All creatures great and smaller: A study in cetacean life history energetics

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All creatures great and smaller: a study in cetacean life history energetics

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This paper reviews some specific studies of cetacean life history energetics over the past 20–30 y that include one of the largest species, the baleen fin whale, *Balaenoptera physalus*, the medium-sized odontocete long-finned pilot whale, *Globicephala melas*, and one of the smallest marine odontocetes, the harbour porpoise, *Phocoena phocoena*. Attention is drawn to the decrease in longevity with size and the differences in biological parameters that reflect this and affect life history strategy and energy utilization. Data from the past whaling industry in Iceland for fin whales, the Faroese 'grindedrap' for pilot whales, and by-catches as well as some live captive studies for harbour porpoise have been used. The studies demonstrate how information can be gathered to compile energy budgets for individuals, relying on carcase measurement and analysis, dietary investigations, biochemical analyses of tissues, and general life history studies including reproduction; as well as from monitoring living animals. The individual examples presented show how food energy storage in the form of fat can be variously important in insulation in the smallest species to controlling reproductive efficiency in large migratory species. The paper concludes by noting that an understanding of energy use in the individual can be an important input in multi-species ecosystem modelling.

INTRODUCTION

Cetaceans span a huge range in body size, from those weighing only a few tens of kilograms to those such as the largest of the Balaenopteridae that can weigh more than 150 tonnes (Lockyer, 1976). Undoubtedly living in a water medium presents some special physical and physiological challenges to cetaceans, such as in the areas of thermoregulation, locomotion and breathing. Nevertheless, the dense water medium provides physical support for the largest animals which might otherwise have not attained such sizes, and also presents some different energetic demands to those faced by terrestrial dwellers; such as the need for good insulation in the form of blubber fat, and also special circulatory developments such as rete and complex blood capillary anastamoses, that can help with thermoregulation and blood circulation during diving.

Cetaceans, as marine mammals, are top predators in the marine ecosystem, alongside man, and frequently there are concerns that cetaceans may be in competition with man for certain fish prey (Lockyer, 2006). As a taxonomic order in the marine ecosystem, Cetacea have the potential to exploit a vast variety and quantity of prey resources which range from small planktonic copepods through euphausiids and other crustaceans, to squid and fish that have a variable energy density content, with levels of 0.3–1.0 kCal (1.3–4.7 kJ) in planktonic organisms and cephalopods to 0.7–2.6 kCal (3.4–12.1 kJ) in fish. Baleen whales are especially adapted to filter-feed on small swarming planktonic prey, but can also take shoaling fish. The toothed killer whales, *Orcinus orca*, will also consume birds and even other marine mammals.

Approach to energetics

Cetaceans in general are elusive and challenging to study by virtue of the fact that many are too large to accommodate in holding facilities, and live in water, often far offshore. In recent years, there have been many studies using telemetry with VHF and satellite tags and time-depth recorders (TDR) that have been able to collect data remotely from both large and small cetaceans on dive patterns, swim speed and potential foraging bouts (Heide-Jørgensen et al., 2002; Bloch et al., 2003; Watwood et al., 2006). In marine mammals generally, especially certain coastal species and also animals maintained in holding facilities, direct observations on metabolic rates (Sparling & Fedak, 2004) and use of isotopic tracers have been possible (Acquarone, 2004; Carlini et al., 2004). Also, the use of ingested transmitters that are able to detect changes in stomach temperature (indicative of feeding), thermistors to monitor heat flux (Willis et al., 2005) and electrodes that can record heart rate changes during diving have been significant (Teilmann et al., 2006). However, all these exciting developments are still only able to contribute to part of the total energy budget of the animal, and many require direct access to the animal either on land or by restricting the animal at the surface, to apply the equipment.

In this paper we will not dwell on the details of individual studies and their techniques, nor energetics of swimming and the more detailed energy dynamics associated with thermoregulation and diving. We will focus on feeding and general energy expenditure at different life phases that may be useful in population energetics. Ingestion of food is a basic essential to acquire energy for growth, metabolism

and reproduction. Although animals may survive without food in the short term, fat energy deposited in the body will still be required in order to meet energy demands at certain times when food is not plentiful. Three case studies will be reviewed here, based on the earlier work of Lockyer.

Energy budget

As an example we will consider the energy dynamics of intake and loss in the individual whale.

Energy taken in and utilized is derived from:
- feeding
- energy storage as fat depots or as glycogen
- developmental growth by adding to the body.

Energy lost from the animal is removed as:
- heat losses via skin, lung exhalations, excretion (urine and faeces—both in terms of undigested food and metabolic loss)
- internal energy transfers in organs (not totally efficient)
- energy loss in assimilation of food
- drag/frictional losses and other costs in swimming
- reproduction (placental transfer, foetal growth and lactation)
- miscellaneous losses, e.g. parasites and disease.

Information that is needed to assess the energy budget for the individual will include the following:
- life history and age parameters
- body size and growth rates in terms of body mass
- reproductive parameters, e.g. age at first reproduction, fecundity, reproductive interval, pregnancy and lactational costs
- activity budget—time and energy spent foraging, resting, mating, etc.
- diet and food (energy) consumption rate
- metabolic rates and energy losses to the environment.

In reality, only some of these items are known for certain species, or are only partially known, so that it is often necessary to make some educated estimates based on comparisons with other better known species.

CASE STUDIES

We will take three different types of cetaceans as our examples: a medium-sized open ocean social odontocete; a large pelagic migratory baleen whale; and one of the smallest coastal marine odontocetes with no special social characteristics.

1. Long-finned pilot whale, *Globicephala melas*, in the north-east Atlantic—off the Faroe Islands
2. fin whale, *Balaenoptera physalus*, in the north-east Atlantic—off Iceland
3. harbour porpoise, *Phocoena phocoena*, in the North Sea—inner Danish Waters and British Isles.

The three types of cetacean will then be compared as to the relative importance of fat storage and mode of energy utilization in relation to their biology.

1. Long-finned pilot whale in the north-east Atlantic: the Faroe Islands

Life history and age, growth and reproductive parameters

The pilot whale lives for up to ~60 y, and the adult male is larger than the female, at ~5.7 m long and weighs

up to 2000 kg, while the female is about 3.8–4.5 m long in adulthood and weighs 600–1000 kg (Bloch et al., 1993). The male is mature by age 17 y (Desportes et al., 1993). The female can reproduce from age 8–9 y, and a single calf of ~180 cm long and 75 kg is born after ~12 months' gestation (Martin & Rothery, 1993). The calf is suckled for 2–3 y. The reproductive interval is up to 5 y.

Activity and body condition

Pilot whales are highly social and have a matriarchal school structure (Kasuya & Marsh, 1984; Amos et al., 1993). Schools may move long distances in a given period of time, and may migrate and follow prey movements. The male is generally more mobile than the female, and may move between different schools. Mating and birthing are seasonal and males particularly may be very active during the mating season and use a lot of energy. Pilot whales store fat seasonally in the winter months and this is used up during the spring and summer months for reproduction (Lockyer, 1993).

In the Faroe Islands, body condition was measured from carcases. Body mass was measured using a 2-tonne tensile link accurate to ±1 kg with a remote digital readout, and suspended from a hoist and pulley system (Lockyer, 1993). All tissues were analysed for composition and energy density (Lockyer, 1993).

Diet

Pilot whales consume almost exclusively cephalopods—representatives from about 13 families in total of which eight are most popular (Desportes & Mouritsen, 1993). The main genera/species in the North Atlantic are squid identified from beaks found in stomachs and include *Todarodes sagittatus* and *Gonatus* spp. from the north-east Atlantic (Desportes & Mouritsen, 1993), *Illex illecebrosus* from Newfoundland (Mercer, 1975), and *Loligo palei* from the north-east USA (Payne & Heinemann, 1993). About 15 genera of fish have been identified from otoliths in the pilot whale stomachs from the Faroe Islands, but the main fish species is mackerel, *Scomber scombrus* in the north-east USA (Payne & Heinemann, 1993). The energy density of squid is low at about 1 kCal (4.7 kJ) per gram, compared to fish species generally, which may vary in energy density both by species, e.g. gadoids are low compared to clupeids, and also seasonally according to the fat content.

Rate of food consumption—ingestion rate

Here we may calculate the amount of food eaten by weighing stomachs from dead animals and also from food consumption records for captive animals. However, this is very variable according to sex, age and size of animal and also its reproductive status. Food consumption can also be calculated from body mass using a formula (Innes et al., 1986) where ingestion rate, IB, is calculated as an allometric function of body mass, M:

$$IB = 0.123 M^{0.80} \qquad (1)$$

where M=body weight in kg, and IB=ingestion rate in kg per day.

Using this formulation method, an adult female pilot whale weighing 1000 kg would consume about 31 kg food per day, which translates to 31×10^3 kCal squid per day and

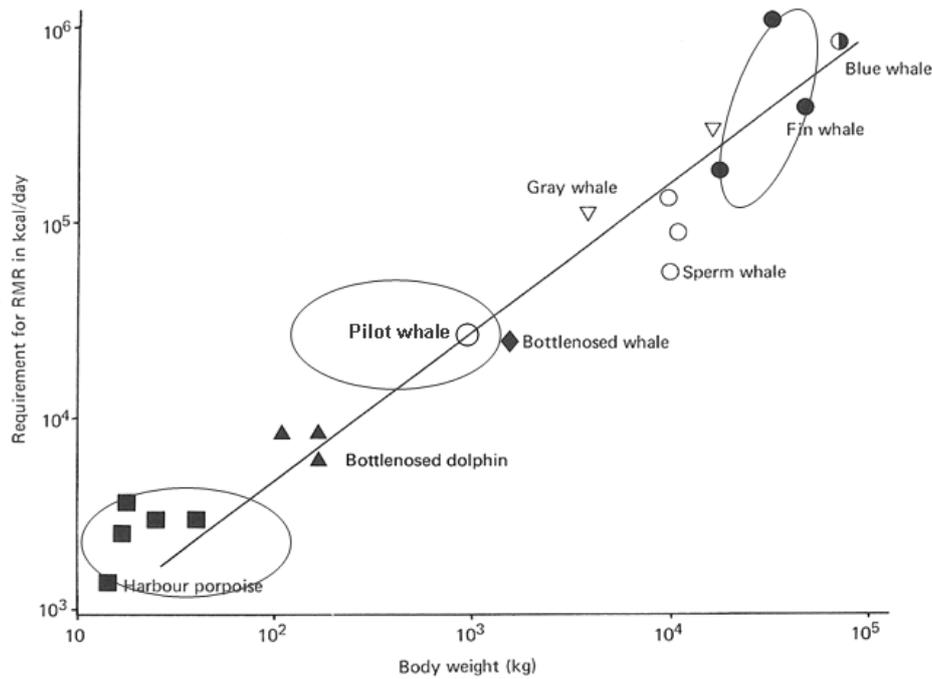**Figure 1.** Resting metabolic rates of cetaceans compared and interpolated (after Gaskin, 1982, based on Lockyer, 1981).

approximately 11.5×10^6 kCal squid in a year (Lockyer, 1993). It should be noted however, that this formula only provides a 'ball-park' estimate of food mass consumed as energy density of prey can be variable. Assimilation efficiency is high in carnivores (Keiver et al., 1984) and is assumed to be 90–95**%** in cetaceans eating a marine animal or fish diet.

Metabolic rates

Metabolic rate, Q, can be calculated from the Kleiber (1975) equation:

$$Q = 70M^{0.75} \qquad (2)$$

This represents basal metabolic rate where Q is in kCal per day, and M, body mass, is in kg. This formulation is based on metabolic rates for a wide range of mammals, and like formula (1) above, is only a guide. An adult female pilot whale weighing 1000 kg would have a basal rate of 1.24×10^4 kCal per day (Lockyer, 1993) according to this formula (2). This is shown on the graphic scale of body size and metabolic rate in Figure 1.

Actual daily energy expenditure is likely to be at least $\times 1.2$–$\times 2$ this level at 1.5–2.5×10^4 kCal per day for maintenance level (including replacement growth). Over a year, this adult female pilot whale would expend up to 9×10^6 kCal (Lockyer, 1993).

Reproductive energetics

Male. The male is reproductively active in spring and summer (Desportes et al., 1993). There is rapid body fat depletion during these seasons (Lockyer, 1993), with muscle fat disappearing first in May, followed by blubber mass in July, and finally lipid content of the blubber decreases in August. By August breeding is over (Desportes et al., 1993).

Female. The chief costs to the female are in pregnancy and lactation. Lockyer (1993) has demonstrated that the pregnancy energy required for gestation of the foetus—costs of the foetal growth and also heat of gestation, Q_G, which covers placental maintenance—can be calculated from Brody (1968):

$$Q_G = 4400 \, M^{1.2} \qquad (3)$$

where Q_G is in kCal, and M is the mass of the foetus in kg.

The suckling calf consumes milk that contains about 15–31**%** fat and lactation demands on the mother require an additional increase in food consumption of about 32–63**%** depending on the stage of lactation (Lockyer, 1993).

Building an energy budget

All the information above can be drawn together to create an energy flow diagram, considering the main energy into the animal and the paths of energy use out in any year. The focus is on the reproductively active adult female over a period of three years, commencing with pregnancy and two years of lactation and the growth of the young calf whose energy budget can be derived in a similar way to the adult. In Figure 2, we can see these component parts of the annual energy budget.

It can be seen that a certain amount of fat storage is necessary and this is stored mainly internally and also in the blubber (Lockyer, 1993). The costs of pregnancy are not as great as the lactational costs, and these are unlikely to increase in the second year despite the growth of the calf because of gradual weaning and independent feeding which is allowed for in the scheme. However, energy storage in the form of fat appears to be important as an energy supplement in reproduction in the pilot whale.
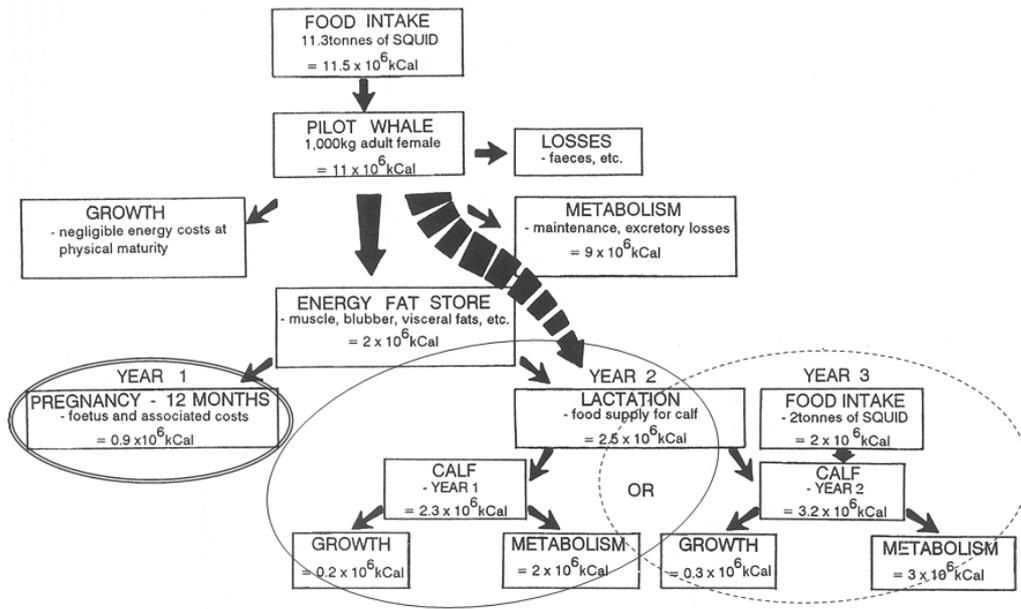
Figure 2. Annual energy flow diagram for an adult female pilot whale during reproduction and for her calf (after Lockyer, 1993). =, Year 1; --, year 2; - - , year 3.
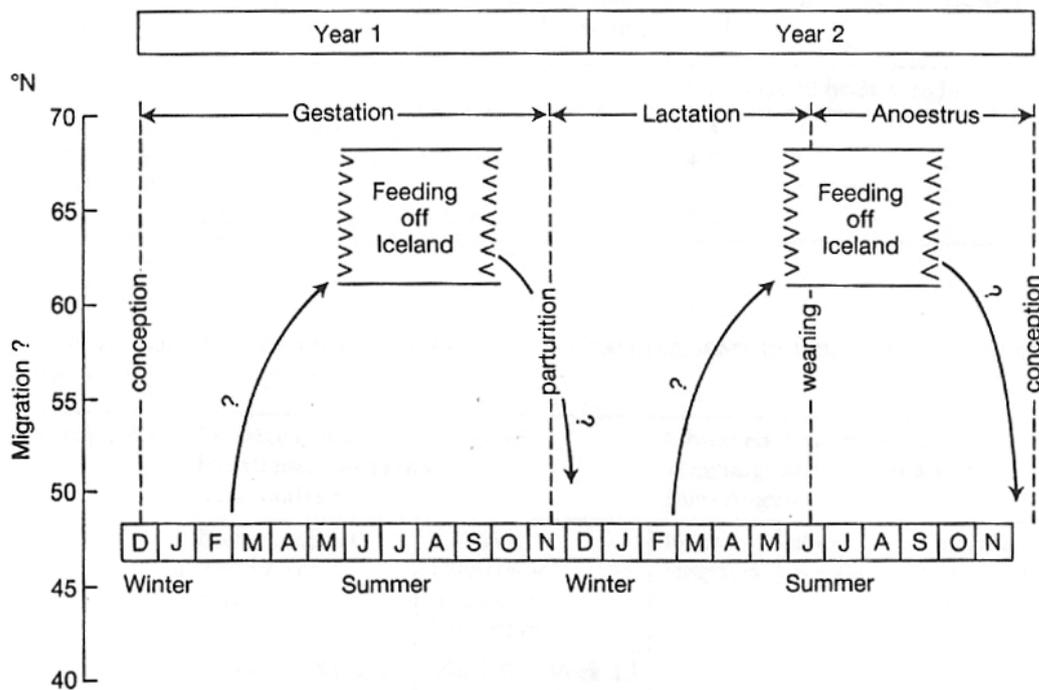

Figure 3. Schematic two-year reproductive cycle for Icelandic female fin whales, showing the relationship of reproductive events with migratory distribution by latitude and feeding activity (after Lockyer, 1987b).

2. Fin whale in the north-east Atlantic: Iceland

Life history and age, growth and reproductive parameters

Fin whales can live up to 80 or more years (Lockyer et al., 1977). Adult females can average 22.5 m and males 21.5 m in length in the North Atlantic and weight can attain 70 tonnes (Lockyer & Waters, 1986; Víkingsson et al., 1988). Both sexes mature between age 6 and 12 y by which time they have achieved about 85% of final body length (Lockyer, 1984; Boyd et al., 1999). Gestation is about 11 months (Lockyer, 1984; Boyd et al., 1999), and at birth, length is

~6.5 m and weight 1.75 tonnes (Lockyer, 1981, 1987a). Lactation lasts 6–7 months (Lockyer, 1981). Fin whales feed mainly on euphausiids and occasional fish when available (Lockyer, 1986, 1987a).

Activity and body condition

The fin whale is essentially oceanic and highly migratory (Lockyer & Brown, 1981) and there is a seasonal cycle of feeding intensity and breeding, separated in time and space by a period of months and often a distance of several thousands

Table 1. *Predicted energy costs of the reproductive cycle of the female fin whale off Iceland—after Lockyer (1987b).*

Energy output		Energy input	
Pregnancy–11 months	Lactation–7 months	Calculated from carcase composition	Estimated from food requirements
Foetal growth to 1750 kg @2940 kCal g⁻¹	Milk production of 72 kg d⁻¹ @3320 kCal kg⁻¹ with 90% mammary gland efficiency	Average difference between pregnant and near-end of lactation female carcase composition after three months of summer feeding	Total food requirement at 80% assimilation efficiency conversion of food
$=5.1\times10^6$ kCal PLUS Heat of gestation – $Q_g=4400*M1.2$ $=34.3\times10^6$ kCal	$=55.8\times10^6$ kCal	$=98\times10^6$ kCal	$=119\times10^6$ kCal

Total energy costs		Total energy costs	
39.4×10^6 kCal + 55.8×10^6 kCal			
$=95.2\times10^6$ kCal		$=98\times10^6$ kCal	$=119\times10^6$ kCal

of miles covered across many latitudes. A schematic 2-year reproductive cycle is depicted in Figure 3 showing the movements of the female fin whales in relation to reproductive events and feeding over the months of the year.

Body condition has been monitored off Iceland during many seasons, most recently by Víkingsson (1990), and it is clear that summer feeding is correlated with massive increases in body fat, and also with the fecundity of the female (Lockyer, 1986, 1987a; Víkingsson, 1990). During the summer feeding season (over 13 weeks) during the recent historic fin whaling in Iceland, adult female fin whales were sampled and measured anatomically for length, girth and blubber thickness, as well as for weight of all organs and tissues and composite body mass. All weights were performed on a weigh bridge with container, the total weight being derived from piecemeal weighings (Lockyer & Waters, 1986). All tissues were originally analysed for energy density using a bomb calorimeter (Lockyer et al., 1984), and these values used to calculate body energy content. The body mass difference between end of season pregnant and beginning of season end of lactation females was found to be an average 18.5 tonnes (range 16–21 tonnes) equivalent to a carcase energy density of 98×10^6 kCal (range $95–102\times10^6$ kCal) in a 19.4 m female. This is a huge difference in body mass which has been shown to be the result mainly of fat deposition internally and in blubber (Lockyer, 1986, 1987a, b). The energy density change is very significant, nearly doubling in the pregnant animal over the summer feeding period.

Diet

Fin whale stomach contents off Iceland indicate that dietary preference is predominated by the euphausiid shrimps, such as *Meganyctiphanes norvegica* (Lockyer, 1986; Víkingsson, 1992, 1995, 1997), although capelin and other

fish may be taken if available. Energy density of euphausiids is 0.93 kCal per gram in Lockyer (1987b), and relatively low compared to that of fish (see earlier).

Rate of food consumption—ingestion rate

In general, the assumption with respect to food consumption has been 4% of body mass (Sergeant, 1969), as used by Lockyer (1981) for baleen whales. The formulation (1) used above for pilot whales can also be used. However, as observed by Lockyer (1981), consumption during winter months may be reduced depending on prey availability. Full stomach capacity has also been used as a guide to meal size. Víkingsson (1992, 1997) estimated that in summertime, a full stomach was usually about 500–600 kg food for a 'standard' 18.6 m fin whale, and feeding rate calculated from digestion speed and feeding activity, indicated a daily intake of around 677–1356 kg with an average 1311 kg daily for a pregnant female. This range represented 1.3–3.3% body weight per day intake. Assimilation efficiency is assumed to be relatively high despite the non-digestibility of chitin in crustaceans, and 80% has been applied to dietary intake in all energy budget calculations, as discussed in Lockyer (1981).

Metabolic rates

The metabolic rate for fin whales can be interpolated from Figure 1, and also from the same formulation as used for pilot whales, above in formula (2). Estimates were originally presented in Lockyer (1981) using several different approaches to determine resting metabolic rate. Víkingsson (1995) has estimated the relative metabolic requirements for pregnant fin whales relative to food consumption during the 4-month summer feeding period, which amount to 1.19×10^8 kCal. This represents about half the estimated total annual metabolic requirement as calculated by Lockyer (1981)—see also discussion below under *Building an energy budget*.
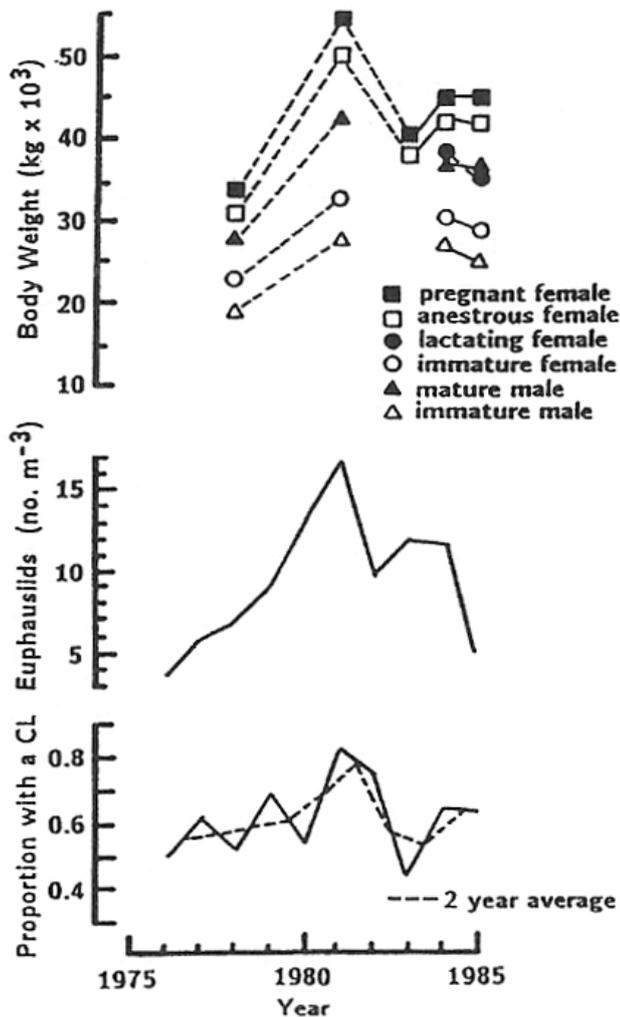
Figure 4. Yearly variations in female fin whale body condition (weight) for different reproductive classes, whale food abundance (euphausiid density) and potential whale fecundity (proportion of females with a corpus luteum) off south-west Iceland (after Lockyer, 1987b), showing the close correlation.

Reproductive energetics

This case study focuses on the adult female and the reproductive costs associated with the annual feeding cycle, and pregnancy and lactation over a two-year period. The study is described in Lockyer (1987a). It is also necessary to consider the growth of the foetus, and this can be estimated using the Huggett & Widdas (1951) foetal growth model based on fin whale foetal data. Foetal growth has been depicted in Lockyer (1984) with the Huggett & Widdas (1951) formula:

$$W = [0.47(t-74)]^3 \qquad (4)$$

where W is body weight in kg, and t is the time in days since conception.

Again, energy densities of foetal tissues and milk, as presented in Lockyer (1987a) can be applied to the gestation and lactation costs, and heat of gestation as given in formula (3) earlier.

Building an energy budget

In this particular case study, focus is on the relative costs of the female reproductive stages. In Table 1, energy intake
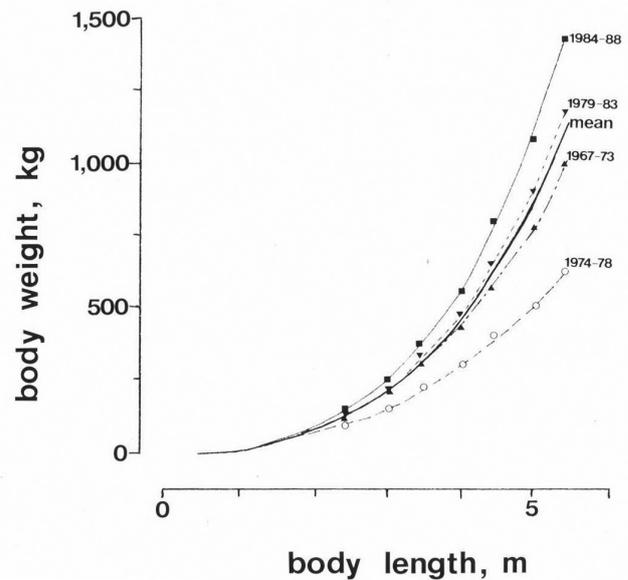

Figure 5. Annual fluctuations in food and subsequent decrease in body fat condition of the mother, as illustrated in Figure 4, can directly influence foetal growth and size in fin whales, as shown by the low body weight of near-term foetuses in the mid-1970s (after Lockyer, 1990).

and output are calculated and compared and found to be in balance. The costs of the combined pregnancy and more costly lactation are satisfied by the fat energy stores laid down by the pregnant female. From an earlier study (Lockyer, 1981), we can estimate that the total reproductive costs (over two years) for the Icelandic female fin whale at about 1×10^8 kCal amount to about half the annual energy demands of the female's total metabolic costs which are estimated to be about 2×10^8 kCal in the slightly larger southern fin whale.

Annual variations in food supply on the energy balance

The topic of environmental effects mediated through food availability and consumption, has been addressed in some detail by Lockyer (1986, 1987a,b, 1990). There appears to be a close correlation between body mass and fat condition and euphausiid prey abundance in all reproductive classes of both sexes off Iceland (Figure 4). The fecundity in the female is also affected. The apparent pregnancy rate varies in a two-year cycle, but this is to be anticipated for a two-year reproductive cycle (Figure 3).

The effect of poor prey availability and the consequential reduction in body fat accumulation for energy storage, also appear to affect foetal growth in weight. Figure 5 shows that in different time periods, foetal growth in mass relative to length varies considerably, with the period 1974–1978 being especially low in body mass. This time period correlates with a period of low prey abundance and also low adult body fat condition reflected in low body weight (see Figure 4). This may have serious implications for survival of the calf immediately after birth, both in terms of poor insulation and lowered buoyancy. However, there are no data on calf survival in different years.

Nevertheless, while mammals may have an innate ability to survive times of poor feeding, reproductive output may well assume low priority during these periods.

Table 2. *Body fat condition in porpoises from British waters, after Lockyer (1995), showing the extreme variation in pregnant and lactating animals and sex differences in newborn that may influence differential survival.*

Reproductive class	Length (cm)	Weight (kg)	Blubber weight (kg)	Mid-girth (cm)	Mid-lateral blubber thickness (mm)	Blubber lipid content % wet weight
Calf ≤90 cm						
Neonate (male)	76.2 ±8.6	7.1 ±2.0	2.7 ±1.8	45.6 ±5.2	9.9 ±4.1	67.3 ±8.6
Neonate (female)	79.3 ±7.2	8.7 ±4.3	4.3 ±2.7	47.1 ±4.1	12.8 ±6.2	69.3 ±11.6
Adult female >140 cm						
Resting	156.9 ±11.6	45.0 ±13.0	11.9 ±1.7	86.6 ±6.9	13.4 ±5.9	85.5 ±8.1
Pregnant	151.5 ±5.3	50.3 ±9.1	13.6 ±2.3	95.4 ±9.1	16.8 ±4.2	86.8 ±6.3
Lactating	156.0	40.0	11.0	82.0	12.0	
Pregnant and lactating	150.0	49.0	11.0	96.0	14.0	83.0

3. Harbour porpoise in the North Sea—inner Danish waters and British Isles

In this case study, feeding, growth and seasonal body changes are analysed for porpoises both in human care and free-living, in predominantly Danish waters. The former were a female and a male porpoise, both studied for several years from the first and second year of life respectively when sizes were around 130 cm in length and weights were 37.5 kg for the male and 40.5 kg for the female (Lockyer et al., 2003a). The free-living porpoises were a combination of past directed catches and Danish bottom-set net by-caught animals which are described in Lockyer et al. (2001) and Lockyer & Kinze (2003). In addition, reference is made to an earlier study made off British coastal waters where by-caught and some stranded animals were investigated (Lockyer, 1995). The review examines the growth, relative body mass and seasonal variations in body fat and food intake, and the role of fat storage in this small cetacean.

Life history and age, growth and reproductive parameters

The following parameters taken from a review by Lockyer (2003) for harbour porpoises from this region indicate that mean size is ~155 cm length and 50 kg in males and 165 cm length and 65 kg in females. Longevity is normally <12 y, but maximum age attained can be 24 y. The age at sexual maturity is 3–4 y for both sexes. The peak birth period is June–July after 10–11 months' gestation, when birth size is ~70 cm length and 5 kg weight. The sex ratio in nature is predominantly 1.2 males:1 female.

Activity and body condition

The harbour porpoise is one of the smallest marine cetaceans with a relatively high surface area to volume ratio, suggesting that energy balance in relation to insulation and heat loss might be important. The relative thickness of blubber also decreases with adulthood and body size, indicating less need for insulation and fat energy reserves (Lockyer, 1995). The harbour porpoise has been described as 'living in the fast lane' (Read & Hohn, 1995), and has to cram its life history into a short life with a fast turnover in reproduction and rapid growth. The harbour porpoise is essentially a coastal animal but has been reported to migrate seasonally in the past years (Kinze, 1995). Recent satellite-tagging experiments in the inner Danish waters have also shown that many individuals may move long distances, but nevertheless return to familiar grounds (Teilmann et al., 1999). In addition, the tagging programme revealed that free-living porpoises are underwater diving more in winter than in summer.

Body condition has been assessed by weighing and measuring the animals in different places on the body: whole body weight, length, and girths and blubber thicknesses (Lockyer et al., 2003a). Blubber thickness in live animals was measured using a Lean Meater portable ultrasound device by Renco, and normally used in pig husbandry for determining sub-dermal fat thickness (Lockyer et al., 2003a). The live animals were also able to beach themselves onto a weighing platform (Lockyer et al., 2003a) whilst carcases were weighed by suspension from a scale.

Diet

The diet of harbour porpoises in Scandinavian waters has been studied in detail by Aarefjord et al. (1995), Lockyer & Kinze (2003) and more recently by Lockyer & Andreasen (2004) using stomach data from by-caught animals in Danish waters. It is clear that in inner Danish waters gadoid fish are important, as also are gobiid fish and ammodytids. Aarefjord et al. (1995) reported that overall, clupeid fish were most important in all Scandinavia, although presently clupeids are not as significant a prey in Danish waters as formerly thought. At the Fjord and Bælt in Kerteminde, Denmark, porpoises in human care were fed mostly with herring that contained a relatively high fat content (Lockyer et al., 2003a) with energy densities normally >2 kCal per gram wet weight.

Rate of food consumption—ingestion rate

Lockyer & Kinze (2003) concluded that full stomach capacity of free-living porpoises from Danish waters, comprised about 1 kg in an adult animal. Animals in human care at the Fjord and Bælt consumed up to this amount approximately five times daily, and most daily consumptions were in the range 2.5–5 kg wet weight herring, depending on the individual and time of year (Lockyer et al., 2003a). Over
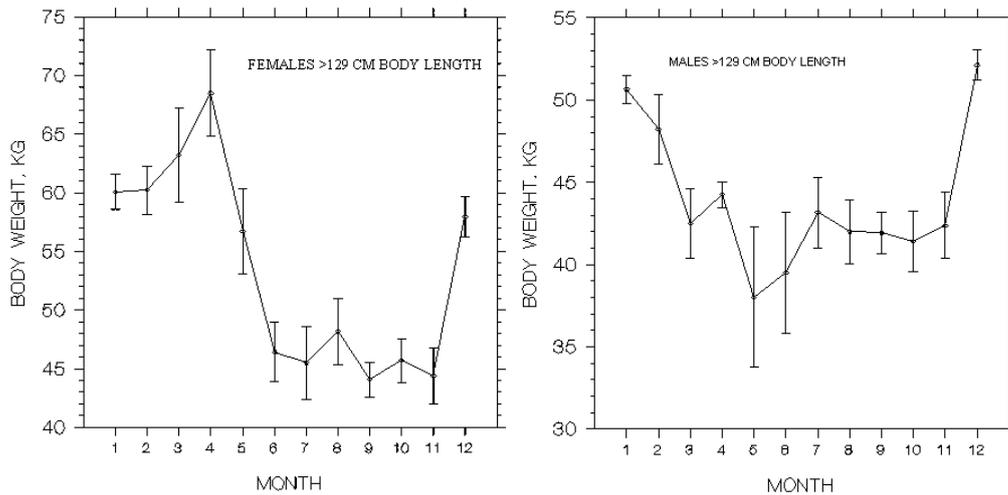
Figure 6. Seasonal variation in body weight in free-living porpoises (length >129 cm) from the Danish waters, showing means and 95% confidence intervals.

a year, consumption might represent between 913–1825 kg (1.83–3.65×10^6 kCal), depending on individual and seasonal variation. This represents almost an order of magnitude less than an adult female pilot whale (see Figure 2).

Metabolic rates

Metabolic rates have been presented in Figure 1. However, Reed et al. (2000) were able to measure oxygen consumption and metabolic rate in a live restrained porpoise to provide a resting rate. They reported a general increased respiration rate with increased activity and metabolic rate. Lockyer et al. (2003a) indicated both seasonal and diurnal variations in respiration rate in two captive porpoises at the Fjord and Bælt. Average daily respiration rate was nearly 50% higher in October than in wintry February when activity levels also showed a decline with a significant increase in 'logging' behaviour where animals lay still at the surface. Activity was also greater in the daylight hours with more cruising around and generally higher breathing rates (Lockyer et al., 2003a). Teilmann et al. (1999) found that as well as being underwater more in winter, the free-living tagged porpoises dived more actively in daytime than at night.

Reproductive energetics

The data shown in Table 2 indicate relative body weight and body fat measured in different ways for neonates and adult females of different reproductive status. It is clear that even at birth, females are larger and heavier than males with more body fat. Extra fat means more energy and also more insulation. It has been suggested that this may cause differential survival rates between the sexes (Lockyer, 1995), and may partly explain the very high male to female ratio in stranded neonates while mortality returns to near parity in the second year of life (Lockyer, 2003).

The pregnant females clearly have greater body fat deposits than other reproductive classes, and lactating animals have the least fat reserves. This is a good indication that reproductive costs are significant in the porpoise. The phenomenon of high body fat in pregnant females relative to other groups has also been shown in Greenlandic porpoises

(Lockyer et al., 2003b), and it is also clear that blubber lipid content is higher in this pregnant group (Lockyer, 1995; Lockyer et al., 2003b; and see Table 2).

Building an energy budget

In this case study, focus has been on seasonal variations in body fat condition correlated with food intake and environment. The study has two aspects, as mentioned earlier: a study of live captive animals—a male and a female— and a study of free-living animals based on caught and by-caught animals and carcase analysis. The daily records of food consumption and food composition and energy density, weekly girth and blubber thickness measurements as well as regular body weighings, made over a duration of more than 5 y, allowed detailed analyses of how environment could affect energy dynamics. Results indicated regular seasonal variations of large amplitude in body mass and blubber thickness as well as food consumption over 5.5 y. The actual peaks of body weight and blubber thickness occurred in winter, with troughs in summer. The food consumption pattern was similar to the body mass changes, but in fact food intake increases preceded body mass increase. Thus the body mass changes echo the food intake pattern (Lockyer et al., 2003a).

The animals live in an open system where fjord water flows freely through their enclosure year-round, thus simulating near-natural conditions. The seawater temperature in the fjord where the porpoises are maintained showed steady seasonal variations with extremes of 18°C and 2°C in summer and winter respectively over a 2-y period (Lockyer et al., 2003a). Body mass, girth and blubber fat thickness were high during the winter with cold temperatures and low during summer higher temperatures, there being a pattern of inverse correlation (Lockyer et al., 2003a). This appears to be a consistent feature of body mass dynamics, and suggests that insulation, in addition to any other energy requirements, may be very critical to this small cetacean, and that blubber fulfils this role.

In order to investigate that this phenomenon was not an artefact of captivity, data over several years from >600

free-living animals were analysed from the Danish past directed catches and by-catches. The studies are not directly comparable as the captive one focuses on individual animals whereas the other is a composite of many animals throughout the year. However, with careful exclusion of most sub-adults (<130 cm length), mean monthly body weights for both males and females could be calculated with 0.95 confidence intervals (Figure 6). Results show that body mass is lowest in the summer and early winter while high body mass occurs in mid-winter. Thus the pattern of weight gain and loss is similar to the captive animals.

DISCUSSION AND CONCLUSIONS

The case studies discussed here include a variety of cetaceans in respect of size, life history, feeding habits, reproductive pattern and longevity. The fin whale represents a filter feeder on organisms lower down the scale in the food web with relatively low energy density. The species does not have a complex social structure, and does not form groups of more than a few animals usually. The strict annual cycle of extensive migration and intensive summer feeding, dictates a life history strategy that will optimize utilization of these factors. Thus fat energy storage is a key feature of surviving poor feeding periods and supporting reproduction.

The pilot whale has a complex social infrastructure and is generally a group-living species, with marked differences in behaviour between the sexes, and dimorphism is also a prominent feature where males exceed females in size: typical for polygynous species. There is no extensive migration, although there may be seasonal preferences in prey consumption, yet prey has a generally low energy density. Whilst breeding has a seasonal trend, the lactational phase of the reproductive cycle is not as short and intense as in the fin whale, and is not geared to fit into an annual cycle. Indeed, nursing in pilot whales may continue for many years, and females other than the biological mother may offer to suckle calves (Kasuya & Marsh, 1984). Here there is also a difference as, unlike fin whales and porpoises, the mother stays with her offspring often through to adulthood. There is evidence of fat storage (Lockyer, 1993), but this appears not to be critical except that the males clearly rely heavily on these reserves in their quest to seek out and mate with females in other schools, and lose most of their stored fat in the process. Much of the fat storage is also internal around organs such as the kidneys. The fat storage may thus act as a buffer in times where there is a prey deficit. The squid provides a low calorie diet, which at times may demand supplementation either from fat stores and/or consumption of higher energy density prey such as fish.

Finally, the non-social harbour porpoise, being a small animal relative to the other two species, may actually encounter negative thermoregulatory challenges at certain times, and needs insulation to conserve heat and also stored fat as an energy supplement when food availability is poor. Lockyer et al. (2003a) remarked how quickly and dramatically both newly captured porpoises lost weight, before they started to eat, with dramatically rapid loss of blubber and also underlying tissue. In comparison, the fin whale whose blubber insulation is extremely thick, may encounter thermoregulatory problems of a different kind

with potential overheating. It is probably advantageous for the fin whale that the actual blubber thickness is not a critical issue in thermal insulation, and that the generally thick blubber may have facilitated survival in polar waters and allowed the species to take advantage of the high food production in these regions. Stored energy would also provide energy during long migrations. Lockyer et al. (1985) noted that much of the stored fat energy was in the posterior dorsal muscle in the fin whale, thus counteracting the likelihood of too thick blubber.

Clearly, fat storage is essential for the porpoise, both as a buffer in normal life, for insulation and also to support the short and relatively intense reproductive cycle. The porpoise may vary its diet throughout the year, but it has been noted often that the species has a very catholic diet and may readily switch from one to another prey type depending on what is available, unlike the other two case studies presented here where there is a definite prey preference. Because of 'living in the fast lane', the porpoise must be able to optimize food energy resource, and clearly there may be advantages in seeking out the higher energy density species when available, in order to minimize energy costs of feeding relative to food intake.

Future more sophisticated studies may incorporate investigations using isotope dilution techniques (e.g. doubly-labelled water) for estimating metabolic turnover, and also leptin dynamics (Guilherme et al., 2004) in the body for understanding fat storage, mobilization and utilization in relation to food intake. However, whenever research focuses on marine mammals, access to the animal is often problematic as well as large size for handling.

Presently, with the growing interest in ecosystem approaches to fisheries management, and associated multi-species management, it will be increasingly important to understand the energy dynamics of food supply to the top predators who may present potential competition among themselves and man. In some ecosystems, consumption of fish may be as much as or exceed that taken by fisheries (Bax, 1991). The primary forces that move energy through the food web also have effects indirectly on cetaceans, as temperatures may affect primary and secondary production in the seas and thence the prey availability to predators higher up. At the very least, a consideration of energy balance in multi-species modelling would be desirable.

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