

How much do large whales eat?

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ABSTRACT

Estimates of the amount of prey consumed by cetaceans have been used in ecological models and also directly compared to human fisheries yields. Most of these estimates have been based on assumptions about energy requirements. However, the lack of direct measurements for large whales has necessitated extrapolation beyond the data points available from smaller species. A number of different parameterisations of general regressions in which energy requirements or consumption are estimated as proportional to body mass raised to some power B , were compared with estimates of Basal Metabolic Rate (BMR) from the widely used Kleiber equation. The choice of values has a large impact on estimates, which can differ by an order of magnitude, but modellers are frequently forced to make rather arbitrary decisions due to lack of data. Nevertheless, neither data nor theory appear to support values of $B > 0.75$. Although some parameter values have obtained status through common usage, these have not always been based on actual data and estimates of consumption by whales need to reflect this uncertainty. Comparison of generalised relationships with data from other sources, including rates of filter feeding, oxygen consumption and seasonal changes in energy stores, suggest upper bounds on average daily metabolic rate of large whales. Estimates based on stomach contents also indicated average daily metabolic rates of less than four times the BMR from the Kleiber formula, but these are critically dependent on estimates of digestion time for which there appear to be little data. Estimates of stored energy suggest that large whales that migrate to seasonally productive feeding areas either have relatively low energy requirements for their size or need to meet a considerable proportion of their annual energy requirements outside of the feeding grounds.

KEYWORDS: ENERGETICS; FOOD/PREY; FEEDING; MODELLING; MANAGEMENT; NORTHERN BOTTLENOSE WHALE; NORTH ATLANTIC RIGHT WHALE; BLUE WHALE; BOTTLENOSE DOLPHIN; NARWHAL; ANTARCTIC MINKE WHALE; COMMON MINKE WHALE; SPERM WHALE; SEI WHALE; KILLER WHALE; FIN WHALE

INTRODUCTION

Several studies over the last three decades have generated estimates of how much prey is consumed by large whales. These studies have arisen both from concerns that whales may have a negative impact on fisheries and also that fisheries be managed in order to leave sufficient prey available for whales. Most estimates have been intended to inform ecological models; others have been used to examine hypotheses that prey resources may be limiting predator population recovery (Baumgartner and Mate, 2003; Kenney *et al.*, 1986), whilst some have been used for direct comparison with human fisheries (Tamura and Ohsumi, 2000). Such comparisons have generated much public debate, often poorly informed. Within the International Whaling Commission (IWC) some Commissioners have stated that ‘whales consume huge quantities of fish making the issue a matter of food security for coastal nations’ (IWC, 2007) despite the conclusion of the IWC Scientific Committee that ‘for no system at present are we in the position, in terms of data availability and model development, to provide quantitative management advice on the impact of cetaceans on fisheries, or of fisheries on cetaceans’ (IWC, 2004). Given such a level of interest over quantities that have not been directly measured, there is a clear need for understanding the uncertainties surrounding the available estimates of food consumption. This paper reviews a number of estimates of prey consumption in an attempt to allow comparisons between different approaches.

Most of the methods for estimating prey or energy consumption of whales are based on generalised formulae related to body size. These formulae usually relate to body mass, although Hunter *et al.* (2000) suggested that maximum body length is a more accurate independent variable than body mass. Most calculations have relied on

estimating the energy requirements of whales and using this to estimate the amount of prey that would need to be consumed to meet these requirements. These calculations face a number of challenges: (1) estimates of metabolic rates in large whales need to be extrapolated well beyond the range of available data; (2) estimates of Basal Metabolic Rate (BMR) need to be adjusted to Field Metabolic Rate (FMR) or Average Daily Metabolic Rate (ADMR) and to allow for the energy requirements of growth and reproduction; (3) large whales may make long migrations and feed for only a proportion of the annual cycle; and (4) energy content of prey needs to be estimated and adjusted for assimilation efficiency (i.e. the amount of energy that becomes available to the whale).

RELATIONSHIPS WITH BODY MASS

Some of the studies reviewed here used direct empirical relationships between mass of food ingested and body mass while others were based on estimates of energy requirements. Where the energy content of the prey can be expressed as an average value per kg, then consumption rates follow directly from the energy estimates. Thus in the cases considered, daily consumption rates, R , can be expressed in the general form

$$R = AM^B \quad (1)$$

Where R is mean consumption rate in kg d⁻¹ over the whole year, A and B are constants and M is the body mass in kg. This equation can also be expressed in terms of energy

$$E = KM^B \quad (2)$$

Where E is the mean daily energy requirement over the whole year (kJ d⁻¹) and K is a constant. The energy balance for an individual is frequently written as

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$$T = E/c \quad (3)$$

Where T is the total energy intake (kJ d^{-1}), E is the metabolisable energy and c is the product of digestive efficiency and assimilation efficiency.

The value of B will clearly become increasingly influential with increasing body mass, and so is particularly significant for large whales.

Energy requirements

Kleiber (1975) suggested the generalised formula of Eqn 2 for BMR (expressed in kJ d^{-1}) in homeotherms, including mammals, with an exponent of $B=0.75$.

$$\text{BMR} = 293.1M^{0.75} \quad (4)$$

Although some studies have suggested that marine mammals have elevated metabolic rates compared to the Kleiber formula, none of these have proved to be consistent with all the available data. The hypothesis that marine mammal metabolic rates are higher than those of carnivorous terrestrial mammals (or mammals generally) has been tested on more than one occasion by comparing all available standardised metabolic rate determinations for marine mammals (specifically pinnipeds and cetaceans) with relationships generated for terrestrial mammals. Lavigne *et al.* (1986) concluded that the previous perception that marine mammals have higher metabolic rates in relation to body size than terrestrial mammals was not supported by data when comparisons were made under standardised conditions. Innes *et al.* (1987) also reached similar conclusions for comparisons of feeding rates and on further analysis of BMR estimates based on O_2 consumption (Innes and Lavigne, 1991). These results were confirmed by Hunter *et al.* (2000) who included additional data, but still were unable to reject the null hypothesis that BMR in marine mammals is the same as in terrestrial mammals of similar body size.

More recently, Williams *et al.* (2001) calculated BMRs of Weddell seals (*Leptonychotes weddelli*) and bottlenose dolphins (*Tursiops truncatus*) resting on the water surface of 1.6 and 2.3 times the predicted levels for similarly sized domestic terrestrial mammals. Their estimates involved measuring oxygen consumption. It is interesting to compare their estimates of BMR in bottlenose dolphins to measurements of actual food consumption of this species in captivity. Kastelein *et al.* (2002) found that estimated average annual food consumption of adult males and non-pregnant, non-lactating females was approximately $176 \times 10^5 \text{kJ}$ for a mean adult body mass of 260kg. This would correspond to a total energy requirement around 2.5 times the predicted BMR from the Kleiber formula and similar to the BMR estimated by Williams *et al.* (2001). There is clearly a discrepancy in this case given the expectation that the total energy content of the prey consumed would be some larger multiple of BMR. However, even if the BMR estimates of Williams *et al.* (2001) were correct, this would not justify their conclusion 'that the metabolic rates of many species of carnivorous marine mammal are elevated when compared to levels for carnivorous terrestrial mammals', since their finding only applies to two species. By taking selected data points for a few other species (as Williams *et al.* did) it is not correct then to reject a hypothesis supported by a much larger and more standardised data base. There have also been suggestions that marine mammals may require elevated

metabolic rates to maintain body temperatures (Kshatriya and Blake, 1988). However, in response to Kshatriya and Blake (1988), Lavigne *et al.* (1990) recalculated the lower critical temperatures of blue whales (*Balenoptera musculus*) and found that they, like many smaller marine mammals, should not be obligated to increase their heat production in order to maintain homeothermy, even in sea water at its minimum temperature of about -2°C .

Based on the evidence that metabolic rates in marine mammals were not exceptional, Lavigne (1996) suggested the following formula for ADMR, based on Eqn 4.

$$\text{ADMR} = \beta(293.1M^{0.75}) \quad (5)$$

Where ADMR is the average daily metabolic rate in kJ , β is a multiplicative factor greater than one and M is the mass in kg (a daily energy requirement of 293.1kJ corresponds to 70kcal or a power output of 3.39W). Based on the assumption that FMR is a simple multiple of BMR, ADMR should approximate average FMR throughout the year. For cetaceans, β is often assumed to be in the range of 2-5. Some authors have used $\beta=2.5$ which was a choice made by Kenney *et al.* (1997) for all cetaceans and subsequently followed by Hooker *et al.* (2002) and Laidre *et al.* (2004) for northern bottlenose whales (*Hyperoodon ampullatus*) and narwhal (*Monodon monocerus*) respectively. Baumgartner and Mate (2003) used a value of two for the ratio of diving metabolic rate to BMR in North Atlantic right whales (*Eubalaena glacialis*) with a note that 'It is very important to bear in mind, however, that the selection of Diving Metabolic Rate=2BMR, though based on sound reasoning, is truthfully only a guess.' This caution is applicable to most studies that assume a value for this ratio. Although some particular values have gained status through repeated use, these are not necessarily supported by actual data.

Alongside the debate about whether marine mammals have elevated metabolic rates is the debate about the value of B . Despite considerable attention being given to estimation of B within the literature (Hunter *et al.*, 2000; Kleiber, 1975; Koteja, 1991; Lavigne *et al.*, 1986) the problem remains of very few data points at higher body mass on which to base regression lines. Regressions that are not significantly different can nevertheless result in different values of B that result in considerable differences in predictions of consumption rates at large body mass. For example, the regression analysis of Lavigne *et al.* (1986) for the relationship between body mass and metabolic rate in phocid seals gave a value of B of 0.87. However, this was not significantly different from Kleiber's equation. The relationship between metabolic rate and body mass in marine mammals has also been reviewed by Boyd (2002). He suggested an allometric relationship in which FMR (expressed in kJ d^{-1}) varied with body mass to the power 0.524.

$$\text{FMR} = 2529.2M^{0.524} \quad (6)$$

Other recent reviews have also challenged the 0.75 figure as a general value for B in mammals. For example, White and Seymour (2005) argue that the best estimate of B for BMR is 0.69 across all mammalian taxa. In an extensive regression of 619 species from 19 mammalian orders, the same authors had previously made the case that BMR in mammals is proportional to body mass raised to the power 0.67 (White and Seymour, 2003). However, it should be noted that large whales are outliers to all these studies in terms of body mass.

COMPARISONS OF DIFFERENT STUDIES OF CONSUMPTION

Comparison of different estimates of the amount of prey consumed by large whales is complicated by whether these estimates are expressed in terms of energy or mass and whether they are mean daily values throughout the year or just for seasonal consumption within a region. For the studies reviewed here, we have presented comparisons in terms of mean daily energy throughout the year, relative to the predicted BMR from the Kleiber formula (Eqn 4).

Estimates of prey consumption by large whales based on allometric extrapolations

Kennedy *et al.* (1997) used the approach of Eqn 5 in a study of the trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. They assumed assimilation efficiency to be 80% and an average FMR/BMR ratio of 2.5. This gave an estimate of total energy intake of 3.125 times BMR. They also applied an additional factor for baleen whales to take into account seasonal differences in feeding rates. The study area was a known summer feeding ground for baleen whales and the calculated ADMR was multiplied by 1.2 to account for higher feeding rates when whales were in the study area. Such corrections highlight important issues when comparing estimates. For some modelling studies, it is the consumption within the area of the model that is of interest; for others it is the average consumption throughout the year. Daily consumption rates may vary by orders of magnitude between areas of high feeding activity and low feeding activity, especially for species that make long migrations and are able to store large amounts of energy.

To move from ADMR to estimates of prey consumption, data are required on the relative composition of the diet and energy content of the different prey species and assimilation efficiency. In many cases, such data are not available. In a study of the North Pacific, Trites *et al.* (1997) used a direct approximation for an individual's daily consumption or ration,

$$R_{i,s} = 0.1M_{i,s}^{0.8} \quad (7)$$

Where $R_{i,s}$ is the daily prey consumption in kg and $M_{i,s}$ is body mass in kg, for each species i and sex s . The value of 0.8 was taken from Innes *et al.* (1987). Okamura *et al.* (2001) used the same formula for an *Ecopath/Ecosim* model of the western North Pacific. Eqn 7 is shown on Fig. 1 assuming a mean prey calorific value of 5,450kJ kg⁻¹ (this is a commonly used value for fish prey and is used in this paper to standardise comparisons between estimates based on intake and estimates based on energy requirements) and an assimilation efficiency of 80% (this value is also used in this paper to standardise comparisons).

Sigurjonsson and Vikingsson (1997) used two different parameterisations to estimate consumption by whales around Iceland, which were used as input in an ecosystem model by Stefansson *et al.* (1997). They used the suggestion of Armstrong and Siegfried (1991), based on the results of Innes *et al.* (1986), that feeding rates could be described as

$$R = 0.42M^{0.67} \quad (8)$$

Where R is the daily consumption and M is body mass in kg. This is shown in Fig. 1 for a prey calorific value of 5,450kJ kg⁻¹ and an assimilation efficiency of 80%.

Sigurjonsson and Vikingsson (1997) also calculated ingestion rates based on estimates of energy requirements using

$$G = 863.6M^{0.783} \quad (9)$$

Where G is the daily requirement in kJ.

This was based on the near-basal metabolic rate of Lockyer (1981) with an assumed assimilation rate of 80% and an activity coefficient of 1.5. Mean daily feeding rates for baleen whales were also adjusted seasonally based on the assumption of 83% of the annual intake being during a 120 day summer feeding period and that feeding rates for the intensive feeding period were ten times that during the rest of the year, also based on Lockyer (1981). Thus the summer ingestion rate was assumed to be 2.53 G and the winter ingestion rate 0.235 G . In the absence of data on the seasonal variation in energy content of prey species they assumed an average of 3,900kJ kg⁻¹ for crustaceans and 5,450kJ kg⁻¹ for fish and cephalopods. These values were then used to calculate consumption rates from Eqn 9.

Tamura and Ohsumi (2000) used three different parameterisations to calculate regional estimates of prey consumption by cetaceans, referred to as Methods 1, 2 and 3 in their paper. Method 1, uses Eqn 8 directly, Method 2 uses Eqn 9 and Method 3 uses the formula suggested by Klumov (1963),

$$R = 0.035M \quad (10)$$

Where R is daily consumption in kg and M is average body mass, kg. This is shown on Fig. 1 for a prey calorific value of 5,450kJ kg⁻¹ and an assimilation efficiency of 80%. The relevance of the data from Klumov (1963) have subsequently been questioned by Reilly *et al.* (2004) who commented that the data used 'do not provide a sound basis for extrapolation'. For Method 2, Tamura and Ohsumi (2000) assumed the mean energy content of prey to be 4650kJ kg⁻¹ for baleen whales in the Southern Hemisphere and 5,450kJ kg⁻¹ for baleen whales in the Northern Hemisphere and odontocetes around the world. Tamura *et al.* (2004) used the mean of Methods 1, 2 and 3 and this is also shown in Fig. 1.

In a study of biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean, Reilly *et al.* (2004) reviewed various options for estimating mean daily consumption for a number of species. They used data on estimates of feeding rates of minke whales (*B. bonaerensis*) in the Antarctic (Tamura *et al.*, 1997) that appeared to be in good agreement with the Blix and Folkow (1995) FMR estimates. At the other end of the body mass range for great whales they extrapolated using Eqn 8 to blue whales. Fitting the generalised relationship between consumption and body mass given in Eqn 1 to these points gave their preferred relationship

$$R = 1.66M^{0.559} \quad (11)$$

for mean daily consumption in kg during the high feeding period in the Antarctic. This is shown in Fig. 1 adjusted for seasonal feeding based on the same assumption as in Eqn 9, of 83% of annual intake during the high feeding period, assuming mean energy content of prey to be 4,650kJ kg⁻¹ and an assimilation efficiency of 80%. However, they did consider a range of possibilities within the model, based on a maximum daily consumption for blue whales as a percentage of body mass.

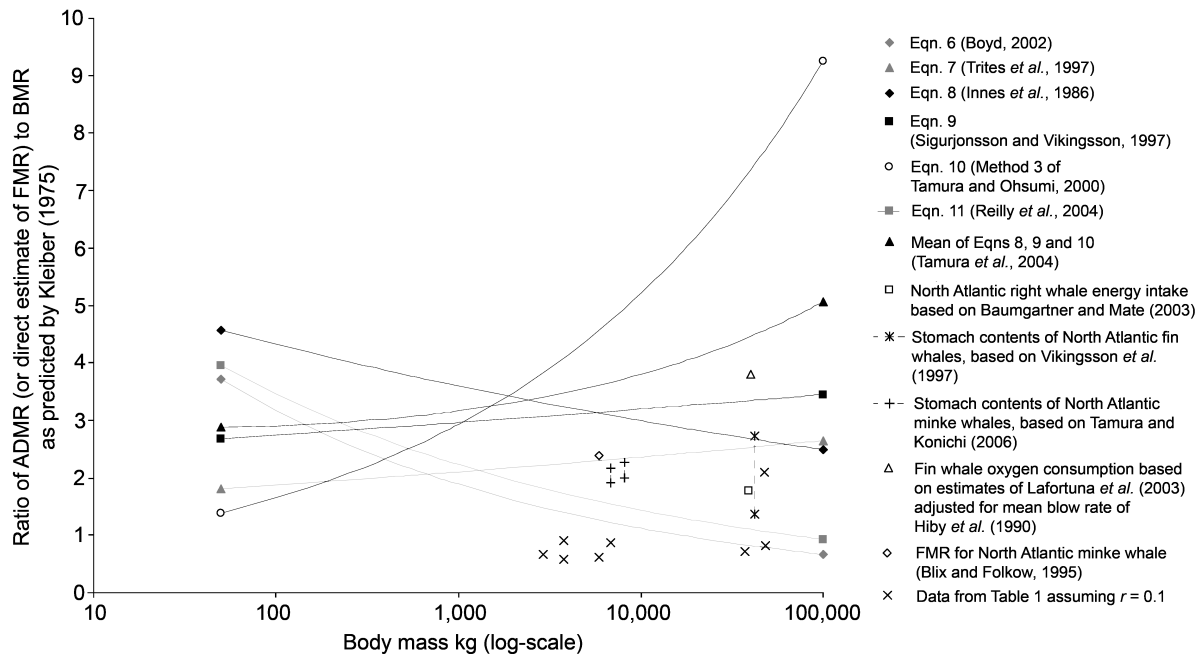


Fig. 1. Comparison of different studies expressed as a ratio to BMR as predicted by the Kleiber formula. For comparative purposes estimates based on seasonal energy intake were adjusted to approximate ADMR throughout the year (direct estimates of FMR were not adjusted for possible seasonal differences). Where estimates were originally expressed in terms of prey mass these were converted to energy based on estimated prey energy content and an assimilation efficiency of 80%.

OTHER METHODS OF ESTIMATING CONSUMPTION RATES

Possible alternative approaches to extrapolation based on allometry include direct measurement of intake from behavioural studies, estimates of intake based on analysis of stomach contents, estimates of respiration based on oxygen exchange, and estimates of energy requirements based on utilisation of energy stored in body tissues.

Direct observations of consumption rates

Estimates of quantity of prey consumed from behavioural studies of free living cetaceans have rarely been possible in the short term and become even more problematic over an annual cycle. For baleen whale species that feed by 'gulping' on prey that may take evasive action, measuring the amount of prey consumed is unlikely to be practicable. However it may be possible to make some inference for filter feeding species such as the *Balaenidae* if it can be assumed that the prey take no avoiding action. This has been done for North Atlantic right whales based on assumptions of swimming speed, projected area of the mouth, proportion of time spent feeding and measurements of copepod densities in the vicinity of feeding whales (Baumgartner and Mate, 2003; Beardsley *et al.*, 1996; Kenney *et al.*, 1986). Such an approach also provides an additional theoretical consideration for the choice of *B*. If body proportions remain constant with growth then the projected area for filtering will increase with body length raised to the power two whereas mass increases with length to the power three. Thus unless larger whales swim faster or spend a greater proportion of their time feeding, then *B* would have to be 0.67 or less.

Kenney *et al.* (1986) estimated a maximum possible daily filtering rate of $9.9 \times 10^4 \text{ m}^3 \text{d}^{-1}$ for right whales in the Cape Cod area assuming that they were feeding around the clock during submerged periods. This was based on a swim speed of 1.5 ms^{-1} . These estimates led them to conclude at the time

that the required prey densities were from one to three orders of magnitude greater than the densest concentrations sampled in the vicinity of North Atlantic right whale aggregations in the Great South Channel. Subsequent studies have tried to measure plankton concentrations in the vicinity of feeding right whales, and the results highlight the large variability in copepod densities. More recent studies of skim feeding right whales suggest that a 1.5 ms^{-1} swim speed may be too high. Leaper *et al.* (1999) observed maximum swim speeds of 1.2 ms^{-1} and a mean of 0.6 ms^{-1} with the mouth open, similar to a mean of 0.64 ms^{-1} for feeding whales observed by Mayo and Marx (1990) in Cape Cod Bay and 0.7 ms^{-1} from Goodyear (1995). The mean density of plankton observed near feeding right whales in the Great South Channel was 5.9 gm^{-3} (Wishner *et al.*, 1995) and 3.9 gm^{-3} in Cape Cod Bay (Mayo and Marx, 1990). Subsequently, Beardsley *et al.* (1996) reported some very high copepod densities in the Great South Channel. They calculated that the highest observed densities from a single bucket sample in front of a feeding whale (3.3×10^5 copepods m^{-3}) would enable a right whale to satisfy its daily energy requirement in around nine minutes of feeding. However, such high densities are not commonly observed and are much greater than mean values close to feeding whales. For example, the mean copepod density reported by Baumgartner and Mate (2003) beside feeding right whales in the Bay of Fundy was 6,618 copepods m^{-3} i.e. only 1/50 of the peak observed by Beardsley *et al.* (1996). Using the mean ingestion rate of Baumgartner and Mate (2003) for feeding right whales provides an energy intake of 2.96BMR. However, right whales are known to make long migrations and clearly do not feed every day of the year. Given the time spent by female right whales on the calving grounds and travel times between feeding areas it seems unlikely that all right whales could feed at this rate for more than nine months of the year. This would suggest a mean annual energy intake of 2.2BMR as predicted by Kleiber. Assuming an assimilation efficiency of 80% would suggest

FMR=1.76BMR and this is shown in Fig. 1 for comparison. No correction was made to this estimate to allow for less than 100% filtration efficiency (Mayo *et al.*, 2001). Baumgartner and Mate (2003) concluded that many of the tagged right whales in their study ingested prey at sufficient rates to meet daily metabolic requirements assuming DMR = 2BMR. However, if DMR values for right whales exceeded four times BMR, then only 4 of the 22 individuals with tag attachments lasting over 1hr would have been ingesting prey at a sufficient rate to meet daily energy requirements.

Stomach contents

Some estimates of feeding rates have been based on analysis of stomach contents including Vikingsson (1997) for fin whales (*B. physalus*) feeding off Iceland, Tamura *et al.* (1997) and Tamura and Konishi (2006) for Antarctic minke whales. Vikingsson (1997) predicted daily feeding rates for fin whales of between 677 and 1,356kg based on quantity of fore stomach contents and assumptions about the evacuation rate of the fore stomach. This range of values is plotted on Fig. 1 assuming a prey energy density of 5,450kJ and an assimilation efficiency of 80%, for a mean body mass of 42 tonnes adjusted to an average daily rate through the year using the assumption of Sigurjonsson and Vikingsson (1997) that $I=2.53R$ where I is the summer feeding rate and R is the mean throughout the year.

The ability of whales to exploit a super-abundance of prey will be limited by the size of the mouth and stomach, the duration of the conditions that maintain prey at high densities, the extent of the dense patches and the rate at which the stomach is evacuated. There is thus a maximum rate of food intake regardless of prey density. In studies of Antarctic minke whales during commercial whaling Bushuev (1986) found that only 3% of Antarctic minke whales caught between 04:00-05:00 hrs had empty stomachs but that this rose to 96% between 17:00-18:00 hrs. He concluded that in good feeding areas Antarctic minke whales only exhibited one period of peak feeding per day. Tamura and Konishi (2006) also reported a similar but less pronounced diurnal pattern in Antarctic minke whale stomach contents and used this to estimate daily consumption based on assumed digestion rates. Their consumption estimates of 4.36%-4.95% of body mass per day, adjusted for a mean daily rate based on 120 days feeding at high rate and 83% of annual energy intake during this period are shown in Fig. 1 for minke whales of body mass 6,800 and 8,100kg assuming a mean prey energy content of 4,473kJ kg⁻¹. Approximate times for digestion cite Bushuev (1986) although in fact this paper does not provide any actual data on digestion times. If the proportion of prey digested in each time interval, d , is constant (i.e. exponential decay) then there will be a linear relationship between estimates of daily consumption and estimates of d . Thus without data on d , it is not possible to relate stomach contents to consumption rates.

Respiration rates

Lockyer (1981) estimated that 30 and 70 tonne fin whales had BMRs of 1.4 and 1.8 times respectively of the values predicted by the Kleiber formula on the basis of lung capacity. Subsequent studies have also attempted to estimate metabolic rates from estimates of oxygen consumption. These are based on measured respiration rates, estimates of lung capacity (tidal volume) and assumptions regarding the exchange efficiency of oxygen. Lafortuna *et al.* (2003) derived a relationship for tidal volume, $V_T=0.074M^{0.9}$, from

measurements for three cetacean species in captivity. Extrapolation to large whales was based on a similar regression of measurements of total lung volume that did include sei (*B. borealis*) and fin whales and also appeared to scale with body mass to an exponent around 0.9. They also made the assumption that whales control their ventilatory output, mainly, if not exclusively, by frequency modulation. This assumption was based on physiology and may be challenged on the basis of numerous reports from field observations of variation in the apparent strength of blows for several species. One implication of the assumptions is that if tidal volume scales as body mass 0.9 and metabolic rates scale as body mass to some smaller exponent, then ventilation rates would decrease with size. There is some evidence of this from intra-specific comparisons. For example, Gordon and Steiner (1992) calculated mean blow intervals of 70.6s for small sperm whales (*Physeter macrocephalus*) and 107.1s for large males. Lafortuna *et al.* (2003) estimated an average oxygen consumption of 150L min⁻¹ for a 40,000kg whale with a conversion factor of 20.1kJ per litre of O₂. The observed blow rate in that study (mean 1.16 breaths min⁻¹) was rather higher than the mean respiration rate from a review of fin whale blow rates (mean 0.87 breaths min⁻¹) by Hiby (1992). Fig. 1 shows the FMR for fin whales based on Lafortuna *et al.* (2003) but adjusted for 0.87 breaths min⁻¹ (giving an O₂ consumption of 113L min⁻¹). This should be a more representative estimate of average FMR values, but nevertheless is only valid for whales on their feeding grounds.

Blix and Folkow (1995) used respiratory rates and lung volumes combined with respiratory data from other cetacean species to estimate an FMR of 80kJ kg⁻¹ per day for North Atlantic minke whales (*B. acutorostrata*). This is shown in Fig. 1 for a body mass of 5,900kg. This estimate has been widely used in a number of studies including the *MULTSPEC* multi-species model for fish and marine mammals in the Barents Sea (Bogstad *et al.*, 1997). In this model, average gross energy intake within the study area, allowing for muscle growth, blubber and visceral fat deposition was assumed to be 125kJ kg⁻¹ per day. Folkow *et al.* (2000) present similar calculations for northeastern Atlantic minke whales but stratifying energy requirements by season and by sex and reproductive status. Their values for gross energy intake range between 88kJ kg⁻¹ for physically mature males in spring to 143kJ kg⁻¹ for immatures in autumn. They estimate an average consumption of all prey by minke whales of 117kg per whale per day over a 183 day feeding season. In a model of interactions between minke whales, cod and herring fisheries in the Greater Barents Sea, Schweder *et al.* (2000) used an average daily consumption of 90kg per whale per day. By contrast, Laws (1977) had previously assumed that minke whales in the Antarctic fed at 3.9% of their body mass a day for 365 days a year. If krill is assumed to have an energy content of 4,500kJ kg⁻¹ then the mean daily gross energy intake would be 175.5kJ kg⁻¹. This is more than double the FMR estimates by Blix and Folkow (1995) and 5.6 times BMR as predicted by Kleiber for an 8,000kg whale and seems highly unlikely.

Energy stores

Brodie (1975) used estimates of the amount of lipid stored by fin whales on feeding grounds in the Southern Ocean and North Pacific to estimate consumption rates on the feeding grounds and energy requirements over the period for which whales are assumed not to be feeding. These estimates were taken from whaling data from 245 whales in the North

Pacific and 1,948 whales in the Antarctic by subtracting mean yields per whale at the start of the feeding season from those at the end. For a 48 tonne Antarctic fin whale he estimated a net gain in oil of 3,585kg over a 120 day feeding period. For a 37 tonne North Pacific fin whale he estimated a net gain in oil of 2,189kg over a 182.5 day feeding period. These would result in average available daily energy from stored reserves over the assumed non-feeding period of 550 and 451MJ per day for Antarctic and North Pacific fin whales respectively, based on an estimate of 38MJ kg⁻¹ from whale oil. These values represent 56% of BMR calculated by the Kleiber formula (Table 1). However, it is possible that whales may also feed during the low-feeding rate part of the year, when they are using up energy stores. To investigate how this would affect the conclusions reached by Brodie, suppose S is the energy stored during the high-feeding rate period, D is the number of days of high feeding rate (where energy available from intake exceeds demands) and L is the number of days of low feeding rate (where energy demands exceed that available from intake; also $D+L = 365$).

Then, while lipid is being deposited

$$S = D \times f(I - FMR) \quad (12)$$

where f is the efficiency by which energy from food intake is converted into lipid and I is the daily energy intake during the high feeding period. If all the stored energy is used during the low feeding period (with an assumed 100% efficiency) and assuming the daily intake during this period can be expressed as a proportion of high feeding intake, rI , then

$$S = (L \times FMR) - (rI \times L) \quad (13)$$

Giving

$$FMR = \frac{S}{(1-r)} \left(\frac{1}{L} + \frac{r}{D \times f} \right) \quad (14)$$

For an assumed set of values of D , L , f the ratio of low feeding rate to high feeding rate, r , will determine FMR. This is illustrated in Fig. 2 based on Brodie's data for the amount of energy stored by an Antarctic fin whale. The solid lines in Fig. 2 assume $D=120$ and $L=245$. The dotted lines assume $D=182.5$, $L=182.5$. In both cases the spread of lines cover the range of values of f from 0.5-0.8. This figure shows that the relationship between FMR and the ratio of low feeding rate to high feeding rate is relatively insensitive to the assumptions made regarding D , L and f within the parameter space explored in this study, particularly for low values of r . Although $0 < f < 1$ there are no data on which to base f for whales.

Some estimates of the rate of low season feeding have been made, but based on rather sparse data. For example, Lockyer (1981) predicted that 17% of annual food intake for Southern Ocean baleen whales was outside the high feeding period. This is equivalent to $r=0.1$ for $D=120$ and $L=245$. This estimate has also been used by other authors including Sigurjonsson and Vikingsson (1997) in the North Atlantic. Based on the energy stored from Brodie (1975) and assuming $f=0.7$ this estimate of low season food intake would result in estimates of FMR of 71% and 81% of the Kleiber prediction of BMR for North Pacific and Southern Hemisphere fin whales respectively (Table 1).

Brodie (1981) also estimated a mean daily energy requirement of 7.98×10^5 kJ for a 46 tonne bowhead whale (*Balaena mysticetus*) based on what he described as

metabolically effective surface area (the surface area of the muscular body core), rather than body mass – this would equate to 0.86 of BMR as calculated by Eqn 5. He estimated a lipid store of 4,000kg built up over the feeding season. This figure would suggest slightly more available stored energy in relation to body size than for Antarctic fin whales (Brodie, 1975). Based on this estimate of energy requirements, Brodie estimated that the lipid store could last the whales up to six months of not feeding. Lockyer (1981) estimated rather more stored energy for Antarctic fin whales (Table 1) than Brodie (1975) based on classifying them as either lean or fat and using total weight difference rather than oil yield. Tamura and Konishi (2006) and Folkow *et al.* (2000) also present analyses of energy stores in Antarctic and North Atlantic minke whales respectively. These are compared in Table 1. For $r=0.1$ all these studies that measure stored energy would indicate FMRs of less than the Kleiber BMR except for Lockyer (1981) where the ratio of FMR to BMR would be 2.1. The minke whale data are consistent with Folkow *et al.* (2000) who concluded that North Atlantic minke whales would be unable to survive the winter on energy stores built up in summer alone. For the studies of minke whales, Table 1 shows the values of r required to support the ADMR of 80kJ kg⁻¹ estimated by Blix and Folkow (1995). These vary from 0.34-0.42 for Antarctic minke whales and around 0.6 for North Atlantic minke whales. These values do not seem consistent with current theories of Antarctic minke whales making long migrations to breeding areas with poor food resources. Although it is perhaps not surprising that minke whales in the North Atlantic appear to store less energy than Antarctic minke whales, some North Atlantic minke whales are still believed to undertake long migrations. Either theories about low season consumption rates need to be revised or these data on stored energy would indicate metabolic rates of minke whales rather lower than other estimates.

DISCUSSION

The current situation is that developers of ecological models involving large whales tend to make rather arbitrary, but potentially highly influential decisions on selecting an approach from published sources on which to base estimates of prey consumption. We have not attempted a comprehensive review of all previous studies, but studies were selected to illustrate the range of estimates. Nevertheless, it is apparent from our review that several of the extrapolated curves, principally Eqn 10 and the mean of 8, 9 and 10 lie outside of the range of available data points for large whales (Fig. 1). These equations involve values of $B > 0.75$ and our conclusion is that they are not supported either by theory or data.

It is also difficult to reconcile data on energy stores and widely held beliefs that large whales spend long periods without feeding without assuming lower values for FMRs than the BMRs predicted by the Kleiber equation. In this regard, observational studies of feeding whales in the low feeding season would be particularly valuable. Estimating relative feeding rates in the field may be easier than absolute values (based for example on prey availability and proportion of time spent feeding).

In terms of predicting food intake, it is the total energy requirement that is of interest and hence FMR is more relevant than BMR. Thus the question of the relationship between BMR and FMR in relation to body size must also be considered. Koteja (1991) found that FMR scaled as body mass to the power 0.61 compared to BMR which

Table 1
Estimates of FMR based on stored energy assuming $f=0.7$.

Species	Body mass (kg)	Total energy stored during high feeding period (S) MJ	High feeding days (D)	Low feeding days (L)	Mean low feeding/high feeding intake (r)	FMR MJ/day	FMR/Kleiber BMR	r required for 80 kJ kg ⁻¹ in minke whale
Antarctic minke - immature male ¹	2,900	13,216	90	275	0	48	0.4	
	2,900	13,216	90	275	0.1	77	0.7	
	2,900	13,216	90	275	0.5	306	2.6	0.42
Antarctic minke - mature male ¹	6,800	32,815	90	275	0	119	0.5	
	6,800	32,815	90	275	0.1	190	0.9	
	6,800	32,815	90	275	0.5	760	3.5	0.40
Antarctic minke - immature female ¹	3,800	22,141	90	275	0	81	0.6	
	3,800	22,141	90	275	0.1	129	0.9	
	3,800	22,141	90	275	0.5	512	3.6	0.34
North Atlantic minke whale - mature ²	5,900	17,589	182.5	182.5	0	96	0.5	
	5,900	17,589	182.5	182.5	0.1	122	0.6	
	5,900	17,589	182.5	182.5	0.5	330	1.7	0.62
North Atlantic minke whale - immature ²	3,800	11,745	182.5	182.5	0	64	0.5	
	3,800	11,745	182.5	182.5	0.1	82	0.6	
	3,800	11,745	182.5	182.5	0.5	221	1.6	0.61
Antarctic fin whale ³	48,000	131,341	120	245	0	536	0.6	
	48,000	131,341	120	245	0.1	769	0.8	
	48,000	131,341	120	245	0.5	2,636	2.8	
Antarctic fin whale ⁴	47,500	344,400	120	245	0	1,405	1.6	
	47,500	344,400	120	245	0.1	2,016	2.1	
	47,500	344,400	120	245	0.5	6,912	7.3	
North Pacific fin whale ³	37,000	80,197	182.5	182.5	0	439	0.6	
	37,000	80,197	182.5	182.5	0.1	558	0.7	
	37,000	80,197	182.5	182.5	0.5	1,507	1.9	

¹Data from Tamura and Konishi (2006). ²Data from Folkow *et al.* (2000). ³Data from Brodie (1975). ⁴Data from Lockyer (1981) for female fin whale at puberty.

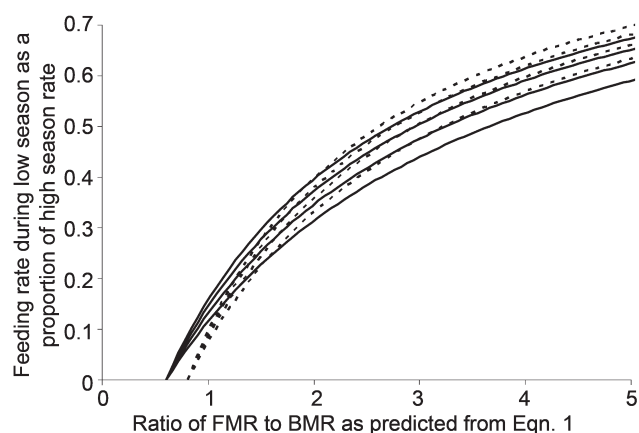


Fig. 2. Sensitivity of relationship between ratio of FMR to BMR as predicted by the Kleiber formula and ratio of feeding during low rate periods to high rate periods for $D=120$ (solid lines), $D=182.5$ (dotted lines) for $f=0.5-0.8$. Based on data for Antarctic fin whales from Brodie (1975).

scaled as body mass to the power 0.71 in his sample of mammal species. Although that study did not include marine mammals and considered mainly smaller species such as rodents, the qualitative result that FMR and BMR tend to converge with increasing body size is supported by Boyd (2002). Boyd suggests that the relationship between the energy cost of locomotion and body size could be one explanation for this. Passive drag is closely related to wetted area of non-propulsive body parts that will scale approximately to body mass to the power 0.67. When this is coupled with other effects such as the reduction in wave-making resistance with body size for a whale swimming at a given speed at the surface, the overall costs of travelling a certain distance at a given speed will scale to body mass raised to something less than 0.67. Locomotion may account

for a substantial proportion of energy expenditure in marine mammals. For example Boyd *et al.* (1994) calculated that locomotion costs were 40 to 60% of total energy expenditure in southern elephant seals. Boyd (2002) did note some caveats to his regression analysis that gave a value of B of 0.52 for FMR in marine mammals, the main concern being that measurements had been made using a number of different techniques. If only measurements of FMR using doubly-labelled water were considered then the slope (B value) was 0.81, although in that case the regression itself was not significant. Excluding the two species with the largest body mass (fin and minke whales) or excluding measurements with doubly-labelled water did not however, change the result. Nagy (2005) also reviewed FMR in relation to body size across a number of taxa. For mammals, there were no significant differences between the slope (B value) for BMR or FMR which both lay between 0.67 and 0.75. There is an ongoing debate about whether the value of B should be closer to 0.67 which would be expected from Euclidean scaling (White and Seymour, 2003;2005) or closer to 0.75 based on theories predicting quarter-power scaling (Savage *et al.*, 2004). However, none of these extensive reviews suggest values outside of the range 0.67-0.75. Thus we conclude that both theoretical and empirical evidence indicate that values of B greater than 0.75 are not appropriate for large whales. Nevertheless, the possibility that large whales might be an exception and scale to a value of less than smaller species that dominate the published data also cannot be rejected.

An additional factor that may contribute to larger whales having relatively lower average metabolic rates than might be predicted from extrapolation from smaller cetacean species may be related to the periods of fasting which tend to be longer for larger species. Periods of fasting are often accompanied by metabolic depression (Markussen *et al.*, 1992; Rea and Costa, 1992). Lockyer (1981) reviewed weight loss in other long fasting mammals (particularly

during hibernation) and found most species tended to lose 0.2–0.3% of body mass per day. If this rate of loss was sustained over an eight month fasting period then total weight loss would be around 50%.

Despite a total lack of theoretical or empirical evidence to support an exponent of 1 when scaling to body mass this value has nevertheless been used in some recent studies. For example, Murase *et al.* (2006) used the estimate of 80kJ kg⁻¹ per day from Blix and Folkow (1995) and apply it to humpback and fin whales to estimate the amount of krill consumed in sectors of the Southern Ocean. Inter-specific extrapolations were particularly important for that analysis which attempted to investigate inter-specific competition. The conclusion that 'humpback whales consumed about twice the amount of krill as Antarctic minke whales in Area IV' was largely the result of the choice of $B=1$. This resulted in estimates of consumption by humpback whales that were more than 50% greater than would have resulted from assuming $B=0.67$.

It is likely that neither population energy budgets nor consumption rates will be the greatest source of uncertainty in modelling interactions in complex ecosystems. Nevertheless it is important to understand the sensitivity of any model predictions to uncertainty in consumption rates. The values for food intake in large whales used in many models to date would appear to be at the high end of the likely range and model runs should be considered using lower values. As an extreme case, the parameterisation used by Tamura and Ohsumi (2000), which they describe as Method 3, gives predictions an order of magnitude greater than one of the other studies considered here (Boyd, 2002). With this level of uncertainty, comparisons of consumption by cetaceans with fisheries catches, which then may be used out of context, are clearly inappropriate and potentially misleading.

One issue not addressed in detail in this review is variation in the energy density of prey. This is clearly critical to calculating mass of prey consumed from estimates of energy requirements and annual and seasonal variation across trophic levels may also be important from a modelling perspective. Although most studies have used average values, several studies have highlighted the high level of variability in prey energy density (De Lorenzo Costa *et al.*, 2006; Mårtensson *et al.*, 1996; Winship and Trites, 2003).

Winship *et al.* (2002) attempted to quantify some of the uncertainties surrounding estimates of food requirements of Steller sealions (*Eumetopias jubatus*). Their conclusion was that 'uncertainty in diet and bioenergetic parameters resulted in the largest variation in model predictions'. Boyd (2002) also examined the sensitivity of estimates of consumption to input variables for a study of Antarctic fur seals (*Arctocephalus gazella*) and macaroni penguins (*Eudyptes chrysolophus*). In these studies, the body mass of the species in question was within the range that allows interpolation rather than extrapolation of bioenergetic parameters and also where there is least discrepancy between the various studies considered here. Unfortunately, due to the need for extrapolation, it is not possible to quantify the uncertainties in predicting food requirements of large whales using similar approaches. While data on feeding rates of small cetaceans and pinnipeds may allow for improved estimates it seems unlikely that reliable estimates of the feeding rates of large whales will become available in the near future. To date, lethal research programmes based on weighing stomach contents have been able to add little to such estimates. For example, Leaper (2007) found that the data

used by Tamura and Konishi (2006) to estimate consumption of krill by Antarctic minke whales were consistent with a range of mean daily consumption on the feeding grounds of 1.5–7% of whale body mass per day. This range covers what might be considered plausible values including all but the maximum two of the lines shown in Fig. 1 over the range of minke whale body mass, and is thus not inconsistent with allometric comparisons. However, despite large sample sizes of 6,777 whale stomachs, the data were not able to narrow the range of values. The IWC Scientific Committee concluded that until questions related to the length of the feeding season, digestion rates and the extent of feeding at night could be resolved 'it would not be possible to move beyond only broad estimates' (IWC, 2008).

In addition to incorporating uncertainty, all studies need to provide a clear justification for the methods and assumptions on which estimates are based. In particular, certain values for some parameters have obtained a status through common usage rather than carefully analysed data. These include ratios of FMR to BMR, digestion rates, the length of time spent on high latitude feeding grounds, the proportion of total annual consumption on these feeding grounds and assimilation efficiency. All these need careful consideration when generating estimates. A constant assimilation efficiency of 80% was used in this paper to allow comparisons between studies (some of which used this value) but this will clearly vary with prey condition, size and species.

In addition to uncertainty in the energy requirements of individuals, estimating numbers of whales in an area is an obvious source of uncertainty in estimating overall prey consumption, although quantifying uncertainties in numbers has received far more attention than most of the other aspects considered here. Estimating the numbers at age and body mass at age of individuals within the population is also challenging. Trites and Pauly (1998) suggest a general relationship for mean mass across the whole population based on maximum length, but such methods may not be appropriate where the population is segregated by age or sex.

Another factor that will affect energy requirements of mature females is the investment in rearing a calf. In terms of population energy budgets this requires data on the number of calves successfully reared until weaning since the energy requirements of lactation are the dominant component associated with reproduction.

Estimates of energy requirements are not just of interest for ecological models, but may also be used to examine the implications of disturbance and changes in behaviour. For example Williams *et al.* (2006) used estimates of energy requirements to estimate the potential impacts of human disturbance on killer whales (*Orcinus orca*). Uncertainties in basic energy requirements may have a substantial impact on the conclusions of such studies.

Resolving the uncertainty in how much large whales eat will not be easy. Our review has concentrated on the implications for Eqn 1 of the value of the exponent (B) rather than the intercept (A). Nevertheless the estimate of the intercept can have a substantial effect. The estimates reviewed were most consistent for body masses between 200 and 1,000kg where the ratio between highest and lowest was around two. This range includes the body masses for which there are most direct data for cetaceans.

From an ecological modelling perspective, tightening the bounds on a range of plausible values may be a useful step, especially given that marine ecological models face so much

uncertainty in other regards. We believe the evidence from this review is sufficient to put upper bounds on the mean daily energy requirements of large whales indicating that studies based on Eqn 10 or the mean of 8, 9 and 10 appear to have overestimated the quantity of prey consumed. Specifically, all of the individual data points reviewed in Fig. 1 fall below a mean annual FMR of four times BMR as predicted by the Kleiber equation. Setting lower bounds is more difficult and will probably have to rely on further bioenergetic models, but at the present time mean annual FMRs close to or even slightly below those predicted by the Kleiber equation for BMR, cannot be ruled out. A parameter space for average energy intake for large whales, bounded at the high end by Eqn 8 and at the low end by Eqn 6 (adjusted upwards for assimilation efficiency) might currently be an appropriate choice. This would cover the individual estimates derived from a number of different methods, with the commonly used estimate of FMR from Blix and Folkow (1995) falling roughly in the middle.

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