type-B orca was consistent with a penguin/mammal-eating habit whereas the movements of several type-C orca were consistent with a fish-eating habit (Andrews et al. 2008). As noted earlier, Type-C orca are reported as being by far the most common form in the McMurdo area (Pitman & Ensor 2003) and are assumed to comprise most orca in the study region. The proportion of Antarctic toothfish in the diet of type-C orca in the Ross Sea is not known. It has been suggested that the diet of the type-C orca in the Ross Sea is 50% toothfish and 50% silverfish (Ainley pers. com.). Type-C killer whales have been photographed carrying large Antarctic toothfish on at least two occasions (Pitman & Ensor 2003, and references therein) so Antarctic toothfish are certainly a prey of orca in the Ross Sea. Orca are also known to take Patagonian toothfish from long-lines around Prince Edward Island and Crozet and to a lesser extent around South Georgia (Kock 2001; Brandao & Butterworth 2005, Kock et al. 2005). Recent observations around Prince Edward Island suggested that two out of every three toothfish on a longline had been attacked and partially devoured by orca (Brandao & Butterworth 2005). However, depredation of toothfish from longlines by orca has never been observed from New Zealand vessels in the Ross Sea (Jack Fenaughty, pers. com.). Also, habitat overlap between Antarctic toothfish and orca in the Ross Sea seems to be low. In other parts of the world, orca tend to spend most of their time foraging in surface waters (<100 m depth), and have a maximum diving depth of about 275 m (Baird et al. 2005). Catch rates of Antarctic toothfish in the longline fishery are greatest between 800 and 1500 m (Hanchet et al. 2007), so for toothfish to be a major prey item of orca, a significant part of the Antarctic toothfish population would have to be in midwater or over shallow ground, or orca would need to spend time feeding much deeper (ca. 3 times their normal maximum depth) in the Ross Sea than elsewhere in the world. Stable isotope analysis of orca and toothfish muscle suggests that orca feed at a very similar if slightly lower trophic level than Antarctic toothfish (Bury et al. 2008), which is inconsistent with toothfish forming a major (greater than about 10%) part of the diet or orca. In general therefore, although not known with confidence, at present it seems unlikely that Antarctic toothfish form a substantial part of the type-C orca diet in the Ross Sea in terms of weight consumed. It is not known if consumption of a small amount of toothfish is ecologically important to orca. We estimate the proportions of different items in the diet of orca in the Ross Sea is: 1% Emperor penguins; 2% crabeater seals; 1% Weddell seals; 5% large demersal fishes; 10% medium demersal fishes; 15% small demersal fishes; 50% silverfish; 5% pelagic fish; 10% squid.

4 Sperm whale

Sperm whales (*Physeter macrocephalus*) are migratory and are distributed from the tropics to the pack ice edges in both hemispheres, although generally only large males venture to the extreme southern portions of the range (e.g., Gaskin 1973). The species was subject to high catches through the 20th century. Global and Southern Ocean population in the mid-1980s was estimated

at 982,200 and 410,700 respectively (Klinowska 1991). In 2000, the global population was estimated to be 360,400 (Baker & Clapham 2004), but there are estimated to be only 28,100 individuals south of 50°S (Kasamatsu & Joyce 1995), and 12,000 south of 60°S (Whitehead 2002; International Whaling Commission 2001). The subtropical convergence at c. 40°S marks the southern limit of females and young males; only the larger males penetrate further south (Knox 2007; Lockyer & Brown 1981). Sperm whales are deep divers, apparently capable of reaching depths of >3200 m, and commonly diving to about 400 m. Sperm whales tend to inhabit oceanic waters, coming close to shore where submarine canyons or other physical features bring deep water near the coast. Any occurrence of sperm whales in the Ross Sea is likely to be along the shelf edge. Kasamatsu & Joyce (1995) reports a southernmost sighting of sperm whale at 74°S in the Ross Sea, and summarise data collected in sighting surveys between 1976/77 to 1987/88 during mid-December to mid-February. The data show that the highest densities of sperm whales in the southern ocean occurred in the area 70–78°S 150°E–180° i.e. along the Ross Sea shelf edge, with the highest densities in the Southern Ocean at 74°S on the Ross Sea slope. Two International Whaling Commission subareas in Sector V shown in Kasamatsu & Joyce (1995) span the study area: subregions V-ES (Ross Sea shelf) and V-EM (Ross Sea slope and north of slope). No sperm whales were sighted in subregion V-ES (Kasamatsu & Joyce 1995). Kasamatsu & Joyce (1995) state that, with no correction for sighting efficiency (the probability of sighting an animal on the ship trackline), the number of sperm whales sighted in subregion V-EM was 828 ± 406 between December and February. This sperm whale abundance corresponds to about 10% of the total Southern Ocean (south of 60°S) summer population (Kasamatsu & Joyce 1995). Taking the most recent population estimate of 12,000 sperm whales south of 60°S (Whitehead 2002; International Whaling Commission 2001) as being reasonable, this leads to an estimate of 1229 ± 602 sperm whales in subregion V-EM (Ross Sea slope and north of slope). The distribution of whales within this region is not known, but many are likely to be feeding along the slope edge in the study region. We assume the number of sperm whales in the Ross Sea study area to be 800 individuals, but note this is subject to considerable uncertainty. Sperm whales migrate northwards seasonally, and we assume that these sperm whales are present in the study region for only 3 months of the year (Kasamatsu & Joyce 1995; Knox 2007).

Newborn sperm whales are 3.5–4.5 m long. Adult females are up to 12 m and adult males are up to 18 m in length. Weights of up to 57 t have been recorded (SeaMap 2005). Other work gives 33 t as an approximate average value (Gaskin 1982; Bradford-Grieve et al. 2003). Here, we use the value for mean weight for male sperm whales of 27 t (Lockyer 1981b).

Prey is taken by seizing individual items. A wide variety of prey items have been found in the stomachs of sperm whales from around the world, but cephalopods (squid and octopuses), and fish (especially demersal fish) are considered to be the major prey items (Nemoto et al. 1985; Jefferson et al. 1993; Perry et al. 1999; Whitehead 2003). Some data suggests that their diet is almost exclusively cephalopods (Laws 1977; Northridge 1984). Sperm whales in the Southern Ocean, and Pacific subantarctic are reported as feeding primarily on squid and secondarily on fish (Clarke 1980; Knox 2007; Evans & Hindell 2004). Knox (2007) gives the ratio of squid to fish in their diet as 9:1. Antarctic toothfish have been described as prey items by Yukhov (1970, 1971) and Abe & Iwami (1989) but proportions are not known. Yukhov (1970, 1971) examined large numbers of stomachs from 12–18 m long sperm whales from the Pacific Ocean sector of the Antarctic from 1965 to 1969 and found that the main prey were cephalopods but that between 1 and 6 or more Antarctic toothfish (97–160 cm long) were also frequently found in the sperm whale stomachs. The sperm whales containing Antarctic toothfish were recorded from 58°S to 73°S (from the Antarctic Convergence to the northern slope of the Ross Sea), and from about 160°E to 100°W (Yukhov 1970). Although some records were associated with seamounts and

ridges, many occurred over deep water (>4000 m) suggesting the sperm whales were feeding pelagically (Yukhov 1970).

Stable nitrogen isotope composition of sperm whale tissue has been reported in the literature; measurements from skin in the Gulf of California were $\delta^{15}\text{N}$ were 17.2–19.9‰ (Ruiz-Cooley et al. 2004), with measurements from teeth in the NE Atlantic of 16.1–18.1‰ (Walker & Macko 1999). Nitrogen isotopic composition varies by a relatively small amount (<1.4‰) between tissues (Kurle & Worthy 2002; Hobson et al. 1996), but $\delta^{15}\text{N}$ values vary more substantially between regions. In general, marine mammals from northern oceans are reported as having higher nitrogen-isotope ratios than those from southern oceans (Kelly 2000). Hence, we suggest that an upper bound for $\delta^{15}\text{N}$ values for sperm whale muscle in the Ross Sea may be 16.1‰. Assuming that colossal squid (*Mesonychoteuthis hamiltoni*) form the major prey item of sperm whales in the Ross Sea, we can use estimates of $\delta^{15}\text{N}$ for this species of 11.5±1.2‰, a value for Antarctic toothfish muscle $\delta^{15}\text{N}$ of 13.6±1.1‰ (Bury et al. 2008) and a fractionation factor of +3.4 ‰ for $\delta^{15}\text{N}$ per trophic level (Post 2002), to estimate that the diet of sperm whale comprises up to a maximum of 56% toothfish. However, if all toothfish production estimated in the trophic model (Pinkerton et al. 2009a) were to be consumed by sperm whales (biomass and consumption parameters as estimated above), toothfish could comprise a maximum of 27% of the diet of sperm whales, so this is likely to be a more realistic upper bound on the fraction of toothfish in the diet of sperm whales. This figure is very sensitive to the change in $\delta^{15}\text{N}$ between regions which is not known. For example, if we assume that $\delta^{15}\text{N}$ for sperm whale muscle in the Ross Sea is nearer 15‰ instead of 16.1‰, the proportion of toothfish in the diet of sperm whales is estimated to be only 3%. In summary, consumption of toothfish by sperm whales remains unknown. For the trophic model, we assume squid dominate the diet of sperm whales in the Ross Sea, and suggest a starting diet of: 25% fish (3% large demersal fishes, 2% medium demersal fishes, 5% small demersal fishes, 10% silverfish, 5% pelagic fish) and 75% squid, thought note that this may underestimate the importance of large fish in their diet. Further data on sperm whale diet is required to improve this estimate. Biopsy samples of sperm whale blubber or skin from the Ross Sea would be especially useful to provide information (albeit indirect) on the trophic position of sperm whales in the study region.

5 Southern bottlenose whale

Southern bottlenose whales (*Hyperoodon planifrons*) seem to be most common between 58° and 62°S in the Atlantic and eastern Indian Ocean, but low numbers have been reported from the Ross Sea (Leatherwood & Reeves 1983; Northridge 1984). Like other beaked whales, they are deep-water oceanic animals and tend to be found in open water beyond the continental shelf in water deeper than 1,000 m. The whale is rarely found in water less than 200 m deep. Southern bottlenose whales are thought to have a circumpolar distribution in the Southern Hemisphere, south of 30°S (SeaMap 2005). They apparently migrate, and are found in Antarctic waters only during the summer, where they tend to occur within about 120 km of the ice edge. They have been found in groups of as many as twenty-five, but mainly appear to travel in units of less than ten. Northridge (1984) and Mead (1989) reported that there were no population estimates or even rough figures on relative abundance of the southern bottlenose whale available at that time. In 1995, Kasamatsu & Joyce (1995) published abundance estimates for south of the Antarctic Convergence (c. 60°S) in January: 599,300 beaked whales, most of which were southern bottlenose whales. Branch & Butterworth (2001a) estimated the population of southern bottlenose whales south of 60°S from two sets of surveys to be nearer 54 000–72 000. These later values are an order of magnitude lower than Kasamatsu & Joyce (1995) suggested. The Ross Sea makes up about 2% of the sea area south of 60°S, so, assuming southern bottlenose whales are

approximately uniformly distributed through this area, there will be c. 1260 southern bottlenose whales in the Ross Sea (using an average of populations from Branch & Butterworth 2001a). Kasamatsu & Joyce (1995) report very few sightings of beaked whales in the vicinity of the Ross Sea, so we reduce this to c. 500 southern bottlenose whales in the Ross Sea. This estimate should be considered tentative. We assume that southern bottlenose whales are present in the Ross Sea for 3 months of the year.

Maximum known sizes are 7.8 m for females and about 7.1–7.2 m for males (SeaMap 2005; Trites & Pauly 1998, and references therein), but there is a small sample size of measured animals. Trites & Pauly (1998) estimated an average weight within a population of 1331 kg (females) and 827 kg (males). This implies an average individual weight of 1080 kg for whole population, assuming equal numbers of males and females. Southern bottlenose whales are thought to take primarily squid (Northridge 1984), but probably also eat fish and possibly some crustaceans. We assume their diet is composed of: 1% medium demersal fishes; 10% small demersal fishes; 12% silverfish; 8% pelagic fishes; 61% squid; 2% *E. crystallophias*, 3% *E. superba*, 3% other macrozooplankton.

6 Arnoux's Beaked whale

Arnoux's Beaked whale (*Berardius arnuxii*) probably has a circumpolar distribution in deep cold temperate and subpolar waters of the Southern Ocean, though most records are from the southeast coast of South America, near the Antarctic Peninsula, South Africa, and the Tasman Sea (e.g., Leatherwood & Reeves 1983; Northridge 1984). Most reported strandings have been around New Zealand and it seems to be relatively abundant in Cook Strait, especially during spring and summer (Cawardine 1995). Sightings of large numbers have been reported recently along the western Antarctic coastal sector during the austral spring (Ponganis et al. 1995), similar to observations by Rogers & Brown (1999) for the eastern Antarctic sector. Sightings have been associated with shallow regions, coastal waters, continental slopes or seamounts (Rogers & Brown, 1999 and refs. therein) and other areas with steep-bottomed slopes (Carwardine 1995). They are known to enter pack ice and may live very close to the ice edge in summer, but likely to move away during winter. "Low numbers" of Arnoux's whale have been reported from the Ross Sea (Waterhouse 2001), though Kasamatsu & Joyce (1995) report very few sightings of beaked whales in the vicinity of the Ross Sea.

Not much is known of the biology of this species, and there are no estimates of abundance. Arnoux's beaked whales are cryptic; they are capable of diving for an hour or more, hence are difficult to observe and identify with confidence. In the southern hemisphere, identification could be confused with *H. planifrons* or *T. shepherdii* (Balcomb 1989). The life history of Arnoux's beaked whale is likely to be similar to that of its better-studied, northern hemisphere relative, Baird's beaked whale (*Berardius bairdii*). The reproductive biology of Arnoux's beaked whales is poorly known. Arnoux's Beaked whales are apparently not as numerous as Baird's beaked whales, which have a reported population of "several thousand" (CMS 2005), or of the order of 30 000 individuals. Assuming the total population of Arnoux's beaked whales is 10 000, and that these are widely distributed through the Southern Ocean (0.5% in Ross Sea), suggests a Ross Sea population of 50 animals. It is not known if this is reasonable. We assume that these whales are present in the Ross Sea for 3 months of the year.

Arnoux's beaked whales are quoted as having a maximum size of c. 9.8 m (SeaMap 2005). The maximum length of males and females is quoted as 9.6 and 8.9 m respectively by Trites & Pauly (1998). Using data given by (Trites & Pauly 1998) we estimate an average weight for individuals in an unexploited population of 1809 kg (females) and 1656 kg (males). Assuming equal numbers

of males and females we estimate the mean weight of individuals in a population to be 1730 kg. The feeding habits of Arnoux's beaked whales are assumed to be similar to those of their northern hemisphere relatives (Baird's beaked whales), thus consisting of benthic and pelagic fishes and cephalopods (Jefferson et al. 1993; SeaMap 2005). We assume a diet consisting of: 1% medium demersal fishes; 10% small demersal fishes; 12% silverfish; 8% pelagic fishes; 61% squid; 2% *E. crystallophias*, 3% *E. superba*, 3% other macrozooplankton.

7 Minke whale

The minke whale is one of the best studied baleen whales in the world. Historically, the taxonomy of minke whales has been plagued by confusion and debate (Stewart & Leatherwood 1985). At that time, scientists identified three geographically isolated populations of minke whales that may be separate subspecies: (1) *Balaenoptera acutorostrata acutorostrata* (North Atlantic); (2) *Balaenoptera acutorostrata bonarensis* (southern hemisphere); (3) *Balaenoptera acutorostrata davidsonii* (North Pacific). Here, we use Rice (1998) as representing the current state of knowledge in the field of cetacean taxonomy, which is that two separate species of minke whale may be found in the Ross Sea: dwarf minke whale (*Balaenoptera acutorostrata* un-named subspecies), and Antarctic minke whale (*Balaenoptera bonarensis*). Progress to this understanding is summarised by an extract from Reeves et al. (2003, p. 34): “Only within the last decade has the species distinction between the Common Minke Whale [*B. acutorostrata*] and the Antarctic Minke Whale (*Balaenoptera bonaerensis*) become widely understood and accepted. The present convention is to regard *B. acutorostrata* as consisting of two, and possibly three, subspecies: the North Atlantic subpopulation, *B. a. acutorostrata*; the North Pacific subpopulation, *B. a. scammoni* (= *davidsoni*); and the “dwarf” minke whale, *B. a. subsp.*, which is found in parts of the Southern Ocean (Rice 1998).” The two species of minke whales found in the Ross Sea (Antarctic minke and dwarf minke) are generally easy to distinguish from the larger rorquals that occur in the Antarctic (blue, fin, and sei whales), but, although they are generally about 2 m longer, it can be difficult to distinguish Antarctic minke whales from dwarf minke whales. In addition, there may be separate stocks of Antarctic minke whales in the Southern Ocean (Anonymous 2006). Historically, work on minke whales in the Southern Ocean does not tend to distinguish between the Antarctic minke whale and the dwarf minke whale. In this work, where we refer to “minke whales” we are referring to the combination of the two species. We are not aware of information that gives the relative proportions of these species in the study area.

Minke whales in the southern hemisphere are pelagic and circumpolar. They are found up to the Antarctic pack ice in summer, moving north by thousands of kilometres to warmer temperate and equatorial waters of the South Atlantic, Indian, and South Pacific Oceans in winter. They are known to occur well into pack ice covered seas (Ribic et al. 1991), though they are often said to prefer coastal and shelf seas to open waters. Minke whales penetrate the Ross Sea at different times of the year (e.g., Saino & Guglielmo 2000; Ainley 1985), possibly because of variations in the Antarctic Slope Front and frontal activity in the western Ross Sea associated with the ice edge and the northward flowing current there. We assume the minke whale population is present in the Ross Sea for 3 months per year (Dec/Feb). The Southern Ocean population of minke whales is c. 380 000 (SeaMap 2005). The southern ocean population of minke whales has been estimated to number around 580 000 animals (International Whaling Commission 1984; Northridge 1984).

Minke are the most numerous whales within the Ross Sea sector, with an estimated 14 300 individuals (Ainley 1985) close to the Ross Sea in densities of 0.02 – 0.05 / km² within the Ross Sea model area. This is considerably fewer than the number estimated to occur in an area 2.5 times larger, but including, the Ross Sea (Butterworth & Best 1982). However, the discrepancy could be explained by the timing of the cruises – Ainley's (1985) cruises occurred primarily

during December, but those of Butterworth & Best (1982) were more than a month later. During the intervening time a heavy band of pack ice that had closed the Ross Sea from the Pacific moved or dispersed, and so this may have enabled more whales to enter the Ross Sea by the time of the later censuses. The figure of 14 300 individuals (Ainley 1985) is well within the confidence limits of numbers of minke whales estimated by Branch & Butterworth (2001a, b). Minke whales tend to be concentrated to the north and in the western part of the Ross Sea. The number of minke whales penetrating into the Ross Sea itself (and hence our study area) is likely to vary substantially between years (e.g. Ichii et al. 1998). During winter cruises to the Ross Sea all minke whales were north of 70°S, with 21 and 9 seen in 1995 and 1998 respectively (Van Dam & Kooyman 2004). Until more information is available to allow this distribution to be estimated, we propose assuming here that typically one third the number of minke whales in the Ross Sea area feed in the study area.

Typical maximum length of “minke whales” within a population is given as 9.8 m (male) and 10.7 m (female) by Trites & Pauly (1998). The references quoted show that this work refers to Antarctic minke whales. Biometrics of Antarctic minke whales given by Konishi et al. (2008) are similar: mature males 6.3–9.6 m (n=2890) and 3.1–11.1 t (n=2766); pregnant non-lactating females 7.6–10.2 m (n=1814) and 4.9–12.5 t (n=1753). Length-weight relationship for minke whales given by Lockyer (1976) was: $W=0.049574 \cdot L^{2.31}$ where W is the weight [t] and L is the total length [m]. This relationship implies maximum weights of Antarctic minke whales of 9.7 t (male) and 11.8 t (female). Average weights within the population were estimated to be 6.1 t and 7.0 t for male and female whales respectively (Trites & Pauly 1998). The Antarctic minke whale is a long-lived species - those sampled by Konishi et al. (2008) were aged up to 63 (males) and 59 (females) years.

Dwarf minke whales are distinctly smaller than the Antarctic minke whale. The female dwarf minke whale is probably larger than the male; the longest female measured was 7.8 m long while the longest male was 7.1 m long (Arnold et al. 1987; Best 1985). These values, and the length-weight relationship of Lockyer (1976), suggest maximum weights for dwarf minke whales in the Antarctic of 2.7 t (male) and 3.5 t (female). Note that even the dwarf minke whales in the Southern Ocean are considerably larger than minke whales in other regions. For example, in Korean waters, minke whale length is reported to be 5.8–6.5 m with weights of 2–2.7 t (Gong 1981). For comparison, minke whales in Southern Ocean waters are reported to have maximum lengths (at physical maturity) of 8.3–8.6 m (males) and 8.8–9.0 m (females) by Stewart & Leatherwood (1985). These lengths are between those for Antarctic minke and dwarf minke whales. The mean weight of individual minke whales in the Ross Sea is calculated assuming that there are equal numbers of Antarctic minke whales and dwarf minke whales, and equal numbers of males and females. The average weight of minke whales in the Ross Sea is hence estimated to be 4.8 t.

The Antarctic minke whale migrates from tropical latitudes to the Antarctic where it spends the austral summer feeding (Kasamatsu et al. 1995). In Antarctic waters they accumulate fat reserves in blubber, which increases in thickness as the season progresses. Using the quantity of blubber as a proxy for energy storage Konishi et al. (2008) found a decrease in energy storage of minke whales from the Ross Sea and adjacent International Whaling Commission regions over an 18 year period from 1988. They concluded that these results primarily indicate an increasing shortage of food for the Antarctic minke whale over at least the last two decades and that the loss of blubber thickness over the 18-year period was equivalent to 36 intensive feeding days during the austral summer. Support for this decline in energy storage among minke whales in the Ross Sea comes from Ichii et al. (1998) who reported that the body condition was lower than that of whales in the adjacent waters off George V Coast. Further evidence for this is suggested by

Ainley et al. (2006) who, on the basis of field work completed around Ross Island, concluded that unusually numerous minke whales, fish-eating killer whales and Adélie penguins that year deplete crystal krill and silverfish stocks.

Minke whales use two forms of feeding: lunge feeding and bird-association feeding. Minke whale diet in the southern hemisphere is dominated by pelagic crustaceans, especially krill (mainly *Euphausia superba* with some *E. crystallorophias*), taken from the continental slope of the Ross Sea (Knox 2007; Ainley & DeMaster 1990; Ichii & Kato 1991; Ichii et al. 1998). Saino & Guglielmo (2000) encountered a large proportion of minke whales where acoustic surveys indicated very large swarms of krill. It seems that minke whales are flexible in their choice of food and adjust their diet according to food availability with few strong preferences (Skaug et al. 1997). Minke whales are certainly able to feed on small pelagic and demersal fish, such as sand eel, mackerel, and anchovy (e.g., Olsen & Holst 2001; Tamura 2003). A single minke whale feeding twice daily is reported as consuming an estimated 21.5 and 33.8 t (male and female respectively) of food over three to four months in the Antarctic (Armstrong & Siegfried 1991), consistent with values based on our Q/B value which gives 24.5 t. Ichii & Kato (1991) estimate higher values of 33.6–39.6 t. It is likely that there will be significant consumption of silverfish as well as krill in the Ross Sea. Proportions in the diet are estimated as 5% small demersal fishes; 20% silverfish; 5% pelagic fish; 20% *E. crystallorophias*; 45% *E. superba*; 5% other macrozooplankton.

8 Fin whale

The fin whale (*Balaenoptera physalus*) is found throughout the southern oceans, from the Antarctic and Indian Ocean to the coasts of New Zealand, Peru, Brazil, and South Africa. Fin whale sightings in the Ross Sea (Bassett & Wilson 1983) indicate that they prefer ice edge habitats, particularly along the continental shelf edge. Laws (1977) has suggested that the stock may have been reduced from around 400 000 animals initially to around 80 000 in the 1970's (Northridge 1984). Grenfell (1981) has estimated the total population in Antarctic areas 2, 3, and 5 (60°W to 70°E and 130°E to 170°W) to be around 80,000 also (Northridge 1984). Tamura (2003) and IUCN (2005) quote a value of 85,200 for the Southern Ocean south of 30°S based on International Whaling Commission (1979) and Perry et al. (1999). The fin whale is classified as endangered by the IUCN. A worldwide population estimate of 115 500 fin whales, with 22 000 in the southwest Pacific was given by Young (2000) and references therein. The food of fin whales in Antarctic waters is restricted to euphausiids, mostly *Euphausia superba*, but also *Thysanoessa macrura* (e.g., Nemoto 1959, 1970). The densest concentrations of fin whales in the Southern Ocean are reported as being where krill (*E. superba*) is most abundant (Brown & Lockyer 1984). This is consistent with the early observation that fin whale blubber thickness increases in summer when krill-whale co-occurrence is maximum (Mackintosh & Wheeler 1929). If fin whales were approximately uniformly distributed throughout the Southern Ocean, we estimate 3% of the Southern Ocean population would be present in the Ross Sea (c. 2560 whales). This is likely to be an overestimate because the Ross Sea does not support major concentrations of *E. superba*. We suggest there are likely to be fewer than 200 fin whales in the Ross Sea in the summer. Indeed, no fin whale calls were detected during an acoustic study at a site in the Ross Sea during the period 2 March to 16 June 2004 (Širović et al. 2009). Zenkovich (1970) estimated that fin whales spent 120 d y⁻¹ in the Antarctic (4 months). We assume that fin whales only penetrate into the Ross Sea proper (study area) for half of this time, i.e. 2 months per year.

The fin whale measures 26 m in the southern hemisphere. Large animals may attain weights of up to 130 t, but most probably weigh much less. Mackintosh (1965) gives 49.7 t as an average fin whale weight. Lockyer (1981a) gives 55 t (female) and 64.5 t (male) as average maximum

weights of fin whales. We assume an average weight for the population of 56 t (Trites & Pauly 1998). We also note that body weight varies seasonally. Fin whales can live to be up to 90–100 years of age (Trites & Pauly 1998; SeaMap 2005). Fin whales in the Southern Oceans feed almost exclusively on krill with small quantities of other pelagic crustaceans (copepods, amphipods). We assume their diet is: 5% *E. crystallorophias*; 86% *E. superba*; 4% other macrozooplankton; 5% mesozooplankton.

9 Sei whale

The sei whale (*Balaenoptera borealis*) lives mainly in the open ocean and not often seen near the coast. They occur from the tropics to polar zones in both hemispheres, but prefer warmer waters to fin and blue whales and are consequently more restricted to mid-latitude temperate zones (Tomilin 1957; Mackintosh 1965). They do undergo seasonal migrations, although they apparently are not as extensive as those of some other large whales. Current global abundance of the sei whale is considered to be about 39,000–80,000 (Young 2000; SeaMap 2005). The population of sei whales in the southern hemisphere has been estimated at between 15,000 and 30,000 (International Whaling Commission 1980). Tamura (2003) gives a number of 10,860 for the southern hemisphere including the Indian Ocean. Zenkovich (1970) estimated that sei whales are present in the Southern Ocean for only 100 days per year. Because of their preference for open-ocean temperate waters, we assume that only a very small minority of the southern ocean population of sei whales spends any time in the Ross Sea. Only two individuals were seen at the edge of the pack-ice near Scott Island in December 1976, but none was seen elsewhere during five cruises in the Ross sea completed between Dec–Jan 1976–1980 (Ainley 1985). Here, we assume there may be of the order of 100 sei whales in the Ross Sea for 2 months per year, and even this may be an overestimate.

Adult sei whales can be up to 18 m in length, although 15 m is a more typical length for adults. Large adults may weigh 30 t (SeaMap 2005). Mackintosh (1965) suggests 22.2 t as an average weight of sei whales. Lockyer (1981a) gives 18 t (female) and 19.5 t (male) as average maximum weights. Here, we use a mean weight for the population of 16.8 t (Trites & Pauly 1998). 90th percentile of longevity is reported to be 69 years (Trites & Pauly 1998). Sei whales skim copepods and other mesozooplankton, rather than lunging and gulping, like other rorquals. The diet, according to Kawamura (1974), includes not only euphausiids but also other swarming crustacea such as the amphipod *Parathemisto* (Northridge 1984). We assume their diet is: 4% *E. crystallorophias*; 87% *E. superba*; 4% other macrozooplankton; 5% mesozooplankton.

10 Humpback whale

The humpback whale (*Megaptera novaengliae*) is better studied than other balaenopterid species, and whales are known to occur in summer in well-defined feeding areas in Antarctic waters. Humpback whales are found in all the major ocean basins and migrate long distances. In the summer, humpbacks migrate poleward to exploit the high productivity of the cold waters. In winter humpbacks travel to warm tropical waters. The latitudinal range of this species whilst in Antarctic waters is reported to fall somewhere between the fin and sei whales (Laws 1977). Globally, there may be about 22 000–40 000 humpback whales (Young 2000; SeaMap 2005). In the Southern Ocean, the population is thought to number a few thousand (Northridge 1984). Laws (1977) gives figures of 100 000 and 3 000 for total southern stock sizes before and after exploitation. Tamura (2003) gives a population size for ocean south of 30°S as 10 000 (International Whaling Commission 2000). Austral summer estimates of abundance in the Southern Ocean from three circumpolar surveys completed in the period 1978–79 to 2003–04 indicated that all breeding stocks are increasing and if the rate of increase is >5%, the total

abundance in the Southern Hemisphere is >50,000 (Branch in press). Humpback whales were absent from the Ross Sea during these surveys, but particularly high densities were recorded north of the Ross Sea (Branch in press). We assume that less than 5% of the southern ocean population spends any time in the Ross Sea study region (c. 150 individuals). Zenkovich (1970) estimated that Southern Ocean populations of humpback whales spent 120 d y⁻¹ in the Antarctic region. Here, we assume that humpback whales are present in the Ross Sea proper for only 2 months per year.

Humpback whales measure 11–17 m as adults and attain a weight of at least 35 t (SeaMap 2005). Mackintosh (1965) gives 33.2 t, and we use 30.4 t as the average weight within a population of humpback whales (Trites & Pauly 1998). Longevity is reported as 75 y (Trites & Pauly 1998). Chittleborough (1965) states that *Euphausia superba* is the main food item, but that the krill *Thysanoessa macrura* is also eaten (Northridge 1984). Humpback whales are generalists, eating krill, copepods, fish, and cephalopods. Humpback whales exhibit a wide range of feeding habits intended to concentrate prey, which may be employed individually or in groups, including lunging, bubble-netting and lob-tail feeding (SeaMap 2005). Bottom feeding has also been documented, though is assumed to be a negligible proportion of humpback diet in the Ross Sea. We assume a diet of humpback whales in the Ross Sea of: 5% small demersal fishes; 25% silverfish; 5% pelagic fishes; 5% cephalopods; 10% *E. crystallophias*; 40% *E. superba*; 5% other macrozooplankton; 5% mesozooplankton.

11 Blue whale

Populations of the Antarctic blue whale (*Balaenoptera musculus intermedia*) migrate seasonally, moving poleward in spring to exploit the high productivity of the cold waters and travelling into the subtropics in autumn to reduce energy expenditures, avoid ice entrapment, and reproduce in warmer waters. Individuals do not stay in one area for very long, travelling solitarily or in pairs, and are found in both coastal and pelagic environments. The Southern Ocean blue whale population is estimated at 400–1400 individuals (IUCN 2005). Three complete circumpolar surveys completed during 1978–79 to 2003–04 indicated a population rate of increase of 8.2% per year, although the total numbers are still under 1% of their pre-exploitation abundance (Branch 2008). When feeding in cold waters, blue whale distribution is thought to be largely determined by food availability. Given that blue whale diet in the Southern Ocean is almost exclusively krill (essentially *Euphausia superba*) and that the Ross Sea proper may not contain major concentrations of krill, it is unlikely that many blue whales will occur in the study area. The Antarctic blue whales appear to be part of a single population, as they make the same call wherever they occur around the Antarctic and at least a part of the population is known to migrate to lower latitudes during the austral winter (Branch et al. 2007 and references therein). Seasonal and spatial variations of blue whale calls were analysed from recordings collected by acoustic recording devices at 4 circumpolar sites during 2003 and 2004, including a site south of 70° in the Ross Sea from 2 March to 16 June 2004 (Širović et al. 2009). The results found that the highest number of blue whale calls was detected at the Ross Sea site during March, but there were no calls there after April. If we assume the Southern Ocean population is approximately uniformly distributed through the Southern Ocean, we would estimate that about 3% of the Southern Ocean population enter the study area i.e. the equivalent of 27 blue whales are present in the study area. As mentioned, the number of blue whales in the Ross Sea is likely to be much fewer than this because of the low concentrations of *Euphausia superba*, and be restricted to the shelf edge. We assume 5 blue whales to be present in the study area. Zenkovich (1970) gives blue whales spending 120 d y⁻¹ in Antarctic (c. 4 months), over the summer period. It is reasonable to assume that they spend a shorter time at higher latitudes as sea ice restricts feeding. Here we assume that blue whales only penetrate into the Ross Sea proper for 2 months per year.

The Antarctic blue whale (*Balaenoptera musculus intermedia*) is larger than its northern relations, and generally measures up to 29 m, although a specimen over 33 m was once taken by whalers. Adults can weigh up to 190 tons, but most adults are 80–150 tons. Lockyer (1981a) gives 102 t (female) and 117 t (male) as average maximum weights of blue whales. Mackintosh (1965) gives 83.8 t as the average weight of a blue whale, and here we use 103 t (Trites & Pauly 1998). Blue whales are long lived, with a lifespan (90th percentile) estimated at 100 years (Trites & Pauly 1998). The age of sexual maturity is uncertain, but estimated to be five to fifteen years for both sexes. Reproductive activity takes place during winter, in the warmer waters of their range i.e. outside the study region. We assume blue whale diet in the Ross Sea is: 5% *E. crystallorophias*; 86% *E. superba*; 5% other macrozooplankton; and 5% mesozooplankton.

12 Summary of data for the model

Biomass, energetic parameters and diet data for the trophic model are summarised in Table 1 and Table 2.

13 Acknowledgements

Funding for this work was provided by the New Zealand Foundation for Research, Science and Technology (C01X0505: “Ross Sea Sustainability”).

Table 1: Summary of data for model parameters for whales.

Model group	Name	Scientific name	Weight (kg)	N in summer in Ross Sea	Time (months)	B (tonnes)	B (gC m ⁻²)	P/B (y ⁻¹)	Q/B (y ⁻¹)
Minke_whale	Minke whale	<i>Balaenoptera acutorostrata</i> , <i>Balaenoptera bonarensis</i>	4838	4766	3	5765	9.0E-04	0.039	15.2
Other_baleen_whale						2979	4.7E-04	0.027	8.4
	Fin whale	<i>Balaenoptera physalus</i>	55590	200	2	1853	2.9E-04	0.026	7.6
	Humpback whale	<i>Megaptera novaengliae</i>	30408	150	2	760	1.2E-04	0.028	9.9
	Sei whale	<i>Balaenoptera borealis</i>	16811	100	2	280	4.4E-05	0.031	10.3
	Blue whale	<i>Balaenoptera musculus</i>	102737	5	2	86	1.3E-05	0.019	6.6
Orca	Orca (type C)	<i>Orcinus orca</i> (<i>O. glacialis</i> ?)	3449	3500	3	3017	4.7E-04	0.047	10.7
Sperm_whale	Sperm whale	<i>Physeter macrocephalus</i>	27000	800	3	5400	8.5E-04	0.022	5.1
Other_toothed_whale						157	2.5E-05	0.066	12.0
	Southern bottlenose whale	<i>Hyperoodon planifrons</i>	1079	500	3	135	2.1E-05	0.066	12.2
	Arnoux's beaked whale	<i>Berardius arnuxii</i>	1733	50	3	22	3.4E-06	0.061	10.6

Table 2. Summary of diet estimates for whales in the Ross Sea study region.

Prey	Predators (diet fractions)										
	Minke whale	Fin whale	Humpback whale	Sei whale	Blue whale	Other baleen	Orca (type C)	Sperm whale	Southern bottlenose whale	Arnoux's beaked whale	Other toothed
Emperor penguins							0.01				
Crabeater seals							0.02				
Weddell seals							0.01				
Large demersal fishes							0.06	0.03			
Medium demersal fishes							0.10	0.02	0.01	0.01	0.01
Small demersal fishes	0.05		0.05			0.01	0.15	0.05	0.10	0.10	0.11
Antarctic silverfish	0.20		0.25			0.07	0.50	0.10	0.12	0.12	0.12
Pelagic fishes	0.05		0.05			0.01	0.05	0.05	0.08	0.08	0.08
Cephalopods			0.05			0.01	0.10	0.75	0.61	0.61	0.61
<i>E. crystallophias</i>	0.20	0.05	0.10	0.04	0.05	0.06			0.02	0.02	0.02
<i>E. superba</i>	0.45	0.86	0.40	0.87	0.86	0.72			0.03	0.03	0.03
Other macrozooplankton	0.05	0.05	0.05	0.04	0.05	0.05			0.03	0.03	0.03
Mesozooplankton		0.05	0.05	0.05	0.05	0.05					
Total	1	1	1	1	1	1	1	1	1	1	1

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