

**CAUSES AND CONSEQUENCES OF VARIATION IN THE
ENERGY EXPENDITURE IN GREY SEALS
(HALICHOERUS GRYPUS)**

Carol E. Sparling

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**CAUSES AND CONSEQUENCES OF VARIATION
IN THE ENERGY EXPENDITURE OF GREY
SEALS (*Halichoerus grypus*)**

Submitted for the degree of

Doctor of Philosophy

School of Biology, University of St Andrews

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I, Carol Sparling, hereby certify that this thesis, which is approximately 40,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Date...17/9/03.....

Signature of candidate

I was admitted as a research student in October 1998 and as a candidate for the degree of Doctor of Philosophy in October 1999; the higher study for which this is a record for was carried out in the University of St Andrews between October 1998 and January 2003.

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ABSTRACT

Oxygen consumption of captive grey seals was measured over a period of 2.5 years at the captive facility of the Sea Mammal Research Unit at the University of St Andrews. The conditions under which in-water resting metabolic rate (RMR) was measured had a significant effect on the resulting estimates. RMR was highest when seals were at the surface breathing periodically. Surface apnoea and periodic submergence reduced RMR estimates by 25 and 35% respectively. There was significant seasonal variation in RMR's of adult females, with rates being highest in the spring and declining throughout the summer months. This variation was unrelated to changes in water temperature. Changes in mass explained some of this variation but this seasonality was still evident when rates were expressed mass-specifically. RMR of juvenile grey seals increased with age, as did lean body mass, although there was no relationship between age and total body mass.

Diving metabolic rate (DMR) was measured while seals were voluntarily diving in a quasi-natural setting. Overall DMR was lower than RMR measured in the same animals. Mean DMR was 1.6 times predicted BMR. Average DMR decreased with dive duration and increased swimming activity during dives increased DMR. A model was developed that predicts DMR given information on the behaviour during the dive. This model was used to predict the at-sea metabolic rate of 5 wild grey seals from telemetry data. Overall, predicted at-sea metabolic rates were similar to DMR of the captive seals. Travelling dives had a higher energetic cost than foraging dives. Feeding during diving caused DMR to be increased 1.4-1.6 times pre-feeding levels.

Metabolic rate data was incorporated into a population energy flux model. Energy requirements of different components of the population were estimated on a quarterly basis and all these were summed to produce an estimate of population annual energy requirements. Error in input parameters were used to calculate confidence limits in these estimates.

Chapter 1

General Introduction

Seals are large, often conspicuous mammalian predators in many biological systems. This has created a perception of conflict in parts of the world where seals are seen as competitors to man, feeding on valuable fish stocks. By studying the energetics of such species we can gain understanding and move towards quantifying their effects on marine communities.

1.1 Seal-fisheries interactions

At present, there is often a rather polarised view of how to manage seal populations. Much conservation attention has been focused on seals, not least because of the appeal they hold for the general public. Concurrent with this are often increasing calls by the fishing industry concerned about the status of fish stocks for culls to be reinstated. Boyd (1993) describes this dichotomy in a succinct fashion:

“[Seals are]..at best mysterious animals inhabiting an inhospitable environment and at worst, pests to be eradicated for denying fishermen their livelihood.”

An example of this is the conflict between fishermen, fisheries scientists and conservationists regarding the harp and grey seal populations in the Northwest Atlantic. The region experienced a dramatic collapse of the cod fishery, leading to the closure of the fishery in the early nineties. This collapse occurred in parallel with the continuing increase of the harp seal population following a ban on hunting whitecoat pups in 1987. Many reasons were suggested for the collapse, such as environmental change and over-fishing by domestic and foreign

fleets, but fishermen did not ignore the coincidence of the growing seal populations.

The concerns of the UK fishing industry are a result of the rate of increase of UK seal populations and the decrease in commercial fish stocks in certain parts of the North Sea. Between 1984 and 1995 the UK population increased at a rate of 6% annually with an overall doubling of numbers (Harwood 1995). The population is presently estimated to be about 130,000 individuals (C. Duck, pers comm.) The Scottish population makes up about 90% of the UK population and 40% of the world's grey seals, therefore it is important in a national context that we have the information in hand to decide how best to make any management decisions with respect to UK grey seals.

UK grey seals are at present protected under the Conservation of seals Act (1970) and shooting them for the purposes of protecting fisheries during the breeding period can only be carried out under licence. At other times of year there are no restrictions. (Although currently shooting them without a licence is illegal at all times of year due to the current phocine distemper virus outbreak).

The best approach to evaluate the nature and extent of seal-fishery interactions is likely to be one that involves quantitative, predictive models. In 1992, a meeting of the Scientific Advisory Committee of the UNEP Marine Mammal Action Plan addressed this issue and recommended that future work concentrated on developing modelling procedures and improving current scientific knowledge as inputs into these (Hammond and Fedak 1994). The data required to provide such a model with all the relevant information are manifold; analysing the effects of

predation by seals on fisheries, or the effects of commercial exploitation of their prey on seal stocks, is a complex and difficult task. There is a requirement for detailed information on the population composition and their associated energetic requirements, diet composition and the spatio-temporal foraging patterns of seals. Mathematical models have been used in a number of ecosystems to synthesise the knowledge of seal biology and extrapolating it to predictions of their impact on prey species (Fedak and Hiby 1985; Hammond et al. 1994a; Mohn and Bowen 1996; Winship et al. 2002). The approach generally taken is to use a bio-energetic framework to predict the energy requirements of the population, coupled with information on the diet composition to model the food consumption of a given population. Normally food consumption is predicted for segments of the population, broken down by age and/or sex, and estimates are summed to provide a prediction of the total prey consumption. The applied aspect of this thesis deals with the bio-energetic inputs to such modelling efforts; more specifically aims to improve estimates of energy requirements of UK grey seals. The more theoretical aspects are concerned with the interface of behaviour and physiology, more specifically how physiology relates to the behaviour and life history of the grey seal.

1.2 Seals: an energetic view

Energy is the common currency in which all organisms deal. Energy gained from food is expended in maintaining body functions and in acquiring and processing prey; any additional energy can be used for growth and reproduction. A study of energetics can lead to an understanding of how animals organise their daily or

seasonal activities in the face of the constraints placed upon them by their life history or their environment. All animals must achieve a balance between the energetic expenditures associated with existence and their ability to acquire energy for growth and reproduction.

Pinnipeds in general remain tied to the land to varying degrees for activities such as rest, giving birth, mating and moulting. Different species and taxonomic groups have evolved adaptations to this in different ways. The otariids (sea otters, fur seals and sea lions) divide their time between land and sea intermittently throughout the year. They have extended lactation periods and spread the costs of provisioning their offspring over this time. They tend to have high rates of energy expenditure, which are balanced by high rates of energy acquisition. Phocid seals (true seals) divide their life cycle into distinct land and sea periods, foraging and breeding are temporally separated. Most phocid species have evolved very short lactation periods that minimise the time they are obligated to spend ashore and delay implantation to synchronise pupping and mating to limit the number of times animals have to come ashore.

There are number of factors which contribute to the energetic needs of wild animals; in the following sections, the major factors affecting the rate of energy expenditure of an animal will be reviewed in turn.

1.2.2 Maintenance requirements

These are defined as the energy needed to maintain the biological processes essential to being alive. Normally referred to as basal metabolic rate (BMR), it is the rate of metabolism that is measured under the conditions outlined by Kleiber (1975), namely that the animal be mature (but not reproducing), post-absorptive, at thermoneutrality and resting (yet awake). In cases where one or more of these criteria cannot be met, the term resting metabolic rate is used (RMR). The concept of basal metabolic rate in marine mammals is a controversial one. The belief that pinnipeds and cetaceans have metabolic rates higher than those of similarly sized terrestrial mammals has its roots in the seminal works of Scholander and Irving in the 1930's and 40's (e.g. Scholander 1940; Irving et al. 1935; Scholander et al. 1942). This view persisted through to the 1980's (Kanwisher and Ridgway 1983; Henneman 1983), however in the early 80's several workers were publishing results that challenged this widely held conception (e.g. Gaskin 1982; Schmitz and Lavigne 1984). In 1986 Lavigne and co-workers published a review paper assessing the hypothesis that seals and whales have higher metabolic rates than other mammals (Lavigne et al. 1986). They conclude that seals and whales only show basal metabolic rates higher than predicted values when the conditions under which measurements were made did not meet Kleiber's criteria for BMR (Kleiber 1975). The metabolic rate determinations that did meet Kleiber's criteria did not differ significantly from the BMR of similarly sized terrestrial mammals. However since then, some studies have reported resting metabolic rates of phocid seals that are higher than

predicted values. Metabolic rates of weddell seals resting in water were 1.6 times the predicted levels for terrestrial mammals (Williams et al. 2001; Castellini et al. 1992).

A few authors have argued that the definition of resting metabolism as it stands in studies of terrestrial mammals, is inadequate for use in marine mammals, given that they frequently exhibit apnoea and can spend considerable proportions of their time submerged (Fedak 1986, Costa and Williams 1999, Williams et al. 1999). Most marine mammals, if ever meet conditions for true BMR in natural conditions. However for comparative purposes, whenever predicted rates of metabolism are mentioned in this thesis, I am referring to the rate predicted by Kleiber (1975) for a similarly sized terrestrial mammal (metabolism (oxygen consumption $\text{l}\cdot\text{min}^{-1}$) = $0.0101 \times \text{Mass}(\text{kg})^{0.75}$).

1.2.2.1. Season, body size and body composition

There are a number of factors that can cause variations in rates of ‘maintenance’ metabolism. Most studies of the metabolism of marine mammals have been short, looking at the costs of isolated processes (e.g. moult, lactation, diving, feeding/fasting regimes), however a few longer term studies of seasonal changes in rates of resting metabolism have shown some interesting patterns. In harp seals (*Phoca groenlandica*), metabolic rates were lower than mass-predicted values in autumn and winter, but were indistinguishable from expected rates in spring and summer (Hedd et al. 1997). Rosen and Renouf (1995) also found that

although yearly mean resting metabolic rates for adult common seals, *Phoca vitulina*, were not significantly different from expected values, there was considerable temporal variation, with a 35% decrease between periods of highest and lowest metabolism. Boily and Lavigne (1997) found that adult northwest Atlantic grey seals had resting rates higher than expected in spring, autumn and winter yet rates were lower than expected in summer. In none of these studies was metabolic rate significantly related to total body mass. Expressing metabolic rates mass specifically or comparison to predictions based on mass is complicated by the dramatic changes in adipose tissue mass that phocid seals undergo on an annual basis. Grey seals may undergo mass changes of up to 40% (Beck et al. 2000). Unfortunately the studies mentioned above did not measure body composition at the same time as measuring metabolism so we cannot determine whether these seasonal changes were a result of changing body composition. Results of studies looking at the effect of body fat on metabolic rate have been conflicting. Some reports have indicated that lean body mass (LBM) is the most important contributor to metabolic rate (Forbes and Brown 1989; Cunningham 1980). Rea and Costa (1992) demonstrated that mass specific metabolism declined 47% in northern elephant seal pups, *Mirounga angustirostris*, when body fat increased from 5 to 50% of BM, suggesting that adipose tissue is metabolically inert. Moreover in a study with adult harp seals Aarseth et al. (1999) found that BMR declined 50% when the amount of fat increased from 13 to 45% of body mass. In contrast to these findings McNiven (1984) found that adipose tissue contributes as much as lean body mass (LBM) to the metabolic rate of sheep. However it is not only changes in the proportion of fat to lean tissue that can affect metabolic rate. In humans resting energy expenditure is not constant per unit of LBM. Variation in the relative proportions

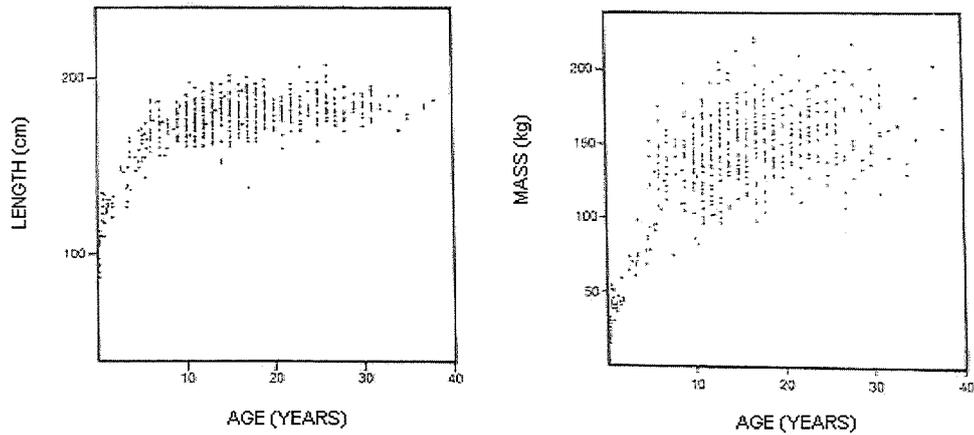
of high and low metabolically active tissues independent of differences in LBM can cause between subject variation in measured rates of resting metabolism (Illner et al 2000). In recent work on migrating birds, Battley et al (2000) found that long distance migration resulted in differential organ reductions as a result of protein catabolism. The authors hypothesise that as the functional role of an organ declines during flight, a reduction in organ size could free up protein without any adverse effects. In this way selective catabolism of tissues that are inactive during flight (e.g. intestines) may buffer other more important organs from increased protein demands. This differential reduction in organ lean tissue mass also results in a more than proportional decrease in both total and mass specific BMR (Battley et al. 2000). The extent if any, of changes in lean, metabolically active tissue in phocid seals in natural situations is unknown. Most phocid seals fast during the breeding period, yet have high energy demands throughout. It is possible that they undergo reductions in some organs to supply protein to maintain metabolic processes involved in fuel supply. Mellish et al. (2000) demonstrated a 12% reduction in lean body mass of lactating grey seals of between early and late lactation. Maternal metabolic rate (MMR) also decreased throughout the same period by 38%. This reduction was evident even when MMR was expressed as a function of LBM. Mellish et al. (2000) account for this decrease with the suggestion that that lactating females employ metabolic compensation, although the mechanism by which this is brought about is not known. Differential reductions of organs that contribute most to BMR of the type seen in migrating birds (Battley et al. 2000) could be a possible explanation.

1.2.3 Growth

Juvenile animals have metabolic rates elevated above adults of similar mass because of the additional energetic cost of producing new tissue (Brody 1945). For growth to occur, animals must acquire energy in excess of the amount needed to support maintenance functions. Reviewing the available data on phocid seals, Lavigne et al. (1986) concluded that juvenile phocid seals had metabolic rates about two times the level predicted for adults of a similar mass. Boily and Lavigne (1997) found that despite considerable individual variation, as juvenile grey seals got older and larger (<1 to 3 years of age), resting metabolic rate approached predicted values for adult mammals of similar mass. Rosen and Renouf (1998) reported a general decline in mass-specific resting metabolism with age in common seals, the youngest seal, a yearling, had a resting metabolic rate of 2 times the predicted rate. The majority of growth in the grey seal occurs throughout the first 4-6 years for females and 6-8 years for males (Figure 1.1) After this age, mass may still increase with age but length doesn't.

As with the adult seals discussed in the previous section, juvenile animals also seem to have seasonal patterns of resting metabolism (Rosen and Renouf 1998, Boily and Lavigne 1997). It is clear that any attempt to quantify the maintenance or resting energy requirements of phocid seals must take both temporal, body composition and age related variations into account.

a) Females



b) Males

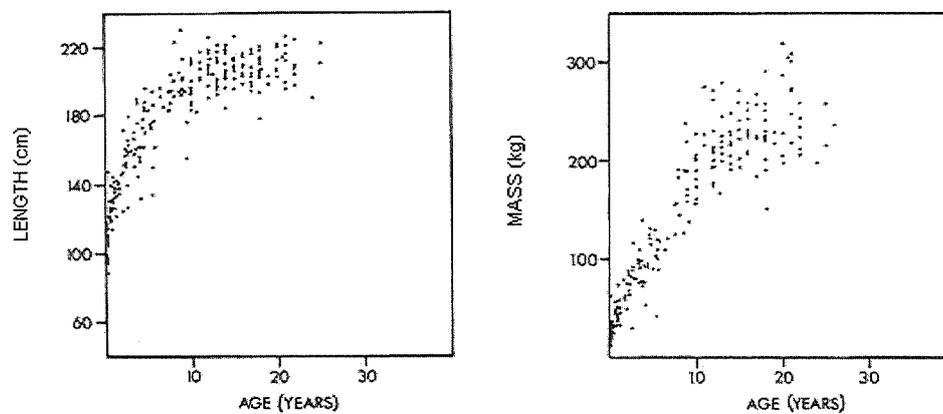


Figure 1.1 Nose-tail lengths and weights of known age Grey seals from specimens taken around the British coast between 1965 and 1982 by the Sea Mammal Research Unit. (a) taken from Anderson and Fedak (1987), (b) from Anderson and Fedak (1985).

1.2.4. Thermoregulation

The thermo-neutral zone (TNZ) defines the range of temperature where metabolic rate of the animal is independent of ambient temperature. The range is delineated by lower and upper critical temperatures. Above the upper critical temperature the animal experiences an increase in metabolic rate as a consequence of the extra metabolic power involved in dumping excess heat to the environment. Below the lower critical temperature the rate of heat production increases with further decreases in temperature as a consequence of extra metabolic power to offset heat loss to the environment. In general, phocid seals have a broad TNZ compared to terrestrial mammals. Gallivan and Ronald (1979) observed that there was no variation in metabolic rate of harp seals in water temperatures between 1.8 and 28.2°C. The TNZ in water was found to vary with body size and season in the common seal (Hart and Irving 1959, Miller and Irving 1975, Miller et al. 1976) with a lower critical temperature in the winter than in summer, probably due to a thicker blubber layer during the winter. Grey seals pups in air have a thermoneutrality that extends from -7 to 23°C (Hansen 1995). Boily and Lavigne (1996) found that the metabolic rate of juvenile grey seals aged 7-19 months did not change between air temperatures of -18 and +35°C. Adult greys have a lower critical temperature in air of below -10°C (Folkow and Blix 1987).

TNZ of greys in water has never been measured although it is likely to be as broad as those found in the phocid species studied to date. However it is important to note that these measurements are made under controlled conditions and animals in these circumstances are not likely to experience the full range of conditions that wild seals encounter. Factors such as wind, rain and solar radiation are likely to effect a free-living seal's thermal balance in ways which may result in wild seals having different TNZ's than determined in these studies.

1.2.5. Activity costs

One of the most obvious costs for an aquatic animal is the cost of swimming. Much empirical attention has been focused on the energetic cost of locomotion in seals. Davis et al. (1985) measured the oxygen consumption of common seals swimming in a flume. Metabolic rate increased over the range 0.5 to 1.4 ms⁻¹. Using a similar approach, Williams et al. (1991), using drag cups to extend the effective swimming speed of the juvenile common seals beyond the flumes maximum water speed, observed an increase in metabolism over the range 0.5 to 3.5 ms⁻¹. Fedak (1986) reported an exponential increase in metabolic rate in swimming grey seals over the range 0 to 1.6 ms⁻¹. Only 2 otariid species have been studied in this way, the California sea lion *Zalophus californianus* (Feldkamp 1987; Williams et al. 1991) and Steller sea lions *Eumetopias jubatus* (Rosen and Trites 2002). Feldkamp (1987) demonstrated an exponential increase in metabolic rate with swim speed in California sea lions. Rosen and Trites (2002) however found a linear relationship between metabolic rate and speed. This latter study was carried out at a lower temperature (8°C) and it is likely that

the increased metabolic power produced in order to overcome drag is used as heat to offset thermoregulatory demands (D.Thompson unpublished data), thereby the apparent cost of swimming at high speeds is low. Results from these studies are often used in bioenergetic modelling to determine the energy consequences of swimming in wild animals. However, how a seal manages its O₂ use in a state of forced exercise may be very different from its natural foraging situation. Although the cost of transport is a very useful concept, when measured in animals swimming close to the surface in swim flumes it has limited ecological significance for phocid seals given that they do not swim in this way in the wild.

Free-living seals exhibit several strategies for reducing the cost of swimming; by remaining submerged they avoid the high drag and associated elevated energetic costs of surface swimming (figure 1.2). Drag is reduced considerably by submerging and the effect of surface drag becomes negligible once an animal has moved three body diameters down into the water column (Williams and Kooyman 1985; Williams 1989). The adoption of different modes of propulsion may also reduce locomotory costs. In a recent study, diving Weddell seals, *Leptonychotes weddellii*, were fitted with backward facing cameras and flipper stroking during swimming (Davis et al. 1999). This revealed several modes of locomotion, including constant stroking, prolonged gliding on descent and burst-and-glide locomotion on ascent. The number of strokes used, and consequently the greater the number of muscle contractions, the higher the post-dive oxygen consumption (Williams et al. 1999). Laboratory flume studies force animals to swim close to the surface and constantly against a water current, therefore

denying animals the opportunity to adopt the same strategies for reducing swimming costs that they use in the wild.

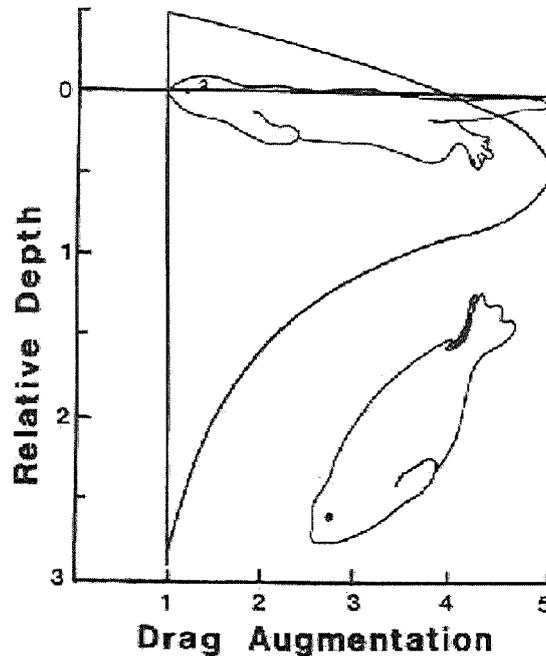


Figure 1.2 Augmentation in drag in relation to relative depth of the swimmer. The horizontal line denotes the surface, relative depth refers to body diameter of the swimmer. Figure taken from Costa and Williams (1999), original data from

Field metabolic rate (FMR) is likely to be a better measure of ecologically relevant costs. FMR has been measured in several otariid species using the doubly labelled water technique (DLW), e.g. New Zealand sea lions *Phocartos hookeri* (Costa and Gales 2000), Antarctic fur seals *Arctocephalus gazella* (Costa et al. 1989; 2000), Australian sea lions *Neophoca cinerea* (Costa and Gales in review, as cited in Costa and Williams et al. 2001), California sea lions *Zalophus californianus* (Costa et al. 1990), Northern fur seals *Callorhinus ursinus* (Costa and Gentry 1986). However FMR's from phocid seals at sea are rare; DLW studies are extremely difficult in this case because of the need for timely recapture. Field metabolic rate measured in this way has only been reported in

one phocid species to date, the common seal. Reilly and Fedak (1991) measured rates of up to 6 times predicted basal rates in males. However this was done during the mating season so the higher costs may reflect the additional cost of mating displays in this species.

One disadvantage of using the DLW technique to measure field metabolic rates is that costs are integrated over periods of days and cannot be partitioned among separate activities, therefore the energetic costs of different types of activities cannot be examined.

The studies on otariids, above, all report FMR's of around six times the predicted basal level, in contrast the metabolic rate, as measured by respirometry, of weddell seals freely diving from an ice hole have been measured at 1.5 to 2 times predicted basal rate (Castellini et al. 1992). The FMR of Northern elephant seals was measured by DLW at 2-3 times predicted basal rate (D. Costa & R. Andrews unpubl. data as cited in Costa and Williams (1999)). Costa and Williams (1999) argue that these differences in foraging energetics between phocid and otariid seals reflect differences in the strategies used by these groups to acquire resources. These differences in foraging strategies are reflected in the dive strategies that each group employs a discussion of which follows in the next section.

1.2.5 Diving

Any consideration of the energetics of free existence in seals is not complete without discussion of the physiology of mammalian diving. Breath-hold diving is an obvious necessity for animals that exploit a prey resource underwater. Maximum dive times among marine mammals varies from less than one minute in the freshwater shrew *Sorex palustris* (Calder 1969) to two hours in the southern elephant seal *Mirounga leonina* (Hindell et al. 1992). Diving among otariids tends to be restricted to short, shallow dives, although there is still variability amongst the otariidae as a group, generally related to the location of the prey. Antarctic fur seals feeding on pelagic prey near the surface at South Georgia have a mean dive duration of around one minute (Costa et al. 1989, 2000) whereas benthic divers have longer dive durations. For example New Zealand sea lions, which are reported to be the deepest and longest diving otariids (Gales and Mattlin 1997), typically dive for around four minutes reaching depths of over one hundred metres (Costa and Gales 2000). Phocids are the elite among seals when it comes to dive performance. Southern and northern elephant seals go to sea for extended periods, diving almost continually day and night, spending up to 90% of the time at sea submerged (Le Boeuf et al. 1988; Hindell et al. 1991, 1992). Weddell seals can dive longer than one hour (Kooyman 1966) and to depths greater than 700m (Testa 1994). Grey seals generally dive for around 3-7 minutes; though occasionally dive for periods over 20 minutes (Thompson et al. 1991; McConnell et al. 1992; Thompson and Fedak 1993).

The amount of time any diving mammal can remain submerged and metabolising aerobically is dependent on two things; the size of the oxygen stores the animal has available for use during a dive, which is fixed the moment the animal submerges to begin the dive, and the rate at which it uses that store during the dive. The most successful diving mammals have evolved adaptations that serve to maximise stores and minimise rate of use, thereby increasing the time they can spend exploiting resources below the surface.

However there is an important distinction between the ability to simply spend a long time submerged and the ability to spend a high proportion of time submerged. The latter is determined by the rate at which animals can return to the initial state after a dive and is related to rates of gas exchange at the surface and rates of recycling of metabolic products. For example the majority of weddell seal dives are short, under 20 minutes, yet some (<6%) are longer, but these dives are always followed by extended recovery periods at the surface (Kooyman et al. 1980). In contrast elephant seals have the ability to dive repeatedly for extended periods (up to 2 hours) with no increase in the time spent at surface between dives (LeBoeuf et al. 1988; Hindell et al. 1991). An important component of the physiological capability of any diving animal is its aerobic dive limit (ADL). ADL is operationally defined as the dive duration beyond which post-dive blood lactate levels begin to rise above resting levels (Kooyman et al. 1980), i.e. the duration beyond which reliance is switched from aerobic to anaerobic metabolism. A disadvantage of reliance on anaerobic metabolism is

the extra time required to metabolise lactate, which limits the proportion of time that can be spent underwater.

The physiological responses to diving are geared towards the conservation of oxygen, so how a seal copes with the metabolic demand of exercise is an important question. A trade off exists between the need to load oxygen at the surface and conserve its use to allow optimal exploitation of a prey resource underwater and the need to utilise oxygen to locomote. There would seem to be no general model to describe how all diving mammals operate during voluntary diving. Field studies carried out on a variety of species over the last 2 decades have helped to clarify the options employed by different groups of animals. Otariids tend to dive with high swimming velocities and have high rates of metabolism, all else being equal dives are much shorter than those exhibited by phocid seals. Weddell seals adopt a mixed strategy, performing principally short aerobic dives and resorting to anaerobic metabolism to extend dive time for longer dives (Kooyman et al. 1980). Grey seals may use a strategy of hypometabolism while submerged to enable them to dive beyond their estimated aerobic dive limit. Studies of freely diving grey seals in a laboratory setting have reported a decrease in metabolic rate with increased dive duration (Reed et al. 1994). Elephant seals can dive consistently beyond their estimated aerobic dive limit without the need for concomitant increases in surface time, and must also be hypometabolic while submerged (LeBoeuf et al. 1988; Hindell et al. 1992). However a study of Northern elephant seals voluntarily diving in a laboratory failed to demonstrate a decrease in metabolic rate with increasing dive duration (Webb et al. 1998). It is likely that the captive seals did not have any reason to

perform such long dives, therefore did not need to invoke any metabolic depression.

1.2.6. Feeding

Not all the energy in ingested food is available to an animal for work, maintenance or growth; some energy is lost during the digestive process. When an animal consumes food, its metabolic rate increases over fasting levels. This increase has been given different terms in the literature; specific dynamic effect (SDE) (Rubner 1902, cited in Kleiber 1975), diet induced thermogenesis (Rothwell 1979), specific dynamic action (SDA) (Jobling, 1983) and heat increment of feeding (HIF) (MacArthur and Campbell, 1994). Most investigations into this effect in marine mammals have referred to this cost as HIF, so for consistency the same term will be used here. HIF is not a fixed amount, and is partly dictated by the size and composition of the meal. In terrestrial mammals, feeding typically elevates metabolism 6-40% over resting rates, depending on the meal composition. Expressed in terms of the energy content of the food consumed, HIF is about 6% for carbohydrates, 13% for fats and 30% for proteins (Blaxter 1989).

The metabolic cost of HIF can be separated into a mechanical component that is due to physical processing and movement of food through the gut, Tandler and Beamish (1979) estimated that the mechanical component of HIF in largemouth bass was between 10 and 30% of the total HIF, depending on meal size. The remainder of the cost is thought to be of a biochemical nature, most likely related to the biochemical costs of nitrogen excretion (Kleiber 1975).

HIF has been investigated extensively in terrestrial mammals (Kleiber 1975; Webster 1983) but HIF has been measured in only a few marine mammal species. Rosen and Trites (1997) conclude that pinnipeds are relatively efficient in utilising ingested energy when compared to terrestrial mammals. In the marine mammals that have been investigated, measured HIF as a percentage of gross energy intake (%GE) ranges from 5% in common seals fed high-energy herring (Markussen et al. 1994), to 17% in harp seals fed a 1kg meal of herring (Gallivan and Ronald 1981). Maximum metabolic rates post-feeding expressed as a multiple of RMR ranged from 1.3 in common seals on high-energy herring to over 2 in Steller sea lions fed 4kg of herring (Rosen and Trites, 1997).

The post-prandial rise in metabolic rate is relatively long lasting. In Steller sea lions the effect lasted 8-10 hours and 6-8 hours for a 4kg and 2kg meal respectively (Rosen and Trites 1997). In common seals, rate was elevated above resting rates 30 minutes after feeding and remained at an increased level for as long as 12 hours (Markussen et al. 1994).

The heat generated as a result of feeding is not necessarily unavailable for use by the animal. The heat can be used to offset an increased requirement such as thermoregulation, something that may be important for aquatic animals that feed at sea. Only one study of HIF in seals measured the effect in water (Markussen et al. 1994), care must be taken when interpreting information derived from measurements made in air.

Given that HIF can be considerable, it is often included as an important component of bioenergetic models, thus errors in estimation of HIF will directly affect estimates of the food consumed by marine mammals.

1.2.7. Reproduction

In most large mammals lactation is prolonged, neo-natal growth is slow and weaning is gradual. In sharp contrast to this reproduction in most phocids is a short period of high-energy demand characterised by a rapid decline in female body mass and rapid pup growth. The typical phocid separation of the annual cycle into feeding and breeding phases has several ecological and energetic advantages (Costa et al. 1986) (The most dramatic example is the hooded seal, *Cristophora cristata*, which has a four day lactation period, the shortest for any mammal (Boness and Bowen 1996)). There is an energetic advantage of minimising the length of time spent suckling. As well as provisioning her pup, the mother has to meet her own metabolic need from her stored reserves. Therefore reducing the period of lactation allows a greater fraction of these reserves to be made available to the pup (Fedak and Anderson 1982).

Females wean their pups then mate before returning to sea. All pinnipeds undergo embryonic diapause. This is a delay in development of the blastocyst after fertilisation (Boyd 1991). It is likely that this phenomenon is related to a need to synchronise the time of breeding and mating so that animals need only to return to land once for both purposes. In UK grey seals, implantation of the embryo is thought to occur around March, the time of the moult. Successful implantation may be related to the body condition of the female at the time, perhaps related to the likelihood of success in producing a viable pup. Boyd (1984) provides some evidence that implantation occurs earliest in female grey seals with large fat reserves, suggesting that the energetic status of the animal

influences the timing of implantation. Stewart and Lavigne (1984) suggest that female harp seals continually assess their condition throughout reproduction and may choose to abort the cycle at the critical points such as ovulation, fertilisation, implantation and birth. Fat reserves of female grey seals are low around the time of implantation, due to the fasting associated with the moult. Therefore as Boyd (1991) argues, they cannot be making decisions based simply on current conditions, but must have some perception that future conditions will allow them to build up enough reserves to raise a pup successfully.

Male phocids invest nothing in parental care to offspring. They devote their efforts to competing for females. Male grey seals are polygynous and will defend a loose cluster of females on a breeding colony, focussing attention on females in the cluster closest to oestrus (Boness and James, 1979; Twiss et al, 1998). This is in contrast to the territory defence strategy of most otariids (Boness et al. 1993). As with phocid females, land breeding phocid male reproductive strategies may also be shaped by energetics. Phocids have lost features for efficient movement on land to a greater extent than otariids (Beentjes 1990; Tarasoff et al. 1972). This results in a higher energetic cost to terrestrial locomotion for phocid seals. Maintenance of territorial boundaries is likely to require more movement than direct defence of females (Boness et al. 2002). The similarity between male and female grey seal breeding strategies is that they both rely on their own stored energy reserves for a period on land when they do not feed. Energetic expenditure by males during this period has been estimated as approximately 83 MJ per day (Anderson and Fedak 1985), which is about two thirds that of females who have the higher demand of provisioning a pup (Fedak and Anderson 1982). However breeding males generally stay ashore for a longer period than

females in order to encounter and mate with several females in one breeding season, because pupping is spread out over several weeks. The duration of stay on a breeding site, the amount of activity and consequently sexual success of males will be related to the amount of stored resources it has. However, Anderson and Fedak (1985) concluded that most males left the breeding site well before all their resources were used up. Depleting body resources to a low level may jeopardise future reproductive success. Only those males which can most easily bear the cost of an active, prolonged and successful breeding season are likely to stay for the full span and gain rewards in terms of number of offspring sired.

1.3 Overview of the thesis

Although a consideration of the metabolic cost of each component that makes up an animals' overall energy budget in isolation may enable us to understand particular energetic adaptations and allows us to compare between species and genera, it is the sum of all these activities that determine the overall energetic cost of existence. The combination of demands therefore shapes the behavioural strategies adopted by an animal and determines how much food an animal has to eat to meet this cost. The integrated cost of activity in an ecological context has rarely been measured in phocid seals. Detailed physiological models of the energetics of individual seals provide a bridge between fine scale experimental observation and the broader assessment of their role within the ecosystem. The work in this thesis is intended to be such a bridge. Many of the relationships and variables explored herein cannot be measured directly in free-living animals so the aim of this work was to measure the energy expenditure of seals in as close to a natural state as was possible within a captive setting.

Chapter 2 provides a background of the species used in this study; the grey seal (*Halichoerus grypus*) and highlights the features of its biology relevant to the work reported on here. Chapter 3 describes the methods used in this study. Because similar methodology was employed to obtain the data presented in subsequent chapters, it seemed useful to provide a separate account of these, to avoid repetition between chapters.

Chapter 4 examines resting metabolic rates of grey seals, attempts to address the problem of definition of resting rates in diving animals, and presents information on variation in resting metabolism caused by season, age, mass and body composition. Having detailed the maintenance costs, chapter 5 moves to an examination of the costs of activity. This chapter presents a detailed exploration of the relationships between metabolic rate while diving, and the behaviour of an animal during the dive. This chapter also takes these relationships a step further and presents a model that can be used to predict the energy expenditure of free-living seals, using information gained from telemetry studies.

Chapter 6 adds an extra element to the work on diving metabolism, by examining the additional costs of feeding during dives.

Chapter 7 goes on to utilise the model presented in chapter 4 to predict the field metabolic rates free-living, satellite tagged animals, thereby providing an opportunity to make the direct link between detailed physiological measurements made in a laboratory setting and the real costs of activity for free-living individual animals.

Chapter 8 moves out of the realm of the laboratory and the individual with an attempt to model the energy requirements of population. A simple bio-energetic model is presented which predicts the energy requirements of the UK grey seal population. Uncertainty in predictions is estimated from the error in input parameters.

The final chapter presents an overview of the thesis. Key findings are discussed in their broader context and some suggestions are made for avenues of further research.

Chapter 2

The grey seal *Halichoerus grypus* (Fab.)

The grey seal is the largest species of the subfamily Phocinae (northern phocids). It is the only species of its genus. Grey seals of the world are composed of three distinct populations: western Atlantic, eastern Atlantic and the Baltic stock (Bonner, 1981). The UK population comprises of approximately 120,000 individuals (C. Duck personal communication). Approximately 40% of the world population of the grey seal breeds on widely dispersed sites around the UK. As discussed in the previous chapter, grey seals in the UK have been at the centre of a heated debate for over half a century. Clearly an informed and constructive debate requires an understanding of the basic biology of grey seals. The Sea Mammal Research Unit (SMRU) have been researching UK grey seals for the last 20 years or so and have gathered a large amount of data on their population size and status, movements, diving and foraging behaviour.

2.1. Life History

Females become sexually mature at 3 to 5 years of age, males at 6. Longevity for females is 46 years and 26 years for males. The reproductive strategies adopted by grey seals were discussed in relation to energetics in detail in the previous chapter so here discussion of breeding is restricted to a short summary. Females give birth to a single pup annually in the autumn. Females appear to return to the same colony, and sometimes to the same site within a colony, to give birth each year (Pomeroy et al. 2000). Males may attempt to copulate with a female from about day 12 of lactation, however copulations are most frequent at the end of lactation.

Grey seals are polygynous, adult males are present near the breeding colony throughout the breeding season. Dominant males may exclude other males from the colony, or attempt to monopolise mating opportunities, however the level of polygyny may vary between sites. Pregnancy rates are high, 90-95% of mature females will pup each year. After giving birth, the female remains with her pup throughout the lactation period (figure 2.1), which normally lasts about 18 days (Fedak and Anderson, 1982). The pups weigh around 14kg at birth and gain weight at a mean rate of 1.6kg per day on a diet of fat-rich milk (Fedak and Anderson, 1982). Pups are normally weaned at a weight of 30-50kg with most of the weight gained since birth taking the form of blubber. Weaning is marked by the abrupt departure of the mother from the breeding colony and pups may remain on land for approximately 2 to 3 weeks after this. When the pups leave the breeding site after the post-weaning fast they are completely naïve and will have no knowledge of where or how to find food.

The most important energetic consequence of the breeding biology of the grey seal is the temporal separation between resource acquisition (feeding at sea throughout the year and building up fat reserves) and resource utilisation (suckling pup for females and maintaining position on a breeding site for males).

2.2 Diet and foraging behaviour

Grey seals feed on a variety of fish species, primarily sandeels and gadoids, although diet may vary between seasons and regions (Hammond and Prime,

1990; Hammond et al. 1994b). Studies carried out in the last 10 years have begun to elucidate the relationships between where grey seals haul out and where they forage (Thompson et al. 1991; McConnell et al. 1992; Thompson et al. 1996; McConnell et al. 1999). These studies have shown that adult grey seals can travel hundreds of kilometres from one haul out site to another, though the majority of movements were local, repeated trips from haul-out sites to discrete offshore areas, with characteristic sediment type, which are likely to be foraging sites. Figure 2.2 shows the movements of 108 individual grey seals, tracked using satellite telemetry (SMRU, unpublished data). Dive behaviour varies with the function of the dive. Travelling is characterised by direct, relatively fast horizontal movement and by V shaped dives whereas during foraging seals swim slower and exhibit square bottom dives spending 60% of dive duration at the bottom depth. Overall dive duration is around 3-7 minutes though seals can dive for 30 minutes or more. Resting involves short dives close to haul out sites and an absence of directed lateral movements (Thompson et al. 1991).



Figure 2.1 Grey seal female with her pup

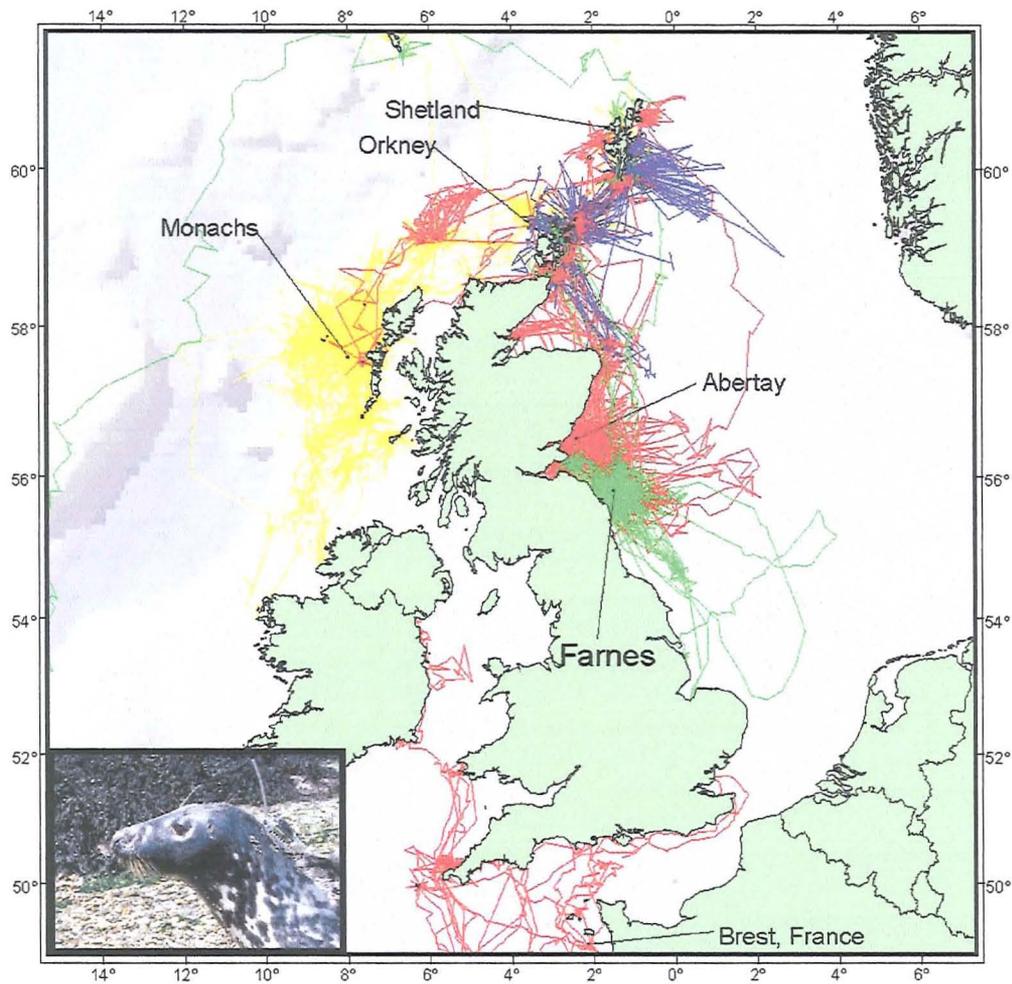


Figure 2.2 Movements of UK grey seals, based on data from deployments of satellite tags on 108 animals. The different coloured tracks relate to different locations that the tags were deployed: yellow – Monach Isles, blue – Orkney and Shetland, Red – Abertay, Green – Farne Islands and orange – Brittany, France. Inset shows a female grey seal with a SMRU satellite tag attached to the back of her neck.

2.3 Assessing seal-fisheries interactions

Given that the UK grey seal population has been increasing for the last few decades, it would be reasonable to assume that at the population level, grey seals are managing to meet their energy requirement. This assumption means that if we can estimate the population energy requirements with some degree of accuracy, we are in a good position to be able to calculate the total food consumption. This, coupled with detailed information on diet composition and foraging effort distribution, we can develop spatially and temporally explicit models of how seals exploit their prey. This will allow us to evaluate the nature and extent of interactions between seal populations and commercially important fisheries.

Satellite tags have been deployed on a total of 108 UK grey seals by SMRU. Work is ongoing to use this information to characterise their movements and foraging areas and to extrapolate this information to the population level. Similarly work is being undertaken by SMRU to characterise diet composition of UK grey seals and seasonal and geographical variations therein. There are good estimates available for the energetic cost of reproduction in grey seals (Reilly et al. 1996, Fedak and Anderson 1982). However, how the energy expenditure of UK grey seals (and hence energy requirements) varies as a function of season, age, sex and activity is less well characterised. The research in this thesis aims to improve current estimates of the energy requirements of grey seals with a detailed investigation into the causes and consequences in variation in energy expenditure.

Chapter 3

Methods

3.1 SMRU captive facility

The Sea Mammal Research Unit at the Gatty marine laboratory consists of three unheated seawater pools. One large pool used for metabolic measurements (42m x 6m x 2.5m) with a capacity of 630000litres, (Figure 3.1) and two smaller circular pools (3 and 5 metres diameter), which are used for holding animals between experiments. The pools are supplied with a constant flow-through of filtered seawater which is pumped into the facility directly from St Andrews Bay. All pools are drained and cleaned every 3-4weeks

3.2 Animals

5 adult and 5 juvenile grey seals were used in this study; all of these were captured from the wild. Names, age classes, origins and masses are shown in table 3.1. Seals at Abertay were caught using either the rush and grab method or beach seining while they rested on exposed sand banks at low tide. Rush and grab is where after a fast landing by boat right in front of the haul out, they are entangled in hoop nets on the sandbank. Beach seining is where nets are deployed by boat adjacent to the shore. The seals get tangled in the net as they try to escape underwater. Seals at the Isle of May were caught on shore on the breeding colony. Two mother pup pairs were caught at the Isle of May in December 2001 (L&K and M&N). All seals were restrained in pole-nets and were transported back to the captive facility by boat. The seals were fed mainly on herring (Lunar Freezing, Peterhead) which were obtained in bulk and stored at -20°C . Prior to use, the fish was thawed overnight in a sink of cold tap water. Adults were given 4-6kg per day and pups 0.5-2.5kg per day.



Figure 3.1 The Sea Mammal Research Unit captive facility. The main pool, in which all respirometry measurements were made, is in the foreground.

Name	Age	Origin	Capture date	Mass at capture (Kg)	Release date	Mass at release (Kg)
Alice	<1	Abertay	31/1/2000	30	7/2/2001	51
Bonnie	<1	Abertay	7/2/2000	25	7/2/2001	45
Cassie	Adult	Abertay	21/3/2000	96	3/4/2001	126
Deirdre	Adult	Abertay	21/3/2000	75	3/4/2001	101
Feefee	Adult	Abertay	15/2/2001	95	11/10/2001	143
Heidi	Adult	Abertay	8/3/2001	118	11/10/2001	148
Jay	<1	Abertay	7/6/2001	32	20/11/2001	50
Kylie	<1	Isle of May	12/12/2001	33	15/11/2002	35
Lola	Adult	Isle of May	12/12/2001	168	25/10/2002	172
Nora	<1	Isle of May	12/12/2001	27	15/11/2002	36

Table 3.1 Details of the seals used in this study.

Adults were given 2 multivitamin tablets (Aquavits, International Zoo Veterinary Group, West Yorkshire) and one iron supplement (ferrous gluconate, 300mg, IZVG) daily. Pups were given 1 multivitamin and 1 iron supplement daily. Animals were normally fed in the afternoon, this allowed at least 18 hours before metabolic rate measurements were made. Animals were inspected by a Veterinary surgeon on a monthly basis and immediately prior to release. All capture and handling procedures conformed to the Animals (Scientific Procedures) Act 1986, under Home Office project licence #60/2589 and followed current good practice guidelines as set out by the Laboratory Animal Science Association (LASA).

3.3 Respirometry

3.3.1 Open flow respirometry system

Oxygen consumption was measured by open-flow respirometry, a schematic of the system used is shown in figure 3.2. A Perspex breathing chamber was set into a modified mesh panel at one corner of the main pool (figure 3.3). An airtight seal was formed by submerging the edges of the box under 6 centimetres of water. Aluminium panels covered the entire pool preventing the seals from surfacing anywhere apart from the breathing chamber during experiments. The breathing chamber had an inlet, which opened to the outside and an outlet which was connected by 1.5inch diameter flexible hosing to a pump situated inside the laboratory (approx 6metres away). Another section of this flexible hose, 2 metres long, was attached to the inlet, acting

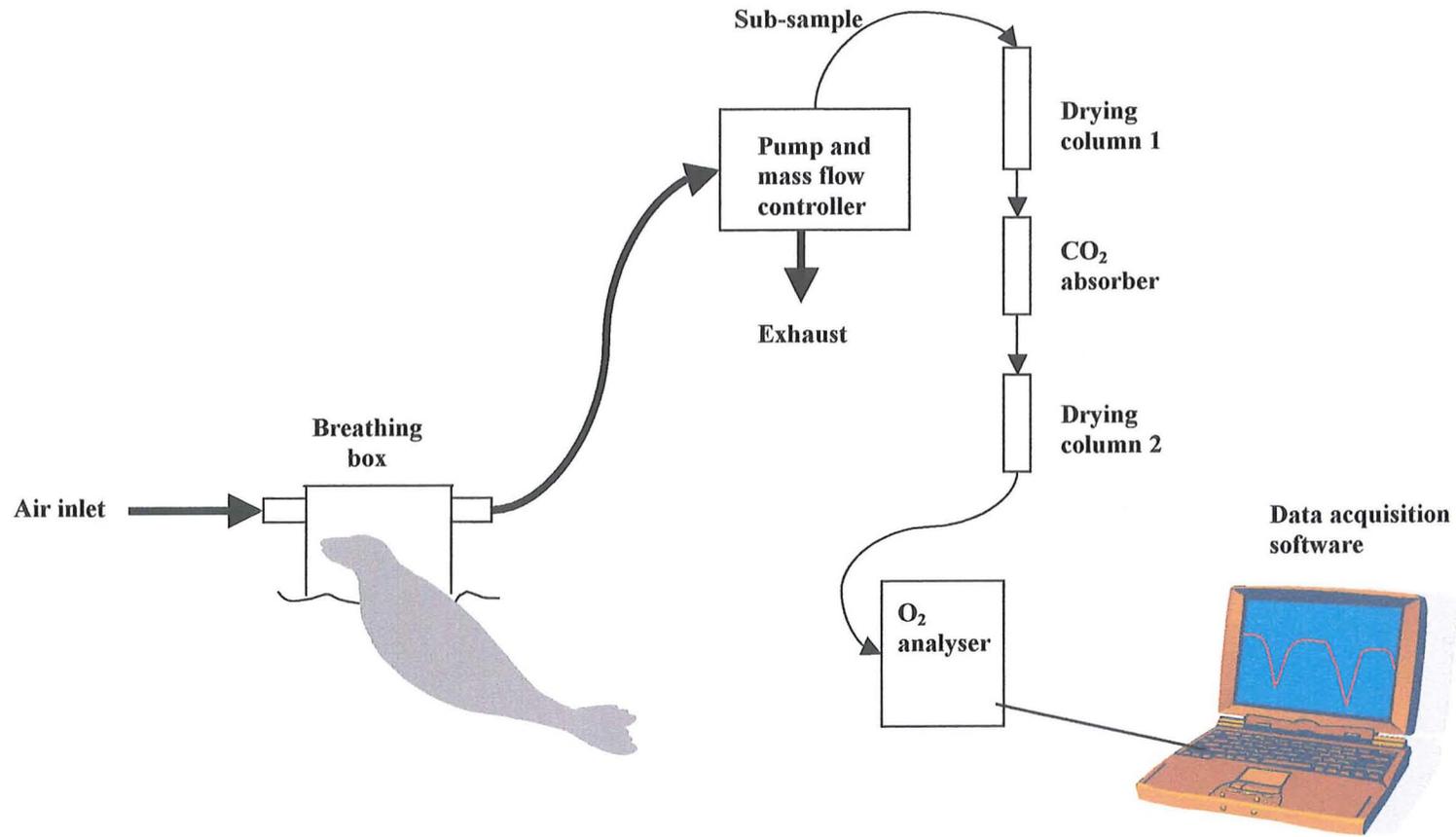


Figure 3.2 Schematic of open-flow respirometry system. The arrows show the direction of air-flow through the system.

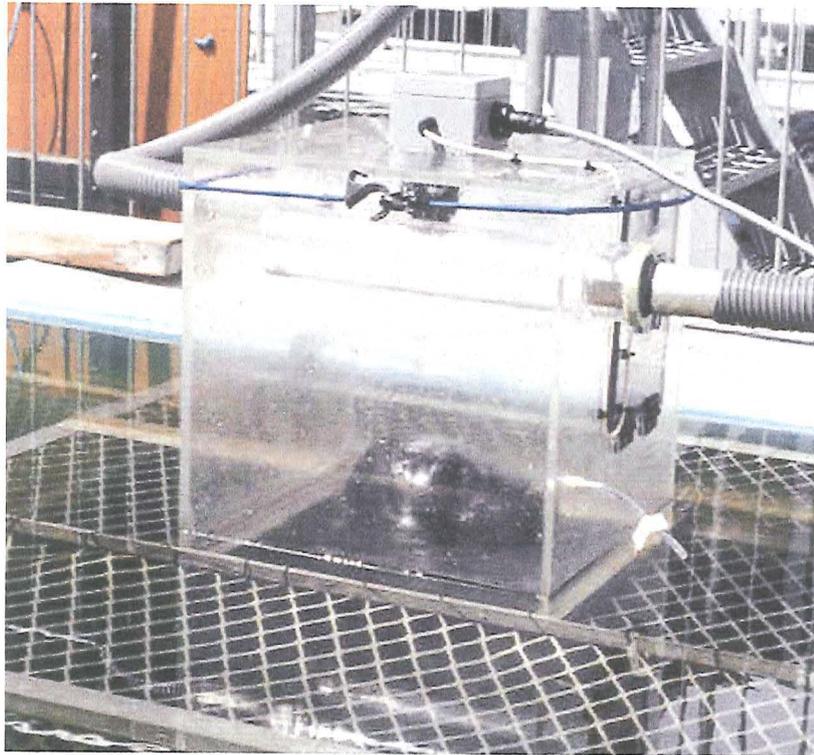


Figure 3.3 Respirometry 'breathing' box

as “dead space” so that none of the seals’ expirations were lost through the inlet. Ambient air was drawn through the box at a rate depending on the animal (200-400l/min), sufficient to avoid accumulation of expired gases within the breathing box (change in oxygen concentration when a seal was breathing in the chamber was approximately 1%). Flow was maintained and monitored using Sable Systems Flow Kit 500H (Sable Systems International). This flow was continuously sub-sampled at a rate of 500ml/min; this sample was pumped at positive pressure through a drying column, a CO₂ absorber and another drying column before entering a ‘Servomex’ paramagnetic oxygen analyser (model OA570, Sybron Taylor, Taylor Instrument Analytics Ltd, UK), which measured the oxygen concentration in the sample gas. The oxygen analyser was connected to a laptop computer using a PCMIA16-bit analogue to digital converter (PC-CARD DAS16/16, Amplicon Liveline). As the animal surfaced and breathed in the chamber it removed O₂ from the flow passing through, the O₂ analyser measured this as a decrease in oxygen concentration. The O₂ analyser output was sampled using a program designed and written for this application in Hewlett Packard Virtual Engineering Environment (HPVEE). Sampling rate was 10/sec. The program calculated and stored a moving average of the fractional O₂ concentration every 10 seconds. These values were read into a comma delimited text file that was time stamped with the date and time at which sampling was initiated, and the identity of the seal under investigation. The system had a lag of approximately 110 seconds from when the seals began breathing until the first deflection on the O₂ analyser, and a 95% response time of 2.5-3 minutes.

3.3.1 Calibration and calculation of oxygen consumption

The respirometry system was calibrated at the beginning of every run using the nitrogen dilution technique described by Fedak et al. (1981). A known flow rate of nitrogen gas is bled into the respirometry chamber (VN_2). As N_2 flows into the chamber, an equal amount of air is displaced. Since air is approximately 21% O_2 , each litre of N_2 that flows in displaces about 210ml of O_2 and thus the O_2 concentration of the gas measured as a deflection on the oxygen analyser decreases. If the N_2 flow rate is adjusted so that the oxygen analyser records the same deflection as it did when the animal was breathing in the chamber, then the N_2 is displacing as much O_2 as the animal was consuming. Since the oxygen analyser in this system has a linear response (see Appendix 1), an exact match was not required and matching flow could be calculated. In this way VO_2 can be calculated directly from VN_2 . This calibration technique has relatively small errors as long as the flow through the system remains constant between measurement and calibration. Flow rates of nitrogen were regulated to arbitrary values using a glass tube flow-meter (Brooks Instruments). This flow-meter was calibrated weekly using a Brooks Vol-U-Meter gas calibrator. All volumes of gas were converted to STPD. Calibration curves relating flow-meter reading to measured flow in l/sec were constructed and equations produced using least squares regression.

Oxygen consumption (VO_2) of the seal was calculated using the following equation:

$$VO_2 = \frac{0.2094VN_2}{0.8} (\Delta C / \Delta C^*)$$

Where ΔC and ΔC^* refer to the deflection of the analyser during measurement and calibration respectively and VN_2 is the volume of nitrogen used in the calibration. For detailed explanation of the mathematical principles underlying the use of this calibration technique see Fedak et al. (1981). A number of tests were carried out to verify the integrity of the system (Appendix 1).

3.4 Measurement of behaviour

The seals' behaviour was measured using a Time Depth Recorder (Mk 8 TDR, Wildlife Computers), attached to the head of the animal (figure 3.4). The turbine housed in the tag rotated as the animal swam and the tag counted and logged the number of revolutions of the paddle wheel per second (measured TDR speed or MTS). MTS was converted from measured TDR speed to estimated true speed (ETS) using a calibration produced from measurements of a seal swimming in a tank where actual speed measured visually was compared with MTS (Jones 2001). Timed runs were undertaken over a 30 metre distance in the pool. The seal swam over this distance following an experimenter walking alongside the pool at different speeds carrying a food bucket. The seal would then receive a food reward at the end of the run. Using a yearling pup, 40 timed runs were made over the 30m with the TDR deployed on the head of the animal. Actual speed of the animal was plotted against the TDR recorded speed for each run. The resulting equation relating measured speed to true speed using least squares regression was:

$$ETS \text{ (m/s)} = 1.403 * MTS \quad (R^2=0.96)$$



Figure 3.4 Juvenile grey seal with TDR attached

A wet/dry sensor measured surface and dive durations. Data from the TDR were downloaded at the end of a set of measurement trials (typically 1 week). A digital watch was synchronised with the TDR clock. The time the seal entered and left the water was noted for each individual trial, which enabled the experimental period to be isolated from the TDR record and matched with the O₂ consumption trace. Data from the TDR were downloaded at the end of a set of measurement trials (typically 1 week) and the following 'sections' isolated: 1. resting at the surface breathing continuously; where TDR sensor was dry for at least 10 minutes and O₂ response showed a stable deflection over this period. 2. Resting at the surface breathing periodically; where TDR was dry for at least 10 minutes and O₂ response showed cyclical change over the same period. 3. Dive periods where TDR alternated between wet and dry and the O₂ response showed corresponding cycles. Where a diving period was identified the following parameters were calculated for each dive: dive duration, surface duration, total length of dive cycle, proportion of dive cycle spent submerged, overall mean speed (in metres per second, average of per second ETS reading), total distance travelled over dive (speed in m.s⁻¹ times duration in seconds), percentage of dive spent swimming and the mean active swim speed (average of per second ETS readings where ETS>0.02).

3.5 Body composition measurement

Body composition was measured using the isotope dilution method (Reilly & Fedak, 1990). The seals were immobilised during the procedures described below using either intravenous or intramuscular injection of a tiletamine/zolazepam mixture (Zoletil, Virbac). Dosage rates were 0.1mg/kg and 0.05mg/kg for im and iv routes

respectively. After blood sampling for determination of background ^2H levels in body fluids, seals were injected intravenously with weighed doses of deuteriated water (0.12ml/kg of 99.9% $^2\text{H}_2\text{O}$, Sigma-Aldrich Chemicals). Blood samples were taken 3-4 hours post injection, after equilibration had occurred. Serum samples were flame sealed into 50 μl capillary tubes. Distilled water was obtained from these serum samples by the method described by Speakman (1997). ^2H enrichment of this distillate was determined using the method described by Ward et al. (2000). Samples were analysed in duplicate and where duplicate samples had a coefficient of variation of greater than 2%, the samples were re-distilled and re-run. Isotopic enrichment of the injection solution was verified by diluting the original source with a known amount of water, mimicking an injection of the dose into an organism's body water pool. These dilution samples were analysed alongside the experimental samples and the exact enrichment of the original solution back-calculated.

^2H dilution space was calculated using an equation from Speakman et al. (2001):

$$N_{mol} = \frac{M_{mol}(E_{in} - E_p)}{(E_p - E_b)}$$

where N_{mol} is the number of moles of water present in the body, M_{mol} is the number of moles of isotope injected into the body, E_{in} is the enrichment of the isotope introduced into the body, the background enrichment of this isotope in the animal is E_b , and the enrichment measured in the body fluids after equilibration is E_p . (Enrichment measured in ppm).

Total body water (TBW), total body fat (TBF) and total body protein (TBP) were calculated using equations from Reilly & Fedak (1991):

$$\text{TBW (kg)} = 0.382 + 0.965 \text{ }^2\text{H dilution space (kg)}$$

$$\% \text{TBF} = 105.1 - 1.47(\% \text{TBW})$$

$$\% \text{TBP} = 0.42(\% \text{TBW}) - 4.75$$

Fat body mass (FBM) and Lean body mass (LBM) were calculated as follows:

$$\text{FBM (kg)} = \% \text{TBF} / 100 * \text{TBM (kg)}$$

$$\text{LBM (kg)} = \text{TBM (kg)} - \text{FBM (kg)}$$

Chapter 4

Variation in resting metabolic rates

4.1 Introduction

Basal requirements form a large component of an animal's total energy requirement. Basal metabolic rate (BMR) is that which is measured under the conditions outlined by Kleiber (1975) namely that the animal be mature, post-absorptive, at thermoneutrality and resting (yet awake). In cases where one or more of these criteria cannot be met, the term resting metabolic rate is used (RMR). Standardised measurements of metabolism are often used to compare between taxonomic groups, species or populations in relation to biotic factors such as body size (Kleiber 1975; McNab 1988), brain size (Armstrong 1983), life history parameters (Read and Harvey 1989; Harvey et al. 1991; Speakman et al., 2002) and food habits (McNabb 1986; Cruz-Neto et al., 2001), and with abiotic factors such as environmental productivity (Mueller and Diamond 2000) and geographical habitat (Lovegrove 2000).

Such measures are also often used as baseline values or starting points for bioenergetic models which estimate the food consumption of marine mammal populations (e.g. Lavigne et al. 1985; Mohn and Bowen 1996; Stenson et al. 1997; Winship et al. 2002). Changes in estimations of basal or resting rates will affect all subsequent calculations; therefore it is important in these models that natural variations in BMR or RMR are represented accurately (Hedd et al 1997).

4.1.1. Conditions of 'resting'

There are obvious difficulties however in standardising measurements of metabolic rate in marine mammals. The definition of resting in diving mammals is not straightforward. Animals sitting quietly at the surface appear at rest, as do animals that periodically submerge (Costa and Williams 1999). The metabolic demands of each state however may differ considerably due to physiological changes associated with the diving response. Hurley and Costa (2001) demonstrated that during submersions the metabolic rate of California sea lions declined to as little as 47% of metabolism measured under standard conditions. It is clear from this and other studies of diving mammals (Castellini et al, 1992; Hindell et al., 1992; Reed et al., 1994) that the metabolic response to diving allows for adoption of a metabolic rate below that which is measured under the typical standard conditions used in studies of terrestrial mammals. This problem is also evident when measurements are made on animals resting out of the water; Boily and Lavigne (1996) found that when grey seals exhibited apnoea while in a metabolic chamber in air, metabolic rates were approximately 20% lower than when the seals were breathing regularly. Sleep is also generally associated with depressed metabolic rates. In most species, sleep reduces overall metabolic rate by about 10% below resting waking levels (Berger and Phillips 1995).

This clearly begs the question of what exactly is basal or resting metabolism in diving mammals? It may be argued that diving or submergence represents a type of 'activity' therefore measurements made under such conditions are not strictly comparable to basal, although all other conditions are met and rates are actually

lower than they would be otherwise. This is somewhat counterintuitive as it is generally the lowest measured metabolic rate that is quoted as BMR. However phocid seals spend so much of their time diving, this could be considered the 'normal' state for these animals. Measurements taken during sleep apnoea, whether on land or in water do not strictly conform to Kleiber's criteria either. In reviewing the literature it is not always clear the exact conditions under which quoted metabolic rates were actually measured. This makes comparisons, both intra and interspecific, difficult.

It is difficult to obtain 'true' resting rates for such large active mammals. Some authors have approached this problem by using variation in swimming rates to estimate basal metabolic rates (Markussen et al. 1992). Rosen and Renouf (1995) and Rosen and Renouf (1998) calculated hourly averages of oxygen consumption over 20-24 hour periods. To obtain a measure of resting metabolism they performed a regression of activity scores on mean hourly O_2 consumption rates in harbour seals in water to yield a VO_2 when activity equalled zero. In the latter study they found no difference between RMR estimated this way and RMR measured during periods where standard conditions were met (i.e. activity did equal zero). However they did not take account of the amount of time the animals spent submerged, a factor that can have a large effect on resulting measurements (Hurley and Costa 2001).

Renouf and Gales (1994) in a study of seasonal changes in harp seal metabolism calculated mean hourly averages of oxygen consumption and presented 3 operational definitions of RMR; firstly the average for the 12h overnight

measurement period, secondly the average of the 3 h between 20.00-08.00 which had the lowest hourly average as its median, thirdly the value from the hour with the lowest value between 20.00 and 08.00. This approach does show some consistency in measurement conditions yet still does not take into account variations that may be a result of differing levels of apnoea and or submergence. Hedd et al. (1997) adopted the last of these 3 definitions in their study of seasonal changes in harp seal metabolism. It could be argued that the seasonal changes exhibited in this study may not have been real changes in basal requirements primarily determined by season but may have been a result of changing proportions of time spent submerged or apnoeic.

Williams et al. (2001) distinguished between metabolic rate of Weddell seals while they were quiescent and alert at the surface as opposed to periods of intermittent breathing while asleep. However the decrease in metabolism between the former and latter states was not statistically significant. This is in agreement with previous studies on Weddell seals, which demonstrated that metabolic rates during sleep apnoea were not significantly different from measured resting rates (Castellini et al. 1992). However Castellini et al. (1992) also found that diving metabolic rates, for short dives were higher than sleeping rates but not different from resting rates. Metabolic rates during long dives were significantly lower.

It is clear that despite the quest for comparability, the conditions under which metabolic rates are measured and the way that data were analysed vary considerably between studies and this may in part explain some of the variation in published metabolic rates in marine mammals. The first objective of this study

was to examine resting metabolic rates measured under the three different conditions in water, which are typically referred to as 'resting' – at surface and breathing regularly, at surface and breathing periodically, and during periods of intermittent non-active submergence. The second objective was to examine some of the other factors that cause variations in metabolic rate, which are relevant to seals in nature.

4.1.2 Season and body mass and composition

Renouf and Gales (1994) reported large seasonal changes in the metabolic rates of adult harp seals. They found that the basal metabolic rate of males averaged as much as 83% higher than the allometric prediction from body mass between the months of April and August. During the rest of the year their metabolic rates did not differ from predicted values. In addition, pregnant females also demonstrated marked seasonal variation in metabolic rates; they exhibited a brief elevation after the breeding season in March and April. In May, levels dramatically dropped well below allometric predictions for a non-pregnant adult of similar mass. Hedd et al (1997) confirmed the interannual consistency of these harp seal energetic cycles in additional studies using the same measurement system.

Such large-scale seasonal variations in the metabolic rates have also been reported in other species; Rosen and Renouf (1995) reported considerable seasonal variation in mass specific resting metabolic rates in captive harbour seals with values for both males and females declining on average by 35% between August and November. Boily and Lavigne (1997) observed that North-western Atlantic

adult female grey seals had resting metabolic rates higher than predicted values throughout the year, except for summer, with rates then being 50% lower than those measured in the winter. However Boily and Lavigne (1997) only measured metabolism in air, there is no published information in the seasonal changes of metabolic rate of grey seals measured in water.

Phocid seals undergo dramatic seasonal changes in body mass and composition throughout the year (Beck et al., 2000). Therefore seasonal changes in metabolic rates may be related to changing body mass or body composition throughout the year. Seasonal changes in the metabolic rate of harp seals (Renouf and Gales 1994; Hedd et al. 1997) were independent of changes in total body mass (TBM) throughout the year but were more closely related to changes in predicted lean body mass (LBM). Absolute resting metabolic rates and total body mass were unrelated within animals in the grey seals studied by Boily and Lavigne (1997). However in this latter study body composition was not measured so the relationship between changes in the various components of body mass and changes in metabolism remains unclear in this species. Results of studies looking at the effect of body fat on metabolic rate have been conflicting. Some reports have indicated that LBM is the most important contributor to absolute metabolic rate (e.g. Forbes and Brown 1989) In humans variation in the size of LBM has been shown to explain 65-90% of the between subject variation in non-mass specific RMR (Illner et al. 2000). Rea and Costa (1992) demonstrated that mass specific metabolism declined 47% in northern elephant seal pups when body fat increased from 5 to 50% of BM, suggesting that adipose tissue is relatively metabolically inert. Moreover in a study with adult harp seals Aarseth et al.

(1999) found that BMR declined 50% when the amount of fat increased from 13 to 45% of BM. In contrast to these findings McNiven (1984) found that adipose tissue contributes as much as LBM to the resting metabolic rate of sheep.

However changes in body composition do not only take the form of changes in fat versus lean mass. Recent work has demonstrated that composition of lean mass can change dramatically at different times. In recent work on migrating birds, Battley et al. (2000) found that long distance migration resulted in differential organ reductions as a result of protein catabolism. The authors hypothesise that as the functional role of an organ declines during flight, a reduction in organ size could free up protein without any adverse effects. In this way selective catabolism of tissues which are inactive during flight (e.g. intestines) may buffer other more important organs from increased protein demands. This differential reduction in organ lean tissue mass also results in a more than proportional decrease in both total and mass specific BMR (Battley et al., 2000).

4.1.3. Age

Juvenile animals are widely believed to have elevated mass specific metabolic rates relative to adults (Brody 1945). Boily and Lavigne (1997) found that juvenile grey seals in their first year of life had metabolic rates on average 1.75 times predicted values for adult mammals of a similar mass. They also found seasonal changes in RMR of juveniles that appeared to be unrelated to changes in body size, but again did not measure changing body composition. It is likely that over the first year of life grey seal pups will undergo considerable changes in body composition and therefore are also likely to have changing metabolic

requirements. In the present study we examine changes in body composition and RMR of grey seal pups from one to fourteen months of age.

4.1.4 Bioenergetic modelling

Present estimates of grey seal food consumption in the North Sea rely on a single figure of average daily energy requirement for a grey seal (Hammond et al. 1994a). This does not take into account any of the variations mentioned here. Given that changes in this parameter will have profound changes in any resulting estimates of food consumption, it is clearly important to have an understanding of natural variations in energy requirements over and above those caused by changing levels of activity throughout the year and between different sections of the population. Grey seals are capital breeders therefore undergo large seasonal changes in blubber thickness and body mass (Fedak and Anderson 1982; Boyd 1984). Therefore it is not unrealistic to suggest that the energy requirements of grey seals in the North Sea may change on a seasonal basis.

This chapter addresses three questions: 1) how do adult and juvenile grey seal metabolic rates vary under different definitions of 'resting', 2) how does metabolism vary at different times of the year, and 3) how do these changes relate to changes in body mass and body composition?

4.2. Methods

4.2.1. Animals

Ten female grey seals were used in this study, four adults of unknown age, one sub-adult female and five pups in their first year life. All animals were captured from the wild and transported to the captive facility by boat. Seals were housed in the outdoor captive facility of the Sea Mammal Research Unit at the University of St Andrews. Chapter 2 (this volume) provides more detailed information on the study animals, the captive facility and husbandry. All animals were handled in accordance with The Animals (Scientific Procedures) Act 1986, under regulations set out under project licence #60/2589.

4.2.2. Respirometry

Oxygen consumption was measured using the open-flow respirometry system described in detail in Chapter 2. Resting metabolic rates were obtained longitudinally from each animal over the entire period they were in captivity. Normally at least 2 months elapsed before an animal coming into the facility and being used in experiments. This was due to the time taken to get the animals accustomed to feeding on dead fish and becoming familiar with the experimental set up.

Metabolic rate measurements were made in tandem with other studies (Chapters 5 and 6, this volume). Since animals were allowed to dive freely in the large pool, and were not forcibly restricted to the breathing chamber, resting metabolic rates were obtained opportunistically under three definitions of resting. These occasions could be identified from a combination of TDR records of the activity of the seals, from visual observation when no TDR was used and from the pattern of deflections on the trace of the oxygen analyser which reflect the pattern of the seals' breathing (see figure 4.1). Resting was defined as (1) when animals were at the surface for more than 10 minutes, awake and breathing regularly (Surface Regular SR), (2) when the seals were at the surface for more than 10 minutes with eyes closed and breathing periodically (Surface Apneic or SA). And (3) when animals alternated between breathing at the surface and remaining quietly submerged exhibiting no activity (Periodic Submergence or PS). Figure 4.1 shows an example respirometry trace from the three different states; estimates of resting metabolism were calculated using the average deflection of the O₂ analyser calculated over the sections shown. Duration of resting periods was variable and ranged in duration from 10 minutes up to 1 hour.

Because of the opportunistic nature of the data collection there are more measurements for some animals than others, and more measurements in some parts of the year than others. Although measurements were carried out over 2.5 years, no animal was measured longitudinally for longer than 1 yr. All RMR measurements were made between the hours of 9am and 4pm, with the seals at least 15hrs post-prandial, but less than 24hrs since their last feed. (Boily and Lavigne (1995) demonstrated a change in RQ after 24 hours of food deprivation). RMR was expressed as oxygen consumption in $l \cdot min^{-1}$, mass specifically as

month $[\cos ((360/12) \times \text{month})$ and $\sin ((360/12) \times \text{month})$. The maximum difference in cosine of month occurs between summer and winter, whereas the difference in sine of month is greatest between autumn and spring. Cosine and sine of month thus provide a measure of seasonality (Fisher, 1993). Because only between 2 and 3 body composition determinations were made on each animal throughout the study period, body composition could not be included as a variable in the above analysis. Therefore a separate analysis was carried out where metabolic rate was regressed against LBM, FBM and TBM.

oxygen consumption in $\text{ml}\cdot\text{min}^{-1}\cdot\text{kg}^{-1}$, or as a multiple of Kleiber's (1975) prediction of BMR for a similarly sized terrestrial mammal (BMR litres O_2 per minute = $0.0101 M (\text{kg})^{0.75}$). If more than one resting bout was obtained on a given day, the lowest measurement of VO_2 was used.

4.2.3. Body composition

Body composition was determined by isotope dilution (see chapter 2 for a more detailed description of the technique). Body composition measurements were not made as frequently as RMR measurements, so every RMR estimate could not be expressed relative to the differing proportions of fat and lean tissue.

4.2.4. Statistical analysis

Differences between measured metabolic rates between the different definitions of resting were examined using analysis of co-variance, with metabolic rate as the response variable, resting state, individual and measurement day as factors and duration of measurement period as a covariate.

To examine seasonal variation, metabolic rates estimated using the only the first of the resting definitions were used (at the surface and breathing regularly).

Metabolic rate (O_2 consumption $\text{l}\cdot\text{min}^{-1}$) data for adults and pups were examined separately. Seasonal, individual and mass effects were examined using general linear modelling. Because month is a circular variable, (for instance month 1 is closer to month 12 than to month 6) it was transformed to the cosine and sine of

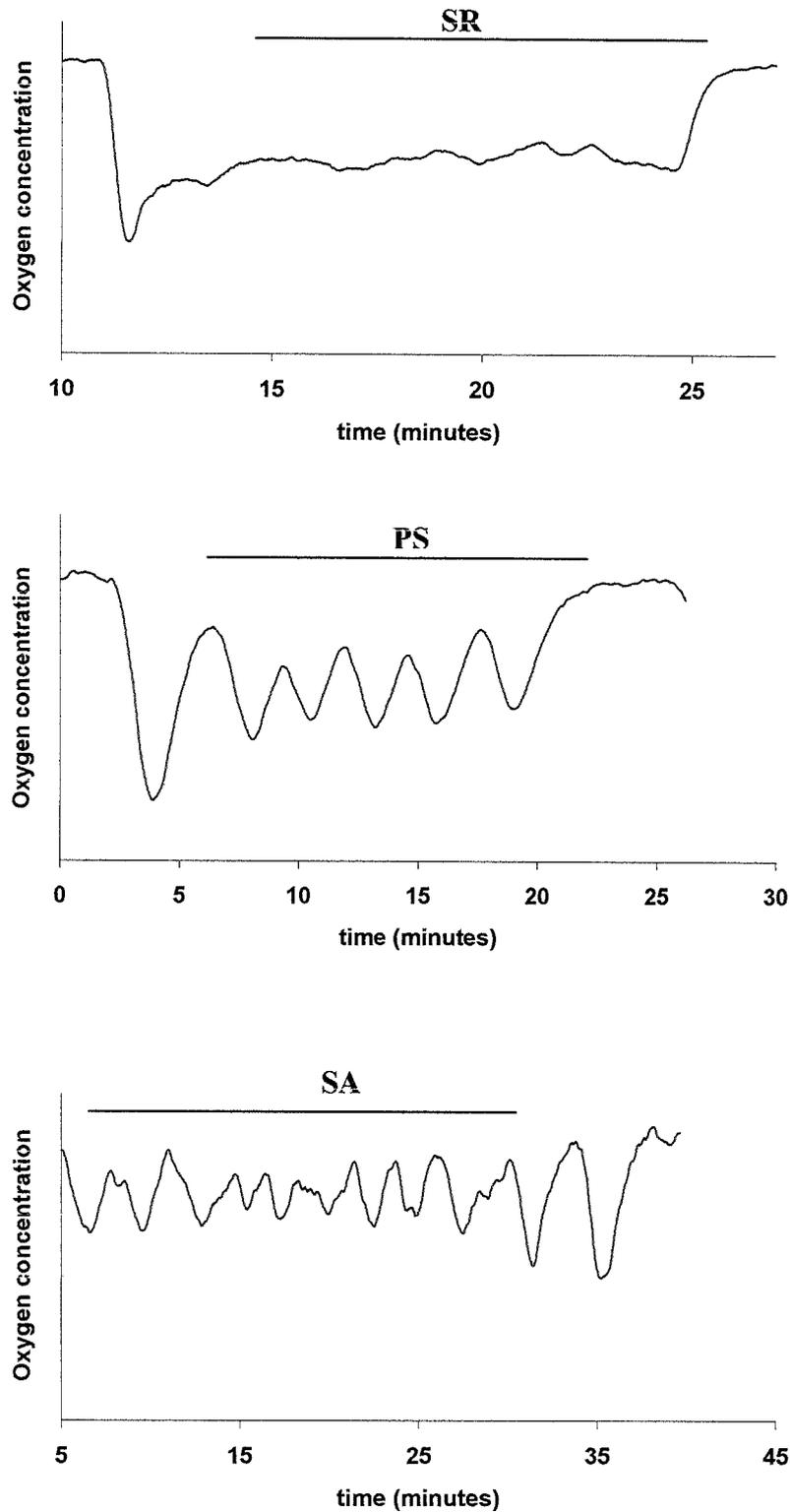


Figure 4.1 Example respirometry traces showing the three different resting states. SR is when the seal is at the surface breathing regularly, PS is when it is periodically submerged and SA is when the seal is apnoeic at the surface.

4.3. Results

4.3.1. Comparison of different resting definitions

i) Adults

Adults tended to spend little time asleep at the surface so a comparison of all 3 states was not possible. There was a mean reduction of oxygen consumption between SR and PS of 25% (table 4.1). An ANCOVA indicated that there was no significant effect of individual, mass or duration of resting period but that there was a significant effect of resting state on metabolic rate ($F=7.32$, $df=1$, $P=0.013$).

ii) Pups

There was a mean reduction of oxygen consumption between SR and PS of 17%, and a mean reduction between SR and SA of 22% (Table 4.2). An ANCOVA indicated that there was no significant effect of individual, age, mass or duration of resting period but that the three means from the different resting states were different from each other ($F=43.15$, $df=2$, $P<0.0001$).

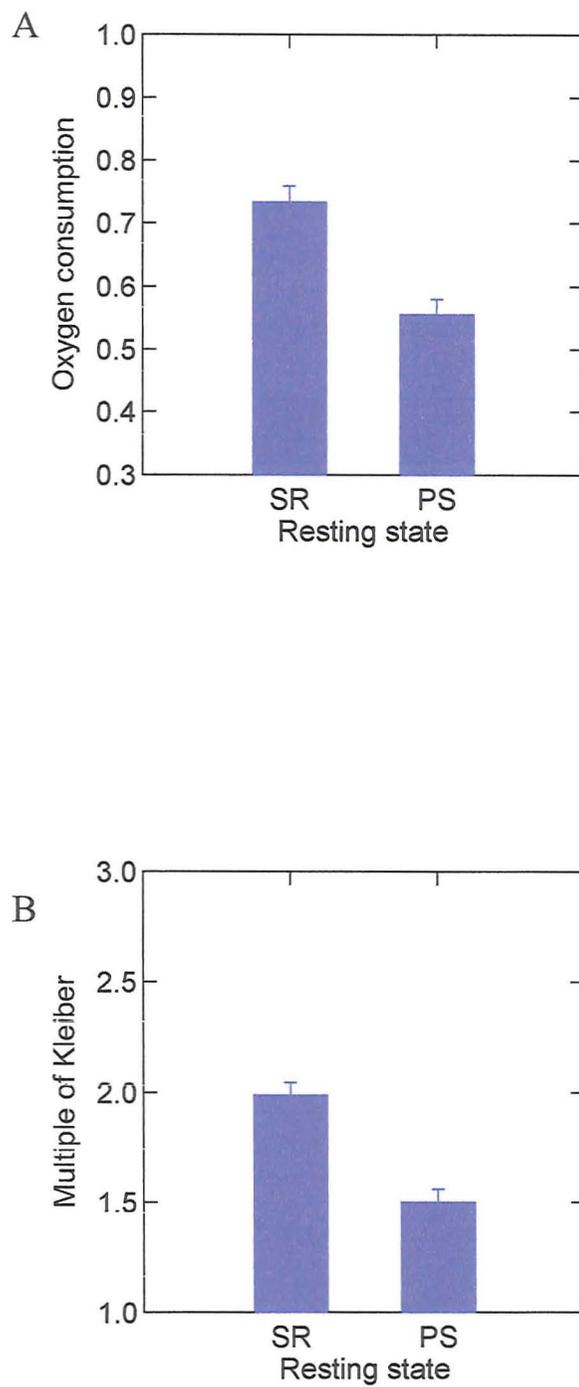
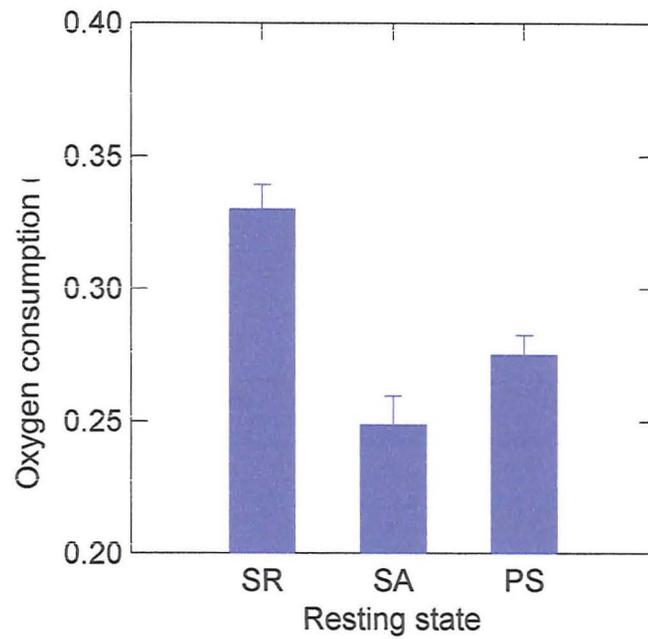


Figure 4.2. Metabolic rate of adults, resting at surface (SR) or periodically submerged (PS). A. is absolute oxygen consumption ($l \cdot \text{min}^{-1}$) and B. is multiple of the metabolic rate predicted by Kleiber. Values are the overall means from the 4 animals detailed in table 4.1 \pm sd.

Seal ID	N	O ₂ consumption (l.min ⁻¹)			Kleiber	
		SR	PS	% reduction	SR	PS
Deirdre	5	0.61 ±0.04	0.41 ±0.02	33	1.8 ±0.13	1.35 ±0.07
Cassie	5	0.77 ±0.12	0.53 ±0.07	31	2.11 ±0.28	1.47 ±0.35
Feefee	6	0.68 ±0.11	0.51 ±0.09	25	1.78 ±0.33	1.33 ±0.20
Lola	15	0.81 ±0.11	0.62 ±0.15	23	2.10 ±0.30	1.62 ±0.39

Table 4.1. Metabolic rates of adult seals under the two resting states (mean ±1 SD), SR=resting at the surface and breathing regularly, PS=periodic submergence. For comparative purposes metabolism is presented in two formats: absolute O₂ consumption and the rate of observed RMR to Kleiber's (1975) prediction of BMR for adult terrestrial mammals of the same size (Kleiber). N refers to the numbers of days which both states were measured.

A



B

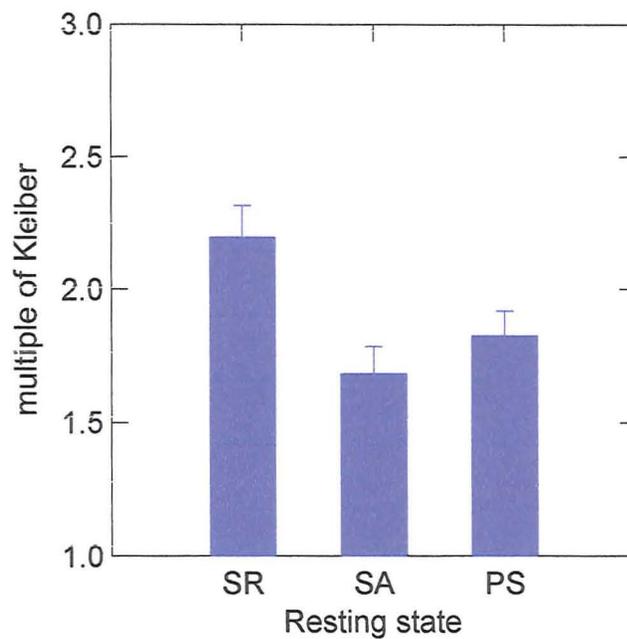


Figure 4.3. Metabolic rate of pups, resting at surface (SR), apneic at surface (SA) or periodically submerged (PS). A. is absolute oxygen consumption (l.min⁻¹) and B. is multiple of the metabolic rate predicted by Kleiber. Values are mean of the values from all 4 pups \pm 1sd.

O₂ consumption (l.min⁻¹)

Seal id	SR	SA	%	PS	%
Bonnie	0.30 ±0.01	0.25 ±0.01	17	0.26 ±0.01	23
Jay	0.33 ±0.01	0.25 ±0.04	24	0.28 ±0.01	15
Kylie	0.32 ±0.01	0.22 ±0.03	31	0.28 ±0.03	12
Nora	0.35 ±0.02	0.28 ±0.02	20	0.28 ±0.03	20
Overall mean:	0.33 ±0.02	0.26 ±0.04	23	0.27 ±0.02	18

Kleiber

Seal id	SR	SA	PS
Bonnie	1.77 ±0.08	1.49 ±0.02	1.53 ±0.04
Jay	1.82 ±0.08	1.45 ±0.21	1.55 ±0.08
Kylie	2.33 ±0.09	1.62 ±0.20	2.01 ±0.20
Nora	2.44 ±0.18	2.00 ±0.14	2.00 ±0.24

Table 4.2. Metabolic rates of pups under the three resting states (mean ±1 SD),

SR=resting at the surface and breathing regularly, SA= surface apnoea,

PS=periodic submergence. For comparative purposes metabolism is presented in

two formats: absolute O₂ consumption (l.min⁻¹) and the ratio of observed RMR to

Kleiber's (1975) prediction of BMR for adult terrestrial mammals of the same

size. % is the percentage reduction between SR and SA, and SR and PS

4.3.2. Season

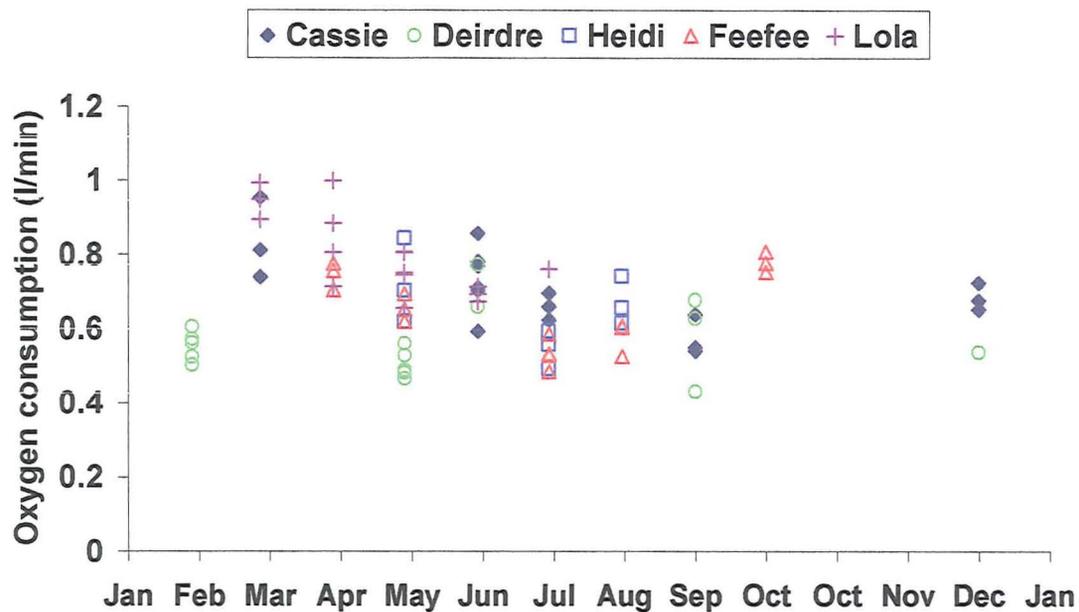
i) Adults

Throughout the 2.5 years of the study absolute resting rates of oxygen consumption ranged from 0.485 to 0.999 $\text{l}\cdot\text{min}^{-1}$ (Figure 4.4A). These correspond to 1.07-2.83 (overall mean 1.95) times the predicted BMR of similarly sized adults (Kleiber 1975). Although there was considerable variation between and within animal, both between and within month, a GLM on data from all 4 adults (excluding Deirdre as she was not fully mature) indicated that RMR ($\text{l}\cdot\text{min}^{-1}$) varied significantly with sine of month ($F=11.596$, $p=0.001$) and mass ($F=6.354$, $p=0.015$). There was no significant effect of cosine of month, individual, or water temperature. This analysis shows that the largest differences in metabolic rates occurred between spring and autumn. The spring elevation and subsequent decline in metabolic rates in all 4 adults can be seen in Figure 4.4A. This pattern is still evident when metabolic rates are expressed mass specifically (Figure 4.4B). Therefore, although mass explains some of the variation in absolute metabolic rate, there are still underlying seasonal changes. Metabolic rates are higher than predicted BMR's for adult mammals of similar mass at all times of year.

ii) Pups

Absolute resting rates of oxygen consumption ranged from 0.200 to 0.404 $\text{l}\cdot\text{min}^{-1}$. These correspond to 1.29-2.30 (mean 1.68) times the predicted BMR of similarly sized adults (Kleiber 1975). As with the adults, inter and intra-individual variation in RMR was observed. Jay was excluded from further analysis because there are only RMR measurements from two times of year.

A



B

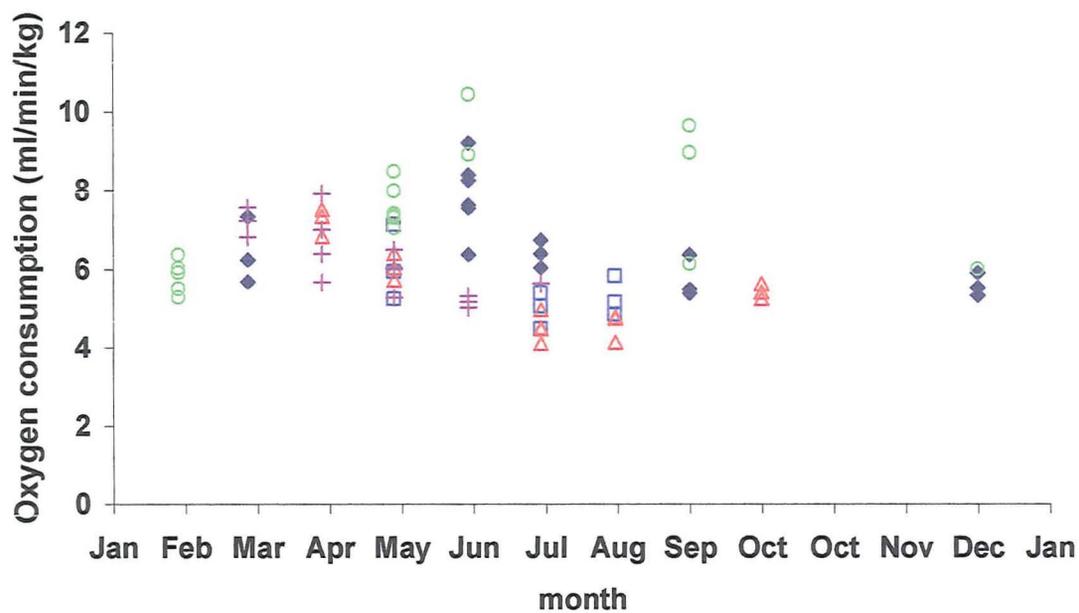
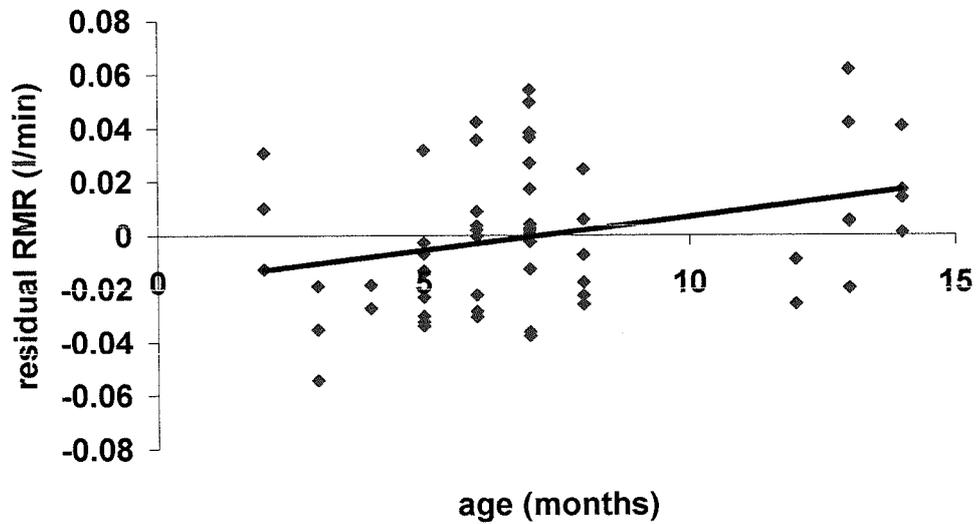


Figure 4.4 Seasonal variation in the resting metabolic rate of 4 adult female seals and 1 sub-adult female (Deirdre), by month of measurement. Each symbol represents one day's measurement. **A** shows RMR as absolute oxygen consumption in $\text{l}\cdot\text{min}^{-1}$. **B** shows RMR expressed mass specifically in $\text{ml}\cdot\text{min}^{-1}\cdot\text{kg}^{-1}$.

A GLM on pooled data from the 4 remaining pups indicated that absolute metabolic rates (oxygen consumption in $\text{l}\cdot\text{min}^{-1}$) varied significantly between animals ($F=39.49$, $p<0.0001$) and that there was a significant positive effect of age ($F=14.77$, $p<0.0001$). There was no significant effect of mass, season or water temperature.

The effect of age is shown individually in Figure 4.5. The effects of all the other variables were removed by performing a separate GLM on RMR including all variables except age, and then the effect of age examined by plotting the residuals of these models against the removed variable.

On an individual level, analysing relationships between mass and age and RMR (Figure 4.6 & Figure 4.7) were complicated by the fact that mass and age were significantly related to each other for two of the animals, Alice ($p=0.005$, $R^2=30\%$) and Bonnie ($p<0.0001$, $R^2=88\%$), whose mass and RMR increased throughout their time in captivity. Mass and age were not related to each other for Kylie or Nora. Using multiple regression with RMR as the response variable and including both mass and age as explanatory variables, Kylie's RMR ($\text{l}\cdot\text{min}^{-1}$) increased significantly with age but not with mass. Kylie's mass specific RMR ($\text{ml}\cdot\text{min}^{-1}\cdot\text{kg}^{-1}$) increased significantly with age. Nora's RMR appeared unrelated to either age or mass (Figure 4.8).



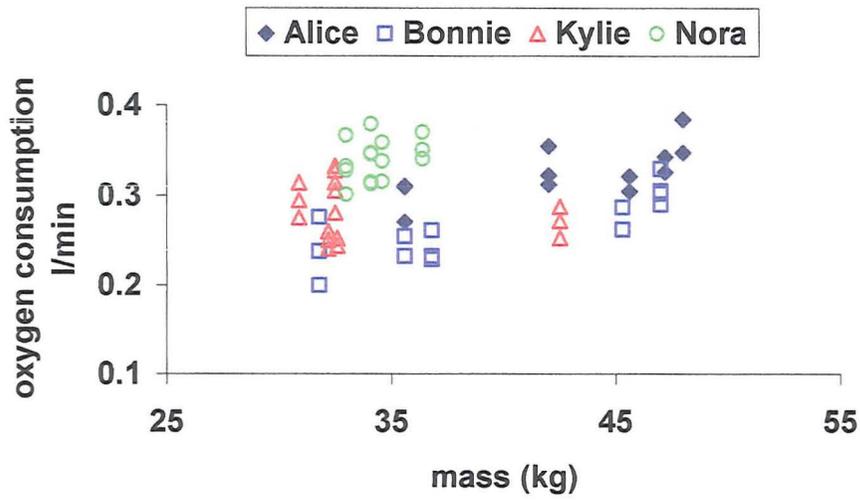


Figure 4.6 Variation in absolute RMR in 4 pups in relation to mass.

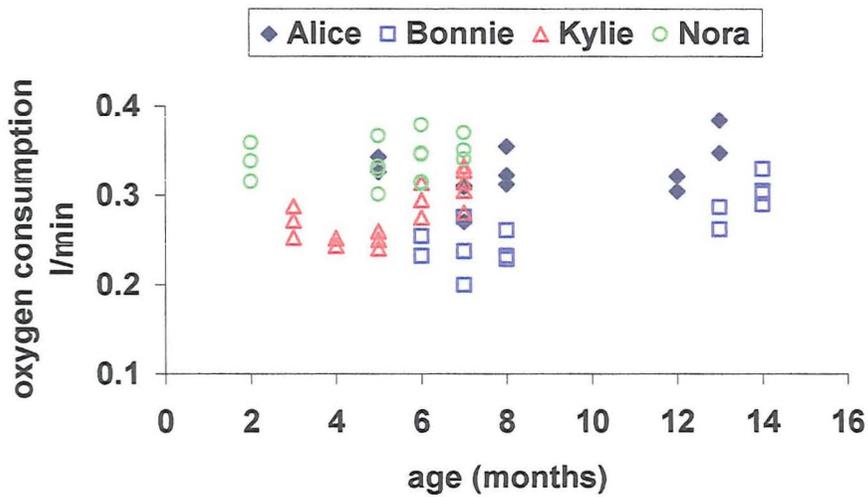


Figure 4.7 Variation in absolute RMR with age in 4 pups in relation to age.

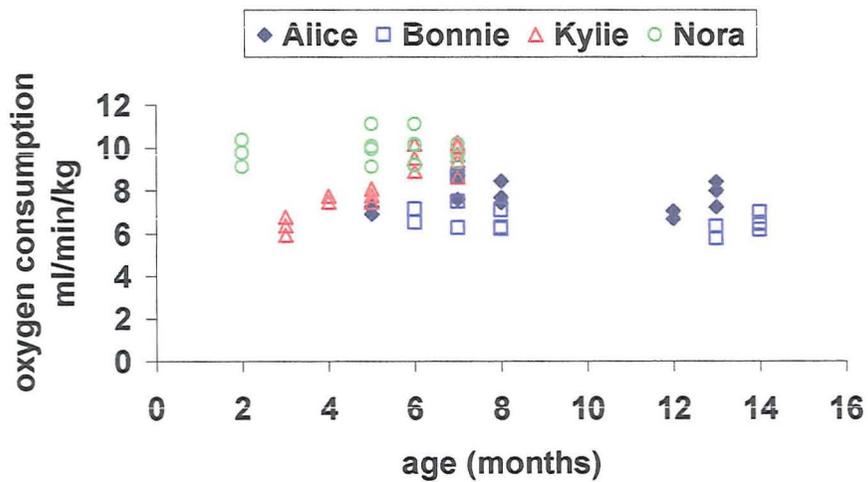


Figure 4.8 Variation in mass specific RMR in pups in relation to age.

4.3.3. Body composition

i) Adults

All 3 adult females for which body composition data were available increased in fat content in the period leading up to the breeding season in autumn, as did the sub-adult Deirdre (Figure 4.9). Deirdre and Cassie further increased in TBM between the breeding and moult period, but this increase was a reflection of increased lean mass rather than fat mass.

RMR ($\text{l}\cdot\text{min}^{-1}$) positively correlated with both TBM and LBM (Figure 4.10), though LBM the largest correlation co-efficient (Spearman's rank correlation, $r = 0.81$, $df = 7$, $p < 0.03$ for LBM and $r = 0.79$, $df = 7$, $p < 0.05$ for TBM).

ii) Pups

All pups increased in lean body mass (LBM in kg) with age (Figure 4.11), although there was variation between animals in the pattern of TBM changes (Figure 4.12). The two pups that came into the facility as whitecoats in December 2001 (Kylie and Nora) had a high percentage fat content at the first measurement (February 2002). This then declined throughout the year. Within this small sample RMR did not vary significantly with TBM or LBM. There was a significant positive correlation between age and lean body mass (Spearman's rank correlation, $r = 0.57$, $df = 9$, $P < 0.05$) but no significant correlation between age and total body mass (Spearman's rank correlation, $r = 0.28$, $df = 9$, $P > 0.05$).

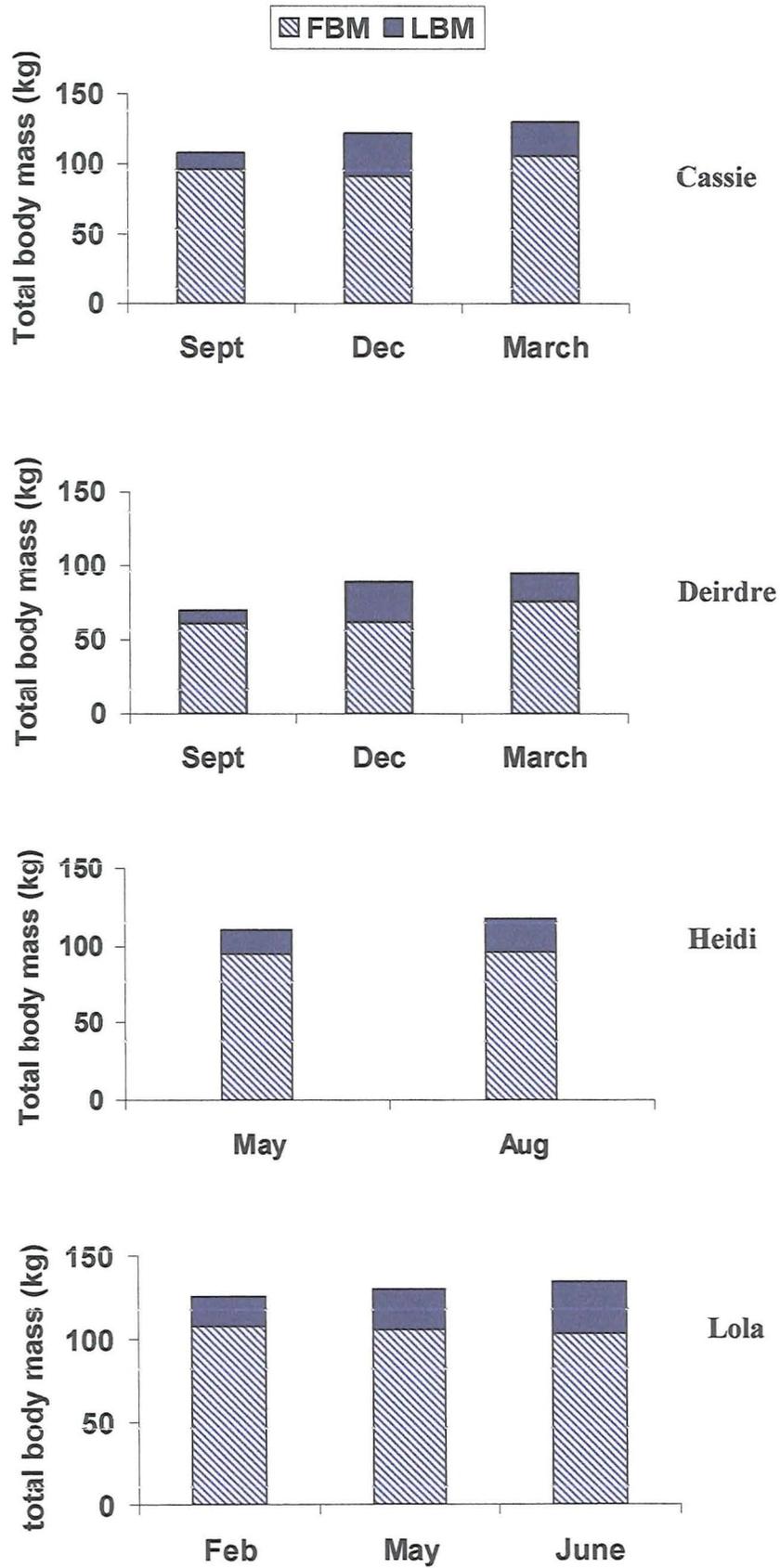


Figure 4.9 Seasonal changes in body composition in 3 adult and one sub-adult females.

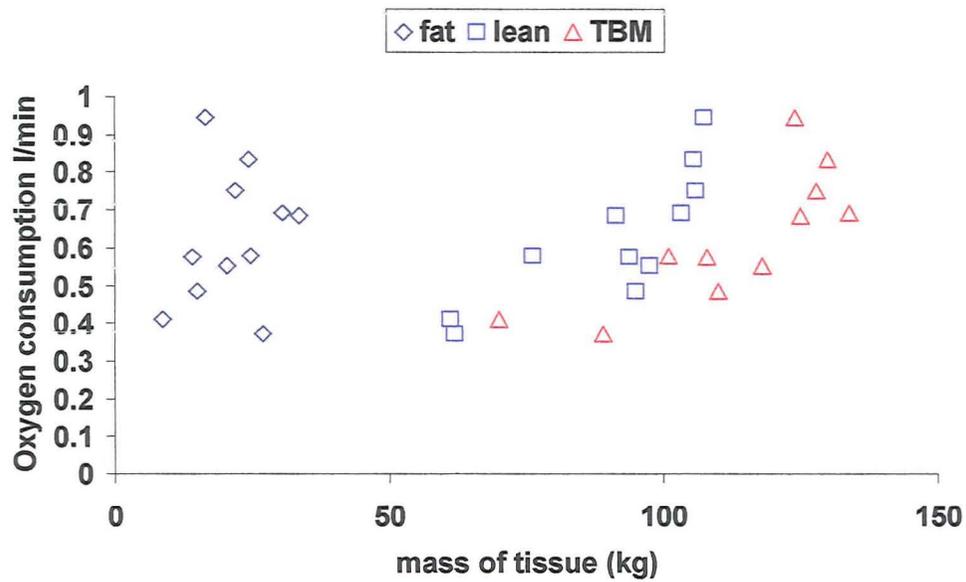


Figure 4.10. Resting metabolic rate of adult seals in relation to body composition.

Data from all 4 adults pooled. Oxygen consumption correlates significantly with both lean body mass and total body mass. (Spearman's rank correlation, $r = 0.81$, $df = 7$, $p < 0.03$ for LBM and $r = 0.79$, $df = 7$, $p < 0.05$ for TBM).

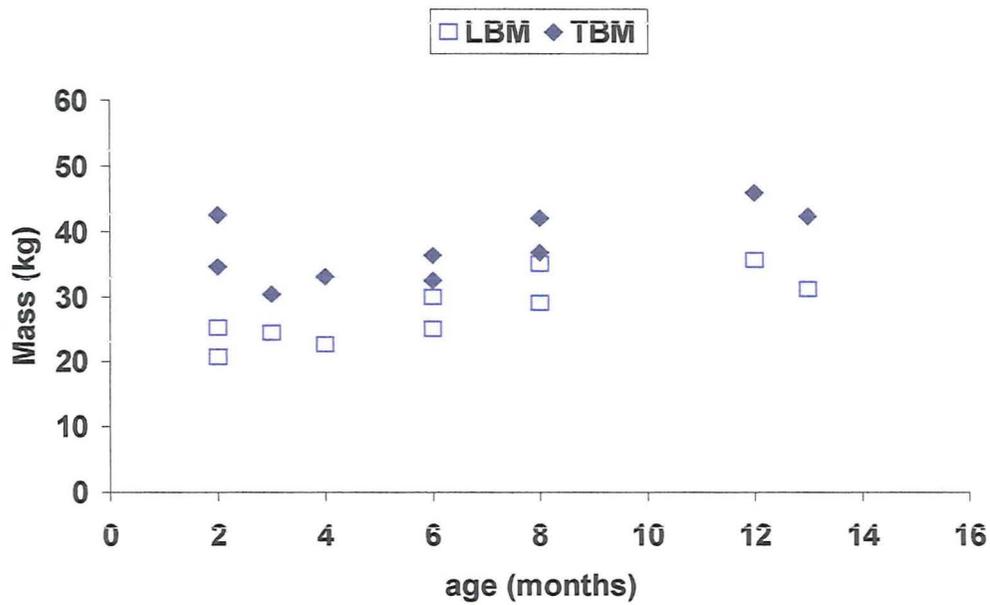


Figure 4.11 Relationships between lean body mass and total body mass, data pooled from all four pups. There was a significant correlation between age and lean body mass (Spearman's rank correlation, $r = 0.57$, $df = 9$, $P < 0.05$.)

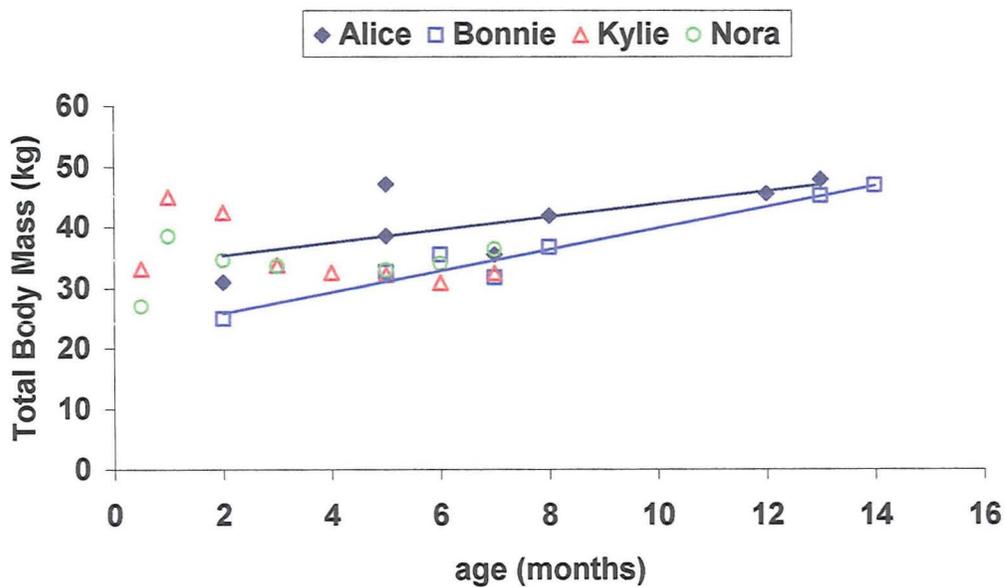


Figure 4.12 Mass changes in relation to age of four pups. A solid line denotes a significant relationship determined by least squares regression. (Alice: $R^2 = 30\%$, $df = 1$, $p = 0.005$, Bonnie: $R^2 = 80\%$, $df = 1$, $p < 0.001$).

4.4. Discussion

4.4.1. Resting conditions

There were clear differences between metabolic rates measured under the different resting conditions. Both periodic submergence and apnoea at the surface resulted in lower rates (17-25%) of oxygen consumption than when animals were breathing regularly while resting at the surface. This is similar to the findings of Hurley and Costa (2001) who found that submergence in Californian sea lions resulted in reductions of oxygen consumption of 47% of levels measured while animals remained at the surface. Savings as a result of periodic breathing are not restricted to animals in water, Boily and Lavigne (1996) found that apnoea on land resulted in metabolic rates 20% lower than non-apneic rates. They suggested that sleep apnoea may be a means by which seals mitigate the thermoregulatory demands of high temperatures, however they found no relationship between the duration of apnoea events and ambient temperature. Ortiz et al. (1978) suggested that one function of sleep apnoea in phocids is to conserve water during periods of heat stress. Whether on land or at sea, the benefit of a reduced metabolic rate as a result of apnoea may be an important energy saving strategy. Fasting seals may have a need for energy and fuel conservation, just as oxygen conservation is important in a diving seal (Andrews et al. 1997).

Regardless of the mechanism behind such reductions in metabolic rate, it is clear that any studies attempting to describe or quantify changes in metabolic rate must

account for variations caused by differing levels of apnoea or submergence.

Accordingly the following discussion of temporal and body composition related variations in metabolic rates refers only to measurements made while animals are at the surface and breathing regularly.

Despite differences between measurements made under different conditions, measurements of marine mammals resting in water are generally higher than those of terrestrial mammals resting in air (Williams et al. 2001), and those of the same animals during diving (chapter 5). Williams et al. (2001) also reported that bottlenose dolphins resting at the surface have metabolic rates 2.3 fold the levels predicted by Kleiber's equation (Kleiber 1975). The Californian sea lions studied by Hurley and Costa (2001) had metabolic rates while resting at the water surface of 2-3 fold predicted values for similarly sized mammals. Sea otters show resting rates that are 2.8 fold predictions when resting quietly on the water surface in a metabolic hood (Williams 1989). Castellini et al. (1992) found the metabolic rates of Weddell seals resting at the surface were 1.6 times predicted values. They suggest that this is because the rest periods followed dives during which feeding probably occurred. It is possible that HIF contributed to the elevated rates in that particular study. This was not the case during the present study where seals were in a post absorptive state and values were still elevated above predicted values. Williams et al. (2001) noted that marine mammals have exceptionally high intestine length to body length ratios. They proposed the hypothesis that the comparatively high metabolic rates of marine mammals resting in water may be associated with the carnivorous nature and aquatic lifestyles of these animals and the cost of maintaining relatively long alimentary tracts. It is suggested that many marine mammal species have relatively long intestines so that they can take

advantage of prey that is patchily distributed or intermittently available (Williams et al. 2001). If this is indeed the case, it is unclear how the elevated cost of maintaining the gastrointestinal tract is balanced against the need for reducing costs for submergence.

Overall, the range of measured RMR's of the adult seals in this study were higher than previously reported values of adult greys in air. Lavigne et al. (1986) reported rates of 0.71 to 0.81 times Kleiber's (1975) prediction; Boily and Lavigne (1997) measured RMR of adults at 1.1-1.5 times Kleiber; those of our adults ranged from 1.1 to 2.6 times predicted values. A similar pattern is seen with the juveniles in this study. Boily and Lavigne (1997) reported an average rate of 1.75 times Kleiber in grey seal pups in their first year, while the values obtained here for our pups were between 1.48 and 2.66 times Kleiber, with an overall mean of 1.98. It was not possible to determine the age of our sub-adult female, Deirdre, but as her mass ranged from 66kg at capture to 95kg at release a year later, we can estimate her age from growth curves to be between 2 and 3 years old (Anderson and Fedak, 1987). Deirdre's RMR ranged from 1.80 to 2.81 times predicted values, compared to 1.35 for 3 year old grey seals as measured by Boily and Lavigne (1997).

It is difficult to obtain 'true' resting rates for such large active mammals.

Satisfying Kleiber's criteria for the measurement of basal metabolic rates is often an impossible task. One or more of the criteria often have to be sacrificed to achieve the remainder. Animals appearing at rest may actually be asleep and distinguishing between these two states is often impossible. To minimise activity, animals are often confined to very small metabolic chambers and this can cause

stress, regardless of training. Some authors have approached the problem by using variation in swimming rates to estimate basal metabolic rates (Markussen et al. 1992). Rosen and Renouf (1995) regressed activity scores against mean hourly O₂ consumption rates to yield a VO₂ when activity equalled zero. However this type of swimming generally involves submergence, a factor that may confound measurements of metabolic rate.

Several authors have called into question the validity of using such standardised measures of metabolic rate in marine mammals. Costa and Williams (1999) argue that the criteria for assessing basal metabolic rate in marine mammals should be re-assessed to conform to their unique lifestyles and physiology. Animals in the wild probably never operate at true basal levels of metabolism (Bartholomew 1977). Therefore if we are investigating metabolic rates as a means to making inferences about wild animals, it is important not to lose sight of the ecological context of the animals in the quest for comparability. In this study, measurements were only made while the seals were resting out of choice, rather than being confined to a small chamber with no alternative. In our study the seals were free to dive and swim around a 42m long, 6m wide, 2.5m deep tank. Thus resting metabolic requirement measured in this context, although elevated relative to predicted basal levels, is likely to be closer to resting requirements exhibited in the wild. Previous estimates of grey seal resting metabolism have been measured while they are resting in air. McConnell et al. (1999) reported that tagged seals spent 38% of their time near haul-outs. However only 12-16% of their time was actually spent on land. Presumably, the remaining fraction of time was spent in the water, resting. Resting at the surface also occurs while animals are at-sea, between periods of foraging (M. Fedak, personal communication). Clearly the

energetic requirement associated with resting in water is likely to be a considerable portion of a seals' annual energy budget.

4.4.2 Seasonal shifts in metabolic rate, body mass and body composition in adult females

There is considerable variation in metabolic rates both within and between individuals. Such variation in RMR measurements is to be expected, especially when data from only a few individuals are included and when each animal can only be measured on a small number of occasions at different times of year. Furthermore, when dealing with large, active wild animals in captivity, many other factors which cannot be controlled for can also affect estimates of metabolic rate. Although care was taken to standardise measurements in this study, the behaviour of the seals was not rigidly controlled. Thus the resting measurements in this study were made on an opportunistic basis. Therefore metabolic rates during these 'rest' periods may have been influenced by additional factors such as the motivational state of the animal or any preceding activity.

However, despite overall variability in metabolic rate estimates both within and between animals, there does seem to be an emerging pattern of a decreasing metabolic rate from the moult/implantation period in March for the adult females in this study. This pattern was still evident when metabolism was expressed mass-specifically suggesting that although metabolic rate did positively vary significantly with total body mass, factors other than variation in TBM were influencing the observed seasonal variation in metabolic rate.

The adult female seals all showed considerable variation in body composition throughout the study period. Lowest percentage fat content occurred in the early months of the year, post breeding season and post moult. Fat content generally increased throughout the year with a corresponding decrease in the amount of LBM as a percentage of TBM. When data from all adults and months were pooled LBM was a better predictor of oxygen consumption than TBM, although both were significantly related to oxygen consumption. These findings are similar to those of Hedd et al. (1997) in that intra-annual changes in metabolic rate of harp seals were related to changes in predicted LBM. However Hedd et al. (1997) found that metabolic rate was not related to TBM in their four adults. RMR in the three adult grey seals studied by Boily and Lavigne (1997) was also unrelated to TBM. However, when examining intra-individual variation of a small number of individuals where the mass changes involved are relatively small it is possible that a lack of power may have meant that any relationship between mass and RMR would not be evident.

These changes in body composition in adult females are likely to be related to the reproductive cycle with fattening occurring prior to the breeding season in the autumn. The interaction between reproductive status, body composition and metabolic rate can be illustrated using two specific examples: Lola was brought into the facility in December 2001 with her whitecoat pup. Lola weighed 168kg at capture and 128kg when her pup was weaned in January. The first body composition measurement was made in March during the moult period and she had a body fat content of 13%. This increased to 17% by May and to 22% by June. Mass-specific metabolic rate declined between February and June by 35%. Blood sampling for progesterone levels indicated that Lola was pregnant at

capture (A. Hall unpublished data) though she aborted her foetus in late June 2002. No body composition measurement was made after this date but her metabolic rate in July had increased from that measured in June by 9%, (although this is only based on one day's measurement).

Another adult female, Cassie, was pregnant at capture in March 2000 and gave birth to a pup in early December. She didn't manage to successfully feed the pup, which died 5 days old, therefore did not experience the same depletion of fat reserves that successfully breeding female grey seals undergo after giving birth. In September she had a body fat content of only 11%, this had increased to 26% by December, 2 weeks after giving birth. Her metabolic rate had also declined between capture and parturition by 12%. Although she didn't need to provision a pup, body fat content still declined after parturition to 19% by March during the moult period. During this period her lean mass increased by 16% and mass specific metabolic rate increased by the same percentage.

Regardless of whether they are expressed in absolute terms or mass specifically, females in this study had lower metabolic rates while pregnant than while not pregnant. This is similar to the findings of Renouf and Gales (1994) and Hedd et al. (1997). Both these studies found that the metabolic rates of pregnant harp seals were depressed from implantation to parturition below values found at other times of year. Lola's (the female for which metabolic rate data and body composition data for 3 months during pregnancy were available) TBM and her LBM as a percentage of TBM increased slightly between the months of March and May, yet her mass specific metabolic rate decreased during the same period. This would suggest that there is an additional metabolic depression operating during the

months of active gestation. This is supported by the fact that she had an increased metabolic rate after aborting her pup. This is similar to Renouf and Gales (1994) who found an increased metabolic rate after abortion in one of the harp seals in their study.

It is surprising that pregnancy is associated with lower metabolic rates given the extra demands of the foetus. However, pregnant women show a reduction in metabolic rate during the first 28 weeks of gestation (Prentice et al. 1989). This reduction was most notable in thin women, suggesting metabolic suppression occurs in response to initial energy status. It is possible that a similar mechanism could be operating in phocid seals. Low body fat levels at implantation could result in a controlled down-regulation of metabolic rate to allow a higher proportion of ingested energy to be stored for future use, thus ensuring that the female can obtain sufficient reserves to successfully produce and wean a pup. A similar mechanism has been demonstrated in hibernating mammals in the period prior to hibernation, where the accumulation of large fat stores are important for survival through the winter (Dark et al. 1989). The fact that the sub-adult female in our study, Deirdre, did not display this seasonal pattern provides further support to the idea that the seasonality of metabolism in our adult seals is related to reproduction rather than solely to changes in body mass and body composition.

The occurrence of metabolic depression during pregnancy in other phocid species has been suggested as an explanation for seasonal variation in diving behaviour. Comparing the mean dive duration of mature female southern elephant seals at different points in their annual cycle, Slip et al. (1994) found that dive duration was longest during the second and third trimesters of pregnancy than during any

other stage in the cycle. They suggested that a lowering of metabolic rate during this period would account for the variation in dive duration throughout the year. However Bennett et al. (2001) found similar seasonality in the dive duration of both male and female southern elephant seals, suggesting therefore that metabolic rate may be changing seasonally in both sexes. Whether male grey seals undergo seasonal changes in metabolic rates is an interesting question that remains to be addressed.

Buoyancy may have an influence on energy expenditure of animals resting at the water surface. An increase in fat content, as demonstrated by our adult females over the summer, may result in seals having to expend less energy to remain at the surface. A number of studies have examined the effects of buoyancy on diving behaviour (Webb et al. 1998; Beck et al. 2000), however the effect of buoyancy on maintaining position at the surface is less well studied. In their study of wild adult grey seals, Beck et al. (2000) found that although seals were always negatively buoyant, buoyancy increased by 47.9% between post-moult and pre-breeding. This would suggest there might be differential expenditures associated with remaining at the surface at different times of year. However, metabolic rate while resting at the surface is unrelated to body fat content in the present study. In fact our females appeared positively buoyant at the surface at all times so it is unlikely that buoyancy-mediated changes in metabolic effort to maintain position at the surface are responsible for the observed seasonal variation in metabolic rates.

An alternative hypothesis is that the high metabolic rates of our females in the spring are a result of the moult. Boily and Lavigne (1997) and Boily (1996)

reported elevated RMR's during the moult in captive grey seals. One suggestion is that elevated metabolic rates during the moult reflect the cost of generating a new pelt. This is contrary to the metabolic depression previously reported during the moult in harbour and spotted seals (Ashwell-Erickson and Elsner 1981; Ashwell-Erickson et al. 1986). Wild grey seals normally haul out for long periods during the moult and are reluctant to enter the water. The reasons for this are unclear, though it has been suggested that, during the moult, animals must maintain circulation to the skin in order to generate new hair growth and because of this, seals experience thermoregulatory problems in water (Boily 1996). Since we measured the RMR of our seals in water the higher metabolic rates during the moult-period in our female seals could be a result of this. Alternatively it may simply be a stress effect of not being able to haul out. However the decline in metabolic rate after the high levels seen in March is a slow one that takes place over several months rather than being an abrupt elevation seen only during the moult. Thus it may be that factors other than the moult are driving these seasonal changes.

Changes in food intake have been reported to be associated with variation in resting metabolic rates (Markussen et al. 1992; Fuglei and Ørtisland 1999; Groscolas and Robin 2001). Since the seals in this study were fed and ate daily, it is unlikely that the seasonal changes in \bar{RMR} reported here were caused by changes in food intake. There is the possibility that these changes in RMR are artificial and have little relevance to wild animals that are likely to have different feeding habits. However until there is more detailed information on feeding rates in wild animals, the importance of feeding habits on metabolic rate cannot be assessed.

The available evidence seems to point to a range of seasonal bioenergetic adaptations, which act throughout the year to allow animals to prepare and respond to changes in energy intake and demand. The fact that these adaptations persist in captivity, despite high availability of food throughout the year, suggests they are under endogenous control. Unravelling the effects of body mass and composition changes, hormonal and reproductive status on metabolic rate changes in such large active animals is a complex task. Further experimental investigations of hormonal regulation of metabolic rate and body composition in conjunction with field investigations into temporal variability of hormonal status and body composition of wild grey seals are useful avenues for further research.

4.4.3 Seasonal and age related changes in metabolism and body composition in juveniles

As with the adults, intra and inter-individual variation in the metabolic rate of pups was high. There was no apparent seasonality in pup metabolic rate, though overall metabolic rate increased with age. Lean body mass increased significantly with age, although total body mass did not. There was no significant relationship between lean body mass and RMR but any relationship may not have been detected due to a lack of power associated with a small sample size. The increase in LBM with age can probably be attributed to growth and development of muscle mass and is likely to be responsible for increases in metabolic rate with age, related to the cost of synthesis of lean tissue, that are not necessarily related to changes in total body mass. Grey seal pups in their first year are highest in mass immediately after weaning, and this is because of stored fat they have gained from

their mothers during the lactation period. This was evident in the two pups, Kylie and Nora, which came into the facility while still being suckled by their mothers. Normally grey seal pups in the wild use this stored fat to sustain them throughout the subsequent postweaning fast which lasts about 2-3 weeks until they learn to forage for themselves (Reilly 1991). At completion of the post weaning fast, pups generally have declined from 40-50% fat at weaning to below 30% (Reilly 1991). Kylie and Nora did not have to undergo this postweaning fast but Kylie had still declined from an initial body fat content of 41% in February to 13% by June. In a similar, but less extreme trend Nora declined from a body fat content of 40% in February to 31% in June. The other two pups, Alice and Bonnie, came into the facility already independent, probably for a period of between one and two months. Consequently their body fat contents were already low at the beginning of their time in the captive facility (20 and 19 % respectively in February). However the pattern of increasing lean mass throughout the year was also evident. No information exists on the changes in body composition of free-living grey seals in their first year of life. Although mass generally doesn't change a much from weaning to being a year old (A. Hall and B. McConnell, unpublished data), it is likely that a similar increase in lean body mass occurs throughout this period. If this is the case then free-living seals probably experience an increase in resting energy requirements throughout the growth period. More information is required to evaluate this.

4.4.4. Implications for modelling population energy budgets and food consumption.

Until recently, most calculations of the energy requirements of phocid seal populations have ignored seasonal changes in resting metabolic rates. Many studies simply calculate the daily energy requirements of individual seals of different ages and sex and multiply these values according to the age and sex structure of the total population (e.g. Lavigne et al. 1985; Olesiuk, 1993; Mohn and Bowen, 1996). To be of most use, models predicting the impact of seal populations should be spatially and temporally explicit. Seasonal changes in diet and energy content of prey have been included (e.g. Olesiuk, 1993), but this has not been paralleled by consideration of the seasonal variation in energy requirements. Given that requirements are likely to vary seasonally, both as a result of changing maintenance requirements and as a consequence of seasonal variation in activity budgets, the impact of seal predation on fish stocks is also likely to change seasonally. Previous estimates of the food consumed by grey seals in the North Sea uses an average daily energy requirement of a grey seal (Hammond et al., 1994a). Considering that information exists on seasonal variation in the diet of this population (Hammond et al. 1994b, 1996), knowledge of seasonal variation in energy requirement would provide a more complete picture of interactions between grey seals and fisheries in the North Sea. It is also clear that during the year, periods of highest energy requirement (i.e. breeding and during the moult) are not necessarily the periods of highest consumption. During moulting and reproductive periods seals can spend a considerable proportion of time on land. Adults lose body mass during these periods, mostly as fat, and these

fat stores have to be replenished before the next fasting event. Information on seasonal variations in body mass, body composition and growth, in tandem with information on energy expenditure can be used to estimate seasonal patterns of consumption.

Models that use the BMR or RMR of individuals as a foundation for calculating the energy requirements of populations assume that changes in RMR directly result in changes in FMR. There is no evidence however that FMR and RMR are functionally linked at the intraspecific level (Koteja 1991). Estimating energy requirements of wild individuals is a task best undertaken using ecologically relevant, empirically derived measures of the costs of various activities coupled with estimates of the extent to which those activities are carried out in the wild. Wild animals do spend a proportion of their time at rest, but these periods of rest may have energetic requirements quite different from those measured under strictly basal conditions. This has been appreciated by some authors, indeed Ryg and Ørtisland (1991) in their model of energy requirements of ringed seals, assumed that resting metabolism of a seal was 1.5 times greater than its basal metabolic rate. Similarly Hammill et al. (1995) assumed that hauled-out grey seals had a metabolic rate higher than basal. However little empirical evidence for this exists. Here we have presented data on the 'resting' energy requirements of grey seals in water, which although do not conform to Kleiber's criteria are likely to be closer to actual levels of expenditure during rest in wild animals. Bioenergetic models which use RMR's derived from strictly controlled experiments as a proxy for resting rates in the wild are likely to under-estimate the energetic requirements associated with periods of rest in the field.

Chapter 5

Diving metabolic rates

5.1 Introduction

Despite technological advances that have given us an insight into the behaviour of phocid seals at sea, measurements of energy expenditure during active diving and foraging in this group are extremely difficult to make. The energetics of diving has received attention from ecologists and physiologists for various reasons. First, the energetic costs of diving are incorporated, explicitly or implicitly in various models of seal prey consumption. Because metabolism while at sea makes up a large component of a seal's annual energy budget, the energetic cost of diving may have a considerable influence on population consumption estimates. Secondly, the rate of energy use during diving is important in understanding the complex balance of behaviour and physiology that shapes the foraging strategies of air-breathing animals exploiting an underwater prey resource. These issues are dealt with in turn in the following sections.

5.1.1 Seal-fisheries interactions

In many parts of the world seals are perceived as competitors to man, feeding on valuable fish stocks, purportedly reducing the numbers available to fishermen. In the UK the grey seal population has been increasing on average by 6% per year since the 60's, and now stands at just over 120,000 animals. This has led to calls for a cull from the UK fishing industry. But before any management decisions can be made, it is necessary to have information on the nature and extent of any interaction between seals and fisheries. One approach is the development of quantitative models that can be used to predict food consumption by a given population of seals, therefore predicting the likely impact of seal populations on local fish stocks (e.g. Winship et

al. 2002, Mohn and Bowen, 1996). These models require information on many elements, including spatio-temporal distribution of seal foraging and the diet composition of the population, coupled with information on population energy requirements.

The energy requirements of seals are the major determinants of how much fish they consume. Metabolism while at sea makes up a large component of a seal's annual energy budget, yet it is this component we know least about. In the Steller sea lion bioenergetic model developed by Winship et al. (2002), uncertainty in metabolism parameters, particularly activity cost parameters had the largest effect on the error in estimates of food consumption.

The doubly labelled water technique (DLW) has been used to measure at-sea field metabolic rates (FMR) of many otariid species, e.g. New Zealand sea lions (Costa and Gales 2000), Northern fur seals (Costa and Gentry 1986) Australian sea lions (Costa et al. 1989; Costa and Gales in review, as cited by Costa et al. 2001) and Antarctic fur seals (Costa et al. 1989; Arnould et al. 1996). To date, at sea metabolic rate has only been measured using this method in one phocid species, the common seal (Reilly and Fedak 1991). The need for timely recapture and the cost involved in dosing large animals with isotopes makes it difficult to apply this technique to phocids such as the grey seal. Grey seals go out to sea on foraging trips that can last several days and move between haul out sites in an unpredictable manner (McConnell et al. 1999). They can be captured at haul-outs but the possibilities of recapturing the same animal are remote. Furthermore DLW can only give measures of the average energy expenditure over a time period of several days and individual metabolic rates cannot be assigned to individual dive types. At sea FMR integrates

the energy expended during all activities including resting periods, so FMR measured in this way has limited utility for examining the relationships between energy expended and dive variables such as depth, duration and swimming speed over periods shorter than an entire foraging trip.

Other approaches to estimate at-sea energy requirements include predicting basal metabolic rate (BMR) based on empirically derived equations relating body mass to metabolic rate (Kleiber 1975), then using a multiplier of BMR to account for activity at sea. This multiplier is generally extrapolated from metabolic rate data from animals in swim flumes or in small tanks (Davis et al. 1985; Fedak 1986; Williams et al. 1991), and are not likely to be realistic models of the varied behaviour of free ranging, unrestrained animals. Flume studies require seals to swim continuously against a current, on or near the surface, something which phocid seals do not do in the wild. Similarly animals restricted to small tanks cannot exhibit the same range of behaviour as their wild counterparts. Free ranging animals need to manage their O₂ stores to maximise foraging time and energy intake (Fedak and Thompson 1993, Thompson et al. 1993). How an animal manages O₂ use in a situation of forced exercise or while diving in small tanks may be very different. A complete understanding of the energetic requirements of the time spent at sea by phocid seals will require an approach that combines laboratory based measurements with data on freely living animals.

5.1.2 Physiology and foraging strategy

In addition to the applied aspects of seal metabolism that relate to questions of food consumption, pinnipeds provide a unique system for studying the relative importance

of physiology in determining foraging behaviour (Costa et al. 2001). The aerobic dive limit (ADL) has been defined previously in chapter 1 but is generally the dive duration beyond which animals start to rely on anaerobic metabolism and is often used to place dive behaviour within a physiological context. The concept of the aerobic diving limit (ADL) has received much attention in the literature over the last few decades (e.g. Kooyman et al. 1983; Kramer 1988; Moss and Castellini 1993; Burns and Castellini 1996; Boyd and Croxall 1996; Butler and Jones 1997; Ponganis et al. 1997; Schreer and Kovacs 1997; Burns 1999; Davis and Kanatous 1999; Cabanac 2000; Costa et al. 2001; Croll et al. 2001; MacArthur et al. 2001; Schreer et al. 2001; McIntyre et al. 2002). However ADL is difficult to measure experimentally, especially in free-living animals. It is more commonly estimated by dividing total body oxygen stores by metabolic rate during diving (DMR). However this presents problems in that actual DMR is itself difficult to measure. Diving metabolic rate can only be measured in animals in captivity, or diving in unique situations such as Kooyman et al.'s (1973) ice-hole experiments with weddell seals. Freely diving metabolic rate in pinnipeds has only been directly measured to date in Weddell seals diving under ice (Kooyman et al. 1973, 1980, 1983, Castellini et al. 1992; Ponganis et al. 1993), and in captivity in northern elephant seals (Webb et al. 1998), grey seals (Fedak et al. 1988; Reed et al. 1994), Baikal seals (Ponganis et al. 1997) and Californian sea lions (Hurley and Costa 2001). In these studies diving metabolism varied with dive type and duration.

However captive studies are limited in the extent to which they can recreate behaviour comparable to that seen in free-living animals. The behaviour patterns actually displayed by seals in the wild are likely to be a result of a number of factors. Hindell et al. (2000) presented data on dive duration and swimming speed that inferred that swimming speed heavily influenced metabolic rate during a dive.

Therefore ADL is not fixed and will vary on a dive-by-dive basis, depending on the situation in which the animal is diving and the behavioural options chosen during a dive. There is currently little information on how metabolic rate during diving relates to the range of behaviour exhibited in free-living animals. While Castellini et al. (1992) measured diving metabolic rates and swimming speed in free-living Weddell seals, the two were never measured simultaneously. Williams et al. (2000) examined the relationship between propulsion mode and post-dive oxygen consumption in free living Weddell seals. They found that stroking dives were energetically more costly than gliding dives. Therefore Weddell seals can extend the duration of a dive by incorporating prolonged glides during diving. This study examines the relationships between dive and surface durations, swimming activity during the dive and oxygen consumption in grey seals diving voluntarily in a quasi-natural setting.

This chapter presents the first estimates of dive-by-dive metabolic rates in grey seals with simultaneous measurement of behaviour in an experimental set-up directly comparable to free-living animals. It also presents a general model that can be used to predict the energy expenditure of diving grey seals from behavioural parameters during the dive. It is proposed that this model be used in conjunction with telemetry-derived behavioural information from field-based studies to estimate the metabolic cost of foraging in free-living animals.

5.2 Methods

5.2.1 Measurements of DMR and diving behaviour

Oxygen consumption of 8 captive female grey seals was measured during voluntary diving in a large pool measuring 42m x 6m x 2.5m. Measurements were made using the 'breathing hole' technique described in chapter 2. The pool was divided into 4 lanes (figure 5.1) to increase the distance that seals could travel in one dive. They were encouraged to dive away from the breathing box by receiving food rewards at feeding holes in a number of training sessions before measurements actually started. The output from the oxygen analyser was monitored continuously in a laboratory inside the building so that seals were not aware of any human presence throughout experimental trials.

The metabolic rate of each dive cycle was calculated by summing the oxygen consumed during the post-dive surface period and dividing it by the duration of the entire dive plus surface period cycle (figure 5.2). Dives were only included in further analysis if the output from the O₂ analyser started at the baseline level and returned to baseline after the surface period. The O₂ output was said to have returned to baseline if it was within 0.01% PO₂ of the baseline value. Only dives with durations of typically over 2 minutes were included for further analysis. This was because the 95% recovery time of the system was 2-2.5 minutes. Where animals exhibited series of shorter dives in succession, an average metabolic rate over the whole period was calculated and dive variables similarly averaged over the same period.

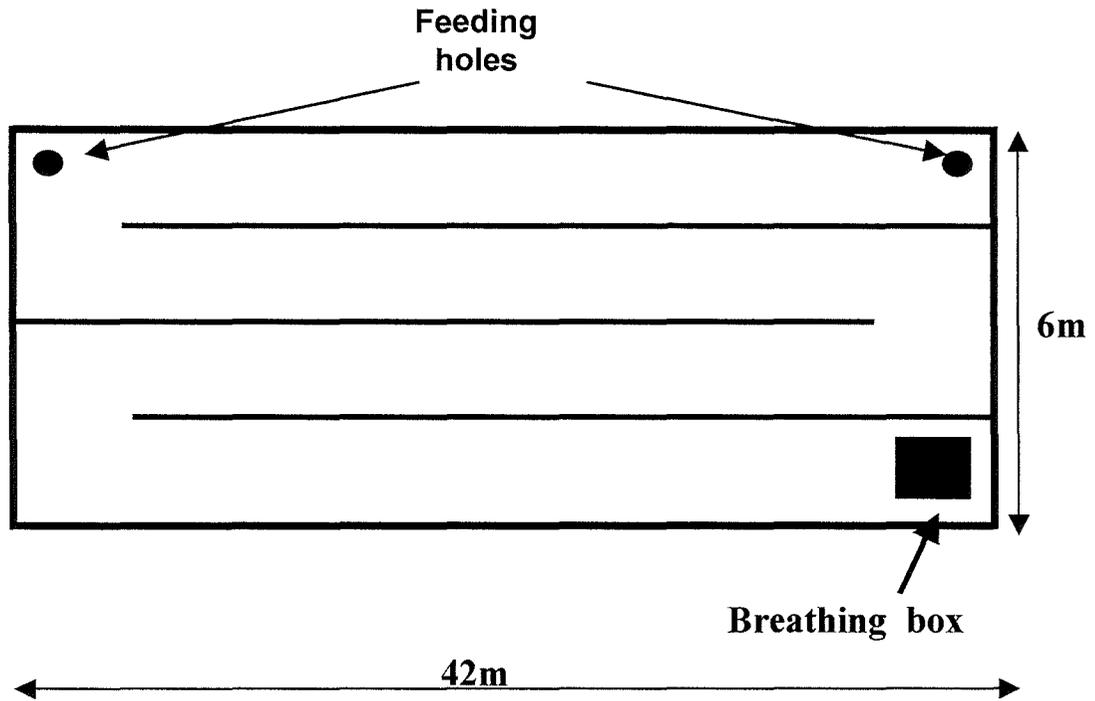


Figure 5.1 Schematic of pool used measurement of diving metabolic rate. The pool is divided into lanes using nets, the seals can travel a maximum of 168 metres away from the breathing box.

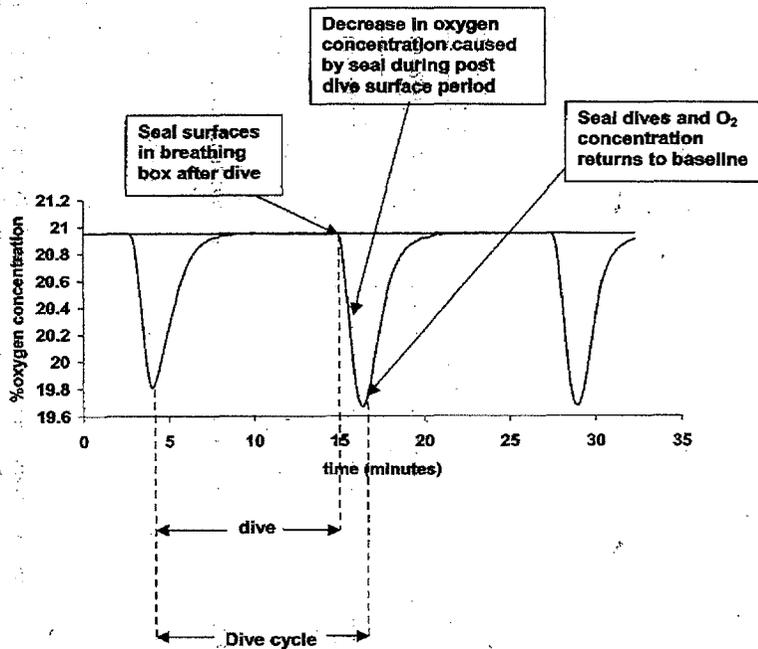


Figure 5.2 Measuring the metabolic rate of a dive cycle. The oxygen consumed during the post-dive surface period is measured by integrating the area of the deflection. The volume of oxygen consumed is divided by the duration of the entire dive plus surface period cycle.

Behaviour during diving was measured using a Time Depth Recorder (Mk 8 TDR, Wildlife Computers), which was attached to the head of the animal (see figure 3.4). The turbine housed in the tag rotated as the animal swam and logged velocity once per second (measured TDR speed or MTS). MTS was converted from measured TDR speed to estimated true speed (ETS) using the calibration described in chapter 3. A wet/dry sensor measured surface and dive durations. A digital watch was synchronised with the TDR clock and the time the seal entered and left the water was noted for each individual trial. This enabled the experimental period to be isolated from the TDR record when it was downloaded. Data from the TDR were downloaded at the end of a set of measurement trials (typically 1 week) and the following parameters calculated for each dive: dive duration; surface duration; total length of dive cycle; proportion of dive cycle spent submerged; overall mean speed during the dive (in metres per second, average of per second ETS); total distance travelled over dive (ETS in $\text{m}\cdot\text{s}^{-1}$ times duration in seconds); percentage of dive spent swimming and the mean active swim speed (average of per second ETS readings where $\text{ETS} > 0.02$).

Each individual dive was assigned a measure of metabolism by matching TDR records with oxygen consumption data. In this chapter the metabolism of a dive is expressed in one of two ways: 1. The rate of whole body oxygen consumption over the dive cycle in litres per minute DMR ($\text{l}\cdot\text{min}^{-1}$), or 2. A multiple of the basal metabolic rate predicted by Kleiber (1975) for a terrestrial mammal of a similar mass ($\text{DMR} (\text{l}\cdot\text{min}^{-1}) / 0.0101 \times \text{Mass}^{0.75}$; referred to DMR (K)). There is debate about how best to control for the effect of mass when comparing metabolic rates between animals of differing mass. Many authors express oxygen consumption on a per kilogram basis. However metabolic rates do not scale, at least inter-specifically, to mass^1 , but to $\text{mass}^{0.75}$

(Kleiber 1975). To determine the relationship between mass and DMR in the seals in this study, \log_{10} DMR ($\text{l}\cdot\text{min}^{-1}$) was regressed against \log_{10} mass (kg).

5.2.2. Factors affecting DMR

To determine which factors had a significant effect on DMR an initial analysis was carried out using a general linear model with DMR (K) as response variable and a combination of factors (age, month, individual), variables (dive duration, surface duration, proportion of dive cycle spent submerged, mean speed, distance travelled, water temperature and interaction terms) as explanatory variables. Non-significant variables ($p>0.05$) were eliminated in a stepwise manner until all remaining variables were significant at $p<0.05$. Relationships between DMR and significant explanatory variables were explored graphically.

Furthermore to investigate if animals behaved similarly between ‘rest’ dives and active dives, dives were split into 2 categories. Inactive dives were defined as dives where distance travelled $<5\text{m}$ (this was chosen because it is the distance that would be recorded if the animal left the breathing box and went to the bottom of the pool at the onset of the dive and returned to the breathing box at the end of the dive with no other movement.) Consequently dives with $>5\text{m}$ travelling distance were classified as active.

5.2.3. Model predicting DMR from behaviour

We also constructed a model that would allow the prediction of DMR ($\text{l}\cdot\text{min}^{-1}$) of free-ranging seals given the sorts of information about their diving behaviour available from telemetry records from wild phocid seals. Only variables that were likely to be measured in telemetry studies of wild animals were included. An initial analysis suggested there were differences in DMR related to the month in which the measurements were made, so some measure of the time of year had to be included as a predictor in the model. Because month is a circular variable, (for instance month 1 is closer to month 12 than to month 6) it was transformed to the cosine and sine of month $\cos((360/12) \times \text{month})$ and $\sin((360/12) \times \text{month})$. The maximum difference in cosine of month occurs between summer and winter, whereas the difference in sine of month is greatest between autumn and spring. Cosine and sine of month therefore provide a measure of seasonality (Fisher, 1993). The model was constructed using the generalised linear modelling function in the statistical package R (R version 1.3.0). The glm was performed using the Gamma distribution and inverse link function, allowing for over dispersion in continuous data and non-homogeneity of variance. The model fit was assessed by examining residual plots and plots of observed versus model fits (see appendix 2 for these diagnostic plots).

The predictive power of these models was assessed in three ways:

1. Predicting DMR of novel animal over periods of short dives (shorter than any dives included in the model) - using novel data from an animal that had not been involved in the model fitting process from periods where both diving behaviour and oxygen consumption were known.

2. On data from animals which had been included in the model fitting process but from periods of diving where diving behaviour and oxygen consumption were known but hadn't been included in the model.
3. By removing one individual from the dataset of all dives, fitting the model to this reduced dataset, and then using that model to calculate the predicted oxygen consumption of the excluded animal over all their dives. This was done with each animal in turn.

5.3 Results

5.3.1 Dive characteristics

A total of 770 dives were recorded with concurrent measures of dive-by-dive metabolic rate for the 8 seals in this study: 593 active and 177 inactive dives. Table 5.1 shows a summary of the dive characteristics for each seal. Across all dives the mean dive duration was 5.3 minutes (s.d. 1.8) and the maximum dive duration was 12.5 minutes. The seals spent on average 83% of the dive cycle submerged. Frequency distributions of dive and surface durations, for both inactive and active dives, are shown in figure 5.4, and frequency distributions of all the behavioural variables measured for active dives are shown in figure 5.5.

5.3.2 Diving metabolic rates

Mean rates of oxygen consumption during diving ranged from 0.25 l.min⁻¹ in a juvenile under one year of age to 0.69 l.min⁻¹ in the largest adult. Regressing the log₁₀ of mass (kg) against the log₁₀ of mean DMR (l.min⁻¹) for each animal resulted in the following equation (see figure 5.6):

$$\text{Log}_{10}\text{DMR} = 0.76\text{log}_{10}M - 1.79 \quad (R^2 = 0.97, d.f. = 7 \text{ } p < 0.0001)$$

Or:

$$\text{DMR} = 0.016 * M^{0.76}$$

Where M = body mass in kilograms, and DMR = oxygen consumption in litres per minute. The slope of the relationship is not significantly different from Kleiber's

Animal	No. of dives	Dive Duration (min)	Surface Duration (min)	Proportion submerged	Total Distance (m)	Mean Speed (m/s)	Mean active Speed (m.s ⁻¹)	DMR (l.min ⁻¹)	DMR (ml.min ⁻¹ .kg ⁻¹)	DMR Kleiber
Bonnie*	81	3.86 ±0.97	0.57 ±0.26	0.86 ±0.05	77 ±86	0.31 ±0.33	0.46 ±0.29	0.28 ±0.09	6.08 ±1.85	1.57 ±0.48
Cassie	19	4.39 ±1.64	1.61 ±0.73	0.74 ±0.08	49 ±44	0.22 ±0.22	0.41 ±0.22	0.55 ±0.13	4.22 ±1.00	1.41 ±0.33
Deirdre	89	4.89 ±1.71	1.08 ±0.50	0.81 ±0.08	80 ±72	0.29 ±0.31	0.69 ±0.34	0.50 ±0.19	5.45 ±2.00	1.67 ±0.62
Feefee	140	5.20 ±1.29	1.23 ±0.40	0.81 ±0.05	27 ±45	0.08 ±0.13	0.21 ±0.15	0.67 ±0.13	4.87 ±0.95	1.65 ±0.32
Heidi	68	6.91 ±0.38	1.10 ±0.31	0.86 ±0.05	54 ±53	0.13 ±0.12	0.37 ±0.12	0.69 ±0.19	4.68 ±1.29	1.61 ±0.45
Jay*	58	4.23 ±2.08	0.88 ±0.45	0.83 ±0.05	79 ±91	0.26 ±0.25	0.40 ±0.25	0.25 ±0.07	5.57 ±1.58	1.44 ±0.41
Kylie*	82	3.97 ±0.62	0.43 ±0.14	0.90 ±0.02	174 ±34	0.73 ±0.13	0.82 ±0.12	0.30 ±0.04	9.33 ±1.21	2.20 ±0.29
Lola	236	5.86 ±1.60	1.26 ±0.43	0.82 ±0.06	89 ±61	0.26 ±0.19	0.69 ±0.18	0.68 ±0.17	5.24 ±1.24	2.18 ±1.51

Table 5.1 Summary of diving characteristics for all 8 seals, *denotes the seal was a juvenile <14 months. DMR (l.min⁻¹) is the mean oxygen consumption over a dive cycle in litres per minute. DMR (Kleiber) is the multiple of the basal metabolism predicted by Kleiber's (1975) allometric equation. All values are mean ± 1 s.d.

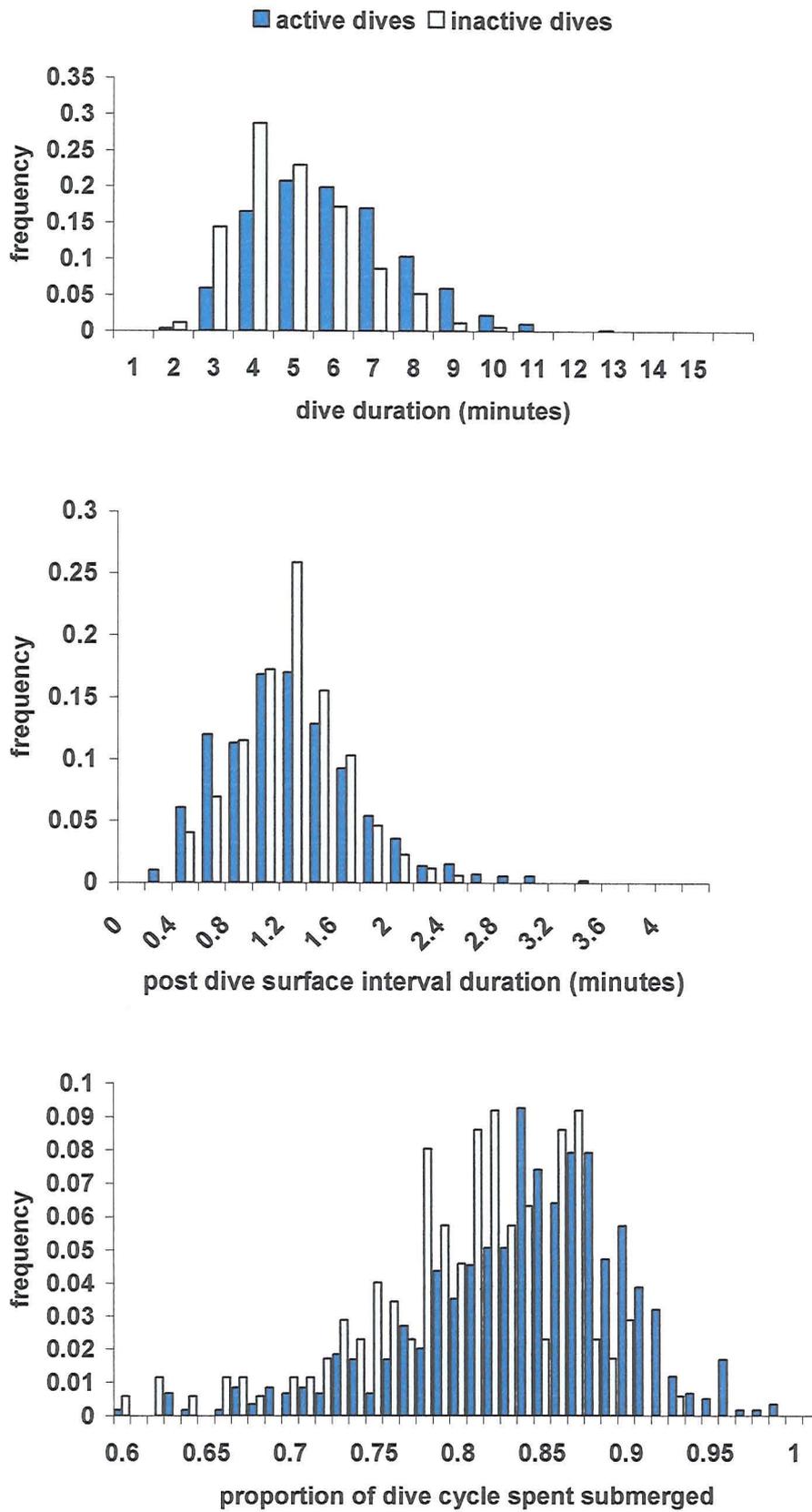


Figure 5.4 Frequency distributions of dive and surface durations of both active and inactive dives from all seals pooled (593 active and 177 inactive dives)

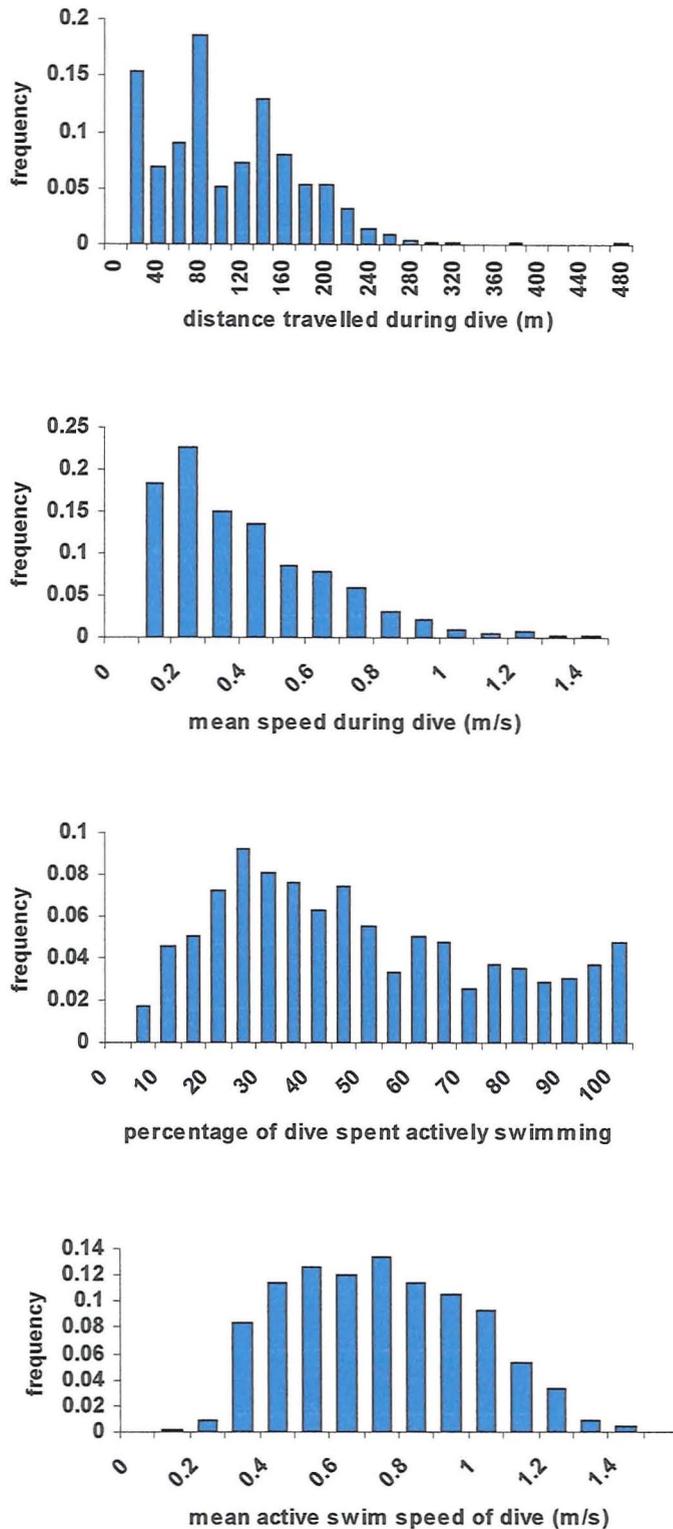


Figure 5.5 Distributions of activity variables during active dives: distance travelled during dive, mean speed during dive, percentage of dive spent actively swimming and mean active swimming speed. Dives from all 8 seals were pooled for display ($n = 593$ dives).

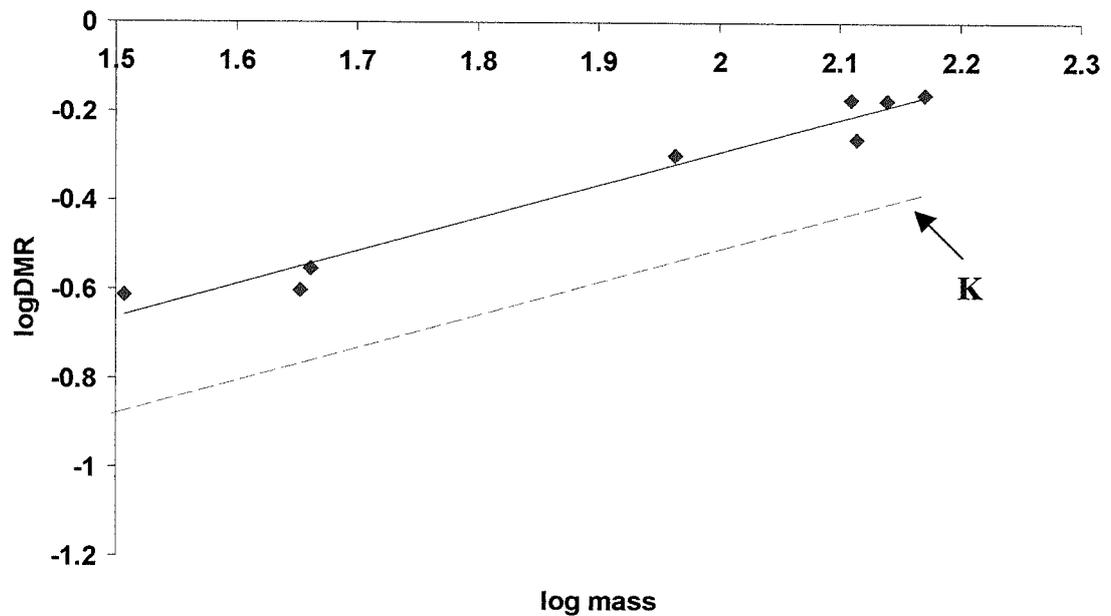


Figure 5.6 Diving metabolic rates in relation to mass. Each point is the mean DMR of an individual seal ($n=8$ seals). The solid line is the line fitted by a weighted least squares regression, weighted by the number of dives from each individual. The equation for this line is: $\text{LogDMR}(\text{l.min}^{-1}) = \text{logMass}(\text{kg}) * 0.76 - 1.79$ ($R^2 = 92\%$, $p < 0.0001$). The line K represents Kleiber's prediction of BMR in terrestrial mammals.

(1975) equation relating basal metabolism to body mass using Bailey's (1959) computation for the comparison of two regression coefficients. Although the number of animals is low and may give an unreliable measure of the scaling exponent, however within the animals studied here at least, DMR did seem to scale to mass to the power $3/4$. All subsequent metabolism measurements, where data are combined from more than one animal, are expressed as a multiple of Kleiber's prediction of BMR for a similarly sized animal (DMR (K)). Expressing metabolism in this way allows us to effectively control for the effect of mass when investigating variation in metabolic rates related to variables other than mass within this sample. When expressed this way DMR in this study ranged from 1.41(K) to 2.2(K)

5.3.3 Factors affecting DMR

An initial analysis (GLM) demonstrated that the variables significantly affecting DMR(K) were month in which the measurement was made ($F = 23.54, p < 0.0001$), dive duration ($F = 120.12, p < 0.0001$) and mean swim speed during dive ($F = 221.85, p < 0.0001$).

Inactive versus active dives

Within individual animals, there was no significant difference between mean inactive DMR and mean active DMR (figure 5.7) (paired t-test, $t = 0.247, df = 6, p = 0.813$).

When all dives were pooled inactive dives were significantly shorter than active dives (pooled variance t-test, $t = 7.743, df = 769, p < 0.0001$), surface periods were similar in duration between the two dive types, resulting in a significantly greater overall proportion of time spent submerged during active dives (Mann Whitney $U = 69631.5, p < 0.0001$).

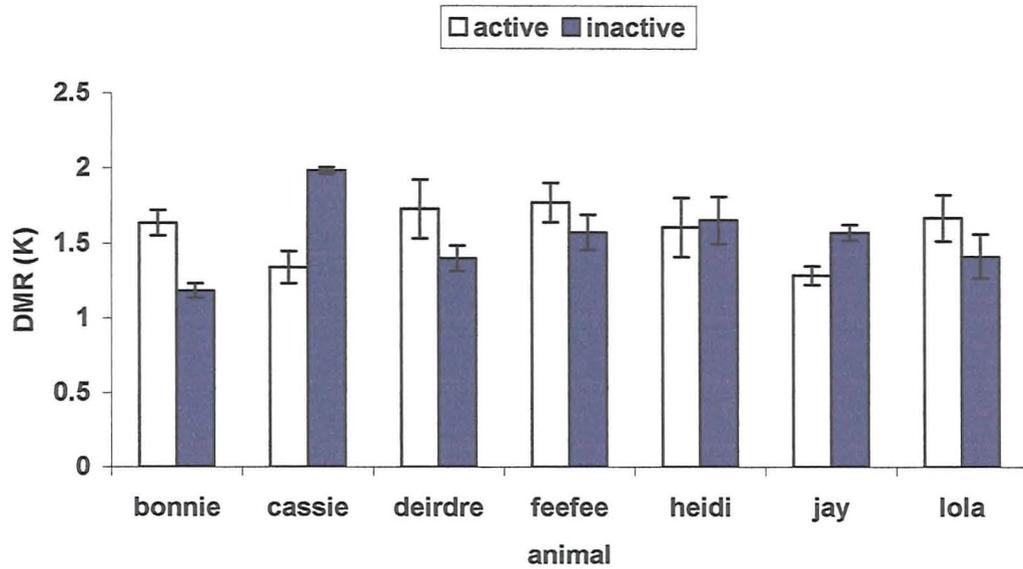


Figure 5.7 Comparison of active and inactive DMR for the 7 animals for which data were available for dives of both categories. Inactive dives were never recorded for Kylie. Values are mean \pm 1sd.

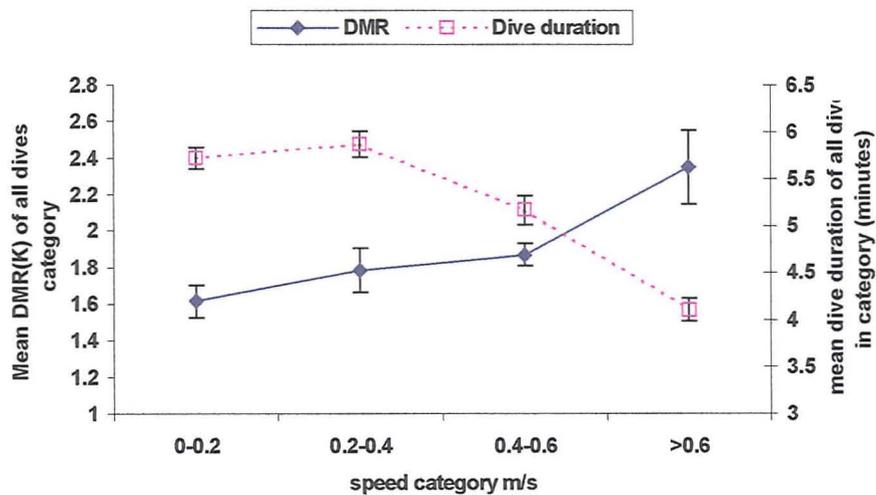


Figure 5.8. Relationships between metabolic rate, dive duration and mean speed during dive. Points are the mean of all dives in that category \pm 1 s.d. Dives from all animals pooled.

DMR and activity

Each dive was placed in one of the following speed bins: 0-0.20, 0.21-0.40, 0.41-0.60, >0.60 m.s⁻¹, the mean dive duration and DMR was calculated for each speed bin.

Mean DMR increases with speed in all speed categories, and there is also a clear decrease in dive duration across all speed categories (figure 5.8.)

The individual rates of oxygen consumption for all dives are shown in Figure 5.9. Figure 5.9A shows dive duration plotted against the metabolic rate of each dive, grouped by speed. This plot shows that the shortest dives, which also have high metabolic rates, tend to have higher mean swim speeds, whereas longer dives tend to have low swim speeds and lower rates of oxygen consumption. Figure 5.9B shows the same dives, with this time mean speed of the dive plotted against the metabolic rate of the dive, here dives are grouped by distance. Similarly, figure 5.9C displays dive duration plotted against the metabolic rate of each dive. From this it appears that the dives with the highest metabolic rate are those that covered the longest distances and had the highest mean speeds. And these dives were also generally shorter than less active dives.

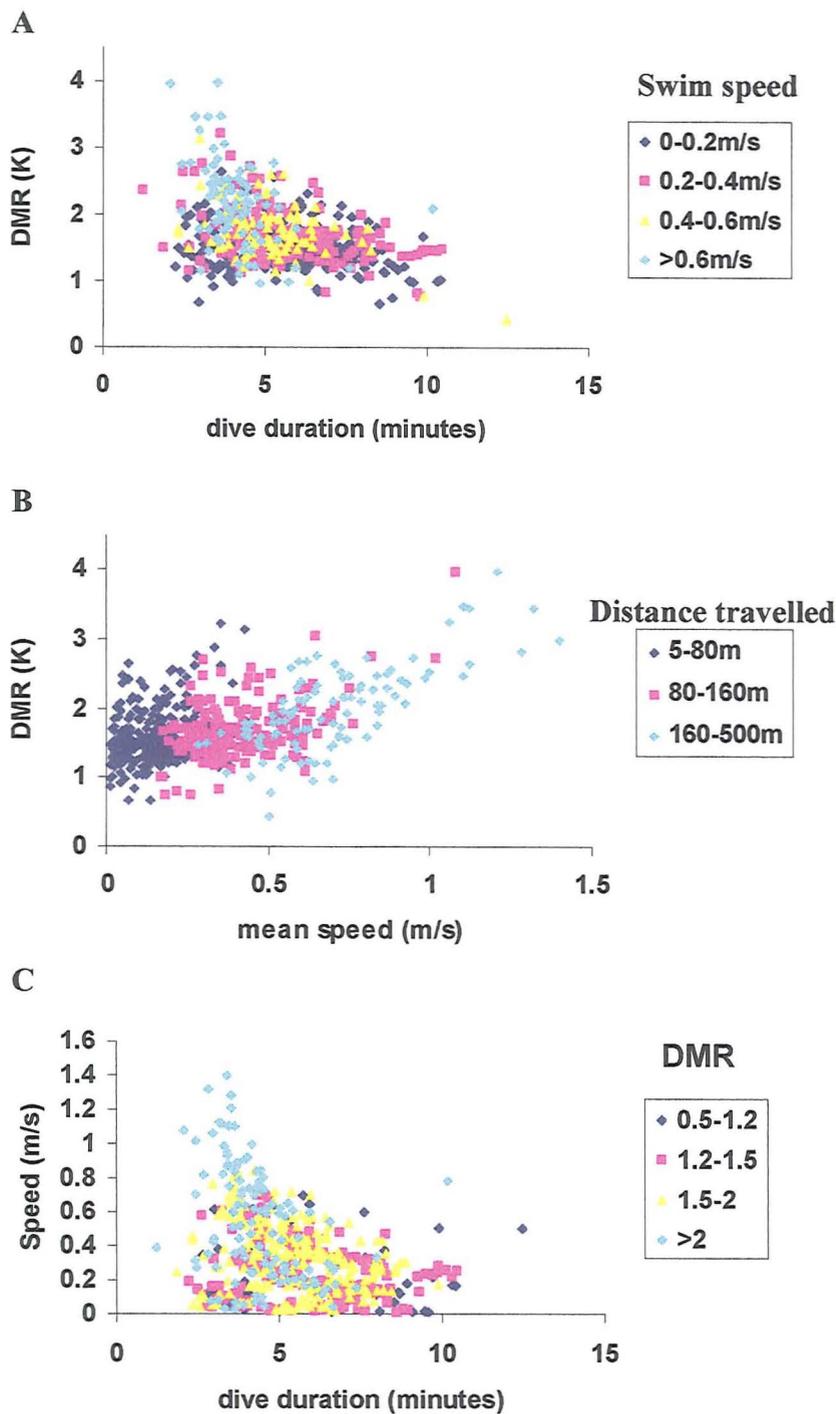


Figure 5.8 Dive by dive analysis of all active dives, each point is an individual dive, metabolic rate is expressed as a multiple of Kleiber. **A.** shows the duration of each dive, plotted against the metabolic rate of that dive, grouped by mean swim speed during the dive, **B** shows the mean swim speed of each dive, plotted against metabolic rate, grouped by the distance travelled during the dive and **C** shows distance plotted against mean speed, grouped by metabolic rate.

The plot of dive duration against DMR shows a cloud of points with what seems to be a pronounced curvilinear upper edge (see figure 5.8A). This was suggestive of a physiological limit, perhaps related to oxygen stores, operating as a constraint to dive duration. We examined the hypothesis that this edge was related to oxygen stores and the rate of their use by fitting a line through the points on this upper boundary. To do this we used the quantile regression function in R to fit a line to the 95th and 99th percentile of the y-data. A theoretical physiological limit was modelled by calculating the mass specific maximum rate of metabolism during a dive of a given duration, given the total body oxygen stores available to the animal. For example the oxygen store available to a diving grey seal of 50kg can be estimated as 3 litres (60 ml O₂.kg⁻¹, Kooyman 1989). Therefore for a dive lasting five minutes, the maximum possible rate of oxygen utilisation during that dive is 0.6 l.min⁻¹ or 12ml.min.kg⁻¹. Likewise a seal of 100kg has an estimated oxygen store of 6 litres, corresponding to a maximum rate of 1.2 l.min⁻¹ or similarly 12ml.min.kg⁻¹ for a five-minute dive. The slopes of the two lines could then be compared. Because of the curvilinear appearance of this edge, and the curvilinear nature of the relationship between maximum possible aerobic DMR and dive duration, the y-axis was log₁₀ transformed to provide linear predictors.

The quantile regression yielded a significant negative relationship between maximum log₁₀ DMR and dive duration for 7 out of 8 seals (see appendix 3 for details of individual regressions). Dives from all animals were combined and the edge predicted by quantile regression was compared to the maximum predicted aerobic DMR (figure 5.10). Regressions were carried out using both the 99th and 95th quantiles on pooled data. The line depicting maximum theoretical metabolic rate lies within the confidence limits of the fitted 99th quantile regression line.

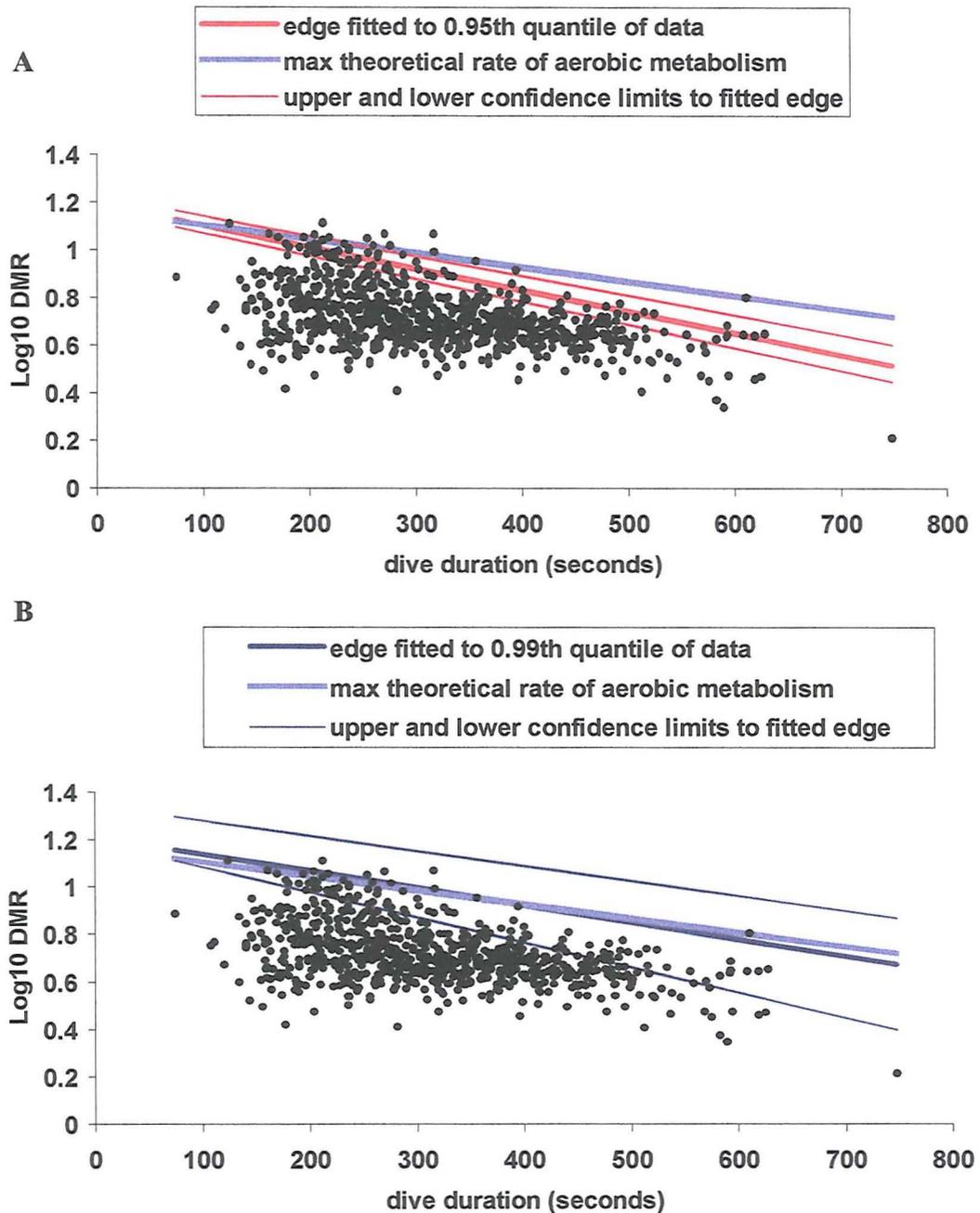


Figure 5.10. Log transformed metabolic rate plotted against dive duration for all dives. Also indicated is the boundary defined by quantile regression (A $\tau=0.95$, B $\tau=0.99$) plus upper and lower confidence limits. The thick line on each plot represents the relationship between maximum possible aerobic logMR and dive duration, based on maximum utilisation of body oxygen stores during the dive.

5.3.4 Predictive model

The complete model is summarised below:

$$DMR (l.min^{-1}) = B_0 - B_1 \text{ mass} + B_2 \text{ sinmonth} + B_3 \text{ dive duration} + B_4 \text{ postdive surface interval} + B_5 \text{ mean speed} + B_6 (\text{mass} * \text{speed})$$

Where $B_0, B_1, B_2, B_3, B_4, B_5$ and B_6 are coefficients. A summary of coefficients, standard errors and significance levels of model predictors is shown in Table 5.5. It is important to note that the inverse link function ($-1/\mu$) of the gamma distribution used to fit the model reverses the sign of the co-efficients (Venables and Ripley 2002).

Table 5.5. (a) Summary of complete predictive model

Predictor	Co-efficient	Standard error of Co-efficient	P
Intercept	4.977	0.1179234	<0.0001
Sinmonth	-0.1605	0.0204335	<0.0001
Mass (kg)	-0.02913	0.0009130	<0.0001
Dive duration (seconds)	0.001744	0.0001394	<0.0001
Post-dive surface interval (seconds)	-0.001068	0.0004882	0.0290
Mean speed (m/s)	-1.938	0.1901924	<0.0001
Speed*mass	-0.01088	0.0016657	<0.0001

Model testing

1. Novel animal

Sections of continuous diving lasting one hour were isolated from the dive records of Nora, an animal who was not included in the model fitting process. Average values for each of the behavioural predictors were calculated for each of the hourly periods. The model was used to calculate the predicted oxygen consumption of Nora during these periods. Predicted oxygen consumption was compared with measured oxygen consumption (figure 5.11). On 4 out of the 7 days where Nora dived continually for 1 hour, measured oxygen consumption fell within the confidence limits of the model's predictions. Predicted rates were on average $0.004 \text{ l}\cdot\text{min}^{-1}$ lower than actual rates, which corresponds to an under-estimate in energy requirement of 1.2 % of actual rates or $3 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$ (based on an energetic equivalent of oxygen of 19.7 kJ per litre of O_2).

2. Novel data from included animals

Predictions of dive-by-dive metabolic rates were compared to actual rates, using 8 dive cycles from Lola (figure 5.12). Differences between actual and predicted rates on a dive-by-dive basis ranged from -0.09 to $+0.17 \text{ l}\cdot\text{min}^{-1}$. Predicted rates were on average $0.01 \text{ l}\cdot\text{min}^{-1}$ lower than actual rates, which corresponds to an under-estimate in energy requirement of 0.8% of actual rates or $1.5 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$.

Sections of continuous diving lasting one hour were isolated from the dive records of Kylie, average values for each of the predictors were calculated for each of the hourly

periods and these were used to estimate metabolic rate over the same period (figure 5.13). Using the complete model, predicted rates were on average $0.008 \text{ l}\cdot\text{min}^{-1}$ higher than actual rates, which corresponds to an over-estimate in energy requirement of 2.3% actual rates or $6.6 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$.

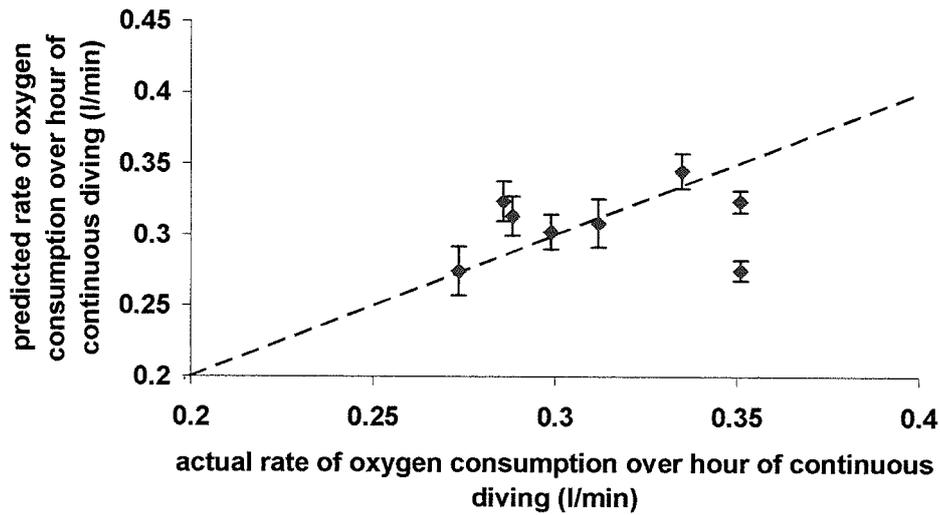


Figure 5.11 Predicted vs. actual rate of oxygen consumption for Nora over 1 hour of continuous diving on 7 separate days (error bars are standard errors of model fits). No data from Nora were used in producing the model. The dashed line represents a 1:1 relationship between predicted and observed oxygen consumption.

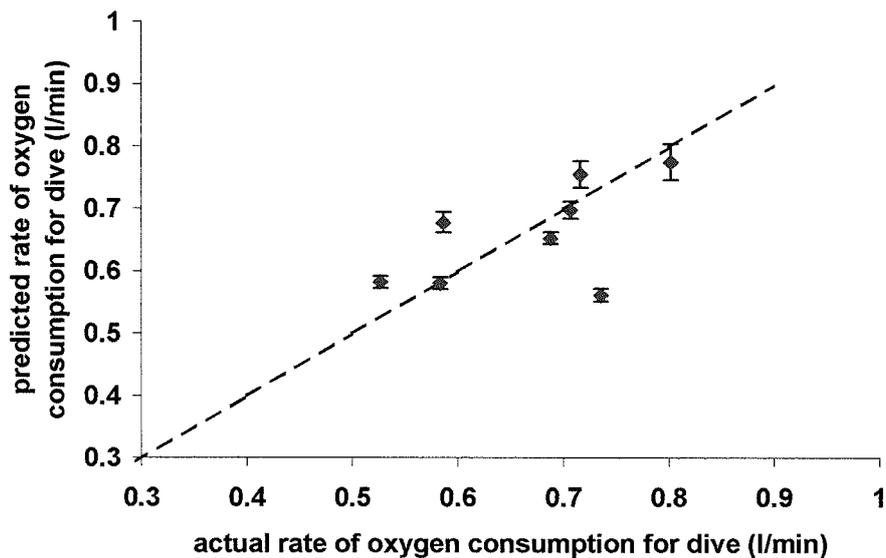


Figure 5.12 Dive by dive predictions of metabolic rate against actual dive-by-dive metabolic rate of Lola for dives that were not included in the model fitting process. Error bars are standard errors of model fits. The dashed line represents a 1:1 relationship between predicted and observed oxygen consumption.

3. Separate models excluding data from one animal

Excluding dives from any one animal from the dataset and refitting the model in R resulted in a set of slightly different models, however the same explanatory variables were significant in each one. The relationship between actual and predicted values across all animals had a slope of 0.995 and an R^2 of 78% (figure 5.14). Predicted oxygen consumption rates across all animals were on average $0.03 \text{ l}\cdot\text{min}^{-1}$ higher than actual rates, which corresponds to an average error in energy requirement of $10.9 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$ or 8% of actual rates.

Model predictions

The predicted metabolic effects of different behavioural strategies were explored by running the model on simulated dive data for a number of scenarios:

1. Increasing dive duration, constant swim speed, mass 50kg (run for a range of speeds from 0.4-2m/s).
2. As above but for animal of mass 100kg.
3. As above but for animal of mass 150kg.

A physiological limit for each scenario was modelled by calculating the maximum possible aerobic metabolic rate for each dive duration as described in the previous section. This maximum rate is shown on fig 5.15 in relation to predicted metabolic rate for a range of speeds.

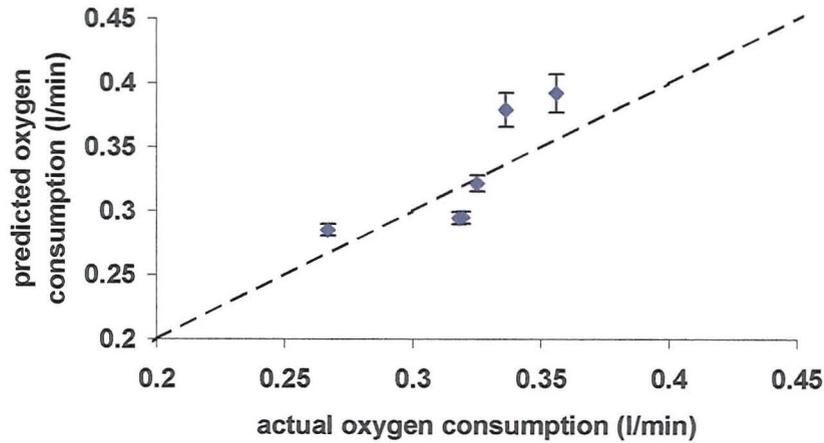


Figure 5.13 Predicted vs actual rate of oxygen consumption for Kylie over 1 hour of continuous diving on 5 separate days (error bars are standard errors of model fits). No data from these days were included in the model. The dashed line represents a 1:1 relationship between predicted and observed oxygen consumption.

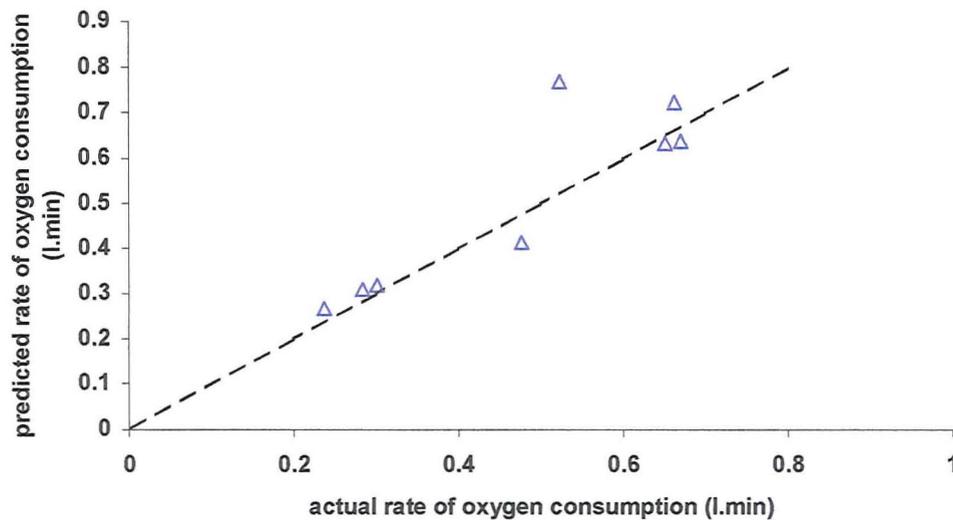


Figure 5.14 Predicted oxygen consumption against actual oxygen consumption. Symbols represent the actual oxygen consumption over all dives for an individual animal plotted against the oxygen consumption over the same dives predicted using the model that excludes data from that animal. The dashed line represents a 1:1 relationship between predicted and observed oxygen consumption.

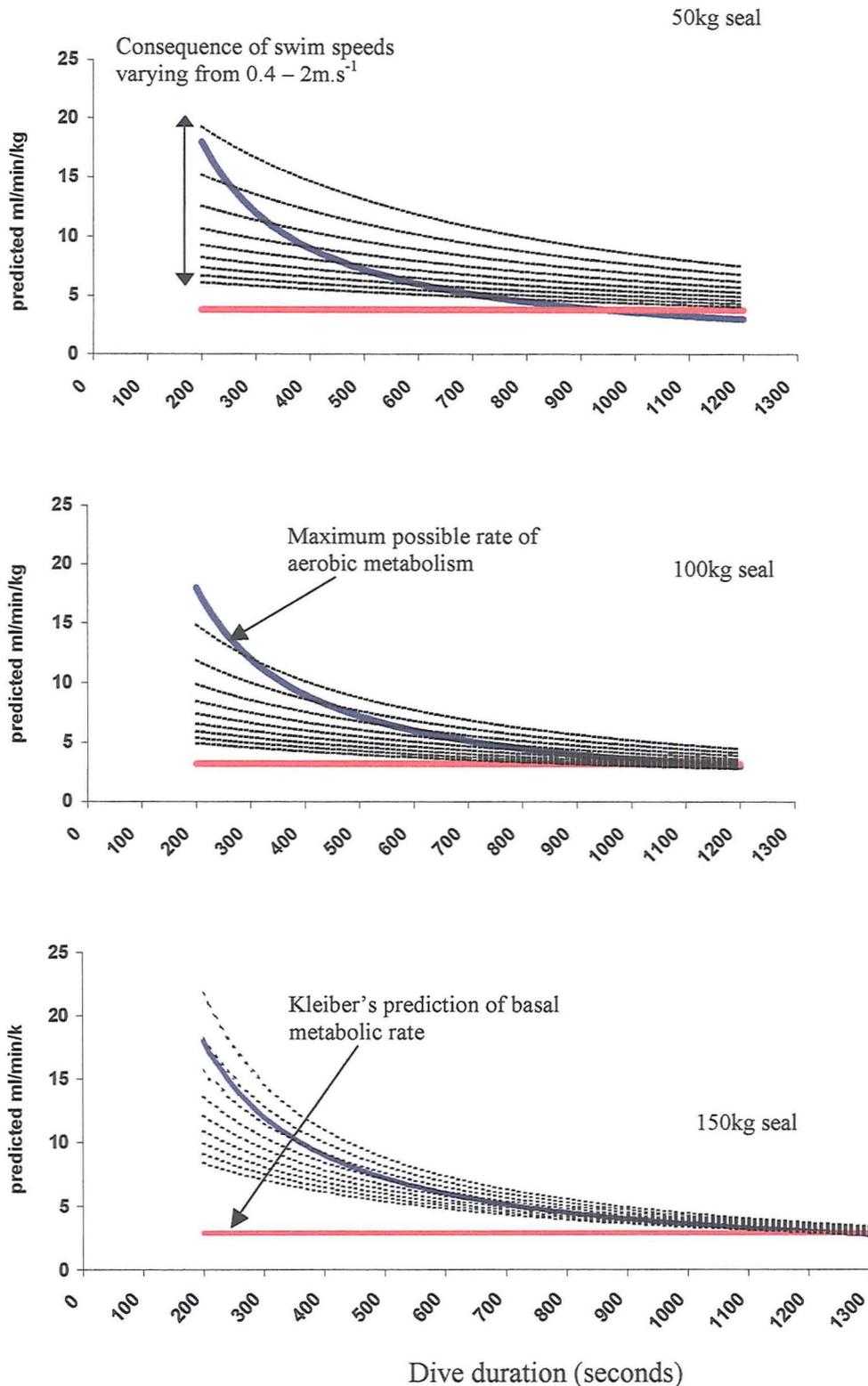


Figure 5.15 Predictions of model given different scenarios. Each plot shows the predicted mass specific DMR for a seal of given mass, against increasing dive duration at different speeds, (dashed lines). Each dashed line represents the relationship between predicted metabolic rate and dive duration for a particular speed. The thick curved line shows the maximum possible rate of metabolism in relation to dive duration (calculated by estimating usable body oxygen stores). The predicted basal metabolic rate is shown by the horizontal line. The range of swim speeds is $0.4-2\text{m}\cdot\text{s}^{-1}$.

5.4 Discussion

The complete cycle of a dive and the subsequent breathing bout can be considered the basic physiological unit in diving seals (Fedak et al. 1988). Metabolic rate measured as an average over this period is estimated easily from gas exchange at the surface.

This rate is likely to exhibit variations directly attributable to variations in behaviour and state on a dive-by-dive basis.

5.4.1. Dive characteristics

The range of behaviour exhibited by the seals in this study is similar to that recorded in wild grey seals using satellite telemetry. Across all animals mean dive duration was 5.3 minutes compared to a mean of 5 minutes calculated from 220000 dives from satellite tagged UK grey seals (figure 5.16; SMRU unpublished data). Mean swim speed from over 3000 dives from 5 grey seals tagged in Orkney and Shetland was $0.42\text{m}\cdot\text{s}^{-1}$ (\pm s.d. 0.24) (Chapter 7, this volume) compared to the average swim speed of dives in this study of $0.32\text{m}\cdot\text{s}^{-1}$ (\pm s.d. 0.25). Although there are likely to be differences in behavioural motivation for performing dives between the seals in this study and freely diving seals in the wild, the physiological processes and consequences are likely to be similar.

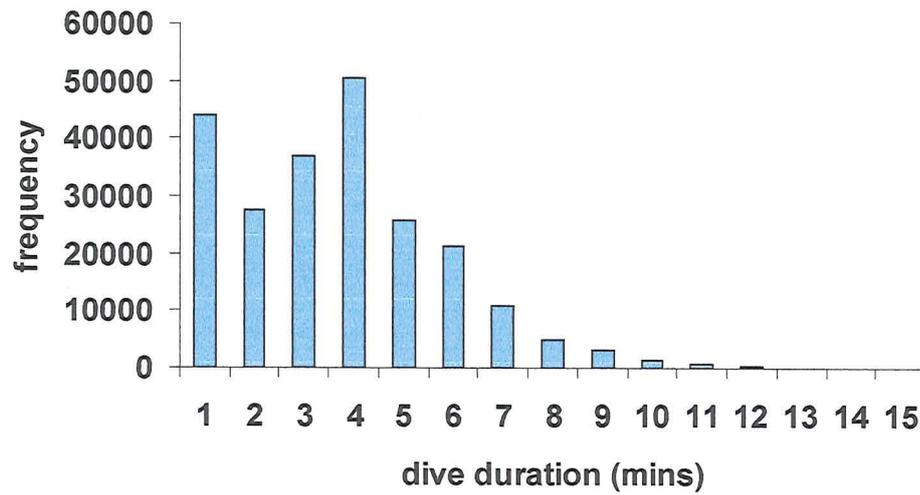


Figure 5.16 frequency distributions of dive durations from satellite tagged UK grey seals (total number of dives > 219000, from 108 seals)

5.4.2 Diving metabolic rate – evidence of hypometabolism?

Mean DMR of all 770 dives in this study was 1.66 K (\pm sd 0.45). This is comparable to 1.6 K in free-living weddell seals diving under ice (Castellini et al. 1992). Given that dive behaviour of the seals in this study was similar to that exhibited by wild seals, we can conclude that ‘natural’ diving behaviour in grey seals is not energetically costly.

80% of all diving metabolic rates, even when seals were active and swimming an average of 100m during dives were lower than resting levels measured in the same seals (Chapter 4, this volume). Kooyman (1989) defined hypometabolism as a rate of metabolism lower than the rate that occurs under the standard conditions of resting in the post-absorptive and normally quiet period of the 24-hr cycle. In this study, diving metabolic rates were lower than those measured under resting conditions, thus providing evidence for hypometabolism during diving in grey seals.

These findings have implications for estimates of food consumption by seal populations. Bioenergetic models of phocid seal populations generally use a multiplier of 2-3 times the Kleiber predicted metabolic rate to estimate the energy requirements associated with at-sea activity in free-living phocid seals (Olesiuk 1993; Mohn and Bowen 1996; Nilssen et al. 2000). If free-living seals spend a significant portion of their time at the lower rates demonstrated in this study, present estimates of energy requirements might be higher than they are in reality. More information is therefore required on the activity budgets and foraging energy requirements of wild seals.

5.4.3. Factors influencing DMR

Mass

Mass had a large effect on diving metabolic rate ($l \cdot \text{min}^{-1}$). This is not surprising since on an individual level, energy associated with maintaining body tissues probably represents the biggest single portion of expenditure and this is obviously higher in absolute terms for larger animals. The relationship between mass and basal metabolic rate is well established between mammalian species in general (Kleiber 1975) and between phocid species in particular (Lavigne et al. 1986). In this study the power exponent of the curve (0.76) was similar to that describing the interspecific relationship between mass and BMR in phocid seals (Lavigne et al. 1986). This allows us to effectively control for mass by expressing metabolic rate as a multiple of the predicted basal rate for an animal of equivalent size (Kleiber 1975). Although on a per kilogram basis pups have a higher DMR than adults, expressed in this way pups had identical metabolic rates to adults (1.66K). Bioenergetic models generally use a higher multiplier of Kleiber's predicted metabolic rate for juveniles than the one used for adults to predict average requirements. This may be a large source of error in such models, especially for populations that are skewed towards juvenile age classes (e.g. Olesiuk 1993).

Season

The month in which measurements were made had a significant effect on the resulting DMR's. When modelled in more detail, the significance of the sine of month term suggested that the biggest differences were between spring and autumn, with DMR's being highest in spring. These changes were independent of body size because the

effect was still evident when we controlled for the effect of mass on metabolic rate by expressing it as a multiple of that predicted by mass^{0.75}. This may be a result of an underlying seasonal physiology related to the timing of the moult and/or reproduction, which may be mediated through changes in body composition or may be a result of changes in hormonal status. There was no seasonality in the dive behaviour exhibited by seals so seasonal changes in DMR are not a result of changing dive behaviour. Seasonal variations in resting rates of metabolism have been reported for harp seals (Renouf and Gales 1994; Hedd et al. 1997), harbour seals (Rosen and Renouf 1995) and previously in grey seals (Boily and Lavigne 1997). Chapter 4 (this volume) reports on seasonal changes in the resting metabolic rates of the animals in this study and the patterns shown are similar. RMR is higher in the spring than in all other times of the year so it is likely that the seasonality in DMR is a reflection of changing resting requirements. These findings are also of significance for bioenergetic modelling. Most attempts to estimate the food consumption of seal populations do not take into account seasonal variations in either basal or activity-related energy requirements (Olesiuk 1993; Boyd et al. 1994; Mohn and Bowen 1996)

Dive duration and swim speed

Plots of DMR as a function of dive duration show that points are scattered below a maximum boundary that decreases curvilinearly with dive duration and above a minimum boundary that is largely independent of dive duration (figure 5.8A). This pattern has also been demonstrated in free-ranging Weddell seals (Castellini et al. 1992) and in previous laboratory studies of grey seals (Reed et al. 1994). The points that form the upper boundary are likely to represent the maximum possible aerobic metabolic rate, a value which is determined by a combination of the dive duration and

the size of the oxygen store available to the animal during that dive. When a line was fitted to this boundary and compared it to the line that resulted from plotting calculated predicted aerobic limits, there was close agreement between the two. The calculations of maximum rate of oxygen consumption assume that all the blood, muscle and oxygen stores are available to the seal. However not all these stores may be universally available within the seal (Reed et al. 1994). DMR fell below this line for the vast majority of these dives, even where dives were highly active, suggesting that the seals were using oxygen-conserving adaptations.

The relationships between dive duration, swimming speed and metabolic rate are not straightforward. When submerged, seals must balance the energetic demands of locomotion with the conservation of a limited oxygen store (Castellini et al. 1985; Skrovan et al. 1999). Swimming activity during a dive influences the rate of oxygen consumption of the actively exercising muscles which in turn sets an aerobic limit to dive duration. Williams et al. (2000) found that dives that consisted of prolonged gliding resulted in lower post-dive oxygen consumption than dives that consisted of continuous swimming. Seals are able to swim at a range of speeds for a range of durations, as long as they remain below the edge. Mean swim speed during the dive had a significant effect on the metabolic rate of a dive, and the dives with the highest swim speeds tended to be the shortest. Hindell et al. (2000) examined the influence of swimming speed on dive duration in free-living southern elephant seals. They show that maximum dive duration is dependent on swimming speed; consequently a seal has a range of different ADL's depending on its activity during the dive. It is clear that exercise performed when submerged requires energy for the working muscles, and this rate of energy usage has implications for the amount of time a seal can remain submerged before having to return to the surface to replenish oxygen stores. This is

somewhat intuitive and has been discussed by many authors (e.g. Kooyman 1989; Hindell et al. 2000) but there have been few empirical studies describing how whole body metabolism varies as a function of variation in pinniped diving activity of the type that is ecologically relevant.

Metabolic rate of grey seals measured in a swim flume displayed a five-fold range with activity ranging from sleep to swimming at $1.6\text{m}\cdot\text{s}^{-1}$ (Fedak et al. 1988).

Furthermore the fraction of time spent submerged decreased as speed increased (Fedak 1986). This pattern was also seen in harbour seals swimming in a flume at speeds over $1.2\text{m}\cdot\text{s}^{-1}$ (Williams et al. 1991). Our seals had metabolic rates that related to between 1 and 4 times predicted basal rates as speeds increased up to a maximum of $1.4\text{m}\cdot\text{s}^{-1}$.

In contrast to the findings of Fedak (1986), we did not observe an increase in the proportion of time spent at the surface when seals were swimming at higher speeds during dives, suggesting that unlike seals swimming in swim flumes, the grey seals in the present study were not reaching levels of exercise where their rate of oxygen utilisation would approach the limit of their rates of gas exchange at the surface, and thus the percentage of the dive cycle spent underwater is not limited by the need to spend more time loading oxygen at the surface. The present study differs from those involving seals swimming in flumes in that any swimming activity is voluntary and occurs as part of a dive. The average swim speed of our seals rarely reached these higher speeds, although the speed reported for each dive is the mean for the whole dive, some dives consist of bursts of fast swimming at speeds over $2\text{m}\cdot\text{s}^{-1}$.

Furthermore seals in a flume are forced to swim just below the surface where drag is much higher than a few metres below, a behaviour that phocid seals do not display in the wild. This will add to the energetic costs for animals in flumes, costs that are not likely to be an issue for free-living, foraging grey seals.

The relationships between swimming speed, duration and metabolic rate found in this study have implications for the interpretation of diving behaviour in wild seals. However a direct extrapolation may be complicated where seals' locomotion is influenced by factors other than active swimming. For example, depth was replicated in the captive facility by the distance that seals could swim away from the breathing box, i.e. depth was translated from a vertical to a horizontal distance. Thus all portions of the dive are within 0.5 and 2.5 metres below the surface, i.e. there is no true ascent or descent phase. However, for a seal foraging in the wild, the interaction between buoyancy and ascent and descent may be of more energetic consequence, especially in a species such as the grey seal that undergoes dramatic seasonal changes in body composition. The speed of movement of a seal through the water may be more a result of buoyancy rather than changes in active propulsion. It could be argued that these changes would cancel each other out in terms of energetic cost i.e. an animal that is positively buoyant will have to swim harder to reach depth but does not have to swim as hard on the way back up to the surface. Conversely a negatively buoyant animal may not have to expend as much energy on descent but may have to expend more energy on the ascent phase of the dive. Distance travelled may not be a good predictor of activity during a dive. Furthermore, buoyant animals also may have to expend considerable energy to remain at depth while foraging in the water column or to maintain position on the bottom for benthic feeding. Beck et al. (2000) suggested that buoyancy significantly affects the rate of descent in grey seals. Similarly (Webb et al. 1998) found a significant inverse relationship between buoyancy and descent rate. The balance of energetic costs related to overcoming buoyancy constraints remains to be addressed. Sato et al. (in press) demonstrated that mode of locomotion during descent in free-living weddell seals was related to body fatness; prolonged gliding while descending was observed in thinner females, but the fatter females exhibited only

swim-and-glide swimming throughout their descent and ascent. The ratio of post-surface time to dive duration was greater in stroke-and-glide swimmers than prolonged gliders, suggesting that prolonged gliding is a more efficient method of locomotion (Sato et al. In press). Relating DMR to stroke frequency or acceleration, rather than mean speed of travel during a dive is a possible avenue for further laboratory studies.

Within the constraints set by physiology, seals can vary their diving patterns to most effectively exploit their environment. This fits with the conceptual framework put forward by Kramer (1988) and developed by Fedak and Thompson (1993), Thompson et al. (1993) and Thompson and Fedak (2001). The diving patterns actually exhibited by seals are likely to be a product of a complex interplay of many interrelated variables. Physiology places an obvious constraint on the behaviour of any mammal that exploits a prey resource underwater but behaviour is also affected by the ecological context of the dive. On an individual dive level the outcome will be particular to a set of circumstances such as prey type, distribution and size. Unravelling these relationships further will require approaches that combine laboratory studies of physiology and behaviour, such as this one, with field observations and further lab studies of a more manipulative nature testing behavioural and physiological responses to differences in prey type and distribution.

5.4.4. Predictive model

The model developed here seems to be a reasonably good predictor of metabolic rate during diving in grey seals. Various tests of the model's capability resulted in errors in predictions ranging from 0.6-2.3%. Across the range of mass in this study, (from juvenile seals of mass 32kg to adults of 150kg) the relationship between predicted and

actual metabolic rate had a slope close to 1. To put these errors into context, predicting rates for the animals in this study by applying a Kleiber multiplier of 2 resulted in over-estimating adult DMR's by 18% and juvenile DMR's by 14%. This latter approach, while useful where data are lacking on the real energetic costs of foraging in the species' concerned, does not allow us to examine variation in requirements as a result of variations in activity/diving type etc. Our model predicted the metabolic rate of seals in captivity, with relatively little error, based on their behaviour. Therefore given that behaviour between our seals and wild seals was not arguably different, we can conclude that applying the model to telemetry derived behavioural data from wild seals would allow us to predict the metabolic costs of dives of different types exhibited in the wild with increased accuracy over the use of a simple multiplier applied over all at-sea behaviour. In addition to exploring the energetic consequences of variations in behavioural strategies, we can then use these predictions as the basis for predicting the energy requirements of the population. There is no method that can be easily used in wild grey seals to measure energy expenditure directly, so direct evaluation of this modelling approach is not possible. However further studies testing the predictions of the model can be carried out using captive seals diving in different circumstances. Given that season was a significant predictor of DMR ($l \cdot \text{min}^{-1}$) it is difficult to see what the applicability of this model would be for other phocid species. More information is required on the general nature of this seasonal effect.

Our model also allows us to explore the physiological consequences of different behavioural options, interpolating to behavioural strategies that were not exhibited by the seals here but may be exhibited by wild seals. For example, figure 5.15 shows an exploration of the effect of varying speeds and durations. From this we can calculate the likely maximum duration for any given speed or mass of animal and compare the

predictions of the model with dive behaviour in the wild (figure 5.17). We have demonstrated that ADL can range, for example, between less than 2 minutes up to 20 minutes for a 150kg animal depending on the activity during the dive. Our model would predict that a dive occurring above the line in figure 5.17 by a wild grey seal must be a result of either metabolic depression to a greater extent than any shown by our seals, or anaerobic metabolism. The results here stress that the behaviour exhibited during the dive must be taken into consideration when interpreting dive durations from wild seals.

Conclusion

The data presented here provide new insights into the relationships between behaviour and energy requirements during natural diving behaviour in the grey seal, and indeed in phocid seals in general. Diving behaviour, similar to that exhibited by wild grey seals, has a low energetic cost, lower than resting costs measured in the same individuals. This study has also demonstrated that in the grey seal oxygen stores provide a real limit to dive duration, and animals can effectively increase the time spent below by reducing the rate at which they use these stores. Furthermore the model we have developed provides us, for the first time, with a means to reliably predict the energy requirements of grey seals at sea given knowledge of their dive behaviour, and provides a context in which to interpret the behaviour of freely diving seals.

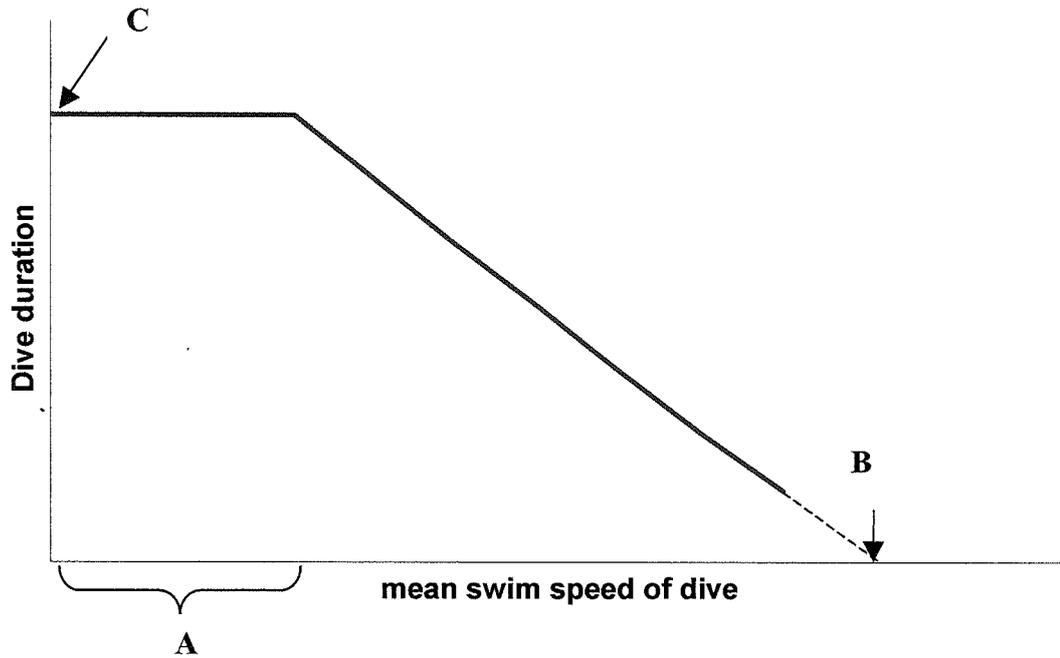


Figure 5.16 Predicted theoretical relationship between swim speed and dive duration.

The area below the line represents the possible combinations of speed and dive duration predicted by the model if seals are metabolising aerobically. **A** represents the range of speeds a seal can swim at during a dive where DMR predicted by the model is between predicted BMR and the maximum theoretical rate of oxygen consumption. **B** represents the maximum swim speed that can occur during aerobic diving. **C** is the calculated maximum possible ADL based on predicted BMR (Klieber 1975) and total oxygen stores available to the seal, for a dive to occur above **C**, metabolic rate would have to be lower than predicted BMR.

Chapter 6

The effect of feeding on diving metabolic rate

6.1 Introduction

As was reviewed in Chapter 1, feeding causes an increase in metabolic rate. This increase will be referred to here as HIF. HIF has been investigated extensively in terrestrial mammals (Kleiber 1975; Webster 1983) but HIF has been measured in only a few marine mammal species. These include sea otters (Costa and Kooyman 1984), harp seals (Gallivan and Ronald 1981), harbour seals (Markussen et al. 1994) and Steller sea lions (Rosen and Trites 1997). When harbour seals were fed herring, metabolic rate increased within 30 minutes of feeding, maximal increase was up to 1.7 times the postabsorptive rate depending on amount of energy intake. Metabolic rate also remained elevated above baseline values in this species for up to 12 hours (Markussen et al. 1994). Rosen and Trites (1997) demonstrated an increase in metabolism of 2.13 times baseline levels after Steller sea lions had been fed 4kg of herring and an increase of 1.76 times baseline after a 2kg meal. The effects peaked at 3.7 hours after feeding for the larger meal and 2.8hr for the smaller meal.

These studies show that the increase in metabolic rate after feeding in seals can be quite considerable. If this effect is similar in wild animals then an increase in metabolic rate may occur during extended periods of foraging diving. An increase in metabolism of this magnitude during diving will have a significant effect on the amount of time a seal can stay submerged.

Delaying digestion, and thus delaying the costs associated with it, has been suggested as a mechanism whereby animals reduce overall metabolic rate during diving. Previous studies have shown that blood flow is markedly reduced to the

intestines during forced dives in Weddell seals (Zapol et al. 1979). Crocker et al. (1997) suggested a trade off between the metabolic demands of maintaining the gastro intestinal tract and processing food and locomotion during diving. Rather than try to meet demands of both, they suggested that northern elephant seals may reduce locomotor costs by drifting when increased energy is needed for processing food. Handrich et al. (1997) suggested that the decreased abdominal temperatures of foraging king penguins may be a result of a local metabolic depression, associated with a slowing down of digestion, which may serve to reduce the penguins' own energy expenditure during foraging and to accumulate food in their stomach for their chicks. Changes in diving behaviour (e.g. decreased dive durations, reduced activity) of a satellite tagged female southern elephant seal towards the last phase of the tracking period led Fedak et al. (1994) to suggest that the seal's aerobic dive limit was reduced during this phase as a result of the additional cost of HIF.

Diving in phocid seals is associated with a relatively low energetic cost, dive times can be extended beyond predicted limits by a strategy of metabolic suppression (Hindell et al. 1992; Reed et al. 1994; Chapter 5, this volume). However the cost of feeding over and above diving costs may serve to elevate metabolic rate during foraging dives thus having implications for calculations of the aerobic dive limit and the reconciliation of field observations with predictions of foraging theory.

Conversely the costs of digestion may be deferred until after a feeding episode in order for the diver to maximise net energy gain.

Here preliminary data are examined to determine if there is any evidence that the HIF is defrayed until after a feeding episode in grey seals in an artificial foraging

situation. Concurrent experiments on the behavioural response of grey seals diving to artificial 'patches' of varying prey densities provided an opportunity to measure the diving metabolic rate of female grey seals during periods of simulated foraging. Specifically the objective of the study was to determine if there are differences in oxygen consumption between fasting, feeding and postfeeding states, and if there are can they be explained solely by differences in behaviour or are they a result of an increased metabolism due to feeding?

6.2 Methods

Two animals were used in this study, an adult female grey seal (Lola) and one female pup in her first year (Kylie). Metabolism was measured during three distinct states: fasting (post-absorptive), feeding and postfeeding. These measurements were made during experiments for another study (Georges et al. unpublished data) on foraging behaviour. These experiments were designed to measure the response of seals to prey patches of different densities and at different depths. The same covered pool and breathing box set-up was used as described in chapter 3. In addition, an automatic feeder (Figure 6.1) which consisted of a motorised belt, in which fish could be delivered to the seals under the surface at varying densities. This feeder was placed at varying distances away from the breathing box to simulate patch depth.

The seals' fasting metabolism was measured in the morning and the feeding experiments started in the afternoon. During the feeding experiments the seals swam from the breathing box to the automatic feeder 40, 80 or 120metres away. Once at the feeder they fed on sandeels (Lola, 5kg per day) or herring tails (Kylie, 2.5kg per day) at different prey densities. Intake per dive varied and depended on the randomly selected prey density they were presented with, although the total mass of food consumed throughout the whole feeding period was constant for each animal between days. Metabolism was then measured for 2 hours after the end of the feeding period. Oxygen consumption was measured using the method outlined in chapter 3, and dive-by-dive metabolic rates calculated as outlined in chapter 5. The

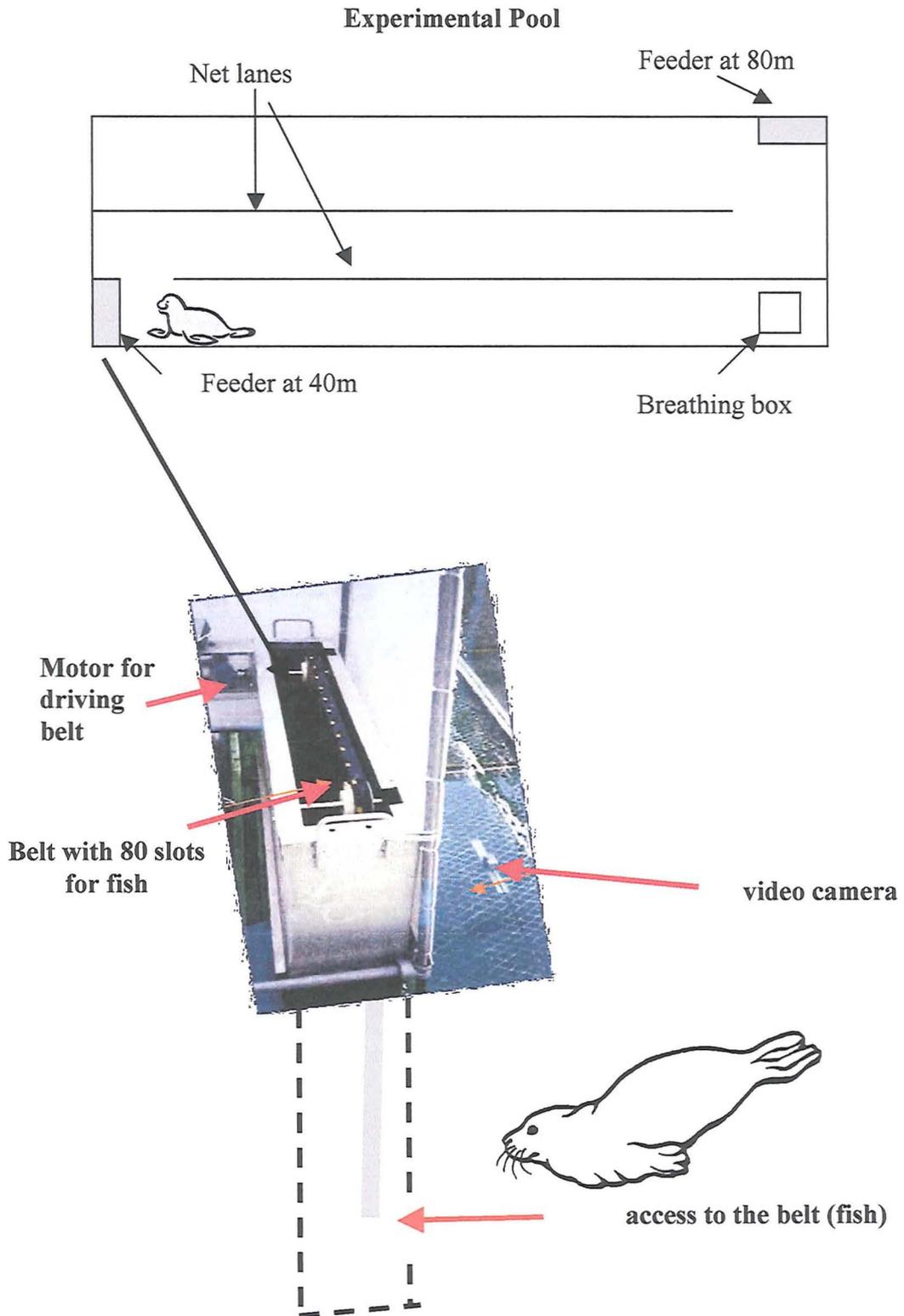


Figure 6.1 Feeding experiments – seals swam from the breathing box to the automatic feeder, which was either 40 or 80 metres from the ‘surface’.

experiment was carried out over 4 days in April, May and June for both animals and additionally in March for Lola. In June Lola's feeding period did not involve any manipulation of food density and her entire 5kg ration was fed over 2 dives on each day. Her metabolism was then measured for six hours after the feeding episode ended.

Metabolism between the 3 periods was compared in a number of ways. Initially overall metabolic rate for the entire period was calculated, and the resulting values compared between the three states. Secondly, dive-by-dive metabolic rates were calculated within each period for individual dives. It was clear that there were significant differences in behaviour between the three states so in order to control for differences in behaviour two different approaches were employed:

1. Principal components and cluster analysis was carried out to characterise dives of similar behaviour. This way, the metabolic rate of behaviourally similar dives could be compared between feeding states. Dives were classified into types according to dive duration, surface duration, distance travelled, average swim speed of entire dive, percentage of dive spent swimming and mean active swimming speed.
2. The predicted metabolic rates of dives from each period were calculated using the model presented in chapter 5, based on behaviour during the dive, these predicted rates were compared with the actual rates of these dives.

6.3 Results

6.3.1 Overall changes in metabolism between the three feeding states

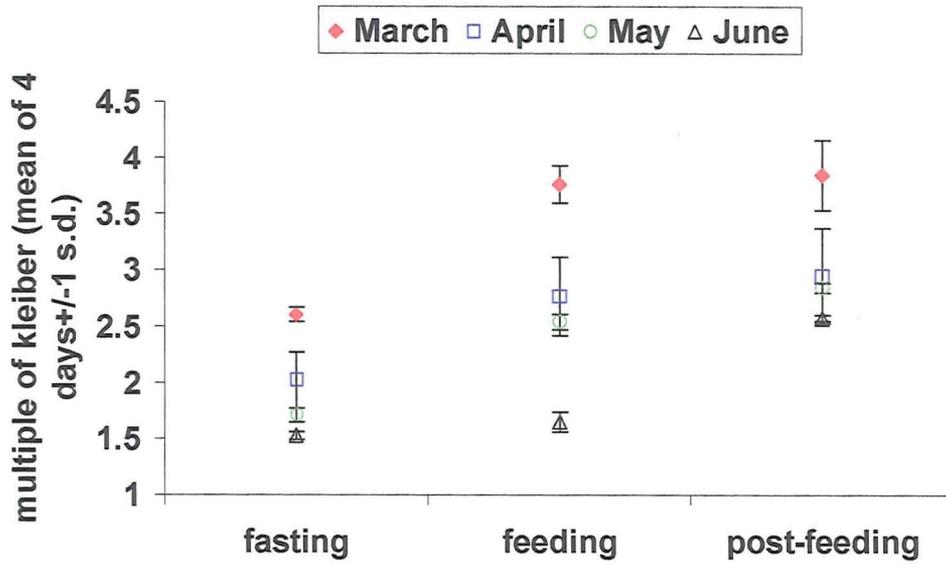
Preliminary analysis indicated that for the adult seal, Lola, there were differences between the three states (figure 6.2) and that there were also differences between months. Analysis of Variance (ANOVA) on these data indicated a significant effect of feeding state ($F=12.222$, $df=2$, $p<0.001$) and month ($F=7.748$, $df=3$, $p=0.002$) on metabolic rate, but no significant interaction ($F=0.160$, $df=4$, $p=0.957$). Sample sizes were too low for post-hoc comparisons. Kylie also exhibited significant differences in metabolism between the different feeding states ($F=42.856$, $df=2$, $p<0.001$), although there was no significant effect of month ($F=0.409$, $df=2$, $P=0.669$).

6.3.2 Comparison of dive-by-dive metabolic rates between behaviourally similar dives from different feeding states

i) Lola

Because of differences in the position of the feeder and because of seasonal variation in metabolism, dives from each month had to be analysed separately. There is considerable variation between months in the number of dive types identified by the PCA analysis, and also variation between the distributions of these dive types among the three feeding states. The results from each month individually are included appendix 4. However, as an example, figure 6.3 displays the behavioural characteristics of the dive types identified in March, and figure 6.4 shows the distribution of these dive types among feeding states. Dives classified as type 1 can

A. Lola



B. Kylie

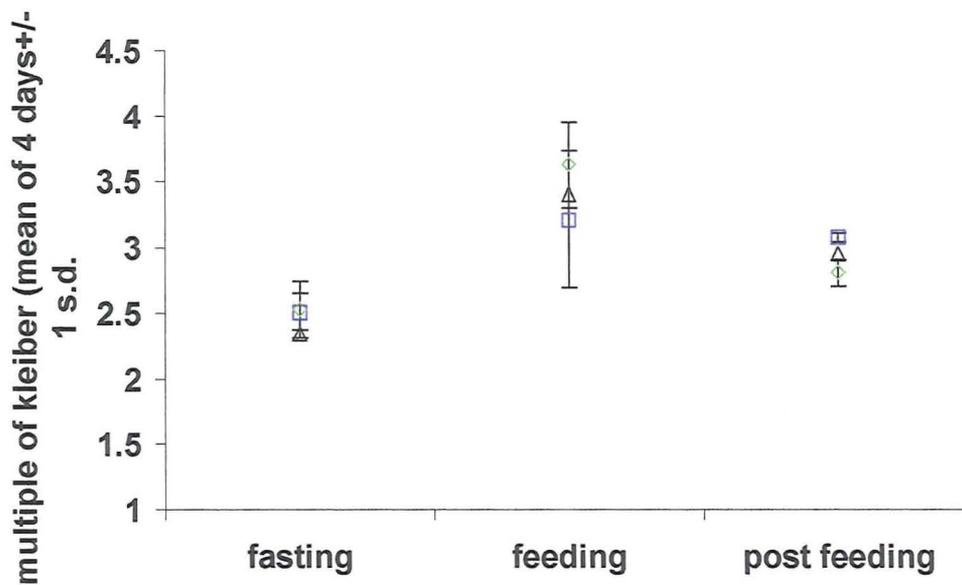


Figure 6.2. Total metabolic rate over the three feeding states by month. Metabolic rate is measured over the whole feeding state and is expressed as a multiple of the predicted BMR (Kleiber 1975).

be interpreted as 'feeder' dives, which consist of the seal swimming quickly and directly to the feeder 40 metres away from the breathing box, remaining there for most of the dive, before returning directly to the breathing box. Dives classified as type 2 can be described as 'exploratory', they are highly active, with the seals swimming for on average 90% of the dive, travelling on average 230 metres during the dive. Dives classified as type 3 can be interpreted as 'resting' dives, which consist of very little activity. 'Feeder' dives were identified in all 4 months, but the behavioural characteristics of the other types identified varied between months (see appendix 4).

Within each month, where there were 3 or more dives in two different feeding states for a particular dive type, DMR's were compared using Mann-Whitney tests. A summary of this analysis is shown in table 6.1. Where there were enough dives to compare between feeding state, there was always a significant difference between fasting and feeding dives of the same behavioural type, and between fasting and post-feeding dives, with fasting dives always having the lower DMR of the two. Sample sizes were not large enough in any month to allow a comparison between dives from feeding and fasting states. On average across all months and dive types feeding DMR was 1.55 times fasting DMR, post-feeding DMR was 1.57 times fasting DMR and 1.09 times feeding DMR.

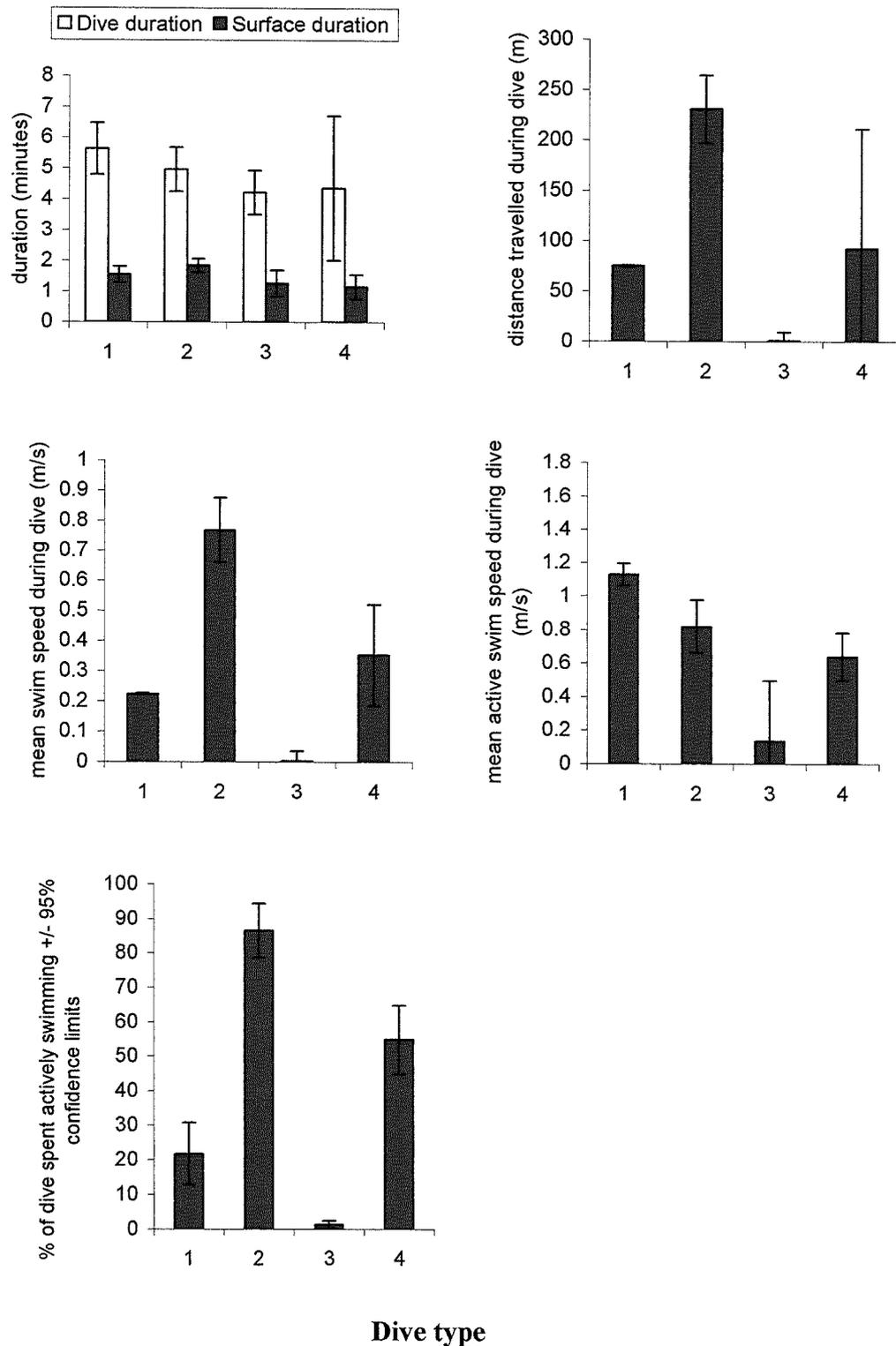


Figure 6.3. Dive classification of all Lola's dives in March, important characteristics of each dive type. Except where otherwise stated values are means of all dives in that category ± 1 s.d.

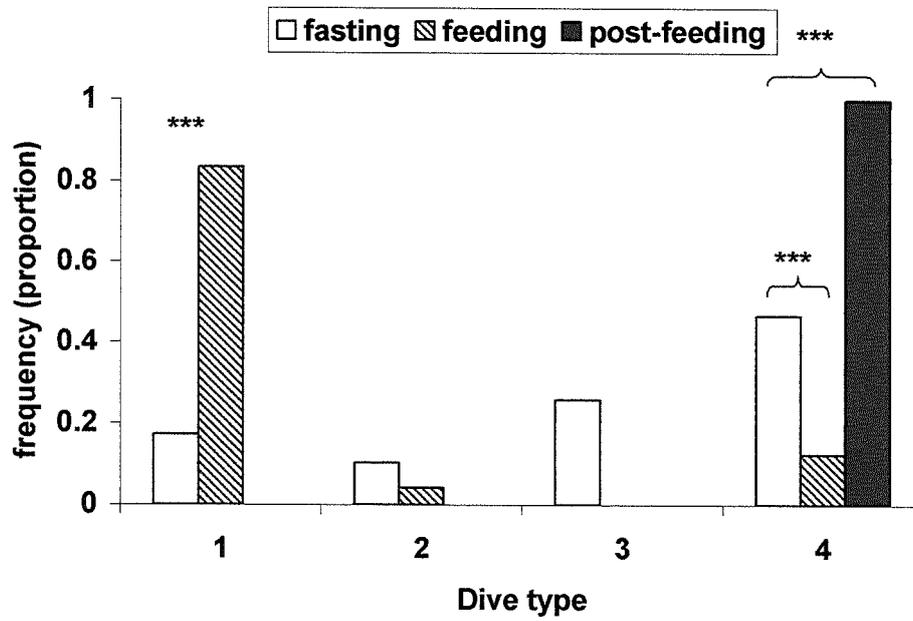


Figure 6.4 Distribution of dive types among feeding states for Lola in March. ** denotes there was a significant difference between the metabolic rate of feeding dives or post-feeding dives compared to fasting dives of the same dive type at $p < 0.001$ (see table 6.1).

month	Dive type	Fasting DMR (Kleiber)	Feeding DMR (Kleiber)	Post-feeding DMR (Kleiber)
March	1	2.14 ±0.25 (10)	3.52 ±0.45 (20)***	-
	2	2.38 ±0.26 (6)	3.24 (1)	-
	3	2.22 ±0.26 (15)	-	-
	4	2.11 ±0.30 (6)	3.06 ±0.33 (3)***	2.99 ±0.24 (3)***
April	1	1.36 ±0.18 (7)	3.01 ±0.19 (21)***	-
	2	1.54 ±0.48 (18)	-	2.20 ±0.67 (13)***
	3	1.51 ±0.19 (8)	2.11 ±0.42 (2)	2.53 ±0.65 (11)***
May	1	1.38 ±0.11 (29)	-	2.38 (1)
	2	1.59 ±0.22 (10)	-	2.19 (1)
	3	1.60 ±0.13 (29)	2.67 (1)	-
	4	-	2.22 ±0.23 (13)	-
	5	1.75 ±0.28 (15)	2.44 ±0.14 (5)**	-
June	1	1.44 ±0.17 (48)	1.67 ±0.19 (4)*	-
	2	1.34 ±0.24 (19)	-	2.37 ±0.04 (7)***
	3	1.50 ±0.14 (13)	-	2.52 ±0.19 (34)***
	4	1.67 ±0.15 (8)	-	2.75 ±0.19 (20)***

Table 6.1 Summary of comparison of behaviourally similar dives across feeding states. Values are mean DMR(kleiber) ±1 sd. Sample sizes are in brackets. Bold type indicates where feeding and post-feeding DMR was significantly different from fasting DMR.

ii) Kylie

Because there was no seasonal effect dives from all months were pooled. The PCA analysis identified 5 dive types (figure 6.5). Feeding dives appeared to have higher MR's than both fasting and post-feeding dives within the same behavioural type. However the distribution of these dive types throughout the three feeding states was such that no statistical comparison could be made between dives of the same type within the same feeding state (figure 6.6 and table 6.2).

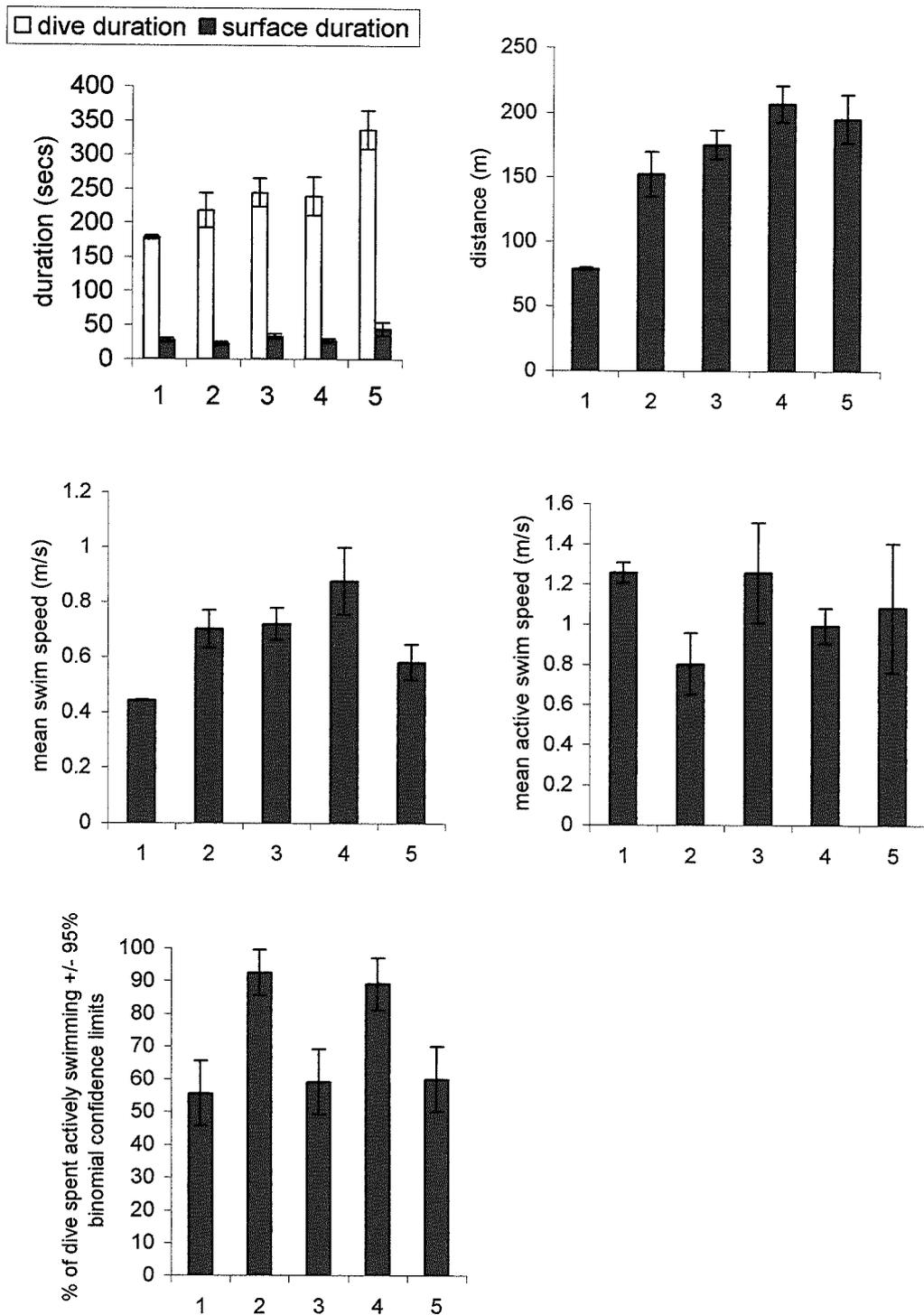


Figure 6.5 Dive classification of all Kylie's dives, important characteristics of each dive type. Except where otherwise stated values are means of all dives in that category ± 1 s.d.

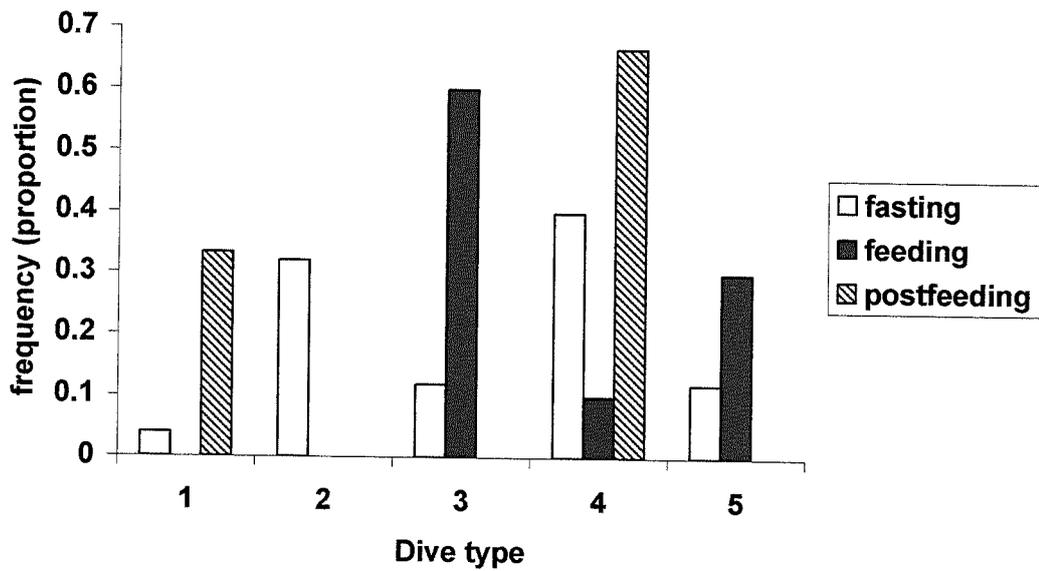


Figure 6.6 Distribution of dive types among the three feeding states for Kylie

Dive type	Fasting	Feeding	Post-feeding
1	2.43 (1)	-	2.50 (1)
2	2.12 \pm 0.30 (8)	-	-
3	2.50 \pm 0.17 (3)	3.05 \pm 0.29 (6)	-
4	2.29 \pm 0.15 (10)	3.21 (1)	2.56 \pm 0.29(2)
5	2.41 \pm 0.33 (3)	2.69 \pm 0.27 (3)	-

Table 6.2. Summary of comparison of the metabolic rate (multiple of Kleiber) of behaviourally similar dives across different feeding states. Values are mean DMR(Kleiber) \pm s.d., sample sizes are in brackets.

6.3.3 Comparisons with model predictions of dive-by-dive metabolic rates

i) Lola

Actual dive-by-dive DMR's during feeding periods were significantly higher than DMR's predicted using the behavioural predictors in the model presented in the previous chapter (figure 6.7, paired t-test $t = 14.052$, $df=69$, $p<0.0001$). The same was found for post-feeding dives (paired $t = 17.975$, $df=84$, $p<0.0001$). On average feeding and post-feeding dives had DMR's of 1.7 and 1.35 and times predicted rates respectively. Predicted rates for fasting dives measured during the same periods were not significantly different from measured rates (paired $t = 0.505$, $df=276$, $p=0.614$).

ii) Kylie

As was the case with Lola, actual dive-by-dive DMR during feeding periods was always higher than the predicted DMR for that dive (figure 6.8). On average, actual rates during feeding were 1.39 times the predicted rates. This difference was significant (paired t-test $t = 10.123$, $df=9$, $p<0.0001$). Predicted and actual rates for fasting dives measured on the same days were not significantly different (paired $t = -1.830$, $df=40$, $p=0.075$). DMR during post-feeding dives were higher than predicted rates but this difference was not significant, however only 3 post-feeding dives had a dive-by-dive measure of metabolism ($t = 2.182$, $df=2$, $p=0.161$).

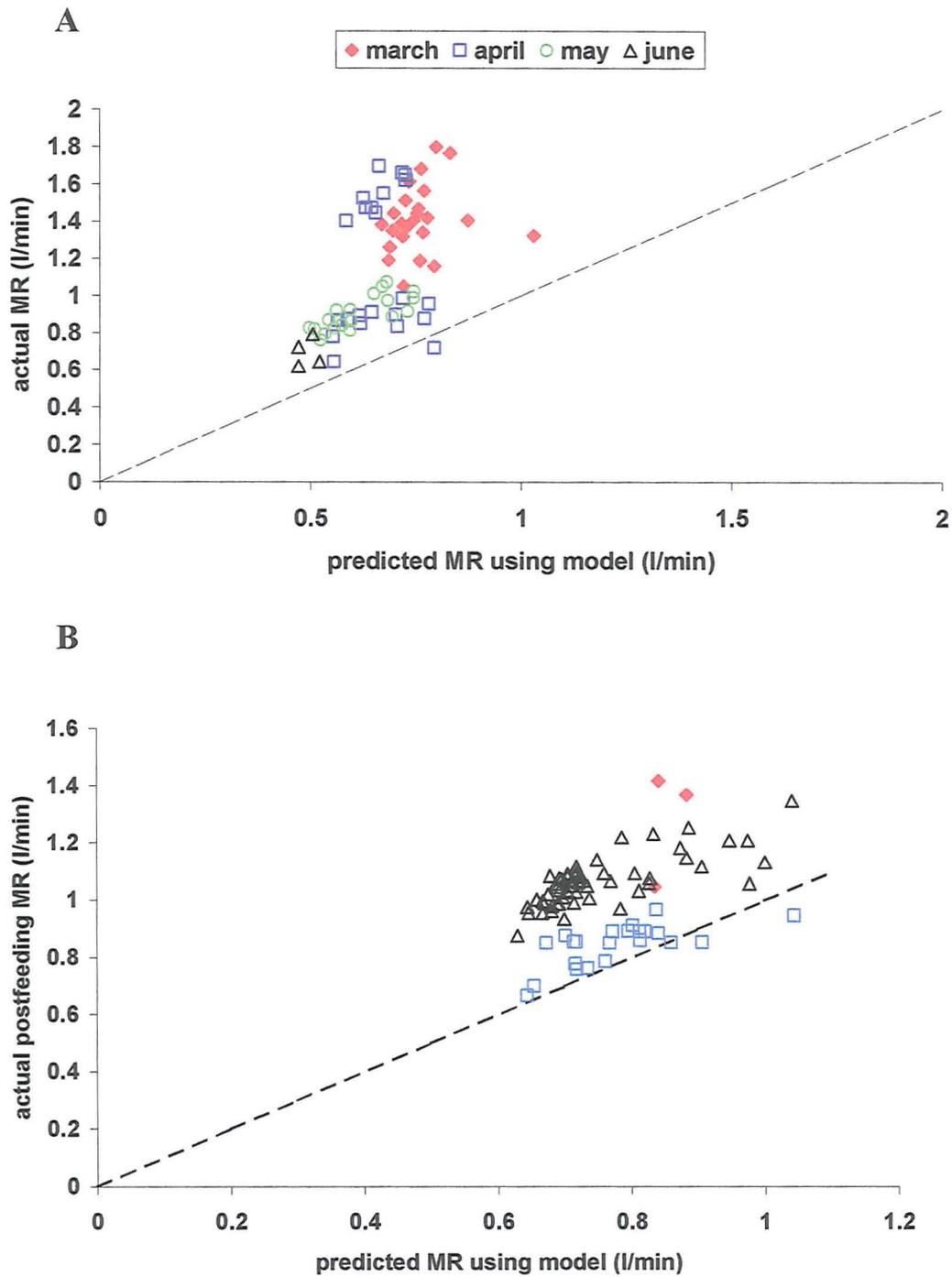


Figure 6.7 Comparison of actual dive-by-dive metabolic rates for Lola's dives against the rate predicted by model. **A.** shows all feeding dives, **B.** shows all post-feeding dives. The dashed line depicts a 1:1 relationship between predicted and actual rates.

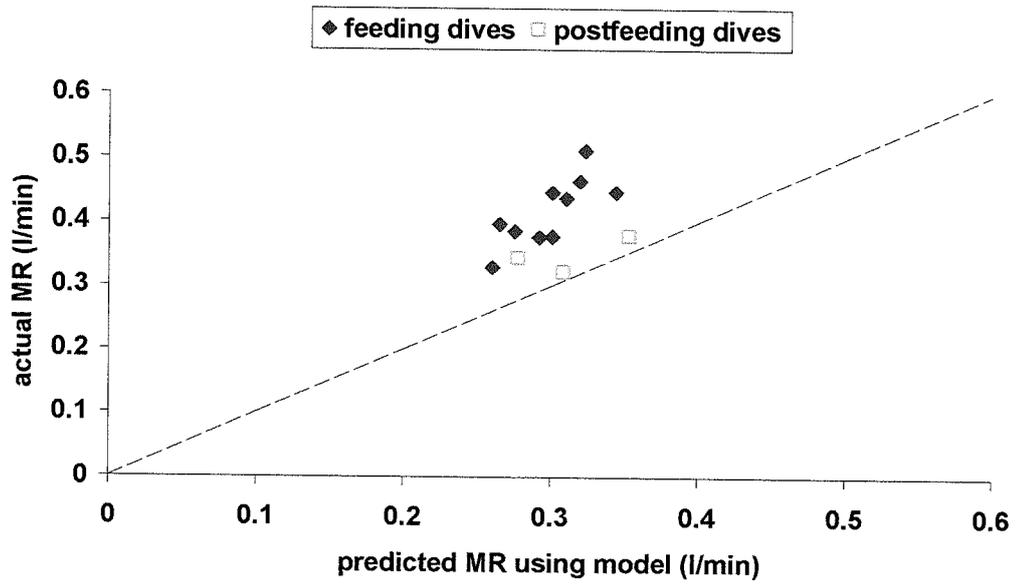


Figure 6.8 Comparison of actual dive-by-dive metabolic rates for Kylie's dives during the different feeding states against the rate predicted by model. The dashed line depicts a 1:1 relationship

6.3.4 Duration of the heat increment of feeding

Dive by dive metabolic rates against time since feeding are shown for Lola (June) in figure 6.9. These post-feeding dives have significantly higher DMR's than those predicted by the model. Predicted rates show a weak but significant decline with time since feeding ($R^2=0.08$, $p=0.021$). Because of this, the difference between predicted and actual rates was plotted against time since feeding (figure 6.10). There was a significant increase in the difference between predicted and actual rates with time ($R^2=0.34$, $p<0.0001$).

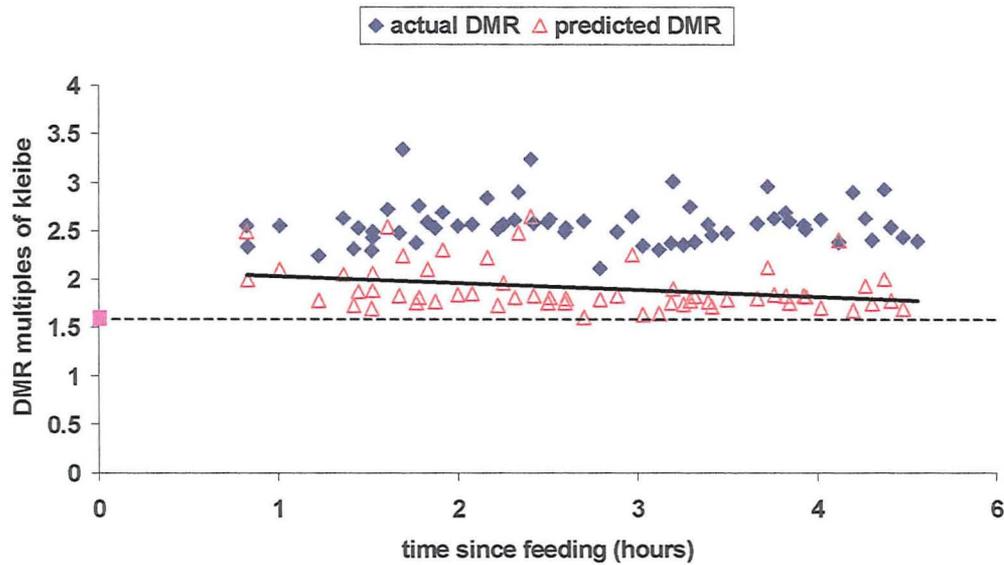


Figure 6.9. Actual and predicted dive-by-dive metabolic rates of Lola in June during the post-feeding period, where she had received 5 kg over 2 dives each day and oxygen consumption was measured for 6 hours of post-feeding diving. The dashed line represents the mean of all fasting dives over the same 4 days of measurement. The solid line represents the line fit by linear least squares regression, the resulting equation is $y = 2.1 - 1.4x$ ($R^2=0.08$, $p=0.021$).

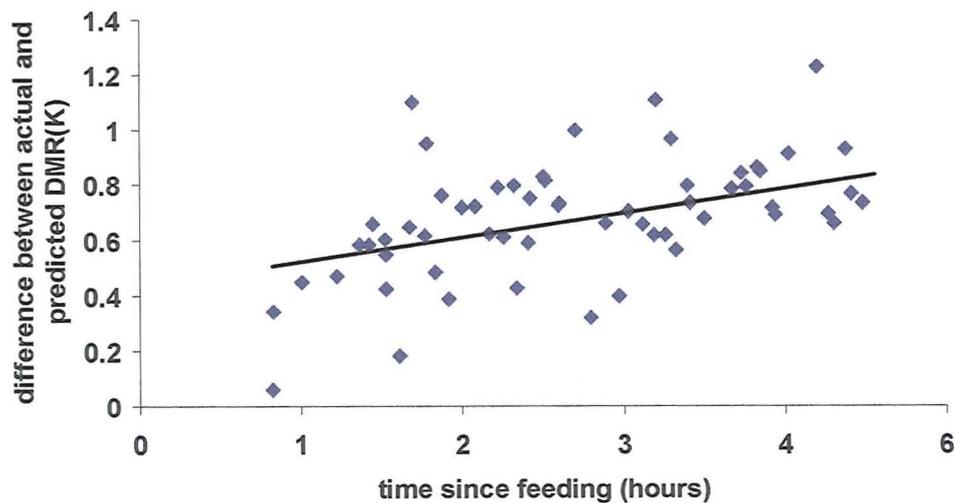


Figure 6.10 Difference between predicted and actual dive-by-dive metabolic rates over time of Lola in June during the post-feeding period. The line is the line fitted by least squares regression, the resulting equation is $y = 1.8x + 0.43$ ($R^2=0.34$, $p<0.0001$).

6.4 Discussion

The results presented here are based on a small sample of only two animals and the experiments were not designed with this type of analysis in mind. Therefore some care must be taken in interpreting these results. However this preliminary study has raised some interesting questions. Overall differences in metabolism between fasted and feeding or post-feeding states are not explained by differences in behaviour, therefore in this setting at least, HIF presents an additional energetic cost during feeding dives. Both approaches used to control for the effect of behaviour yielded similar results. Either comparing the metabolic rates of dives which were similar behaviourally but from different feeding states, or by using the DMR model to predict what the metabolism of a feeding or post-feeding dive would have been had it taken place while the animal was post-absorptive, then comparing that prediction to the actual measured rate. This latter method is simpler and less time consuming than the former. A further justification for using this method is that our DMR model successfully predicted the metabolic rates of the dives that took place during the pre-feeding (postabsorptive) period (chapter 5, this volume).

Even though there was variation in the amount and the timescale over which the animals were fed, the average extent of the increase in metabolism was consistent across months within each animal. Differences in experimental conditions makes direct comparison with other studies of marine mammals difficult. However despite this, the estimated HIF for the two grey seals in this study is within the range of those for other marine mammal species (table 6.3). The increase in DMR of the adult seal after eating 5kg of sandeels of 1.55 – 1.7 times pre-feeding levels is higher than the 1.3-1.4 times baseline in harbour seals fed on 0.8 – 2.65kg herring (Markussen et

al. 1994). However the value for our juvenile seal fed 2kg of herring lies within this range (1.39 times postabsorptive). In comparison harp seals fed on varying amounts of herring experienced increased metabolic rates 1.4 to 1.67 times baseline (Gallivan and Ronald, 1981). The energy content of the food was not measured in this study so comparisons cannot be made in terms of HIF as a percentage of GE. The effect of HIF in other seal species is long lasting. Metabolic rate stayed elevated above resting rates for as much as 15 hours after feeding in harbour seals (Markussen et al. 1994), and 8-10 hours in Steller sea lions (Rosen and Trites, 1997). The effect in Lola, our adult female lasted at least six hours post-feeding and showed no signs of decreasing. Clearly further experiments are needed to determine how long the effect lasts in grey seals.

Most studies of HIF in marine mammals have measured the increase in metabolism after a meal while animals are at rest. The effect of exercise on HIF is uncertain, some authors have indicated that HIF is potentiated by exercise in lean but not obese women (Segal and Gutin 1983) whereas Belko et al. (1986) reported that exercise did not affect HIF in either lean or obese humans. Markussen et al. (1994) assumed that the same relationship between metabolic rate and swimming speed exists for post-prandial and postabsorptive states. The seals in this study were actively exercising, swimming to the automatic feeder, which was between 40 and 80 metres away from the breathing box. In two out of three months for which data are available the biggest differences between fasting and non-fasting states occurred for those dive types that were higher in activity. Clearly further experiments are necessary to determine any effect of swimming on the HIF in seals.

Species	Food Source	HIF (%GE)	VO ₂ (as a multiple of postabsorptive MR)	N
*Grey seal	2kg herring	-	1.39	1
	5kg sandeel	-	1.58	1
Steller sea lion	2kg herring	9.9	1.76	6
	4kg herring	12.4	2.13	6
Northern elephant seal	2kg herring	9.1	1.46	4
	4kg herring	11.4	1.65	4
	2kg capelin	11.5	-	3
	4kg capelin	13.0	-	3
Sea otter	squid	13.2	-	3
	clam	10	1.54	3
Harp seal	1kg herring	16.82	1.40	1
	2kg herring	15.74	1.67	1
	3kg herring	-	1.64	1
Ring seal	Unknown	-	1.80-2.00	2
Harbour seal	Low energy herring	9.0	1.4	3
	High energy herring	5.1	1.31	4
	1.8kg herring	4.7	1.90	3

Table 6.3 Estimates of the heat increment of feeding (HIF) for 7 species of marine mammals. Adapted from Rosen and Trites (1997). HIF is expressed as a percent of the gross energy intake and as metabolic rate (oxygen consumption) as a multiple of baseline postabsorptive rates. The number of animals used in each study (N) is also given. *This study.

HIF is often an important component of bioenergetic models; thus errors in estimation of HIF will directly affect estimates of the food consumed by marine mammals. Most previous studies of marine mammals have measured HIF in air. The combination of diving and activity while feeding in this study provides a more ecologically relevant situation. The energy generated from HIF is not necessarily lost to the individual. The heat can be useful when retained by the animal when

below their thermoneutral zone. Thereby decreasing the energy the animals need to generate to maintain heterothermy. Sea otters use heat generated from HIF to offset thermoregulatory costs when water temperature is low (Costa and Kooyman 1984). The experiments here were all carried out in the spring and summer months so thermoregulatory pressure was probably not significant for our grey seals.

Air breathing divers are faced with a trade off between obtaining oxygen at the surface and exploiting a food resource underwater. Optimal foraging theory predicts they should evolve a variety of characteristics that enable them to minimize energy expenditure and to maximize energy gain while searching for prey underwater. According to these theories, divers should adopt strategies that maximise the proportion of time spent at the foraging site by minimising the proportion of time spent travelling and/or recovering (Kramer 1988; Houston and Carbone 1992). Although decisions on when to return to the surface may be influenced by other factors, they are ultimately constrained by oxygen balance.

Many of the predictions of models of oxygen balance do not fit with observed patterns of dive behaviour in air breathing divers. A high proportion of observed dives are below theoretical limits (Kooyman et al. 1980; Fedak et al. 1988; Thompson et al. 1991; Croxall et al. 1993; Hindell et al. 1992). The marginal value theory predicts that to maximise energetic gain an optimally behaving animal should be approaching these limits regularly (Kramer 1988). These limits are calculated from the size of the oxygen store available to the animal, divided by the rate at which it utilises this store. We have already shown, in chapter 5 that this rate of utilisation can be very variable depending on the behavioural options chosen by the

animal during the dive. The implication of a variable metabolic rate dependent on how long since the seal has eaten and how much it has eaten adds further complexity. Alternatively factors other than physiological constraints may be influencing diving behaviour. Thompson and Fedak (2001) presented a model that provides evidence that foraging decisions are more influenced by perceived prey density.

The results here suggest that grey seals do not defer the costs of feeding until after diving periods. Including these costs in estimates of DMR may help to reconcile predicted behaviour with that actually observed in wild animals. Total body oxygen stores for a 150kg grey seal can be calculated as 7.49 litres (Kooyman, 1989). At the metabolic rate of 1.83 times Kleiber (mean fasting DMR for Lola, the adult female) this would give an ADL of 9.45 minutes. However if the post-feeding metabolic rate of 2.88 times Kleiber is used (mean post-feeding DMR for Lola), this gives an ADL of only 6 minutes. Most dives performed by wild grey seals are between 3 and 7 minutes.

However how closely does our artificial foraging situation resemble the feeding habits of grey seals in the wild? Advances in telemetry have enabled us to gain a clearer picture of the diving behaviour and movements of seals at sea (e.g. McConnell et al. 1999; Boyd et al. 1997; LeBoeuf et al. 2000) and techniques such as faecal analysis, fatty acid analysis and stable isotopes are providing us with information on diet composition (e.g. Iverson et al. 1997; Rau et al. 1992; Hammond et al. 1994b). However, we are still lacking good information on the actual feeding behaviour of wild seals. Recent studies using cameras mounted on seals (e.g. Davis

et al. 1999; Hooker et al. 2002, Bowen et al. 2002) have begun to provide some information on a few species. However logistical problems associated with this technique limits its use (i.e. recovery of the device, battery and memory size, cost). Further manipulative experiments on animals in captivity of this type, combined with investigations into the feeding habits of wild seals are required to fully understand how the heat increment of feeding affects the behaviour of diving, foraging grey seals.

Chapter 7

Predicting energy expenditure during diving in wild grey seals

7.1 Introduction

Measurements of energy requirements during foraging are very difficult to make in free-living grey seals. Energy requirements are a major parameter in models that predict food consumption of marine mammal populations and activity requirements make up a large portion of total energy requirements. Most studies use a simple multiplier of basal metabolism to account for the additional requirement of activity. Winship et al. (2002) found that uncertainty in activity cost parameters resulted in the biggest uncertainty in estimates of food consumption of Steller sea lions. It is therefore important to develop methods to estimate the energy requirements of free-living seals. The reasons why the energetic costs of free-living activity are unknown in many phocid seals have been discussed in detail elsewhere in this thesis. Here we present a preliminary analysis using the model developed in chapter 5 and telemetry data from wild grey seals to predict the energy requirements of grey seals diving in the wild. This combined approach has been used previously to estimate the energy requirements of free-living sharks (Sundstrom and Gruber 1998; Lowe 2002).

Telemetry studies carried out by the Sea Mammal Research Unit over the last 10-15 years have begun to elucidate the diving and foraging behaviour of wild grey seals around the UK (Thompson et al. 1991; McConnell et al. 1992; Thompson et al. 1996; McConnell et al. 1999). Given the detailed information that exists on dive behaviour, in terms of parameters such as dive duration, surface duration and swim speed, we attempted to use an empirically derived model (chapter 5, this

volume) which uses the relationships between these parameters and metabolic rate to predict the energy expenditure of grey seals in the wild.

This approach can be used to investigate the energetic consequences of different patterns of behaviour. For example, McConnell et al. (1999) characterised movements of grey seals tagged at the Farne islands and Abertay on two geographical scales. Some seals undertook long and distant travel (up to 2100km away) to other haul-out sites, and far offshore into the North Sea and the East Atlantic. At a smaller scale, there were local, repeated return-trips from haul-out sites to specific areas at sea (20-60km). Within these short scale movements, behaviour was further classified into and fast movement at sea (FAS, travel to and from foraging areas) and slow movement at sea (SAS, foraging at sea), determined by assessing whether overall travel rate was above or below a threshold travel rate (McConnell et al. 1999). If these different behaviours result in differences in energetic costs, variability between individuals and/or populations may have important implications for patterns of resource use.

The first objective of this study was to provide an estimate of the typical energy requirement of generalised foraging activity. In addition to this, we attempted to see how much differences in behaviour would result in different predictions of metabolic rates.

7.2 Methods

7.2.1 Deployment and telemetry

Information on the movements and behaviour of grey seals was obtained using Argos Satellite Relay Data Loggers (SRDL's) deployed on 5 animals at Orkney and Shetland in 1998 (see figure 7.1). The process by which dive data were collected and processed by the SRDL's is detailed by Fedak et al. (2002); a summary is provided here. The SDRLs (Sea Mammal Research Unit, University of St Andrews) measure 18 x 10 x 5 cm and consist of a data logger interfaced to an Argos transmitter unit. Data from depth, wet/dry and speed sensors are used to determine the activity of a seal. Activity is classified either as 'diving' (deeper than 6m for at least 6 s), 'hauled out' (dry for at least 240 s) or 'at surface'. Distance swum is determined by a turbine odometer mounted on the tag. Individual dive records include information on maximum depth, depth profile, distance swum and dive and surface duration. Series of dive and haul-out records are temporarily stored in memory and selected for transmission by a pseudo random process such that all times of day were adequately represented, irrespective of diurnal satellite availability and animal behaviour.

7.2.2. Diving behaviour during foraging trips

Seal tracks and dive behaviour was reconstructed on the MAMVIS computer visualisation system that allows movements to be replayed and animated against a background of coastline and bathymetry (Fedak et al. 1996). Using this system,

foraging trips were identified as starting when a seal moved outside a 10km radius of a haul-out site and ending when it returned to within 10km of a haul-out site (either the same haul-out site or returning to a different one). Due to errors in location estimates, haul-out and dive records were also used as independent cues to help determine trip start and end. Approximately 3300 dive records were obtained from a total of 28 trips.

7.2.3. Predicting energy expenditure

Metabolic rate (in $l \cdot min^{-1}$) was predicted for each individual dive cycle using the model presented in chapter 5. The following parameters were used: mass of animal, sine of the month in which the dive took place, dive duration, surface duration and mean swim speed during the dive (distance swum during the dive divided by the duration of the dive). Metabolic rate was averaged over each 'trip' to give the average rate of energy expenditure of the trip, using the following method. The predicted rate of each dive cycle was calculated (in litres per minute), then multiplied by the duration of the dive cycle (in minutes) to give an amount of oxygen consumed for each dive cycle. These were then summed to give the total oxygen consumed for the period over all the dives recorded during the trip. This total was then divided by the total time over all dives during each trip to give an average rate of oxygen consumption weighted by dive cycle duration over the dives that we had records for. The assumption that the dive records from the trip were representative of diving behaviour across the whole trip meant we assumed the average predicted energy expenditure across measured dives was representative of the predicted metabolic rate across the whole trip. Once this

weighted average in $l \cdot \text{min}^{-1}$ had been calculated it was then expressed as a multiple of Kleiber's predicted basal metabolic rate for the mass of each animal DMR (K).

7.2.4 Foraging vs. Travelling

In order to investigate whether different types of diving had different predicted energetic costs, foraging trips were further classified as follows:

Long duration trip (LT) – defined as periods of diving activity associated with movements away from the haul-out site (>20km of haul-out site).

These trips were split into 2 parts – travelling and foraging. These were allocated according to travel rate. Travel rate is defined for each location as the mean of the speeds of travel from the previous location and to the next location. This provides an index of whether the seal was travelling rapidly or was relatively stationary in a localised area. Following the methods of McConnell et al. (1999), for each seal, a frequency distribution of travel rates across the whole trip was examined and a threshold travel rate chosen based on the discontinuity of the distribution. This travel rate threshold was generally $0.5\text{-}0.7 \text{ m} \cdot \text{s}^{-1}$; any dives above the threshold were classified as travelling and any below it, as foraging.

Short duration trip (SD) – periods of diving activity with movements away from a haul-out site further than 10 but less than 50km of haul-out site. Dives during short trips could not be further classified because there was not a clear discontinuity in travel rate.

7.3 Results

7.3.1 Movements

The movements of the 5 seals can be characterised on two geographical scales. 3 seals performed long foraging trips between 100 and 330km away from a haul-out site. These trips lasted in duration from 4 to 13 days. The other two seals performed regular trips closer to shore that lasted 2-3 days.

7.3.2 Dive behaviour

Mean dive duration ranged between 2.2 minutes for the 58kg male up to 5.4 minutes for the 136kg female. Maximum dive durations ranged between 6.9 and 15.9 minutes. Mean speed of dives ranged between 0.34 and 0.58 m.s⁻¹. (Table 7.1)

Travelling vs. foraging dives

Seal 1549 performed foraging dives that were longer and had lower swim speeds than travelling dives. For seal 1550 foraging dives were also longer than travelling dives but there was little difference in swim speeds between the two. For seal 1551, there was no difference in duration between the two dive types but foraging dives had slower swim speeds than travelling dives.

7.3.3. Predicted costs of diving

At-sea activity of the grey seals in this study has an estimated energy requirement of 1.4-1.8 times predicted basal metabolism (Kleiber, 1975). Across all trips and animals the overall average metabolic rate was $1.61(K) \pm s.d. 0.16$. A general linear model with predicted metabolic rate as the response variable, and individual and trip type as factors, demonstrated significant variation between animals ($F=7.78$, $df=4$, $p<0.0001$), but no effect of trip type (long or short trip: $F=1.44$, $df=1$, $p=0.243$). Post-hoc comparisons showed that one seal (1553, 105kg female) was predicted to have a significantly lower DMR than the other 4 (figure 7.3). This female also had the longest average dive duration once expressed in terms of physiological time, i.e. dive duration divided by $mass^{0.75}$ (table 7.1).

When this animal is removed there was no significant variation in predicted DMR between the remaining animals ($F=0.19$, $df=3$, $p=0.902$) or trip type ($F=1.82$, $df=1$, $p=0.20$).

Of the 3 animals that performed long foraging trips, all had significantly higher predicted metabolic rates during travelling than during foraging (figure 7.4).

Seal ID	Sex	Mass (kg)	N dives	Mean dive duration (minutes)	Mean surface duration (minutes)	Mean dive duration/mass ^{0.75}	Max dive duration (minutes)	Speed (m.s ⁻¹)	Predicted foraging DMR(K)*
1548	F	136	738	5.59 ±1.51	1.41 ±0.86	0.14	15.88	0.26 ±0.13	1.71±0.11 (7)
1549	M	113	755	3.21 ±1.26	1.02 ±0.53	0.09	7.9	0.43 ±0.23	1.68 ±0.11 (7)
1550	M	104	910	4.02 ±1.88	1.18 ±0.57	0.12	10.45	0.58 ±0.25	1.65 ±0.05 (3)
1551	M	58	541	2.19 ±0.95	1.26 ±0.86	0.10	6.88	0.40 ±0.22	1.62 ±0.07 (4)
1553	F	105	554	5.14 ±1.97	1.26 ±0.82	0.16	13.17	0.34 ±0.22	1.41 ±0.14 (7)

Table 7.1 summary of dive information for the five seals. *is the predicted metabolic rate averaged over all foraging trips analysed, numbers of foraging trips by each animal are in brackets.

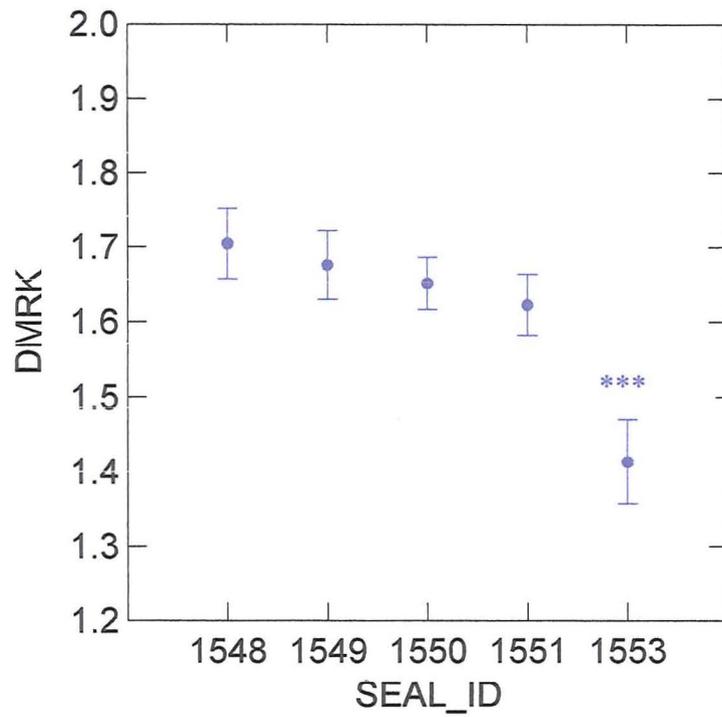


Figure 7.3 Predicted metabolic rate across all foraging trips for individual animals. DMRK is the mean of all trips \pm se. ***denotes that seal 1553's DMR was significantly different from all other animals (Bonferroni post-hoc comparison).

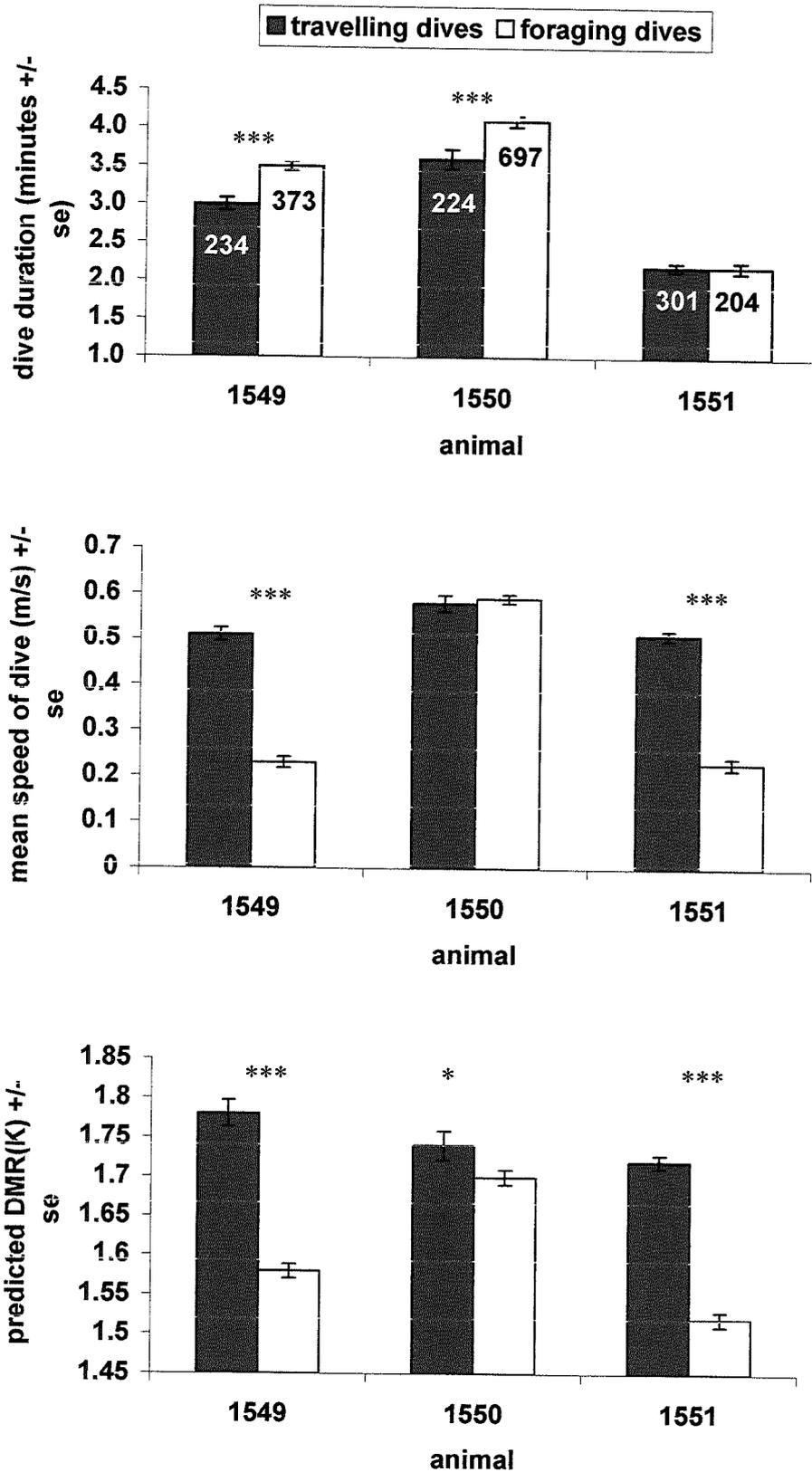


Figure 7.4 Comparison of travelling and foraging type dives.

7.4 Discussion

The overall average over all dives was 1.6 K, which is almost identical to the mean DMR for captive grey seals (chapter 5). This result is not surprising in that dive behaviour in terms of dive durations, surface durations and mean speeds during dives was similar between the captive seals reported on in chapter 5 and the wild seals in this study. Predicted metabolic rate during diving in wild grey seals is lower than the allometric prediction of field metabolic rate (FMR). Other studies have suggested that phocid field metabolic rates are lower than FMR in other species. Castellini et al. (1992) and Williams et al. (2001) measured the metabolic rates of freely-diving Weddell seals of 1.6 times the Kleiber (1975) predicted basal metabolic rate. Hindell and Lea (1998) estimated the metabolic rate of a free-ranging Southern elephant seal weighing 396kg to be $0.88 \text{ l} \cdot \text{min}^{-1}$, which is 1.2 times the predicted level. The factor of 2-3 times BMR is normally used in bioenergetic models to account for activity in phocid seals (Olesiuk 1993; Mohn and Bowen 1996; Nilssen et al. 2000). Attempts to estimate food consumption based on allometric relationships of body size and field metabolic rates have the potential to be serious over-estimates.

There may be important differences in energy expenditure between dives of different types. Travelling DMR was significantly higher than foraging DMR for the three animals that performed long trips. McConnell et al. (1999) classified activity at sea in a similar manner, using travel rate to distinguish between what they termed fast movement at sea (FAS) and slow movement at sea (SAS). They inferred that FAS may represent travelling and SAS foraging. In the present study

it was difficult to satisfactorily split the time spent travelling and foraging during short trips due to the temporal and spatial resolution of the data. The method used here to distinguish between foraging and diving here was relatively crude.

Inclusion of dive type information (e.g. Fedak et al. 2001) or the use of clustering techniques may increase our ability to recognise and thereby assign costs to different types of dives.

Despite these limitations there were differences in the predicted metabolic rates between the two classifications of diving. This deserves further investigation, for example, there may be differences in energetic requirements between populations that forage in different areas, either locally, close to haul-outs or further offshore. The differing energetic consequences of the two strategies may have implications for the impact of each population on their prey resource.

One potential problem with predicting metabolic rate over time is the mass of the animals tracked. The DMR model uses mass of animal in the prediction of metabolic rate. The mass of each animal is only known at capture, however this is likely to change over time, either as a result of mature adults gaining mass in the form of fat for the breeding season, or juvenile animals growing. If the mass of an animal changed considerably during the period between capture and the time for which metabolic rate is being predicted, we may be under or over estimating energy requirements depending on the direction of the mass change. In this study, we used trip and dive data for a relatively short period after deployment (maximum 100 days) however mass change within this period may still result in significant errors in predicted metabolic rate. If mass change is mainly due to

differing amounts of adipose tissue, then it could be argued that the effect on metabolic rate would be minimal, because fat is relatively metabolically inert. However if the amount of lean tissue is changing then the accuracy of predictions of DMR may be affected. Because of the difficulties associated with recapture, it is impossible to measure mass of a satellite-tracked animal after deployment. However, when applying model to data over longer time, it is possible to estimate the mass change of tagged animals based on empirical data on seasonal variation in mass of the type presented by Boyd et al. (1984) for adult females. Or mass at the breeding season e.g. Pomeroy et al. (1999) for females and Anderson and Fedak (1985), for males. There is less available information on mass changes in juvenile animals but growth curves could be used to estimate annual mass change in juvenile seals. There is also some information on mass change in pups in their first year of life (A. Hall and B. McConnell, unpublished data).

The scope of this investigation is limited given that it is only based on a small sample of 5 animals, and only 3 animals for the comparison of travelling versus foraging. However this small study has highlighted that important differences in energy requirements may exist between individuals, depending on their activity. SMRU currently has a large data set of movement and dive behaviour from grey seals satellite tracked over the last 10 years. Future work could examine this data in detail to elucidate seasonal, geographical, age and sex related variation in behaviour and activity budgets. If there are significant differences in behaviour at different times of year, or between animals in different locations, this could have important implications for energy requirements and consequently for the temporal or spatial effects of seals on prey populations.

Chapter 8

Population energy requirements

8.1 Introduction

In order to assess the impact of seals on fish stocks it is necessary to quantify the consumption of different fish species by the seal population. Lavigne et al. (1982) outlined how the prey requirements of pinnipeds could be addressed using a bioenergetic approach, and how this could be extended to the population level. Combining information on the energetic requirements, diet, size and structure of the population allows estimates of fish consumption to be made. The energy requirements of marine mammal populations have frequently been estimated using such an approach (Hiby and Harwood 1985; Lavigne et al. 1985; Ortisland and Markussen 1990; Markussen and Ortisland 1991; Ryg and Ortisland 1991; Markussen et al. 1992; Olesiuk 1993; Mohn and Bowen 1996; Stenson et al. 1997). These models vary in detail from simple equations with a few parameters representing an average individual's annual energy consumption to detailed energy budgets for each age/sex class and time of year.

Breaking down the entire population into classes based on age and sex and reproductive status allows an estimation of the consumption of each class individually. This approach also enables the prediction of the impact of any changes in population structure as well as changes in total population size.

The first objective of this study was to construct a model that predicts the energy requirements of grey seals, applying the new knowledge concerning seasonal changes in energy requirements and activity related energy requirements from

the previous chapters of this thesis. The second objective was to use this model to answer the following questions: 1) what is the estimated annual energy requirement of the UK North Sea grey seal population? 2) How do population energy requirements vary by season? And, 3) Does using this level of detail in energy requirement parameters result in a significantly different estimate of population energy requirements than those previously developed?

The third objective was to calculate confidence limits for the estimates of energy requirement based on the error structure of the model parameters.

8.2 Methods

8.2.1 Model framework

Individual empirically derived energy costs have been combined to estimate the energy required by the North Sea grey seal population in each quarter of the year. This model takes into account age specific metabolism, plus the energy costs of activity and reproduction. This information is combined with the age structure of the population and the time they spend at sea and at shore to estimate the energy needs of the population on a seasonal and annual basis.

First, gross energy requirements were calculated for each age, sex and reproductive class for each quarter. Next, the amount of energy required by each class was multiplied by the effective number of individuals of each class alive each quarter, to give a total population energy requirement for each quarter. These quarterly estimates were then summed to give an estimate of the annual population energy requirement.

95% confidence intervals were calculated using Monte Carlo simulations. In each run of the model, parameter values were randomly sampled from their distribution, defined by a mean and a standard deviation. The model was run 1000 times using the Monte Carlo analysis tool in the Microsoft Excel add-in PopTools (version 2.5).

8.2.2 Population parameters

Age-structured population estimates for the North Sea population (Orkney, IOM, Farnes, Donna Nook) are given in table 8.1. Estimates of the female component of the population were calculated from a population model (Hiby and Duck, in press). Corresponding estimates for the age structure of the male population are not available, but following Hiby and Duck (in press) they were derived here by assuming a one to one sex ratio from birth to sexual maturity, beyond this age, the male component of the population was set at 0.6 of female numbers.

Numbers of each age and sex class were calculated for each quarter using the age and sex specific estimates of mortality (from Hiby and Duck, in press), assuming mortality occurred linearly throughout the year.

Table 8.1 Age-structure and population size of North Sea grey seal population
(Including Orkney).

	Males	Females	Totals
<1	10684	10684	21296
1	3658	3658	7316
2	3197	3197	6394
3	2956	2956	5912
4	2673	2673	5346
5	2431	2431	4862
6+	13375	22291	35666
total	26994	37206	64200

8.2.3 Activity Budget

An activity budget for North Sea grey seals were derived from information on satellite tagged grey seals (McConnell et al. 1999). McConnell et al. (1999) produced a seasonal activity budget based on information from 14 grey seals tagged at the Farne Islands and Abertay. They classified activity as NH – near haul-out activity, FAS – fast movement at sea and SAS – slow movement at sea in two-week bins. This data was bootstrapped to provide quarterly estimates of activity for the following classes of individuals: adult females, adult males and sub-adults, with associated variance. FAS and SAS were combined into a general ‘at sea’ category. NH activity was assumed to be resting. No animals were tracked over the moult so to incorporate the time spent hauled out during the moult, the moult was assumed to last approximately one month for each individual (McConnell et al. 1994). The moult occurs during a protracted period between January and March so estimates of the proportion of time hauled out during the first quarter of the year were adjusted accordingly. Data were lacking for adult females in the first and second quarter so estimates derived for males were used. Similarly data were lacking for the first two quarters for sub-adults so the data from adult males were used for this period for sub-adults. Time spent in reproduction was calculated using an average 18-day lactation for females (Fedak and Anderson 1982) and an average length of stay on the breeding site of 19 days for males (Anderson and Fedak, 1985). These estimates were incorporated into the activity budgets of adult males and pregnant females for the

4th quarter only.

The segment of the population for which least is known in terms of activity is that of pups in their first year of life. A project ongoing at present (K. Bennett, personal communication) seems to be providing evidence that newly weaned pups behave at sea in a similar manner to older seals. In light of this and given that no other information exists, activity budgets for pups in their first year of life were assumed to be the same as those of sub-adult pups, not including the moult related haul-out adjustment in the first quarter.

8.2.4 Bioenergetic parameters

First, body mass (kg) of individuals for each age, sex and reproductive state was calculated on a quarterly basis. For immature animals (<6), body mass of each age and sex class was calculated according to sex specific Gompertz growth curves (Anderson and Fedak, 1985; Anderson and Fedak, 1987). Standard deviations for each mass estimate were calculated using the residuals of the fitted Gompertz models. Quarterly estimates of mass were calculated by assuming mass gain for each age class during the year was equivalent to the difference between the mass in present age class and the mass in the following age class (table 8.2). Seasonal changes in the body mass of reproducing adult males and females were not included to obtain estimates of seasonal expenditures because mass gain of mature adults throughout the year is in the form of blubber mass

(Boyd 1984; Fedak and Hiby 1985). Therefore this energy is expended during the breeding season and this expenditure is accounted for in the empirically derived estimates of reproductive costs. Mass change of weaned pups in their first year of life was from A. Hall and B. McConnell (Unpublished data).

Basal metabolism (BM, in kJ d^{-1}) of individuals was calculated from Kleiber's (1975) equation:

$$\text{BM} = 292.88 \times M^{0.75}$$

Where M is body mass (kg).

The energy cost of activity was incorporated using empirically derived multipliers for each age and reproductive state for each quarter. These age and season specific multipliers for each activity classification shown in table 8.3. Resting metabolism estimates for adult females and juveniles were taken from chapter 4. At-sea estimates were taken from the predicted costs of foraging in chapter 7, with quarterly adjusted values calculated using the model in chapter 5. Estimates of the energy requirement of reproduction were taken from Reilly and Fedak (1996) for females, and Anderson and Fedak (1985) for males. The average cost of male reproduction (83MJ/day) is approximately 4.5 times Kleiber's predicted BMR for a sexually mature male of average mass. For female grey seals the average cost of lactation is 99.8MJ/day, which is equivalent to approximately 6-7 times predicted BMR for a reproducing female of average mass.

No estimates are available for seasonal variation in resting or diving metabolic rates in adult males. In the absence of information on adult males, the female multipliers were used for all mature adults. Similarly all the measurements made on juveniles were done on female animals. However there is no *a priori* reason to expect juvenile males to have higher metabolic rates than females, except as a result of higher mass.

Energy requirements of each activity for each activity, for each quarter, for each age and sex class were calculated as follows:

$$E_{\text{activity}} = A_{\text{activity}} * M_{\text{bm}}$$

Where A_{activity} is the activity related multiplier and M_{bm} is mass predicted basal metabolic rate. Thus the energy requirements for each age, sex and reproductive status were calculated for each quarter as follows:

$$ER = E_{\text{rest}} * \text{rest} + E_{\text{at-sea}} * \text{at-sea} + E_{\text{reproduction}} * \text{reproduction}$$

Where *rest* is the proportion of time spent resting, *at-sea* is the proportion of time spent at sea and *reproduction* is the proportion of time spent in reproduction.

Finally following Fedak and Hiby (1985), energy requirements were converted to estimates of energy consumption by dividing by an overall efficiency value of 80%.

Table 8.2 Estimated mass (kg), by quarter

(a) Sub-adult females

Age	<1	1	2	3	4	5
Quarter						
1	27	41	56	71	85	97
2	33	44	59	74	88	100
3	37	48	63	78	91	103
4	41	52	67	81	94	106

(a) Sub-adult males

Age	<1	1	2	3	4	5
Quarter						
1	27	43	58	74	90	105
2	33	47	62	78	94	109
3	37	51	66	82	98	113
4	41	55	70	86	101	116

(a) All adults

Females	Males
154 ±15.4	214 ±21.4

Table 8.3 Activity multipliers of mass predicted metabolic rates by quarter. Standard deviations, where available are in parentheses. Sources are detailed in the text.

(a) adult seals (6+)

Quarter	Rest	At-sea	Reproduction	
			Females	Males
1	2.28 (± 0.24)	1.81 (± 0.19)	*	*
2	2.08 (± 0.13)	1.75 (± 0.17)	*	*
3	1.76 (± 0.23)	1.57 (± 0.12)	*	*
4	1.86 (± 0.22)	1.61 (± 0.13)	6.6 (± 1)	4.5 (± 1)

(b) Sub-adult males and females 1-5 years

Quarter	RMR	DMR
1	2.10 (± 0.26)	1.66 (± 0.13)
2	1.91 (± 0.19)	1.66 (± 0.11)
3	1.91 (± 0.19)	1.66 (± 0.06)
4	1.91 (± 0.19)	1.66 (± 0.07)

(c) All animals <1 year.

Quarter	RMR	DMR
1	1.91 (± 0.19)	1.66 (± 0.13)
2	1.91 (± 0.19)	1.66 (± 0.11)
3	1.91 (± 0.19)	1.66 (± 0.06)
4	1.91 (± 0.19)	1.66 (± 0.07)

8.3 Results

8.3.1 Individual daily energy expenditure

i) Pups

The model predicted that pups in their first year exhibited a gradual rise in daily individual energy expenditure from 6.1 (4.7-7.8) MJ.day⁻¹ to 8.7 (6.7-10.7) MJ.day⁻¹ (Figure 8.1). This change was mainly due to an increase in mass throughout the year given that they were assumed to spend a fairly constant proportion of time in the water.

ii) Sub-adults

Predicted mean daily energy expenditure of sub-adult males and females changed very little seasonally (Figure 8.2). Males have a slightly higher requirement due to having a higher mass. Predicted daily energy expenditure, averaged across all quarters increased for both sexes between age 1 and 5 (figure 8.3).

iii) Adults

Predicted adult female daily energy expenditure was fairly constant throughout the first two quarters of the year, at an average of 25.5 MJ.day⁻¹ over the first three quarters. The model predicted a decline in daily expenditure in the third quarter to 20.1 MJ.day⁻¹, which then increased to 42.4 (30.6-56.6) MJ.day⁻¹ in the 4th quarter (figure 8.4). Males showed a similar pattern, although during the first three quarters, average male daily expenditure was 23% higher than expenditure of females. In the 4th quarter this difference was reduced to 7%.

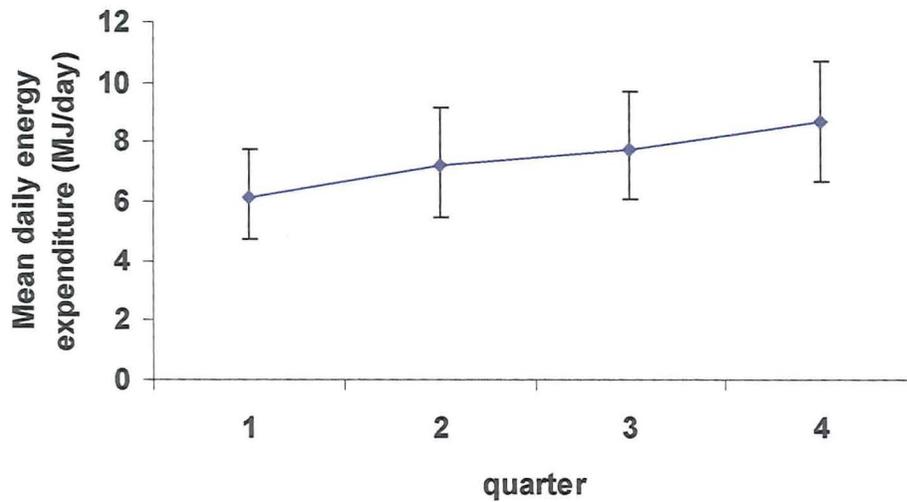


Figure 8.1 Predicted individual daily energy expenditure of grey seal pups between weaning and 1 year of age by quarter. Error bars are 95% confidence limits, generated by Monte Carlo simulations (1000 runs).

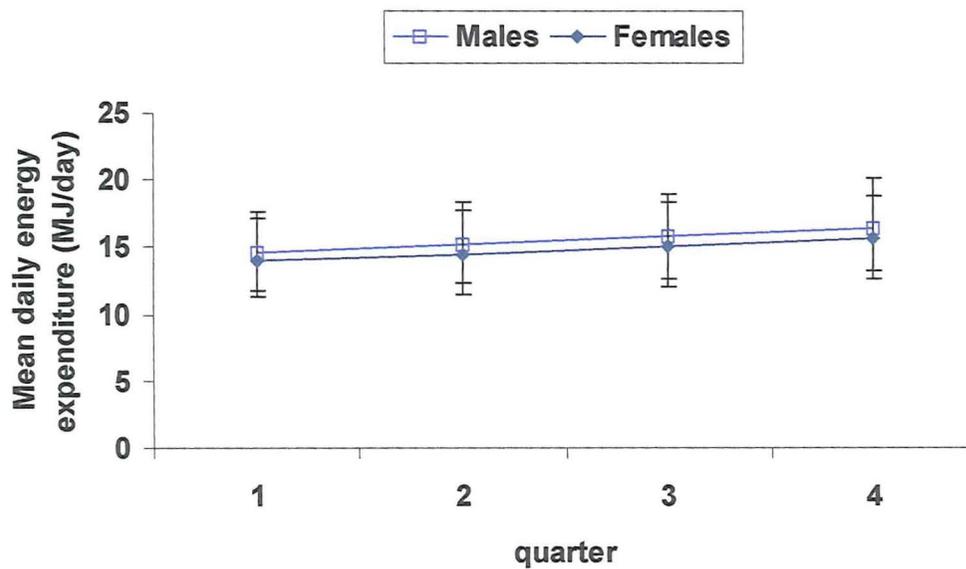


Figure 8.2 Predicted individual daily energy expenditure of sub-adult male and female grey seals by quarter. Error bars are 95% confidence limits, generated by Monte Carlo simulations (1000 runs).

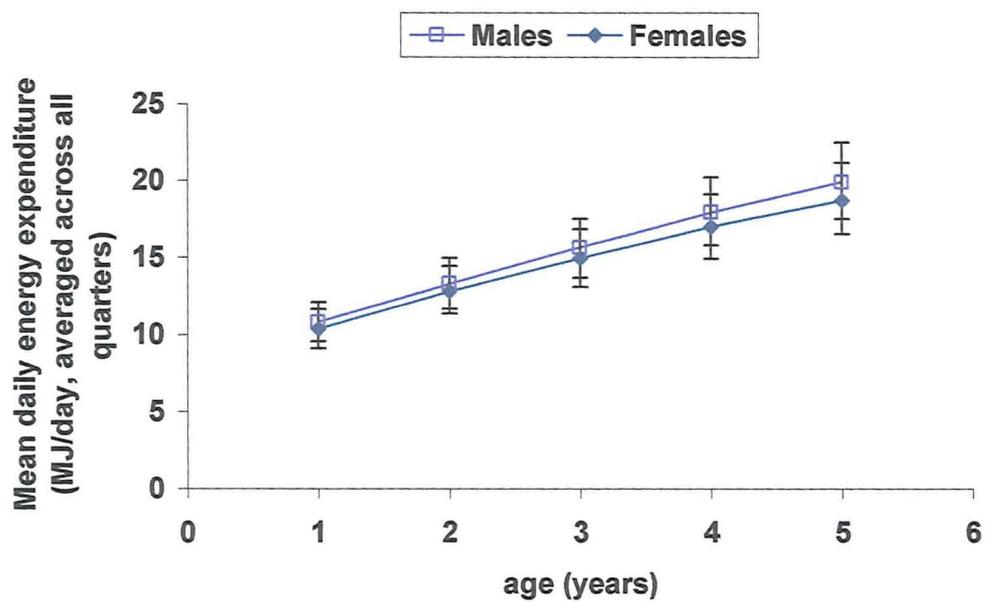


Figure 8.3 Predicted individual daily energy expenditure of sub-adult male and female grey seals by age. Error bars are 95% confidence limits, generated by Monte Carlo simulations (1000 runs).

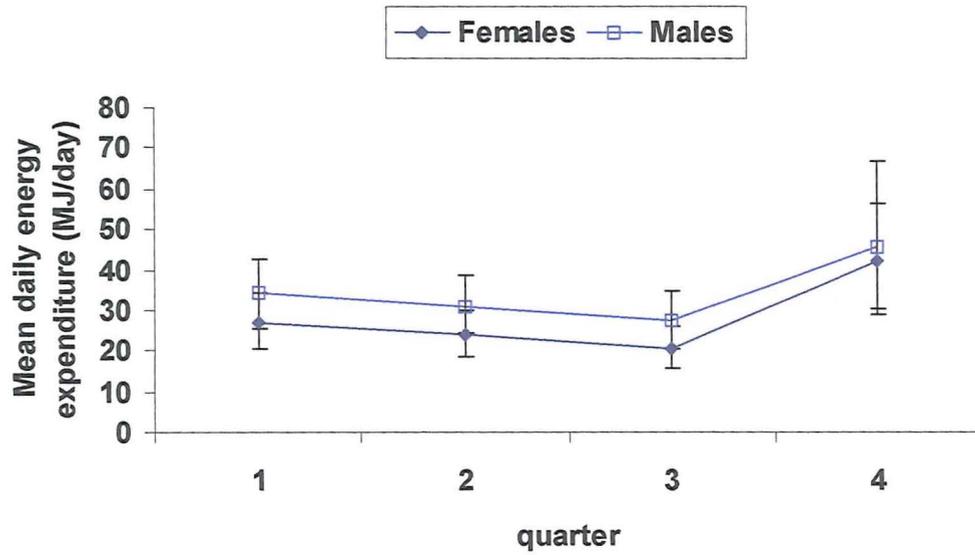


Figure 8.4 Predicted individual daily energy expenditure of adult male and female grey seals by quarter. Error bars are 95% confidence limits, generated by Monte Carlo simulations (1000 runs).

8.3.2 Total energy expenditure

i) Pups

Predicted total energy expenditure of pups (average daily expenditure multiplied by numbers of individuals present multiplied by number of days) decreased throughout the year from 1.2×10^7 ($9.3 \times 10^6 - 1.5 \times 10^7$) MJ in the first quarter, to 6.8×10^6 ($5.3 - 8.7 \times 10^6$) MJ in the fourth quarter (figure 8.5). Although individual energy expenditure increased due to mass increase throughout the year, high mortality of young animals was reflected in decreasing total requirements.

ii) Sub-adults

As with daily energy expenditure, predicted total energy expenditure of the sub-adult part of the population changed very little throughout the year (figure 8.6). Total annual expenditure increased from age 1 to age 3 (change in mass was greater than mortality). After this, mortality cancelled out the increase in mass throughout the year and annual expenditure did not change (figure 8.7).

iii) Adults

Total energy expenditure of the adult male and female segment of the population followed similar trends to individual energy requirements (figure 8.8). Total requirements of the male component of the population were lower than that of females throughout the year. This difference was greatest in the 4th quarter, when total male expenditure was 60 (44-73) % of female expenditure.

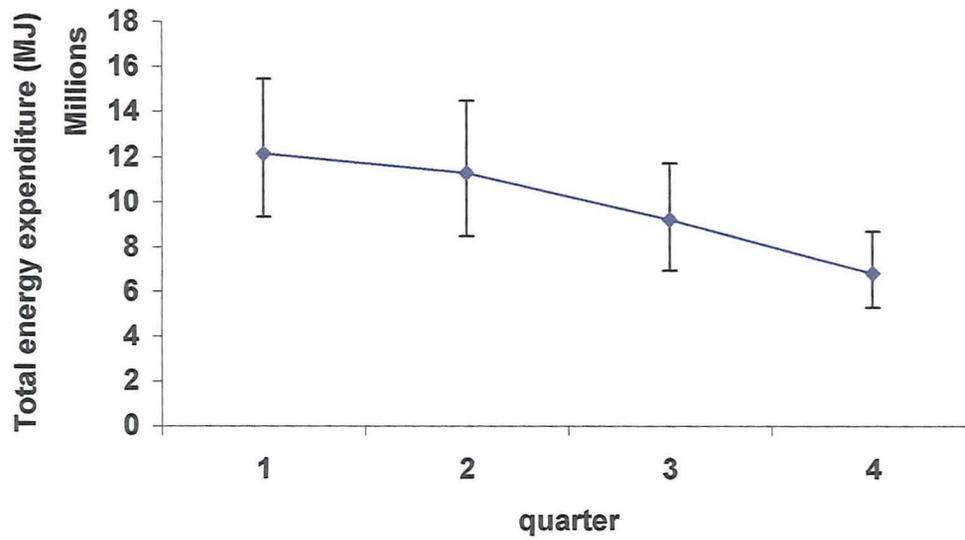


Figure 8.5 Predicted total energy expenditure of grey seal pups between weaning and 1 year of age. Error bars are 95% confidence limits, generated by Monte Carlo simulations (1000 runs).

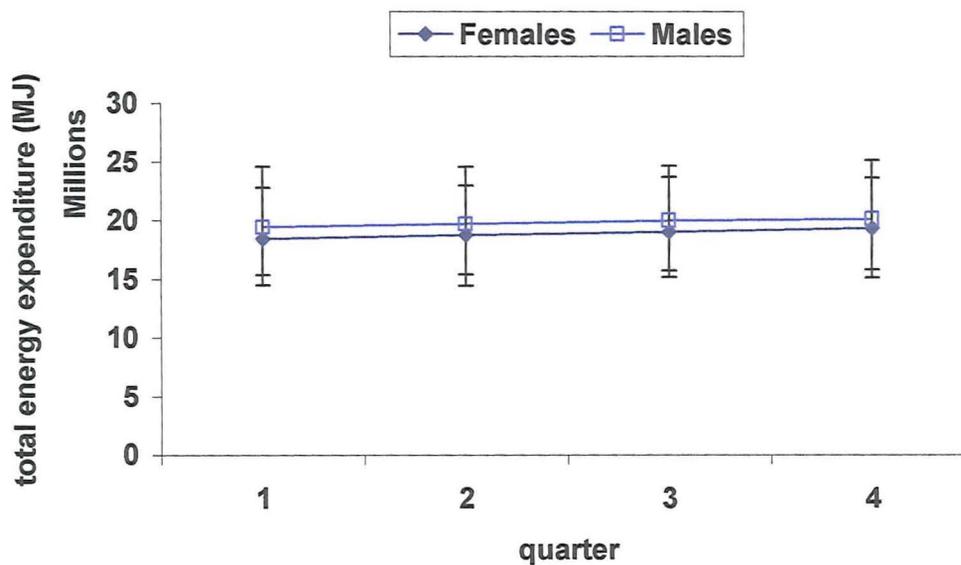


Figure 8.6 Predicted total energy expenditure of sub-adult male and female grey seals by quarter. Error bars are 95% confidence limits, generated by Monte Carlo simulations (1000 runs).

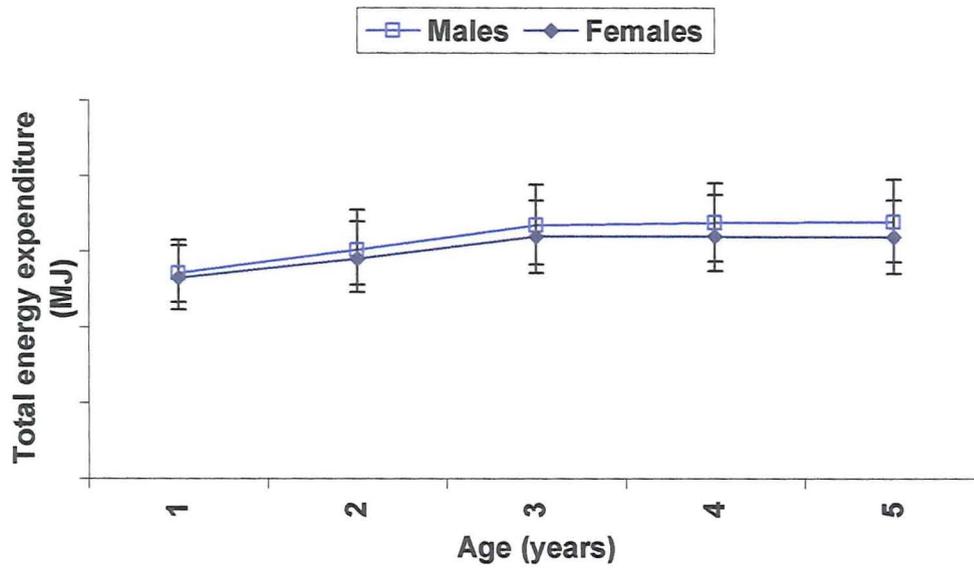


Figure 8.7 Predicted total energy expenditure of sub-adult male and female grey seals by age. Error bars are 95% confidence limits, generated by Monte Carlo simulations (1000 runs).

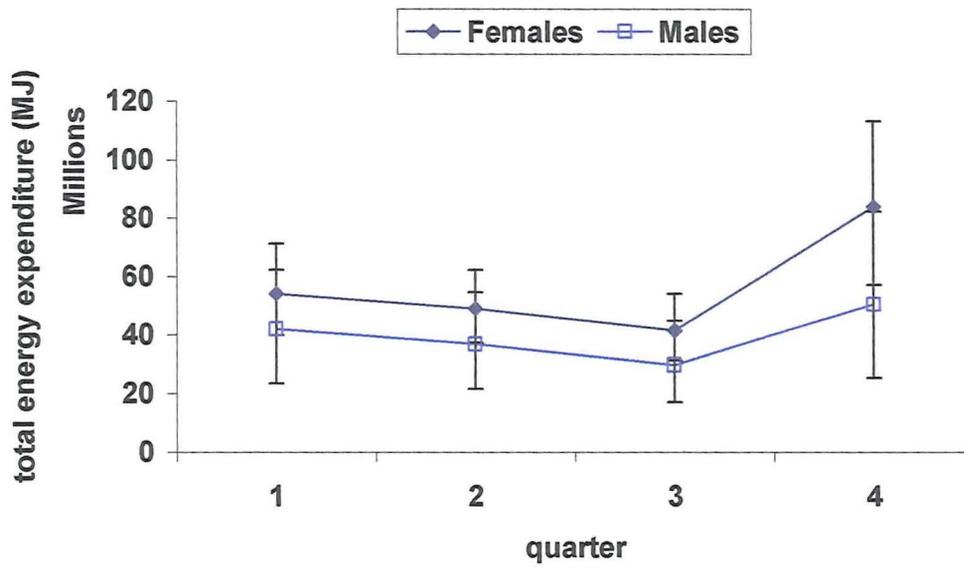


Figure 8.8 Predicted total energy expenditure of adult male and female grey seals by quarter. Error bars are 95% confidence limits, generated by Monte Carlo simulations (1000 runs).

8.3.3 Total population expenditure

Total population energy expenditure by quarter is shown in table 8.4 (also shown graphically in figure 8.9). Upper and lower confidence limits deviate from the point estimate of total annual population energy expenditure by approximately 12%.

Total energy requirements by age/sex class are disproportional to population composition (figure 8.10). 41% of total population energy requirement is accounted for by the adult female segment of the population, but adult females consist of only 30% of total population numbers. Similarly adult males account for only 17% of population numbers, yet account for 28% of population energy requirements. Pups make up only 7% of total population energy requirement, yet account for 21% of population numbers.

Dividing the total annual energy expenditure of 5.8×10^8 MJ by the number of individuals in the population and by 365 gives an average daily energy expenditure for an 'average' grey seal of 20.2 (18.3-22.2) MJ.day⁻¹. Dividing these values by an efficiency of 0.8 gives a total annual energy consumption of the population of 7.25×10^8 (6.1-8.4 $\times 10^8$) MJ and an average daily energy consumption for an 'average' grey seal of 25.3 (22.8-27.8) MJ.day⁻¹, or 5497 (4964-6042) Kcal.day⁻¹.

Table 8.4 Total population energy requirements

Quarter	Total population expenditure (MJ)	Lower 95% C.I. limit	Upper 95% C.I. limit
1	1.5×10^8	1.2×10^8	1.7×10^8
2	1.3×10^8	1.1×10^8	1.6×10^8
3	1.2×10^8	1.0×10^8	1.4×10^8
4	1.8×10^8	1.4×10^8	2.3×10^8
Total	5.8×10^8	5.2×10^8	6.4×10^8

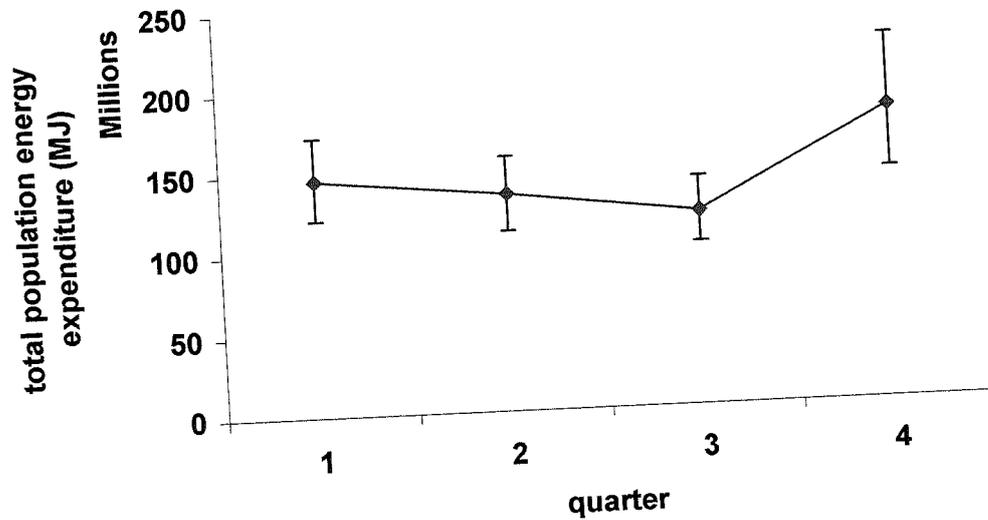
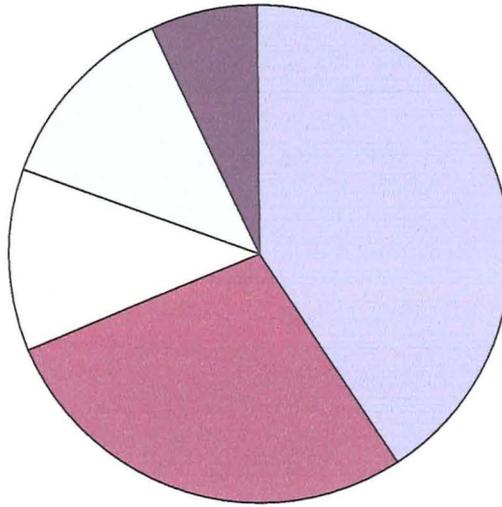


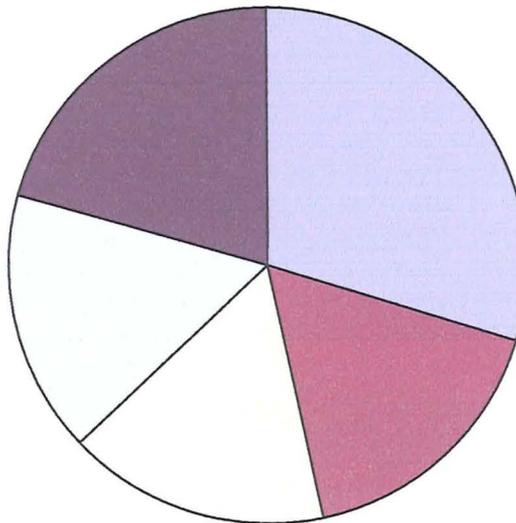
Figure 8.9 Predicted total energy requirement of UK North Sea grey seal population by quarter. Error bars are 95% confidence limits generated by Monte Carlo simulations (1000runs).

Figure 8.10 a) Proportion of total population energy requirement by age/sex class

■ adult females ■ adult males □ sub-adult females □ subadult males ■ pups <1



b) Proportion of total population number by age/sex class



8.4 Discussion

The overall energy requirements of life in the wild are impossible to measure in phocid seals. The best approach to quantify this is likely to be the development of quantitative models that make use of empirical data on the costs of various activities coupled with information of the extent of those activities in the wild populations, together with detailed information on the size and composition of the population. Chapters 4-6 of this volume were an attempt to measure the combined costs of activity of wild grey seals in captivity under similar thermoregulatory and behavioural regimes to those in the wild. Similarly field metabolic rates were calculated from a combination of laboratory measurements of the cost of activity, in tandem with data derived from telemetry studies of the activity of wild grey seals. In this study bioenergetic parameters were calculated based on these empirical data wherever possible. Information on the cost of reproduction was also derived from empirical studies on wild grey seals.

This study tried to include as many parameters as possible in the model. This however, can lead to error in the resulting estimates as a result of inaccurate approximations of unknown parameters. One way of addressing inaccuracies in this type of model is to include error terms for all estimates of model parameters. Most model inputs had error estimates associated with them and using the error distributions allowed us to calculate upper and lower confidence limits on our

estimates of energy requirements. Monte Carlo simulation techniques have been used in a similar manner by Mohn and Bowen (1996), Stenson et al. (1997) and Winship et al. (2002). Given that some input parameters were unknown and there may be a high degree of model error due to some of the assumptions made, these limits represent minimum error. Future work aims to carry out a sensitivity analysis similar to that carried out by Winship et al. (2002). Sensitivity to input parameters can also be examined by systematically incorporating uncertainty in each of the parameters one at a time, while holding all other parameters in the model constant at their mean/median values (Winship et al. 2002). This will allow us to determine the sensitivity of the model to inaccurate approximations of input parameters.

There are a large number of terms included in this model, approximations of which are likely to be potential sources of error in estimates of energy requirement. Hiby and Duck (in press) report that 95% confidence limits of pup production are within 14% of the point estimate. The comparable figure for the total female population estimate at regularly surveyed sites is 18%. However, confidence limits are not available for the population as a whole because of uncertainties in the male component of the population and animals associated with less frequently surveyed sites. The confidence limits around estimates of energy requirement produced here are based on a CV in population size of 20%.

The model used an average efficiency of energy utilisation of 80% to convert estimates of energy expenditure to energy consumption. Ronald et al. (1984)

reported a mean value of 82.7 (\pm 4.8%) for grey seals fed on herring. Efficiency covers two main terms. The first is the efficiency of digestible energy i.e. the proportion of ingested food that is not lost in faeces and urine. The second is the efficiency of utilisation of metabolisable energy, which is the proportion of digested energy that is not degraded to heat through the processing of food energy into usable forms (termed the heat increment of feeding, HIF). Previous studies have shown that HIF is variable according to meal size and composition, the nutritional state of the animal and the composition of growth (Rosen and Trites 1997). During energy deposition (growth) the proportion of energy lost as the heat increment of feeding is greater (Webster 1983; Blaxter 1989). The data presented in chapter 6 however show that the HIF in terms of proportion of total energy expenditure was similar between juvenile and adult grey seals during feeding while diving. This was only measured in two animals, clearly more information is needed on how the HIF operates in diving animals. Whether a differential cost appears after a diving episode remains to be investigated.

Given a lack of data about males and sub-adults, a number of assumptions had to be made. The estimates produced here assume that activity related metabolism and seasonal variation in resting rates were similar for males and females. Future work at the SMRU's captive facility will hopefully enable the development of a clearer picture of sex and age related variation in metabolic rates.

The activity budget for grey seals was based on information from 15 satellite-tracked animals (McConnell et al. 1999). SMRU has a large database of

information from 108 satellite tag deployments on UK grey seals; future work could examine this information to give more detailed activity budgets. There are also a number of assumptions concerning the interpretation of activity budgets that may be important sources of error. It was assumed that all near haul-out activity (NH) was resting. However, this may be underestimate foraging close to haul-out sites. It would perhaps be better to split NH time into time actually spent hauled-out on land, and time spent in water. However, this depends on having land and water specific resting rates. At present there are no estimates of the actual rate of energy expenditure of grey seals resting on land in the wild. The estimates of resting metabolic rate used here may have been overestimates. Periodic breathing, either on land or in water can result in metabolic rates lower than those measured while animals are breathing regularly. In Chapter 4 resting metabolic rates of adult females resting in water decreased by as much as 25% as a result of periodic submergence. Similarly, Boily and Lavigne (1996) demonstrated that apnoea while on land resulted in metabolic rates 20% lower than regular breathing. There is no information on the extent of apnoea in hauled out grey seals.

Estimates of at-sea metabolic rate did change seasonally, but it was assumed that dive behaviour is similar throughout the year. This may not be the case, Beck et al. (2000) noted that there were important seasonal changes in the diving behaviour of North-west Atlantic grey seals. Both sexes increase their dive effort as the breeding season approaches (in terms of higher dive durations, and increased bottom time). If this were also the case for grey seals in the North Sea,

the model developed in chapter 5 would predict a lower at-sea metabolic rate for this period for reproducing animals.

It was assumed that all at-sea behaviour was similar in terms of energetic cost, however data presented in Chapter 7 suggests that there may be important differences in cost depending on the types of dives performed by the animal, for example between travelling and foraging. Further information on the occurrence of different types of behaviour and their associated costs is required.

The cost of at-sea activity was estimated using data from only 5 free-ranging animals (chapter 7), although these 5 seals covered a large range of sizes, there still may be important differences between groups of animals. Future work could involve examining individual differences in behaviour with a view to assigning age and sex specific at-sea multipliers, relating to the behaviour of each group of animals.

The assumptions concerning mass change of individuals throughout the year are also possible sources of error. Deciphering exact seasonal patterns of growth is difficult without longitudinal measurements of immature, growing animals throughout the year. Some data exists for pups in their first year of life (A. Hall and B. McConnell, unpublished data.) However, not enough is known about the seasonal growth patterns in sub-adult animals.

It is important to note that the results of this model are estimates of energy requirements and not estimates of food consumption. On an annual basis, food consumption would probably equal energy requirements, but on a daily, or even seasonal basis, animals do not always consume the food they need to meet their energy demands. Mature seals undergo a period of starvation during the breeding season, and lose up to 40% of their body weight. Therefore estimates of energy requirement by quarter will not be reflected equally in consumption. Estimates of requirement will translate into consumption (by sexually mature animals at least) over truncated periods, between the end of the breeding season and before the moult, and then between the moult and the beginning of the next breeding season. Estimating actual energy expenditure coupled with time spent at sea and changes in the body energy content of seals during these periods can be used to follow actual food consumption at these times of year.

Estimated energy required by each segment of the population is not proportional to the composition of the population. This has implications for predicting what will happen with projected changes in population structure. For example there has been speculation that the UK grey seal population is undergoing density dependent changes (Boyd, 2002b). If this density dependence is operating at the level of pup survival, this will have little effect on total population energy requirements in the immediate future, given that pups only account for 7% of population energy requirements. However if density dependence effects are operating at the level of adult mortality or fecundity, their effects on population

energy requirements may be more significant. The model presented here can be used to predict the outcome of changes in many parameters related to density dependence, and not only those directly related to demographic changes. For example, foraging patterns may increase as prey becomes scarce, seals may spend longer at sea, or switch to alternative prey that require greater energy expenditure to capture. This model would allow the assessment of these types of effects on population and individual energy requirements.

Any modelling process is one of building on previous information, adding new information as it becomes available. Although there are still large gaps in the information required to provide a fully comprehensive energy budget, the present study represents the most complete bio-energetic model of UK grey seals to date. Previous estimates of grey seal energy requirement did not include seasonal variation in individual requirements, nor seasonal changes in activity, aside from those related to reproduction (Fedak and Hiby 1985). However, the estimate of the daily energy requirement of an average grey seal of $24.5 \text{ MJ}\cdot\text{day}^{-1}$ produced here is very close to Fedak and Hiby's (1985) estimate of $25.4 \text{ MJ}\cdot\text{day}^{-1}$. Grey seals in the Eastern Scotian Shelf in the West Atlantic were estimated to have mean daily energy requirements of $31.8 \text{ MJ}\cdot\text{day}^{-1}$ (Mohn and Bowen, 1996). These higher values are a reflection partly of the larger body masses of Canadian grey seals. However, they did not include an efficiency term in their bio-energetic model. If an efficiency term of 0.8 was included in the estimates of Mohn and Bowen (1996), their estimated DEC would be even higher, in the

region of $40\text{MJ}\cdot\text{day}^{-1}$.

An assessment of population consumption broken down by fish species relies on detailed information on the diet composition of the population and the energetic density of each prey species. However, to put the model predictions of energy consumption into context, to satisfy a daily requirement of $24.5\text{MJ}\cdot\text{day}^{-1}$, a seal would need 7.2kg of fish per day if it were feeding on cod alone. However, it could satisfy the same energy requirements with a daily consumption of about 3.9kg of sandeels. (These calculations are based on energy densities of 3.4 and 6.3 KJ per kilo for cod and sandeels respectively, taken from Hammond et al. (1994a)).

The model presented here, like all models of biological systems, is a simplified representation of the real system. Nevertheless, models such as this can aid in predicting properties of the real system that are difficult or impossible to measure. A large amount of information is required to fill the gaps present in the data needed to completely parameterise this model. It is hoped that the approach started here can be developed and used in conjunction with information on diet composition and the energetic density of prey to model interactions between UK grey seals and their prey.

Chapter 9

General discussion

Lavigne et al. (1982) stated that an understanding of energetics in marine mammals is pivotal to the management of most large-scale marine ecosystems. Given that seals are top predators, they are influential components of such ecosystems. Echoing this statement, Boyd (2002) maintained that we couldn't begin to understand the role of marine mammals in relation to other biological components of a system without a common currency - energy. It is also true that this currency is important for examining the behaviour of marine mammals on a smaller scale – how animals dive for food, building into progressively larger scale behaviours involving foraging trips and eventually to whole life histories. This leads to a more fundamental interest in seal energetics in terms of how physiology constrains diving and foraging behaviour and shapes the way these fascinating animals exploit their environment.

The energetics of individual seals in captivity provided the focus for chapters 4 to 6. A priority during these studies was to allow the seals to behave as 'naturally' as possible within a captive setting. This meant not confining them to small chambers and restricting their choice of movement. It also meant leaving them undisturbed during all measurements. This hopefully resulted in measurements that were made on animals that were relatively stress free. Rather than create 'a laboratory in the field' (Butler and Jones, 1997), the idea here was to create the field within the laboratory, or at least a semblance of field behaviour in the laboratory.

Nevertheless it is an important distinction that the objective was not to measure energy requirements of grey seals in captivity and make a direct extrapolation to their wild counterparts. Rather, the metabolic requirements (with associated

error) associated with various activities were determined, with a view to combining this with information on what wild seals do to estimate what the likely energy requirements are of seals in the wild.

However we must still exercise caution in making generalisations at the population level based on measurements of a small number of individuals. This study made measurements of 10 seals in captivity of varying ages and although there was variability, certain patterns were repeatedly observed. One such pattern was the decreasing metabolic rate throughout spring and summer in adult females, which was reflected in both resting and diving metabolic rates and was seen in animals in 3 separate years. Another example was the consistent relationships between diving activity and metabolic rate in all the seals. Similarly the estimates of the heat increment of feeding in chapter 6 were similar in both animals that were measured. The persistence of such patterns provides confidence that data of this nature can be incorporated into future models of seal-fishery interactions, upon which management decisions may be based.

A truism of scientific research is that it often raises more questions than it answers. This study is no exception and in the following sections, the findings of this thesis will be discussed in turn, along with suggested avenues for further research.

9.1 Resting metabolic rates

Chapter 4 detailed seasonal and age-related variation in resting metabolic rates in adult and juvenile female grey seals. There was a significant effect of resting

conditions on resulting estimates of RMR which confirms the view held by other authors (Fedak 1986; Costa and Williams 1999; Boyd 2002) that the concept of standardising metabolic rate for comparison needs to be carefully addressed when dealing with diving animals. The concept of BMR is used to demonstrate the minimal level of metabolism i.e. the energy requirement for maintaining the living state. It is most often used to make comparisons between different groups of animals. In practice, as is the case with most animals, the conditions for BMR are easier to define than to achieve (Hulbert 2003). When dealing with such large active animals, one or more of the criteria is often sacrificed to achieve the others.

In seals minimum metabolic rate is not always that which is measured under Kleiber's criteria for the measurement of BMR. Submergence and apnoea can result in metabolic rates lower than those measured under 'standard' conditions. An interesting question is that if seals can 'maintain life' at these lower rates of metabolism, i.e. while diving, why don't they do this all the time? It may be that they can't sustain this hypometabolism indefinitely and require periods of higher metabolism to compensate. This may explain the elevation in metabolic rates above 'predicted' levels when resting in water. The energetic cost of 'rest' in the wild is not known. Grey seals hauled out in the wild appear to be resting, and appear to spend a great deal of this time asleep. But one possibility is that hauling out represents a 'payback' of hypometabolism during diving. Brasseur et al. (1996) demonstrated that hauling out is a necessity for harbour seals. If this is the case then metabolic rate during haul out is likely to be elevated above estimated 'resting' values. One way to potentially explore this would be to measure

'resting' metabolism of seals after diving activity of varying extent. A useful exercise would be to test the hypothesis that seals have a higher metabolic rate while resting after dives of longer duration. The automatic feeder and pool set up at SMRU would enable experiments of this type.

Chapter 4 also demonstrated that there were seasonal patterns in the metabolic rates of adult female grey seals, which were not necessarily related to changes in mass. It is likely that this seasonality is related to the life history of these animals. It would be useful to examine natural variations in body composition, not only changing adipose levels but also to investigate if proportions metabolically active tissues changed seasonally. The nature and extent of seasonal variation in the metabolic rates of adult males also remains to be addressed. Although challenging to undertake, this research would provide a more complete picture of the causes and consequences of seasonality in metabolism.

In growing seals, variation in metabolic rate was related to changes in lean body mass. As young seals grew larger their absolute metabolic rates increased. However, mass specific rates generally did not change, which suggests that the metabolism of young seals may be a consequence of the relationship between body mass and metabolic rate rather than an additional cost of growth.

It would seem that seals have a high degree of control over their metabolic rate and even basal metabolism may not be a constant. Boyd (2002) accepted that the

concept of BMR is useful as a benchmark against which all measurements of metabolic rate can be compared, however he rejected the notion that BMR is quantifiable in a practical sense in marine mammals. I would tend to agree with both these statements. Seals seem to have flexibility over their metabolic rates that may be related to their aquatic lifestyle (clearly exhibited in our seals, for which metabolic rates were lower during active diving than while at rest at the surface). Temporal separation of resource acquisition and resource utilisation is a feature of the strategies employed by phocid seals, both in terms of foraging behaviour and overall life history patterns. The flexibility in metabolic rates that they appear to have is likely to be related to this.

9. 2 Diving metabolic rates

Chapter 5 demonstrates that 'natural' diving does not seem to be metabolically costly in grey seals. Diving metabolic rates were lower than 'resting' metabolic rates measured in the same seals. This contributes to a growing body of evidence that phocid seals are capable of hypometabolism to effectively exploit their underwater food resource.

Chapter 5 also presents a model developed from empirical data that can be used to estimate the metabolic rates of free-ranging seals from telemetry derived information on their diving behaviour. The model accurately predicted the metabolic rate of diving captive seals. The main motivation for using this approach to estimate diving metabolic rate was because other methods to do so in wild seals were unavailable. This presents a problem in that our predictions

cannot be tested in wild seals. Heart rate telemetry has been used in many species to estimate field metabolic rates (Butler et al. 1992; Butler 1993; Butler et al. 1995; Bevan et al. 1995; Boyd et al. 1995). However, heart rates of naturally diving grey (Thompson and Fedak 1993), and elephant seals (Andrews et al. 1995) appear not to be related to swimming speed. Hindell and Lea (1998) actually found a negative relationship between the mean swimming speed of dives and the mean heart rate of those dives in free-ranging Southern elephant seals. Given that physical activity during a dive has a large effect on the metabolic rate of a dive (Chapter 5, this volume, Williams et al. 2000), it is difficult to see how heart rate would provide estimates metabolic rates on a dive-by-dive basis in the way that our model can. Heart rate telemetry is also more logistically difficult to use than measures of behaviour. Standard SRDL's are deployed on seals much more regularly than heart rate tags, therefore a method that can predict metabolic rate based on behaviour alone, that doesn't depend on measurement of physiological variables could potentially have a much larger applicability.

If the estimated body oxygen store used in chapter 5 represents all the oxygen available to the seal, only 2% of the dives measured exceeded the theoretical capacity of the animal to provide all the energy for the dive aerobically. In which case we can probably conclude that in grey seals oxygen stores provide a real limit to dive duration (as discussed by Butler and Jones, 1997) and grey seals preferentially rely on aerobic metabolism to support activity while submerged. The metabolic rates of 80% of all dives were below the resting rates reported in chapter 4. If these resting rates represent a true maintenance requirement then the

seals in this study were hypometabolic on 80% of all dives. This is even more remarkable considering that these dives consist of active swimming. We have also probably over-estimated the rate of oxygen utilisation over the submerged part of the dive cycle, since 'excess' oxygen is consumed during the surface period and not utilised during the dive (Butler and Jones 1997). It would seem that grey seals can reduce their metabolic demands during diving to divert aerobic power to muscles to enable submerged activity.

The nature and mechanism of how they achieve this is unclear. A number of hypotheses have been proposed. During a dive, the spleen of the Weddell seal contracts and injects red blood cells into the circulation (Hurford et al., 1996). The benefit to the seal is an infusion of circulating oxygen within the red blood cells for the working tissues. Oxygen rich red blood cells could be sequestered during periods of rest.

The low heart rates during longer dives in many seals indicate reduced tissue perfusion. In grey seals diving heart rate is lower during longer dives and may fall to as low as 4 beats per minute (Thompson and Fedak 1993). The pattern of diving heart rates in southern elephant seals are similar to those in grey seals (Hindell and Lea 1998). Reduced blood flow to liver, kidney, spleen, intestines and reproductive tract, could result in a substantial lowering of metabolic activity. However elephant seals make long dives with only short intervening surface periods for periods of months. The splanchnic organs are required for vital activities such as digestion and reproduction, and it is therefore important for circulation to be maintained to these organs for substantial parts of an animal's

life. However grey seal foraging trips are much shorter in duration than those of elephant seals and they spend days, rather than months at sea.

It has been suggested that diving animals can reduce their metabolic demands through reductions in body temperature. This idea has developed mainly from studies of diving birds, which appear to make use of regional heterothermy as a means of reducing their metabolic rate (e.g. Bevan and Butler 1992; Butler et al. 1995; Bevan et al. 1997). Only a few studies have examined body temperatures of diving mammals. Aortic temperatures in Weddell seals decline by 1-3°C during and after prolonged dives (Hill et al. 1987). In juvenile elephant seals making short dives (15 min), subcutaneous temperature fell to within 1°C of water temperature, and non-active muscle temperature fell by as much as 8°C (Andrews et al. 1995). In contrast, rectal temperatures remained normal during diving in captive harp seals (Gallivan and Ronald 1979). More experiments are needed to determine how much of a role regional heterothermy plays in diving metabolism in diving mammals.

Different species probably utilise different strategies, or in fact different combinations of more than one. Determining exactly how this is achieved in grey seals is impossible to determine without detailed physiological measurements of a number of variables including blood distribution and tissue perfusion during the dive, tissue specific metabolic rates and body temperature during diving. Achieving these types of measurement however would probably compromise the 'quasi-natural' setting of this kind of study.

An interesting avenue for research is extending the study of the interaction between physiology and behaviour described here, to an inclusion of ecological context. Although behaviour of the seals in the captive setting was similar in terms of swimming speed, dive duration and surface intervals to free-living grey seals, our seals did not actually have to forage and find food. The artificial 'feeding patch' set-up described in chapter 6 can allow investigators to simulate foraging dives, to allow experiments of a more manipulative nature. The simultaneous measurement of behaviour and energy expenditure in this situation can allow a direct measurement of the strategies employed by these seals, and the testing of theoretical models of the type presented by Thompson and Fedak (2001). Indeed experiments of this type are already underway at SMRU and Future work intends to include variable foraging costs.

9.3 The heat increment of feeding

Chapter 6 is the third and final chapter that was concerned with measurements made on captive animals. The presence of a concurrently running project simulating foraging at a prey patch enabled an investigation of how the cost of feeding affects diving metabolism. The additional cost of feeding has previously only been measured in air in marine mammals. But given that the HIF can potentially have a large effect on the amount of time a diving animal can remain submerged, it seemed appropriate to investigate this in a more ecologically relevant context. Although the constraints of the other study meant that the experiments were not ideally designed with this analysis in mind, there is evidence that ingestion of prey increased the diving metabolic rate of seals

'foraging' in a captive setting. There is also evidence that the increased metabolic rate caused by feeding can be long-lived. How this affects the dive behaviour of free-living seals is an interesting question, which remains to be addressed. One potential way of investigation this is a detailed examination of dive behaviour (from telemetry records) in wild seals to see if there is any evidence that dive duration's are related to time spent foraging previously (i.e. feeding).

9. 4 Predicting costs in free ranging grey seals

Chapter 7 aimed to provide a link between measurements made on animals in captivity, and the application of such data to their wild counterparts. This was only a small demonstration of the applicability of the model developed in chapter 5 and includes only a very small sample of animals; nevertheless it appears that diving in the wild is no more costly than for our captive seals. It has also suggested that there may be important differences in terms of dive behaviour and movements, and consequently energy expenditure, between individuals. This could be expanded to look at how differences in diving behaviour (geographically, seasonally, by age and sex) relate to predicted energy expenditure, and how this relates to patterns of resource utilisation. For example, a population of seals which exploit a food resource local to the areas that they haul-out in may expend less energy travelling to these areas, and consequently need to eat less, than seals which travel to a feeding site hundreds of kilometres offshore. As more and more telemetry-derived information on the behaviour of

wild grey seals becomes available this could be a valuable avenue of future research.

9.5 Population energy requirements

Chapter 8 extended the previous work to the population level by attempting to bring all the new information in the previous chapters together to model the energy requirements of the UK North Sea population of grey seals. Predicted energy requirements were not conceivably different from previous estimates (Fedak and Hiby 1985), although the uncertainty surrounding these previous estimates was much higher. The value of taking a detailed rather than simplified view of population energy requirements is being able to assess the importance of individual components, and being able to predict what will happen given any hypothesised changes in input parameters.

As pointed out by Boyd (2002), two requirements of strategic modelling of energetics are to provide a realistic view of the uncertainty of the results and to identify the critical experiments that are required in order to progress the models towards a more realistic and therefore a more certain representation of how marine mammals function in their environment. It is hoped that the model presented here can be the starting point for such a process.

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Appendices

Appendix 1

Verification of open flow respirometry

A number of tests were carried out to establish the validity of assumptions of the open-flow respirometry system used in this study.

The N₂ calibration method outlined in Chapter 2 requires the oxygen analyser to have a linear response at the full range of gas concentrations measured. Known volumes of nitrogen gas were flowed through the system and the resulting response (in terms of area of deflection) of the oxygen analyser examined for linearity. Figure A1.1 shows some sample deflections that resulted from varying volumes of nitrogen gas and the response times of the system. Figure A1.2 shows the relationship between volume of nitrogen and area of deflection when flow rate through the system was 300l.min⁻¹. (This was also verified for all other flow rates used during the experiments).

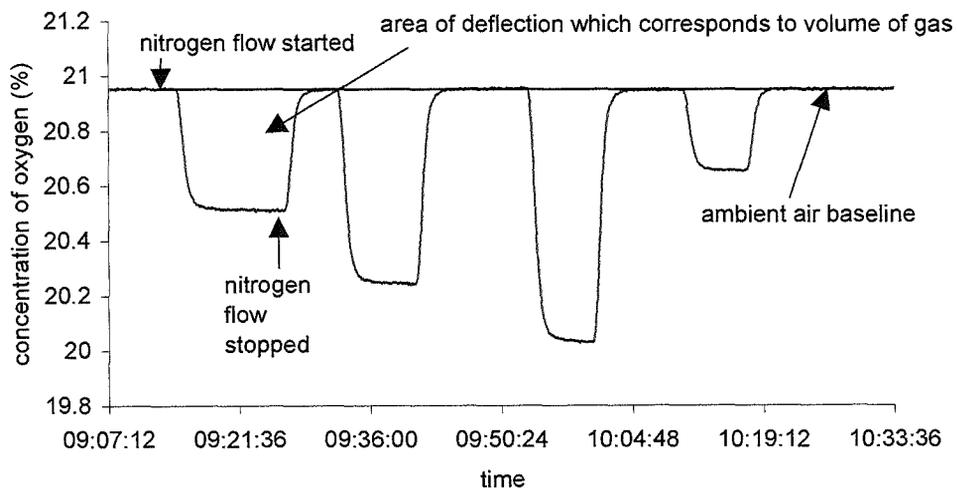


Figure A1.1. Deflection of oxygen analyser when nitrogen gas is bled into respirometry system at different rates and for different durations. The area of deflection corresponds to the total volume of nitrogen flowed through the system.

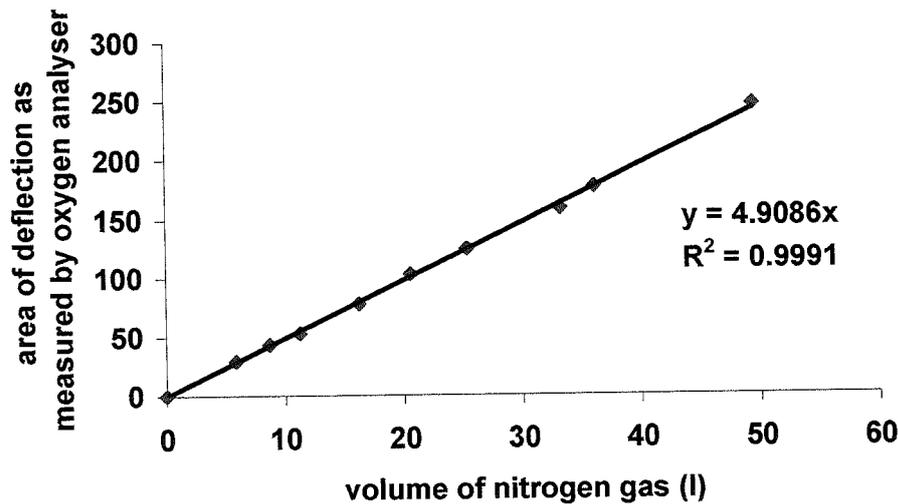


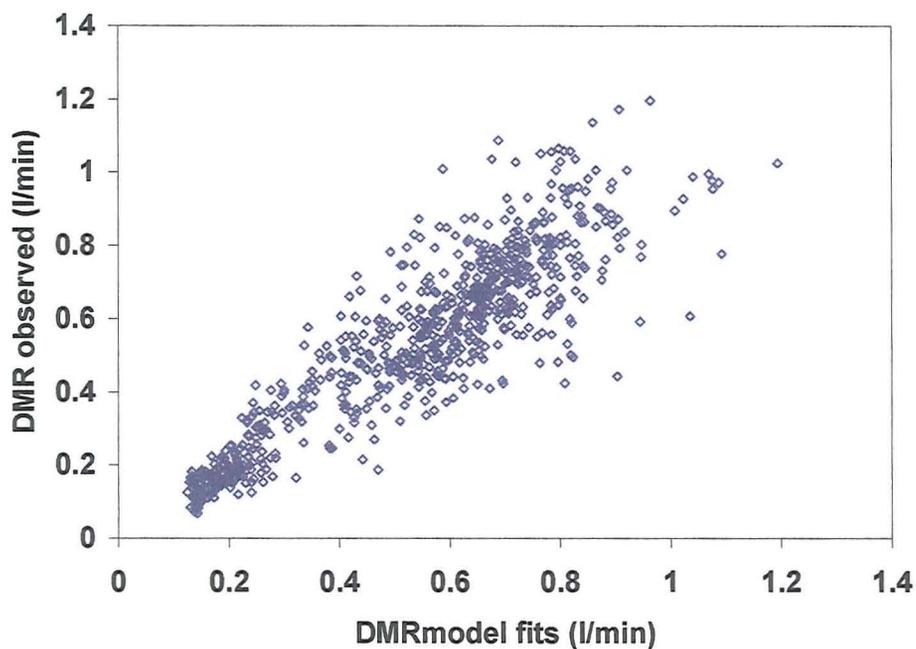
Figure A1.2. Linearity of oxygen analyser

2. To demonstrate that none of the seals' expired air could be lost through the inlet hose of the breathing box, nitrogen gas was bled into the port of the inlet hose at a known rate and the recovery rate of the system compared to that obtained when nitrogen was bled directly into the outlet tube or into the breathing box itself. This was repeated 10 times. The ratio between volume of gas and area of measured deflection did not change with the position of the nitrogen flow into the system (one-way ANOVA, $F = 0.56$, $P = 0.58$).

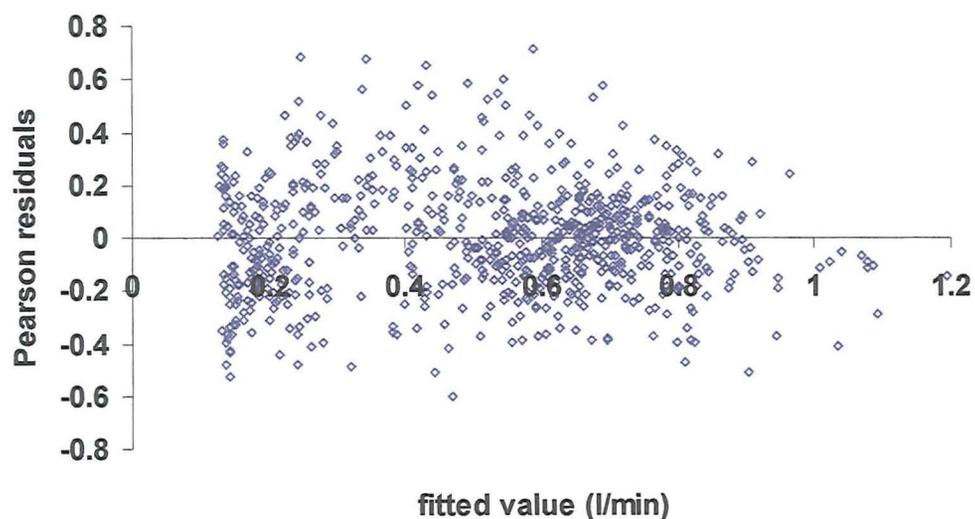
Appendix 2

Figure A2 Diagnostic plots of DMR predictive model (chapter 5)

a) Fitted values of DMR model against observed DMR values. N=593. The model explains a total of 77% the variation in observed DMR.



b) Fitted values of DMR model against pearson residuals.



Appendix 3

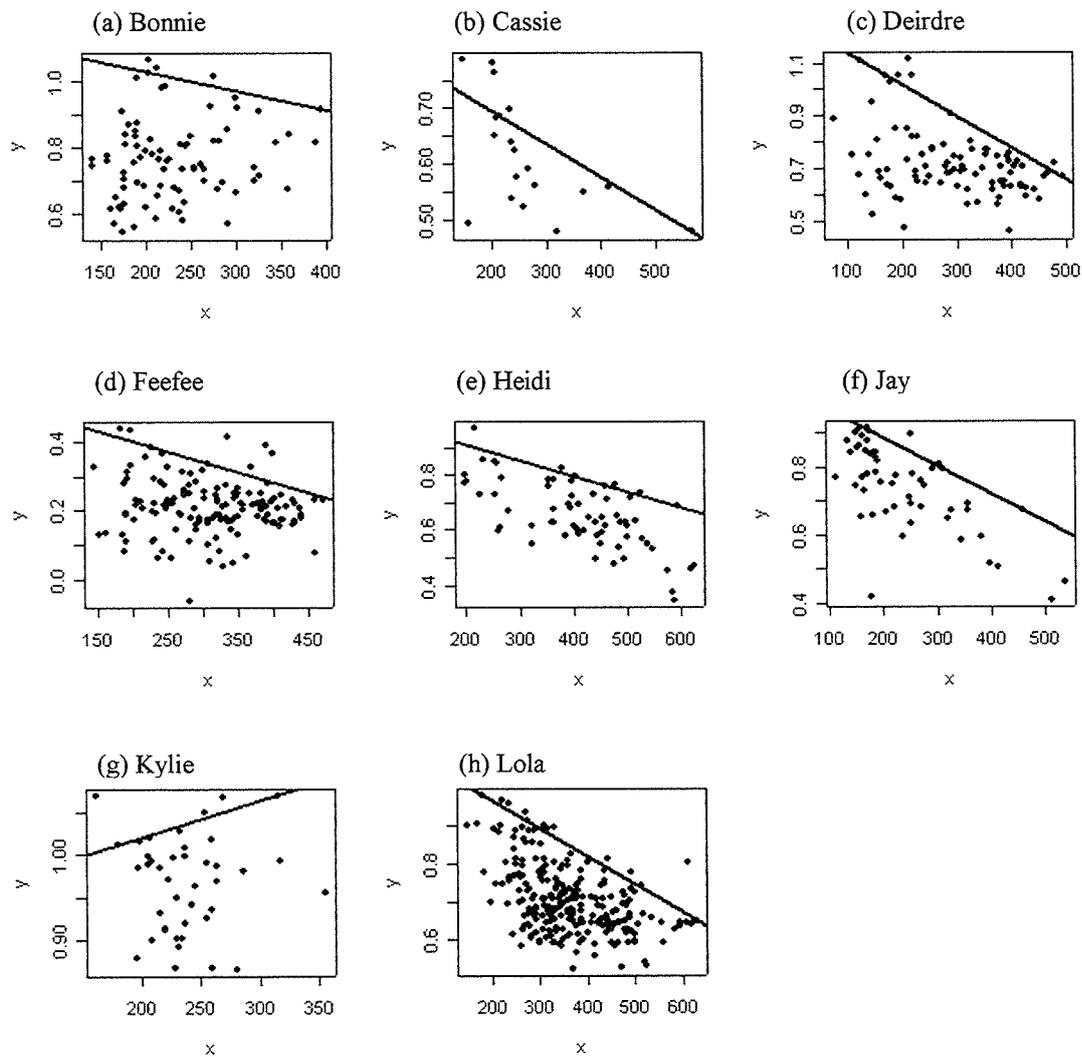


Figure A3 Quantile regressions of dive duration (x) on \log_{10} DMR (y), for individual animals. DMR is oxygen consumption in $\text{ml} \cdot \text{min} \cdot \text{kg}^{-1}$. All regressions are significant ($p < 0.001$) except Kylie.

Seal	Slope	Intercept	quantile	P
Bonnie	-0.00058	1.1454	0.95	<0.0001
Cassie	-0.00059	0.8131	0.74	<0.0001
Deirdre	-0.00121	1.2615	0.95	<0.0001
Feefee	-0.00061	0.5256	0.95	<0.0001
Heidi	-0.00568	1.0231	0.93	<0.0001
Jay	-0.00083	1.0515	0.92	<0.0001
Kylie	0.00042	0.9365	0.89	ns
Lola	-0.00073	1.1097	0.95	<0.0001

Table A3 Summary of quantile regressions for each individual animal.

Appendix 4

Results of month by month PCA analysis to identify behavioural dive 'types' of Lola, for comparison between fasting, feeding and post-feeding states.

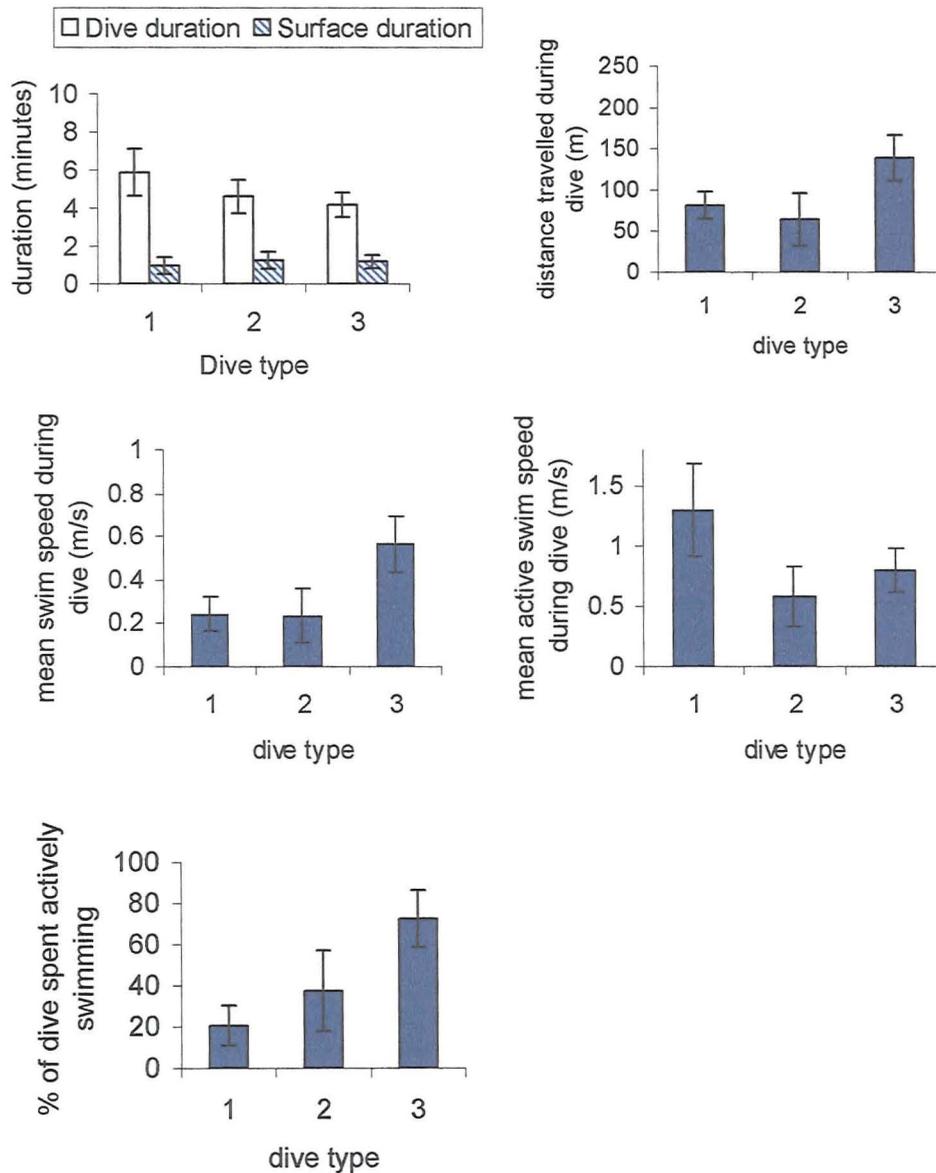


Figure A4.1 Behavioural characteristics of dive types for Lola in April (feeder positioned 40m away from breathing box). See Chapter 6 for explanation. Bars show mean over all dives in that category, error bars are 1 sd.

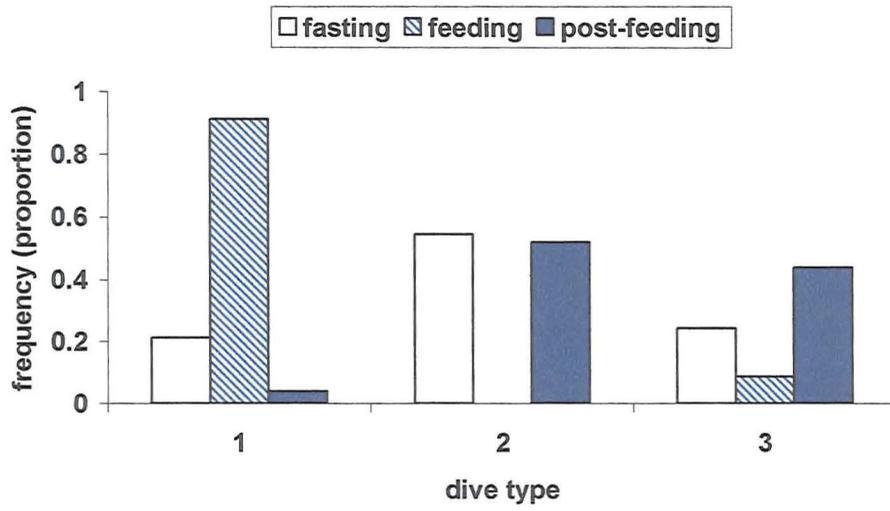


Figure A4.2 Distribution of dive types among feeding states for Lola in April

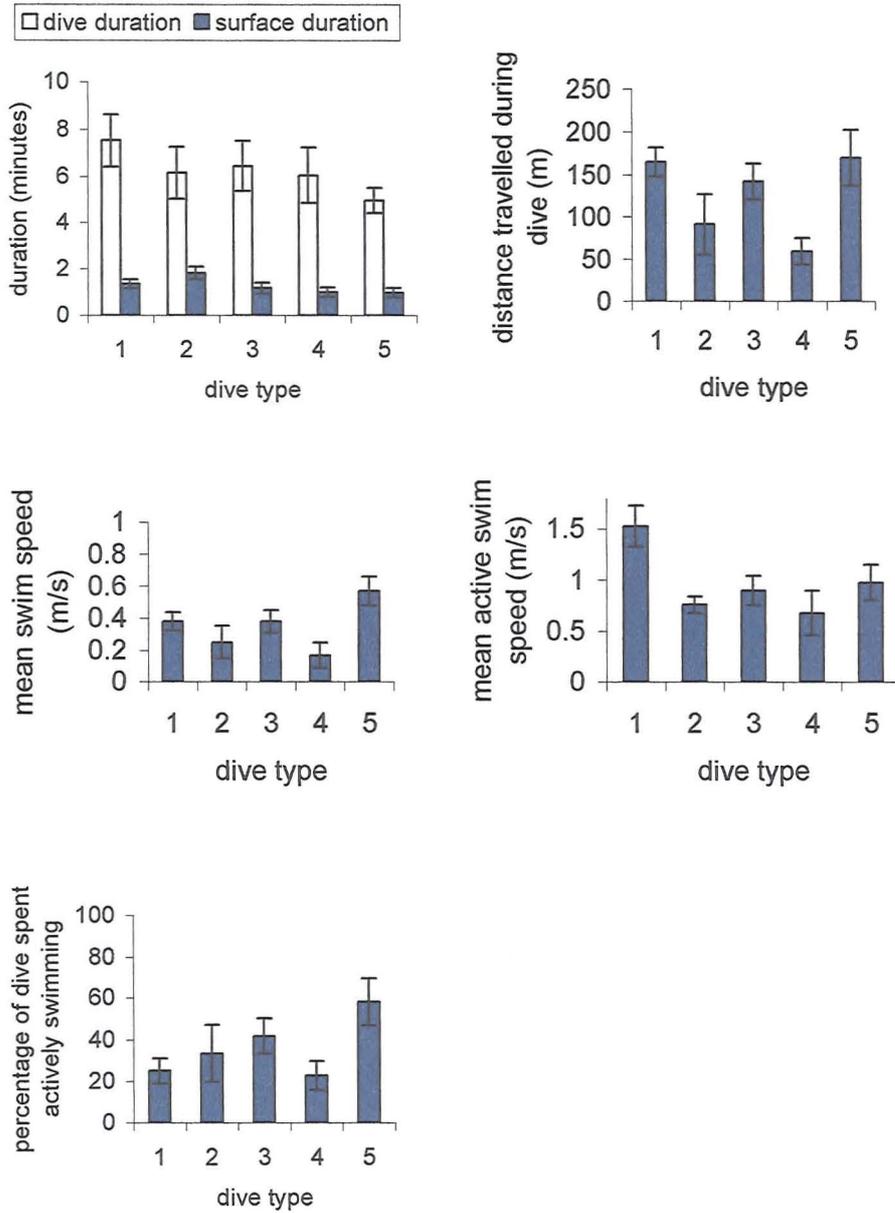


Figure A4.3 Behavioural characteristics of the dive types identified in May (feeder positioned 80m away from breathing box). Bars show mean over all dives in that category, error bars are 1 sd.

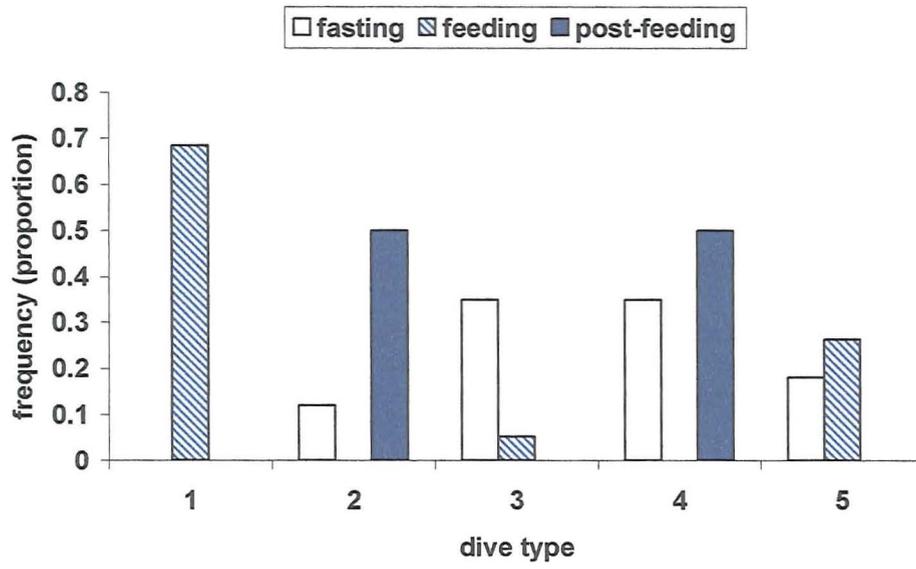


Figure A4.4 Distribution of dive types among feeding states for Lola in May

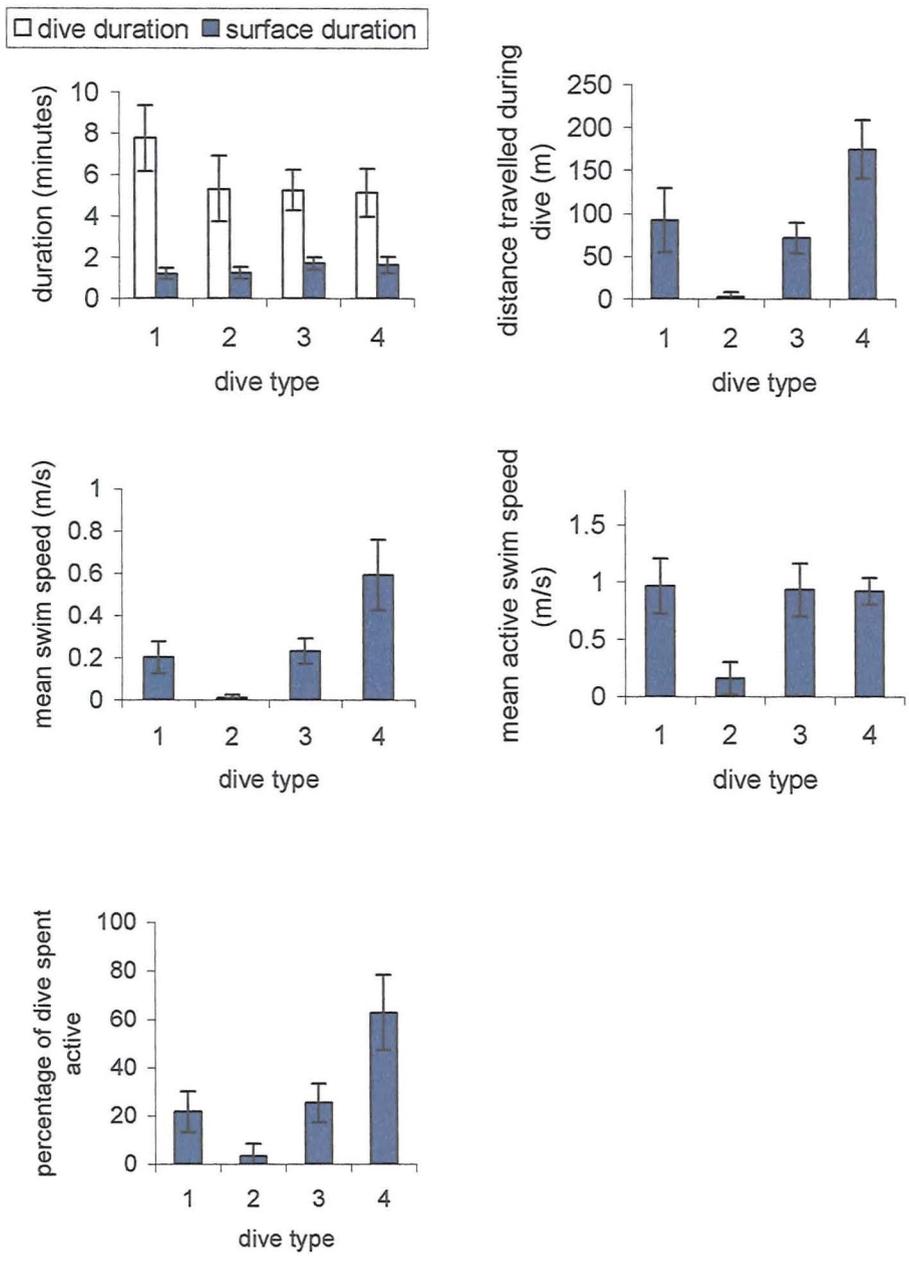


Figure A4.5 Behavioural characteristics of the dive types identified in June (feeder positioned 40m away from breathing box). Bars show mean over all dives in that category, error bars are 1 sd.

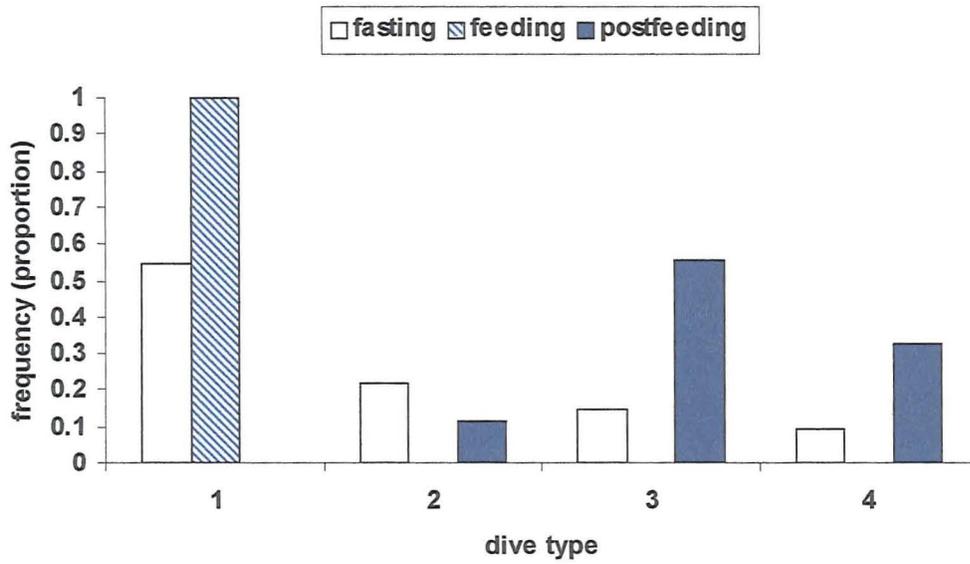


Figure A4.6 Distribution of dive types among feeding states for Lola in June.